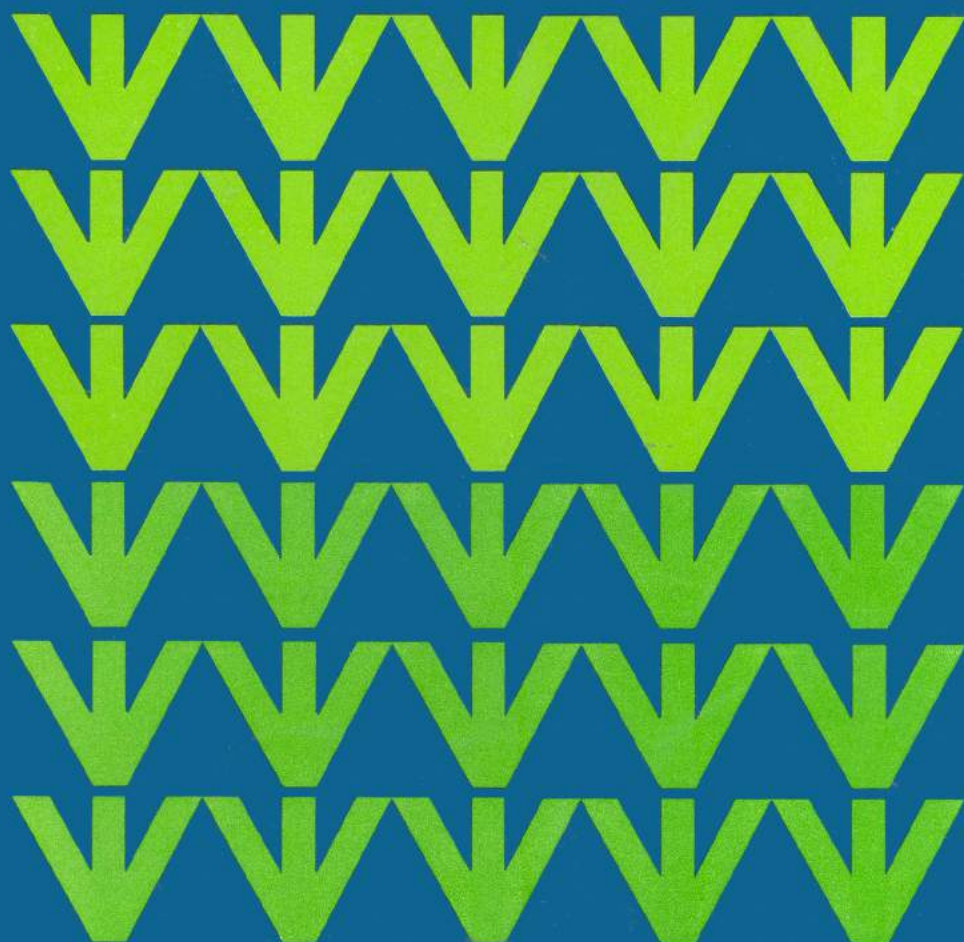


FUNDAMENTALS OF RICE CROP SCIENCE

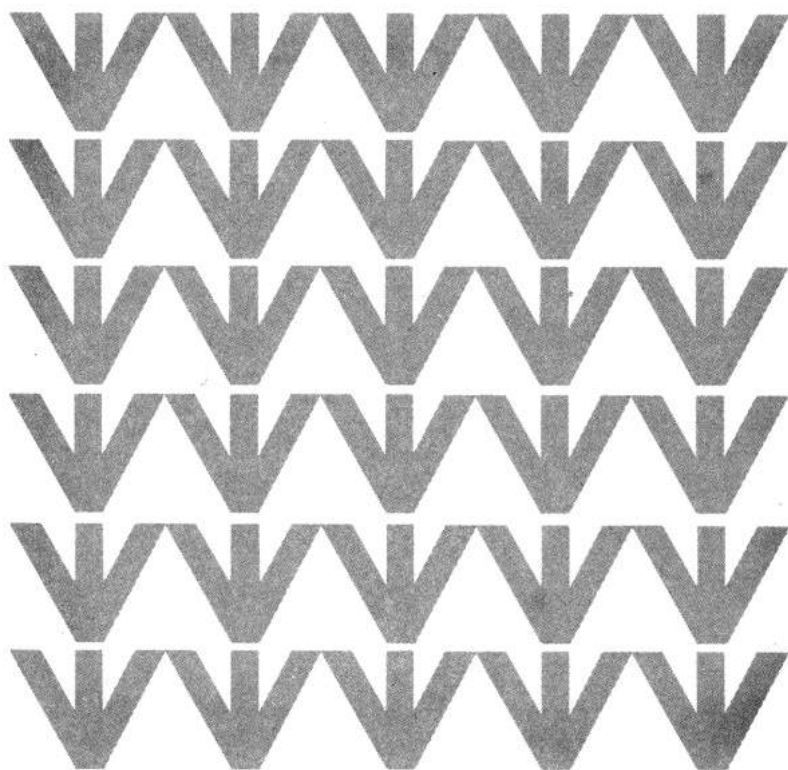
SHOUICHI YOSHIDA



INTERNATIONAL RICE RESEARCH INSTITUTE

FUNDAMENTALS OF RICE CROP SCIENCE

SHOUICHI YOSHIDA



1981

THE INTERNATIONAL RICE RESEARCH INSTITUTE

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FOREWORD

Rice is vital to more than half the world's populations. It is the most important food grain in the diets of hundreds of millions of Asians, Africans, and Latin Americans living in the tropics and subtropics. In these areas, population increases are high and will likely remain high at least for the next decade. Rice will continue to be their primary source of food.

In the 1960s, high-yielding, lodging-resistant, and fertilizer-responsive rice varieties helped initiate the worldwide expansion in food production called the *green revolution*. Additional rice improvement provided varieties that were resistant to several major diseases and insect pests and required growth periods of only 3.5-4 months. New production practices were designed to fit these modern rices into a wide range of environments, providing small-scale farmers in developing countries with higher yields and the potential for multiple cropping. The possibilities these scientific advances provide for expanded food production are being recognized, not only by the farmers but by government leaders who are concerned with national food self-sufficiency. These leaders have responded by expanding support for rice research efforts as well as practical food production programs.

Improved rice production technologies have created an increased demand for scientists, educators, and practical food production specialists. More than ever young students of rice science are seeking information that will help them fulfill the promise of self-sufficiency for their countries. The primary objective of *Fundamentals of Rice Crop Science* is to provide such information.

This excellent book brings together sources of rice information not heretofore found in a single textbook. Through it, Dr. Yoshida shares with students of rice science information from his wide-ranging experience as a plant physiologist at the International Rice Research Institute (IRRI) and from the experience of rice scientists from Japan and other countries. Dr. Yoshida has served as head of IRRI's Department of Plant Physiology since 1966. Previously he was on the staff of the National Institute of Agricultural Sciences in Japan.

Fundamentals of Rice Crop Science is not a textbook on rice physiology alone, although this important field provides the skeleton to which Dr. Yoshida adds current information from agronomy and soil science. His multidisciplinary approach provides the reader with a well-integrated view of rice science, which will help prepare him for future endeavors.

The International Rice Research Institute is grateful to Dr. Yoshida for having prepared this important volume. We feel it will be a primary source of rice information for young scientists for a long time to come.

N. C. Brady
Director general

PREFACE

When I started working as a plant physiologist at the International Rice Research Institute (IRRI) in 1966, I soon realized that there was a vast number of references before me, including those on plant ecology, climatology, soil science, and agronomy. Although I looked for a single textbook that would give me a brief account of the crop physiology of rice, I was unable to locate one. The need for such a textbook became even more obvious as my contacts with young scientists and students from developing countries increased. The primary objective of *Fundamentals of Rice Crop Science* is to meet such a need.

In writing this book, I have tried to present a synthesis of the current understanding of rice crop physiology. I attempt to explain how high rice yields can be achieved with the proper combination of variety, environment, and cultural practices. I also present some means to identify the cause or causes of low and high yields under a given crop environment.

The choice of subject matter discussed here is based primarily on my own experience at IRRI, and is perhaps broader than one might expect. Affected by dialogues with my colleagues from different disciplines, this book contains material of an interdisciplinary nature, which should help crop physiologists improve their communication with plant breeders and soil scientists. For this reason, I have chosen to call this book *Fundamentals of Rice Crop Science* instead of *Fundamentals of Rice Crop Physiology*.

This book would not have come out without the generosity and encouragement of Dr. N. C. Brady, director general of IRRI. Most of the book was written from August 1978 to June 1979, during a sabbatic leave at the University of California at Davis. The manuscript was reviewed by Drs. B. S. Vergara, Z. Uchijima, I. Nishiyama, C. S. Park, H. Shiga, and T. Ando. Mr. Robert Cowell and Ms. Corazon Mendoza of IRRI's Office of Information Services edited the manuscript. I am specifically indebted to Dr. S. K. De Datta for his advice on the preparation of the manuscript. I am also indebted to many others who helped make this book possible.

Shouichi Yoshida

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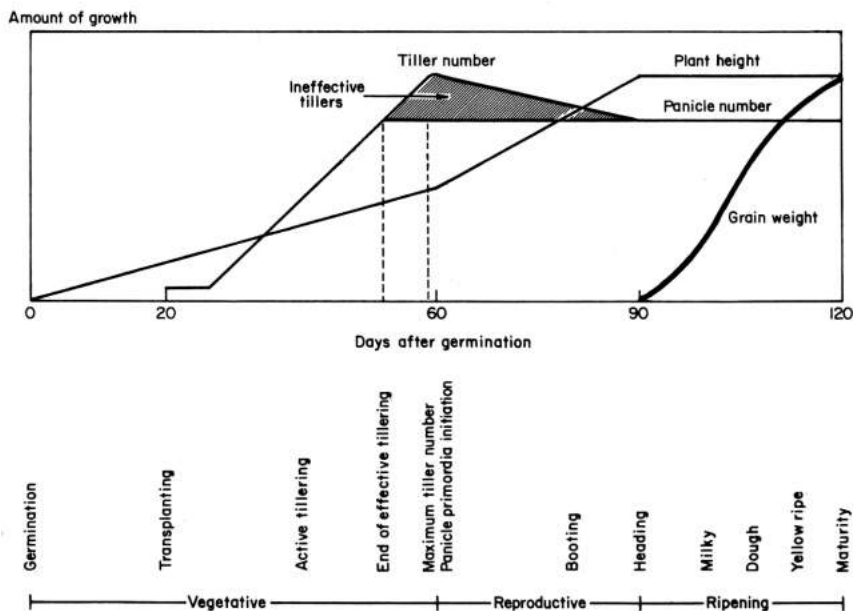
GROWTH AND DEVELOPMENT OF THE RICE PLANT

1.1. OUTLINE OF THE LIFE HISTORY

The rice plant usually takes 3–6 months from germination to maturity, depending on the variety and the environment under which it is grown. During this period, rice completes basically two distinct sequential growth stages: vegetative and reproductive. The reproductive stage is subdivided into preheading and postheading periods. The latter is better known as the ripening period. Yield capacity, or the potential size of crop yield, is primarily determined during preheading. Ultimate yield, which is based on the amount of starch that fills spikelets, is largely determined during postheading. Hence, agronomically, it is convenient to regard the life history of rice in terms of three growth stages: vegetative, reproductive, and ripening. The vegetative stage refers to a period from germination to the initiation of panicle primordia; the reproductive stage, from panicle primordia initiation to heading; and the ripening period, from heading to maturity (Fig. 1.1). A 120-day variety, when planted in a tropical environment, spends about 60 days in the vegetative stage, 30 days in the reproductive stage, and 30 days in the ripening period.

The vegetative stage is characterized by active tillering, gradual increase in plant height, and leaf emergence at regular intervals. All contribute to increasing the leaf area that receives sunlight. Tillering may start when the main culm develops the 5th or 6th leaf. Active tillering refers to a stage when tillering rate —

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1.1. Life history of a 120-day variety grown in the tropics under the transplanting cultivation system (schematic).

the increase in tiller number per unit of time — is high. The maximum tiller number stage follows active tillering. It is a stage when tiller number per plant or per square meter is maximum — before or after the initiation of panicle primordia, depending on a variety's growth duration. Because tiller number declines after the maximum tiller number stage, there is a period before that stage (often called the *end stage of effective tillering*) when the tiller number becomes numerically equal to panicle number at maturity. That does not necessarily mean that tillers developed after the end stage will not bear panicles. But tillers developed at early growth stages normally produce panicles, while those developed later may or may not.

The reproductive growth stage is characterized by culm elongation (which increases plant height), decline in tiller number, emergence of the flag leaf (the last leaf), booting, heading, and flowering. Initiation of panicle primordia usually dates back to about 30 days before heading.¹

Agronomists often refer to topdressing nitrogen fertilizer at *panicle initiation* — a stage about 25 days before heading when the panicle has grown about 1 mm long and can be recognized visually or with a magnifying lens. But initiation of panicle primordia can be recognized only under a microscope. Internode elongation

¹Detailed studies have been done on development of rice panicles in Japan, which is in the temperate region (Matsushima 1970). The results of these studies should perhaps be applied to tropical regions since temperature, which is considered to have a great influence on initiation and subsequent growth of the panicle, is similar during the reproductive growth stage in the temperate region and the tropics.

usually begins around the initiation of panicle primordia and continues until heading. The top five internodes may be elongated at heading. For this reason, the reproductive growth stage is sometimes called the internode elongation stage.

Heading means panicle exertion. Spikelet anthesis (or flowering) begins with panicle exertion, or on the following day. Consequently, heading is considered a synonym for anthesis in terms of calendar days in the life history of rice. It takes 10–14 days for a crop to complete heading because there is variation in panicle exertion within tillers of the same plant and between plants in the same field. Agronomically, heading is usually defined as the time when 50% of the panicles have exerted. Anthesis normally occurs between 0800 and 1300 in tropical environments. Fertilization is completed within 5–6 hours later. Only a very few spikelets have anthesis in the afternoon. When the temperature is low, however, anthesis may start late in the morning and last until late afternoon. Within the same panicle it takes 7–10 days for all the spikelets to complete anthesis; most spikelets complete anthesis within 5 days.

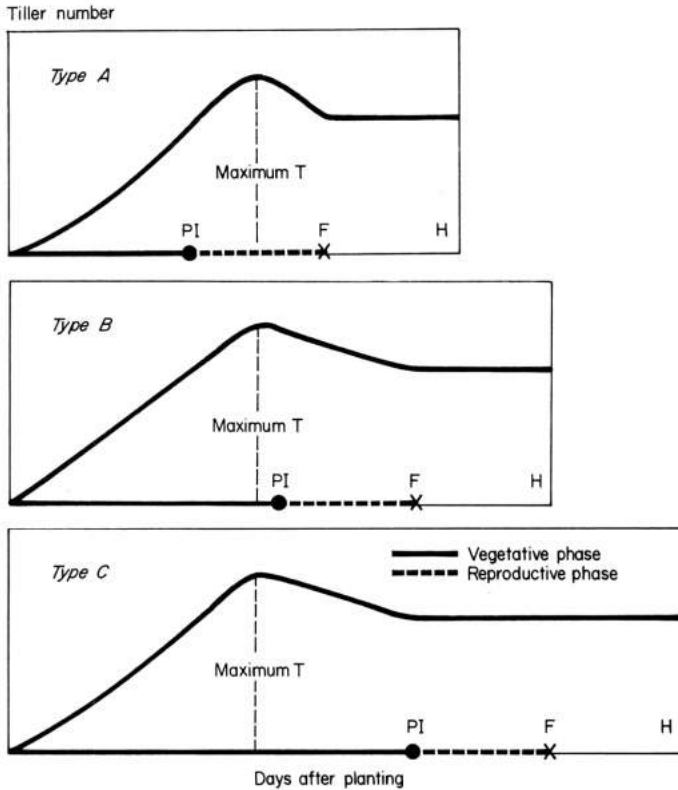
Ripening follows fertilization, and may be subdivided into milky, dough, yellow-ripe, and maturity stages. These terms are primarily based on the texture and color of growing grains. Ripening is characterized by leaf senescence and grain growth — increases in grain size and weight and changes in grain color. During active grain growth, both fresh and dry grain weights increase. Toward maturity, however, dry weight increases slowly but fresh weight decreases as a result of water loss. The length of ripening, largely affected by temperature, ranges from about 30 days in the tropics to 65 days in cool, temperate regions such as Hokkaido, Japan, and New South Wales, Australia.

The basic processes in the life history of rice can be applied to any cultivation system, with some modifications.

First, differences in growth duration are primarily due to differences in the length of the vegetative growth stage. The length of the reproductive stage plus the ripening period may be considered about the same for any variety under a given environment. Early maturing varieties have short vegetative stages. As a consequence, they may initiate panicle primordia before the maximum tiller number stage (Type A in Fig. 1.2) and heading may be staggered because later tillers may produce panicles. Late-maturing varieties have long periods of vegetative stage and may reach the maximum tiller number stage before initiation of panicle primordia (Type C in Fig. 1.2). The period from the maximum tiller number stage to initiation of panicle primordia is sometimes referred to as *vegetative-lag phase* (Tanaka et al 1964). When the length of the vegetative stage is adequate, the plant initiates panicle primordia right after the maximum tiller number stage (Type B in Fig. 1.2). In the tropics, this is normally attained by a 120-day variety.

Second, direct-seeded rice normally starts tillering earlier than transplanted rice because its growth proceeds without the setback caused by growth damage during uprooting. Each direct-seeded rice plant, however, usually produces 2–5 tillers while each transplanted rice plant produces 10–30. Thus, tillering is much less important in direct-seeded rice.

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1.2. Phasal development of the rice plant (adapted from Tanaka 1976). PI = panicle primordia initiation, F = flowering, H = harvest. Maximum T = maximum tiller number stage.

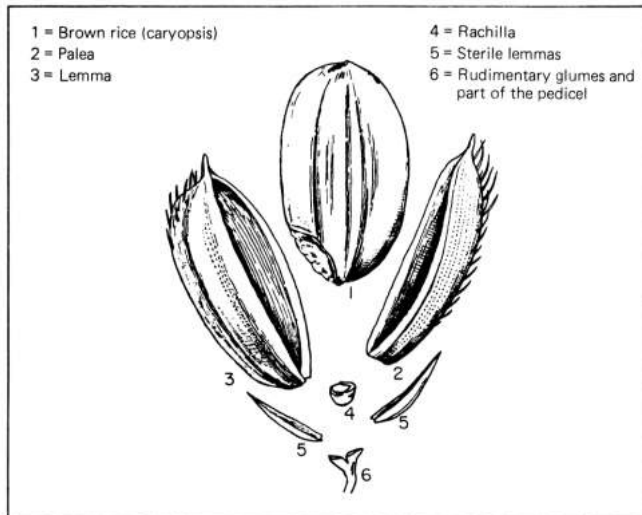
Third, growth duration of the same variety may be slightly different between the transplanted and direct-seeded crops. Transplanted rice usually takes about 1 week more to mature because its growth has been disturbed by uprooting.

1.2. SEED AND GERMINATION

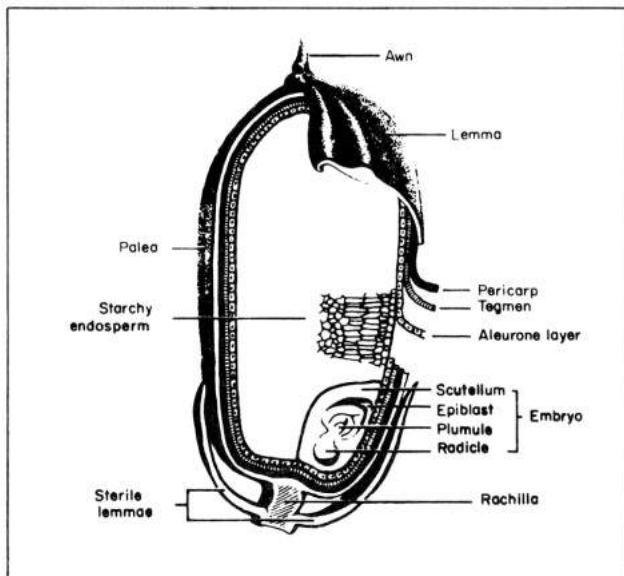
1.2.1. Morphology

The rice grain, commonly called a seed, consists of the true fruit or brown rice (caryopsis) and the hull, which encloses the brown rice (Fig. 1.3). Brown rice is largely composed of embryo and endosperm. The surface contains several thin layers of botanically differentiated tissues that enclose the embryo and endosperm (Fig. 1.4).

The palea, lemma, sterile lemmas, and rachilla constitute the hull of indica rices. In japonica rices, however, because of the nonshattering characteristic, the hull usually includes rudimentary glumes and perhaps apportion of the pedicel. The



1.3. Structure of the rice grain (adapted from Hoshikawa 1975).



1.4. Cross-section of the rice grain (Juliano 1972).

lemma is larger than the palea, and covers about two-thirds of the surface area of matured brown rice. The edges of the palea fit inside those of the lemma so that the hull closes tightly.

A single grain weighs about 12–44 mg at 0% moisture content. Grain length, width, and thickness vary widely among varieties. Hull weight averages

Table 1.1. Grain characteristics of 11 varieties.^a

Variety	Country of origin	Wt (mg/grain) (moisture free)	Length (mm)	Width (mm)	Thickness (mm)	Hull (%)
Khao Lo	Laos	44.4	11.30	3.20	2.53	18.6
Cseljaj	Hungary	36.6	9.43	3.67	2.52	21.5
Ku 70-1	Thailand	34.7	8.91	3.93	2.32	19.6
Hiderishirazu	Japan	26.4	7.98	3.66	2.21	20.9
Rikuto Norin 21	Japan	23.1	6.94	3.48	2.19	20.6
Bergreis	Austria	21.8	6.81	3.25	2.21	19.3
Ai Yeh Lu	China	20.8	6.82	3.08	2.05	20.8
IR747B2-6	IRRI	16.4	7.61	2.46	1.81	20.4
Bangarsal	India	14.7	7.73	2.03	1.72	20.1
Bomdia	Portuguese Guinea	11.6	5.89	2.45	1.65	25.4
Kalajira	Bangladesh	11.9	5.81	2.43	1.89	21.8
Mean						20.8

^aIRRI (1977).**Table 1.2. Percentage germination of seed of 27 rice varieties heated for 4 days at 49°C.^a**

Variety	Origin	Germinated seed (%)	
		Untreated	Treated
Seraup 27	Malaya	1	7
Milbuen 5(3)	Philippines	6	22
CO 29	India	7	26
Mayang Ebos 80	Malaya	1	32
H6	Ceylon	9	46
Tiere mas	Philippines	7	56
Tangkai Rotan	Malaya	7	72
Tam Vuot	Vietnam	10	72
Siam 29	Malaya	11	77
BE-3	Philippines	11	90
H 105	Ceylon	13	81
Leuang Rhaeng	Thailand	15	74
Reyong 6	Malaya	16	71
Peta	Philippines	21	85
Lua Thuoc	Vietnam	21	86
O Tre	Vietnam	22	95
Raminad Str. 3	Philippines	23	98
SLO 15	India	27	75
Serendah Kuning	Malaya	27	87
FK-165	Philippines	29	93
FB-121	Philippines	32	76
Trang Doc	Vietnam	33	89
Taipei woo-co	Taiwan	54	73
Woo-gen	Taiwan	54	87
I-geo-tze	Taiwan	89	73
H 5	Ceylon	95	95
MTU 15	India	95	98

^aIRRI (1963).

about 21% of the total grain weight (Table 1.1). For convenience, the proportion of hull to grain is considered 20%. Conversion factors of 0.8 and 1.25 are usually used to obtain brown-rice weight from grain weight, and grain weight from brown-rice weight, respectively.

1.2.2. Dormancy

Most indica rices have a grain dormancy of several weeks or longer, a desirable varietal trait in tropical areas where rains frequently occur during the harvesting period and temperature stays at optimum for germination all the year round. Nondormant or weakly dormant grain often germinates in situ under such conditions and especially when the crop lodges into standing water.

Several methods to break rice dormancy are available. The simplest is to heat the seed at about 50°C in an open system for 4–5 days. Seed exposed directly to heat is not injured, but seed sealed to prevent loss of moisture may be killed when heating is prolonged. Varieties differ markedly in their response to the heat treatment. As shown in Table 1.2, the dormancy of most varieties was broken by the 4-day heat treatment at 49°C. Five varieties, however, had under 50% germination even after the treatment. The dormancy of variety Seraup 27 was only slightly broken, but increased to 84% after a 10-day heat treatment at 50°C. Within a range of 50°–65°C, the treatment's duration was more effective in breaking dormancy than the temperature.

1.2.3. Germination

Germination starts when seed dormancy has been broken, the seed absorbs adequate water, and is exposed to a temperature ranging from about 10° to 40°C.

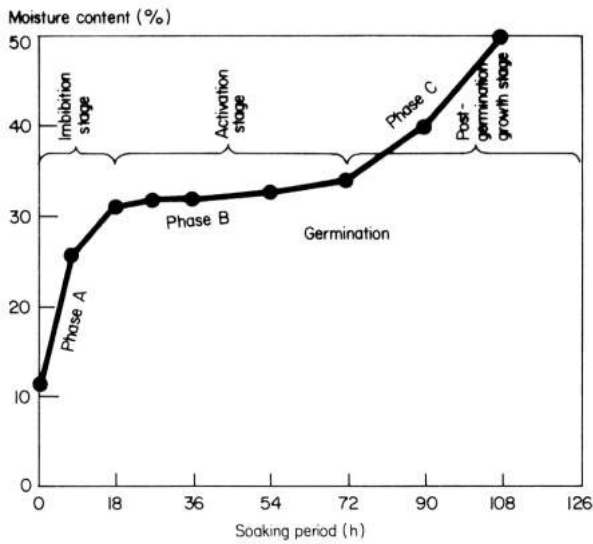
a. *Water absorption.* The germination process may be subdivided into imbibition, activation, and postgermination growth stages (Fig. 1.5). When soaked, a seed rapidly absorbs water for the first 18 hours. This water intake, caused by imbibition forces, increases the seed's water content to between 25 and 35%. Although the duration of this stage is almost independent of temperature, temperature influences water content (Fig. 1.6). Water absorption is not affected by respiratory inhibitors, and the Q_{10} value is much lower than 2.

Water absorption at the activation stage is negligible compared with that at the imbibition stage. The duration is dependent on temperature and increases at lower temperatures. Germination occurs as a consequence of very active metabolic changes during the activation stage (Takahashi, N. 1965). The water content of the seed at the onset of germination varies with temperature; it ranges from about 30 to 40%.

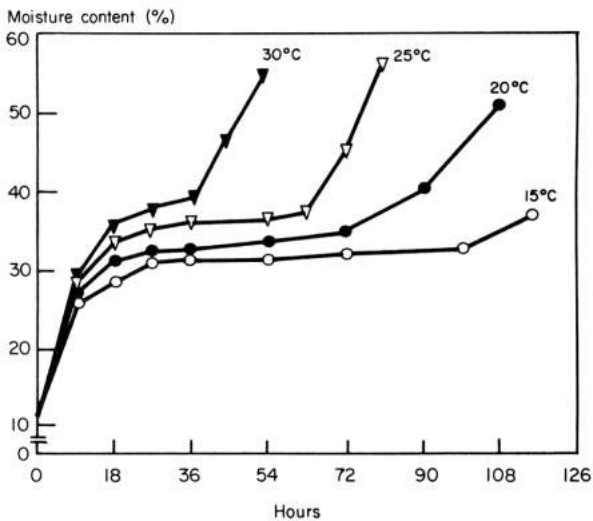
At the end of the activation stage, the white tip of the coleoptile emerges from the ruptured seed coat. This stage is called germination. Subsequently, the coleoptile grows and the first leaf appears.

b. *Effect of temperature.* Temperature has a profound influence on germination by affecting the activation stage and postgermination growth.

The effects of temperature on germination can be examined in three aspects: temperature, time, and germination percentage.

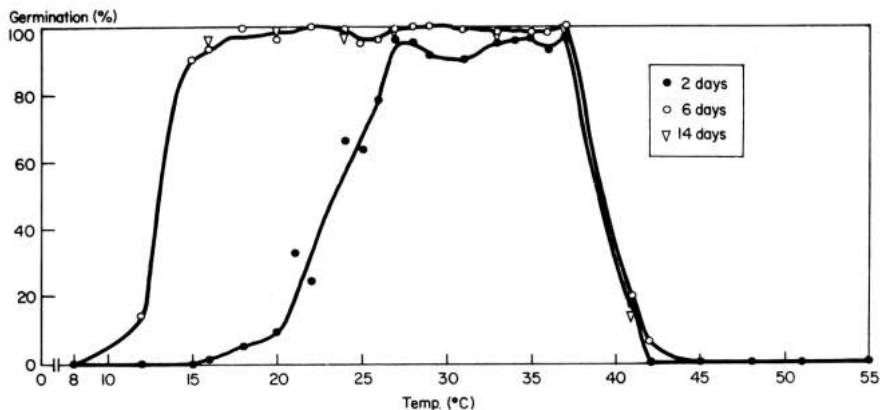


1.5. The pattern of water absorption during the germination of rice seed (variety: Ōu-no 200) at 20°C on filter paper (Takahashi, N.1961).



1.6. The water absorption of rice seed (variety: Ōu-no 200) at different temperatures on filter paper (Takahashi, N. 1961).

In Figure 1.7, 90–97% germination was attained in 2 days' incubation at 27°–37°C. The germination percentage dropped sharply below or above this range. When the incubation time was extended to 6 days, germination was 90% or higher at temperatures between 15° and 37°C. At 8° and 45°C, no germination occurred.

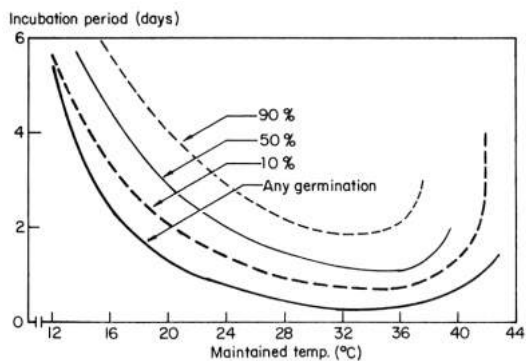


1.7. Germination percentages of rice seeds at different temperatures after 2, 6, and 14 days of incubation (drawn from Livingston and Haasis's 1933 data).

Figure 1.8 gives the shortest incubation time for specified germination percentages at different temperatures. For example, to give 90% germination, about 6 days of incubation are needed at 15°C, about 3 days at 25°C, or about 2 days at 31°–36°C. If the incubation time is extended, rice seed may germinate even at 0°–5°C. At such low temperatures, germination proceeds very slowly and may take a month or longer.

c. Effect of oxygen. Rice seed appears to germinate under anaerobic conditions, if germination is defined as the appearance of the coleoptile from the ruptured seed coat (Takahashi, T. 1905). Under such conditions, however, the subsequent growth of the coleoptile, true leaves, and roots become abnormal.

d. Varietal difference in germination at low temperature. There are clear varietal differences in seed germination at low temperatures. It is, however,



1.8. Smoothed graphs showing for each maintained temperature the average lengths of incubation period required for any germination and for germination percentages of 10, 50, and 90 (Livingston and Haasis 1933)

difficult to relate them to ecological, botanical, or agronomical characteristics.

Geographical distribution of indica and japonica rices suggests that the latter may germinate better at low temperatures. In fact, some japonica rices germinate better than indica rices at low temperatures. But it is also true that some other indica rices germinate better at low temperatures than some other japonica rices. Thus, it is difficult to generalize a simple relationship between the two rices.

Germination at low temperatures may be complicated by seed dormancy. There is clear evidence that some indica rices, when the dormancy has been broken, can germinate at low temperatures as well as or better than japonica rices (Table 1.3). Local selection pressure, related to either cultural practices or local environments, may have caused differential selection of varieties better adapted to low temperature. At 15.6°C, a California variety, Caloro, germinated and grew better than most Japanese varieties tested (Ormrod and Bunter 1961). In California, rice is directly sown into cool-water irrigated fields, while in Japan rice seedlings are grown in the protected nursery beds where high temperatures are maintained. Quite often, traditional varieties in Japan germinate better than improved varieties at low temperatures. Before the use of protected nursery beds, those traditional varieties were raised in unprotected nursery beds and thus were inadvertently selected for low temperatures (Toriyama 1962).

1.3. SEEDLING

1.3.1. Germination and seedling emergence

Germination, defined as the appearance of the white tip of the coleoptile, and subsequent growth of the coleoptile are a continuous phase that occurs within a short time after a seed is placed in soil or water. Seedling emergence is the time

Table 1.3. Germination of indica and japonica varieties at the fastest germination stage^a under low temperatures (9–11°C).^b

Variety	Germination (%)	Average number of days required for germination
<i>Indica</i>		
Kaladumai	99	7.5
IR8	99	10.6
Dharial	96	13.8
Stirpe	86	9.6
<i>Japonica</i>		
Koshihikari	96	16.6
Toyonishiki	66	20.8
Sasanishiki	60	20.1
Honenwase	82	21.3

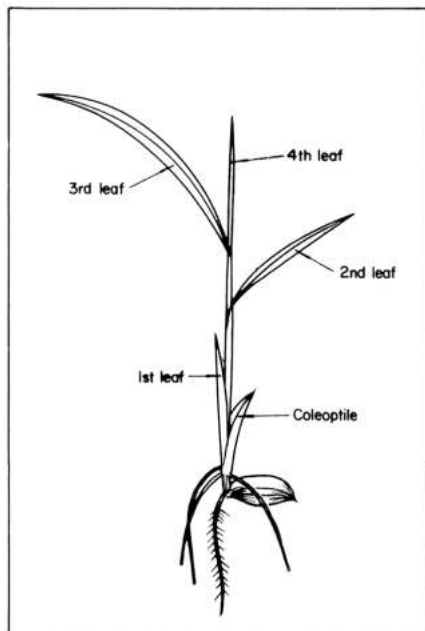
^aThe fastest germination stage refers to the time when dormancy has been broken and consequently germination rate is maximum. ^bIkehashi (1973).

when the tip of a seedling emerges from the soil or water surface and, thus, includes both germination and postgermination growth. Seedling emergence is an appropriate term for the very beginning of rice growth in the field.

1.3.2. Counting the leaves

The age of a rice plant is conventionally expressed in calendar days after germination or seeding. This is convenient for a particular variety under a particular environment. The calendar day, however, cannot be used when comparing growth under different temperature and water regimes because the rate of leaf development, hence, physiological age, is very much affected by environment. Even for the same location and variety, variable weather conditions affect the rate of seedling growth.

Counting leaves on the main culm is the best way to provide a physiologically meaningful age for the rice plant. At germination, the coleoptile emerges and grows about 1 cm. after which the first leaf begins to emerge. The first leaf appears to lack a leaf blade and grows about 2 cm long. The second leaf has a well-developed leaf blade and starts to emerge before the first leaf has completed elongation. The third leaf and succeeding leaves emerge after each preceding leaf has fully elongated (Fig. 1.9). Because the first leaf appears to lack a leaf blade, it is sometimes called a *prophyll* or incomplete leaf. Following this terminology, the second leaf is counted as the first. Hence, special attention must be paid to the



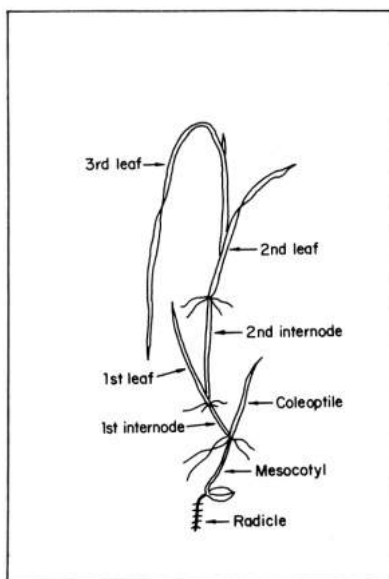
1.9. Counting leaf number of the rice plant.

method of counting leaves, particularly when the reader refers to works published in Japan. The first leaf, however, is known to have the same anatomical characteristics as succeeding leaves (Hoshikawa 1973).

In experiments, the leaf on the main culm is marked with dots of white or red enamel and the observation date is recorded. The n th leaf on the main culm is described as $n/0$, where 0 implies the main culm. Thus, 3/0 refers to the third leaf on the main culm. In this way, the leaf number can be recorded and related to the calendar day. When the first leaf is fully developed, the plant age is counted as 1.0. Similarly, when the second leaf attains its maximum elongation, the plant age is 2.0, and so on. A leaf is considered to have fully developed when the tip of the succeeding leaf emerges. In cases where observations must be made before a leaf's elongation is complete, leaf age may be estimated by the ratio of the length of an elongating leaf to that of the preceding leaf. For instance, if the 6th leaf is still elongating and its length is estimated at about 50% the length of the 5th leaf, the plant's age is 5.5. This estimation is, however, subject to error because the two leaves are not of the same length. Recording the time of maximum leaf elongation is more accurate.

1.3.3. Seed reserve for seedling growth

At initial stages of seedling growth, growth of the coleoptile and subsequent leaves is largely dependent on the seed reserve — nutrients accumulated in the endosperm. When a seed germinates and grows in the dark, it continues to grow until the tip of the 4th leaf emerges (Fig. 1.10). Darkness induces extraordinary elongation of the mesocotyl (the axis between the node of the coleoptile and the base of the radicle), the coleoptile, the first and second leaves, and the first and second internodes.



1.10. Rice seedling growth in the dark (Hoshikawa 1975). The reserved nutrients of the seed support seedling growth up to the third leaf.

Table 1.4. Growth of IR8 seedlings at different temperatures.^a

Mean temperature (°C)	Endosperm wt ^b (mg/grain)	Growth (mg/plant)			Ratio (photo-synthe- sis total)
		Total	Attributable to		
			Seed reserve	Photo- synthesis	
First week					
22	9.2	8.1	7.3	0.8	0.10
25	6.9	10.7	8.7	2.0	0.19
28	4.3	13.7	10.3	3.4	0.25
31	3.1	15.7	11.0	4.7	0.30
LSD (0.05)	—	1.8	—	—	—
Second week					
22	2.6	25.7	4.0	21.7	0.84
25	1.3	49.6	3.4	46.2	0.93
28	1.2	62.0	1.9	60.1	0.97
31	1.0	71.4	1.3	70.1	0.98
LSD (0.05)	—	8.5	—	—	—
Third week					
22	1.1	81.9	0.3	80.7	1.00
25	1.0	201.8	0.2	201.4	1.00
28	1.2	239.2	0.0	239.2	1.00
31	1.1	286.4	0.0	286.4	1.00
LSD (0.05)	—	32.5	—	—	—

^a Yoshida (1973). ^b Initial wt of endosperm was 21.4 mg/grain.

During postgermination growth in the dark, about 60% of the seed weight is converted to new organs. This 60% is called growth efficiency. The growth efficiency is almost constant over a range of temperatures from 21° to 32°C. In other words, temperature changes the rate of growth but not the efficiency with which the seed reserve is used for growth (see Chapter 5).

In light, photosynthesis contributes to seedling growth even at early stages. Assuming that the growth efficiency value is the same in both light and darkness, and measuring the amount of growth, it is possible to calculate the portions of measured growth contributed by seed reserve and by photosynthesis. In the first week of postgermination growth, with temperature ranging from 22° to 31°C, photosynthesis is responsible for less than 30% of growth (Table 1.4). In the second week, it is responsible for more than 84%, and by the third week it totally supports growth. Relative to leaf development, photosynthesis supports 95% of the total growth of a plant at age 3.7. In other words, the rice plant becomes autotrophic at age 3.7.

1.3.4. Factors affecting seedling growth

a. Temperature. In the first week of postgermination growth, weight growth is very sensitive to temperature (Table 1.5). Between 22° and 31°C, the growth rate increases linearly as temperature increases, indicating that chemical reactions

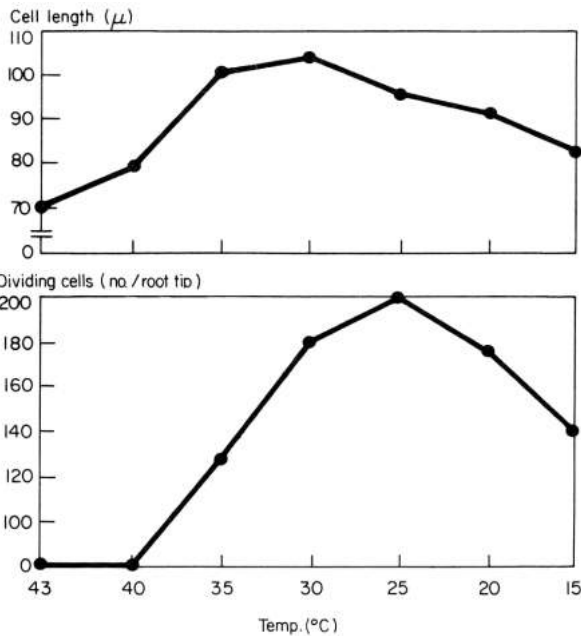
Table 1.5. Growth rate of IR8 at different temperatures up to 5 weeks after sowing^a

Mean temperature (°C)	Growth rate				Ratio of growth rate			
	0-1 wk (mg/plant per wk)	1-2 wk (g/g per wk)	2-3 wk (g/g per wk)	3-5 wk (g/g per wk)	0-1 wk	1-2 wk	2-3 wk	3-5 wk
22	8.1	1.16	1.16	1.40	1.0	1.0	1.0	1.0
25	10.7	1.53	1.40	1.50	1.3	1.3	1.2	1.1
28	13.7	1.51	1.35	1.62	1.7	1.3	1.2	1.2
31	15.7	1.52	1.39	1.62	1.9	1.3	1.2	1.2

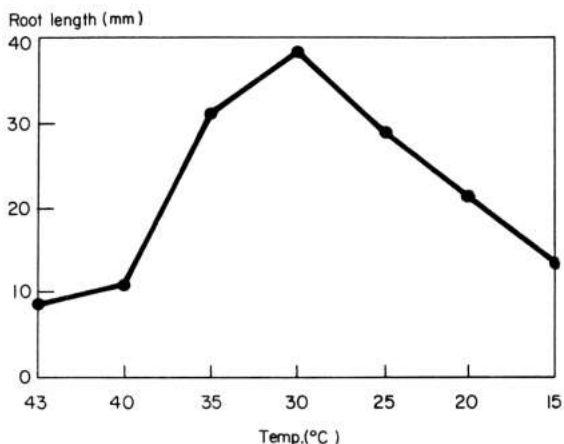
^a Yoshida (1973a).

dominate growth. During this week the seed reserve supports more than 70% of growth, and the breakdown of the seed reserve is enzymatic.

Temperature influences growth less after the first week. Relative growth rates are about the same at 25°, 28°, and 31°C after the first week, and 22°C is considered subnormal for seedling growth. These results indicate that 25°–30°C is best for seedling growth. Growth may be reasonably good up to 35°C, above which it declines sharply. Above 40°C seedlings may die. The critical minimum tempera-



1.11. The effects of temperature on cell division and cell enlargement of the cortex of the radicle tip (Yamakawa and Kishikawa 1957).



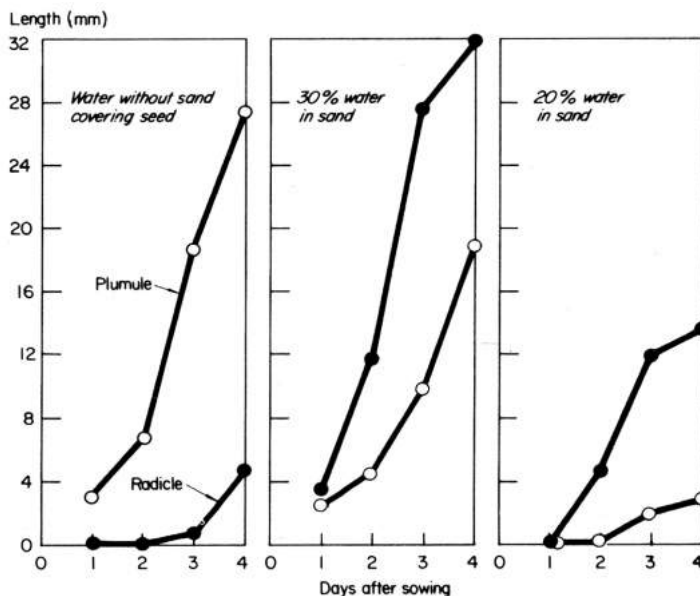
1.12. The effect of temperature on the elongation of the radicle (Yamakawa and Kishikawa 1957).

ture for shoot elongation ranges from 7° to 16°C and that for root elongation from 12° to 16°C (Nishiyama 1977). Hence, about 10°C may be considered as the critical minimum for elongation of both shoot and root. These critical temperatures may vary with variety, seed history, and cultural management.

The elongation of tissue results from two components of cell growth: cell division and cell enlargement. The optimum temperature for cell division of the radicle tip is 25°C, and that for cell enlargement, 30°C (Fig. 1.11). The elongation of the radicle as a whole, however, is optimum at 30°C, indicating that cell enlargement dominates the elongation. Elongation of the radicle stops below 15°C and above 40°C (Fig. 1.12).

b. Light. As mentioned earlier, darkness induces elongation of the coleoptile, mesocotyl, and first and second leaves.

c. Oxygen. Rice seed can germinate under anaerobic conditions but subsequent growth is greatly affected by oxygen supply. In flooded soil where oxygen is limited, germination occurs normally, but the coleoptile becomes unusually long and the first leaf, radicle, and nodal roots may not grow at all or their growth may be highly impaired. As shown in Fig. 1.13, the elongation of the plumule was accelerated and that of the radicle was highly impaired in water. When rice seed was germinated in sand with adequate moisture and oxygen, the radicle grew faster than the plumule. The radicle and plumule were both retarded under inadequate moisture. The oxygen concentration required for the appearance of the radicle is 2 ppm; for root elongation, 4ppm; for active root elongation and development, more than 5 ppm; and for growth of the first leaf, 5–6 ppm (Mitsuishi 1975). Hence, 5–6 ppm oxygen is necessary for seedling growth after the appearance of the coleoptile. In rice cultivation, appearance of the coleoptile itself is not meaningful unless it is followed by the roots and the first and second leaves.



1.13. Effect of water regimes on germination and rooting of rice seeds from sand media (Yokoi 1898).

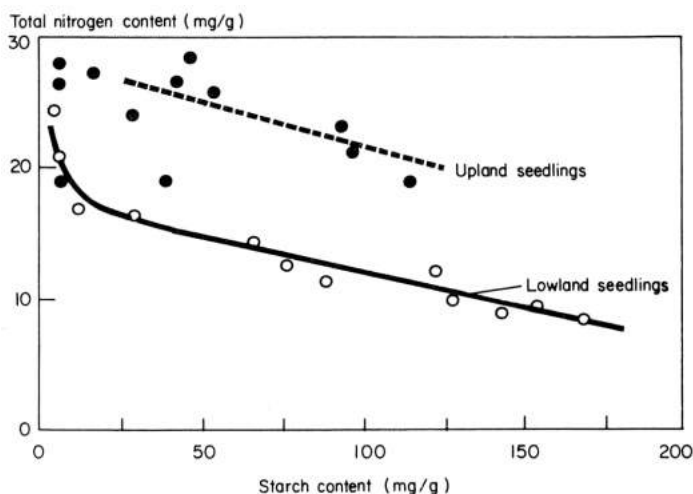
In lowland direct-sowing cultivation, particularly when the seeds are covered with soil, lack of oxygen causes poor seedling emergence. Under such conditions, coating the rice seeds with calcium peroxide is very effective in improving seedling emergence and subsequent growth (Ota and Nakayama 1970, Mitsuishi 1975). In wet soil, calcium peroxide releases molecular oxygen as it reacts with water:



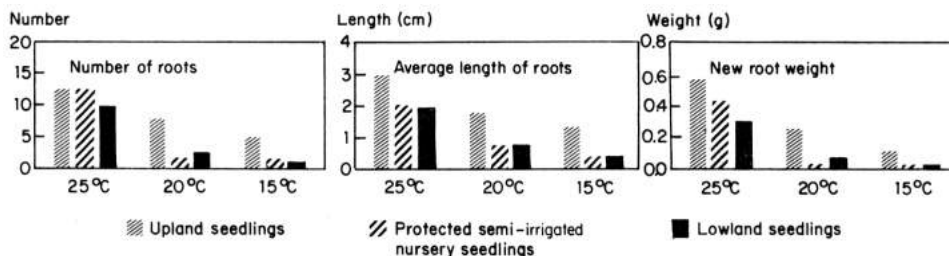
Thus, oxygen is made available for seedling growth even in an anaerobic soil.

d. Water regimes. Seedlings for transplanted rice are normally raised in lowland nurseries. However, experience in northern Japan indicates that upland-grown seedlings have better rooting ability and, hence, recover more quickly after transplanting. The upland-grown seedlings are shorter, have smaller leaves and more highly branched roots, and contain more nitrogen and starch than the lowland-grown seedlings (Fig. 1.14). Reduced leaf surface minimizes water loss during the recovery after transplanting. At the same time, high contents of nitrogen and starch help seedlings develop new roots (Fig. 1.15). These characteristics appear to result from the water stress imposed on the seedlings in the nursery.

Upland-grown seedlings perform well when temperatures are cool at transplanting, the growing period is short, and hence, quick recovery from transplanting is desirable. At low altitudes in the tropics, however, temperatures are favorable for rice growth all year round and growth tends to be excessive. Under such condi-



1.14. Nitrogen and starch content in lowland- and upland-grown rice seedlings (Yamada and Ota 1957).



1.15. Rooting ability of rice seedlings raised in upland and lowland nurseries (variety: Norin 17; 45-day old seedlings) (Yatsuyanagi 1960).

tions, seedling quality may not have much effect on grain yield, as shown in Table 1.6.

In some parts of the Philippines, seedlings are raised by the *dapog* method. Presoaked seeds are thickly spread on banana leaves to prevent contact with the soil. Seeds can also be enclosed with wooden frames and spread on a concrete floor. They are watered carefully and, in about 11 days, the thick mat is taken to the field where the seedlings are separated and transplanted. In this method, seedling growth is almost entirely dependent on the seed reserve.

1.4. LEAF

1.4.1. Morphology

A typical rice leaf is composed of the sheath, the blade, the ligule, and the auricles (Fig. 1.16). The sheath is an elongated, ribbon-shaped leaf base rolled into a

Table 1.6. Effect of nursery method and direct seeding on grain yield, total dry weight, and harvest index of 3 varieties. IRRI, 1970 dry season.^a

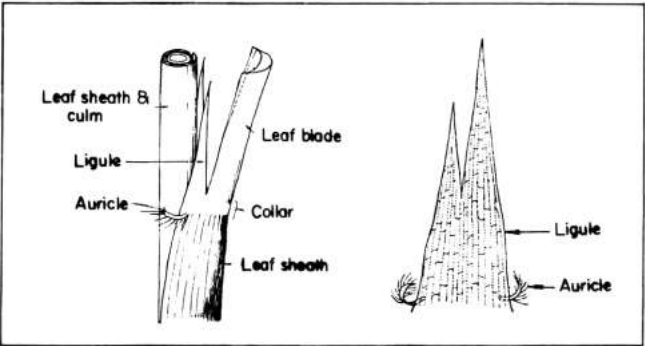
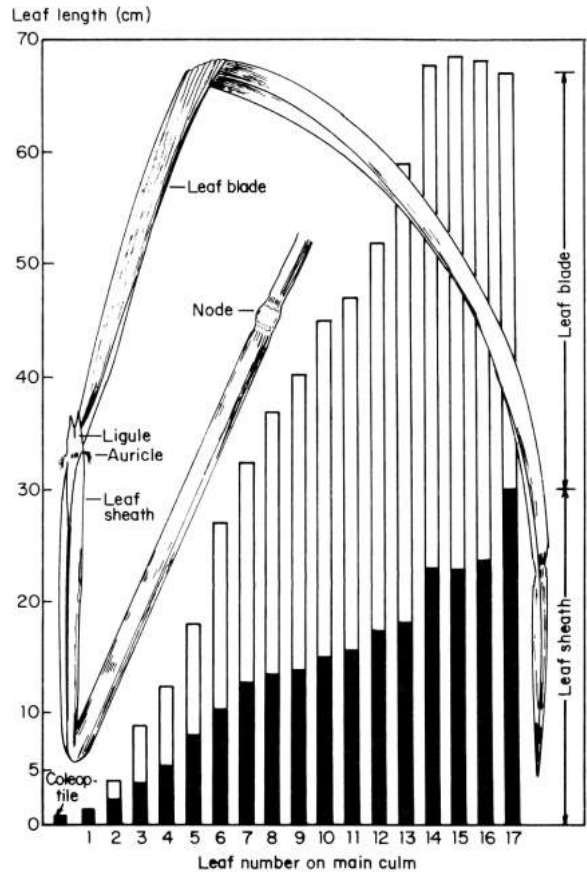
Nursery method ^b	Spacing (cm)	Growth duration ^c	Grain yield (t/ha)	Total dry wt (t/ha)	Harvest index ^d	Grain production per day in main field (kg/ha)
<i>IR74782-6-3</i>						
Wet-bed	10 × 10	98	7.92	14.1	0.48	102
	20 × 20	98	7.23	12.1	0.51	93
Upland	10 × 10	102	7.48	15.5	0.42	91
	20 × 20	102	7.32	12.5	0.50	89
Dapog	10 × 10	102	7.88	14.7	0.46	87
	20 × 20	102	7.61	13.9	0.47	84
Direct seeding	10 × 10	98	7.36	14.0	0.45	75
	20 × 20	98	7.37	13.3	0.48	75
<i>IR154-18-2-1</i>						
Wet-bed	10 × 10	110	7.23	15.2	0.41	80
	20 × 20	110	6.98	13.8	0.43	78
Upland	10 × 10	112	6.75	14.7	0.39	73
	20 × 20	112	6.75	14.4	0.40	73
Dapog	10 × 10	110	7.22	16.1	0.39	73
	20 × 20	110	7.13	14.2	0.43	72
Direct seeding	10 × 10	102	6.89	14.9	0.40	68
	20 × 20	102	6.82	13.5	0.43	67
<i>IR8</i>						
Wet-bed	20 × 20	132	8.61	17.2	0.43	77

^aIRRI (1971). ^bSeedlings were grown for 20 days in the wetbed nursery and the upland nursery and for 11 days in the *dapog* (submerged concrete-lined seedbed) nursery. ^cFrom sowing to harvest. ^dRatio of grain to total dry matter.

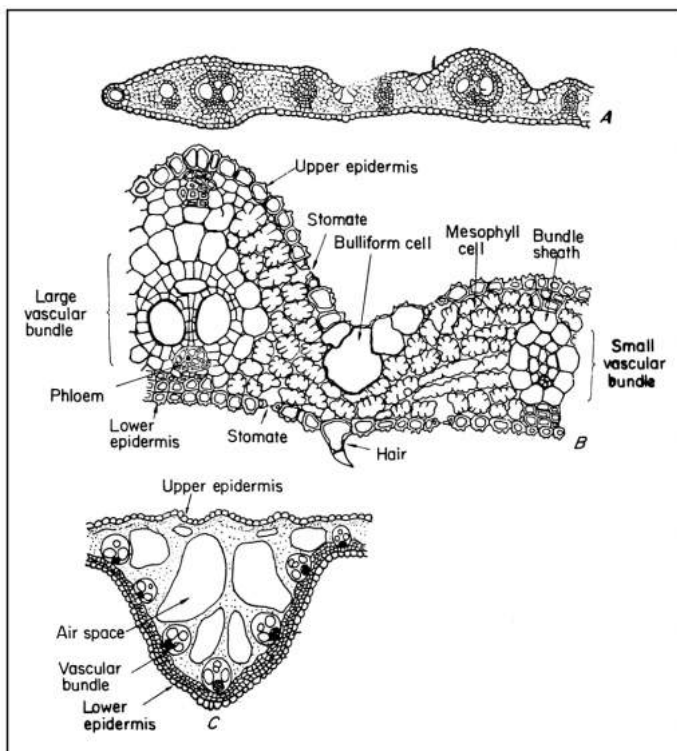
cylinder that encloses all the younger parts of the shoot. The blade is narrow, flat, and longer than the sheath in all leaves except the second. The ligule is a small, white, triangular scale that looks like a continuation of the sheath. At the base of the blade, i.e. around the junction between the blade and sheath, there is a white band called the *collar* (Fig. 1.17). A pair of hairy and sickle-shaped auricles are located at the junction between the collar and the sheath. The presence of well-developed auricles is often used as a convenient guide for differentiating rice from barnyard grasses, which lack auricles. Some rice varieties, however, lack the ligule and auricles (liguleless rice).

Most early- to medium-maturing varieties develop about 10–18 leaves on the main culm. In photoperiod-insensitive varieties the number of leaves is constant under most conditions. For instance, IR747B2-6 develops 13 leaves and Tainan 3, 15 leaves at Los Baños, Philippines, regardless of the planting season. On the

1.16. The form and dimension of rice leaf components (adapted from Hoshikawa 1975).



1.17. Morphology of the area between the leaf blade and the leaf sheath of the rice plant (adapted from Hoshikawa 1975).



1.18. Cross sections of the leaf blade: A-overview of the cross section of the blade; B-cross section of large and small vascular bundles; C-cross section of the midrib (adapted from Hoshikawa 1975).

other hand, weakly photoperiod-sensitive Peta develops 16–21 leaves and strongly photoperiod-sensitive BPI-76, 13–23 leaves, depending on the planting season.

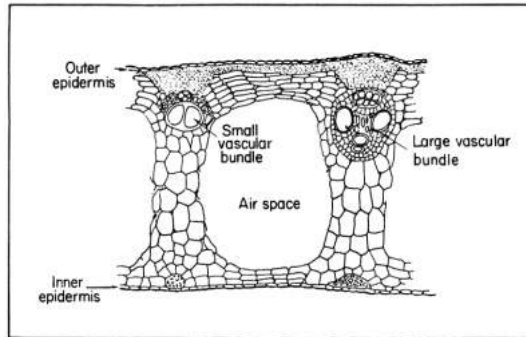
Leaf length increases as leaf number advances. In most varieties, the second or third leaf from the last is the largest. The last leaf is called the flag leaf.

In cross section (Fig. 1.18), the blade contains many large and small vascular bundles; stomates are on both sides of the leaf surface, and large air spaces are developed in the midrib.

In the sheath (Fig. 1.19), large, well-developed air spaces are found between the vascular bundles. These air spaces are connected to stomates and to air spaces in the culm and roots, constituting an efficient air passage system from shoot to root.

1.4.2. Growth of single leaves

At a given time, the rice plant is composed of leaves that are physiologically different in age and activity. Before the initiation of panicle primordia, a leaf emerges about every 4–5 days; afterwards about every 7–8 days. The rate of leaf

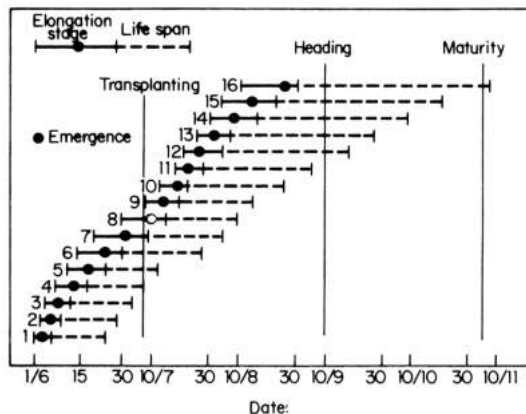


1.19. Cross section of the left sheath (adapted from Hoshikawa 1975).

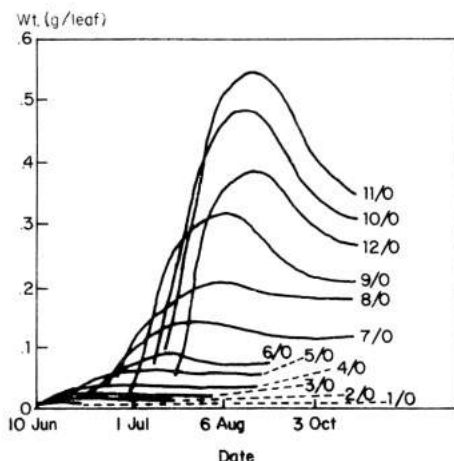
emergence is affected by temperature: an increase in temperature speeds leaf emergence. In terms of the temperature summation index (see page 45), the development of one leaf requires about 100 degree-days before the initiation of panicle primordia and about 170 degree-days thereafter. Thus, when the rice plant is grown at 20°C, leaves emerge every 5 days ($100 \text{ degree-days}/20^\circ\text{C} = 5 \text{ days}$); when it is grown at 25°C, they emerge every 4 days before panicle primordia initiation. Leaves elongate quickly after emergence, complete their elongation, and start functioning.

The life span of individual leaves after elongation differs widely among leaves (Fig. 1.20). Upper leaves have longer life spans than lower ones; the flag leaf has the longest life span. From the initiation of panicle primordia to around heading, the rice plant usually has five leaves that are functioning.

The rate at which the weight of individual leaves increases follows patterns shown in Fig. 1.21. Leaf weight increases sharply, reaches the maximum, and declines.



1.20. The life span of individual rice leaves (adapted from Arashi 1955).



1.21. The growth of individual leaves on the main culm of the rice plant (adapted from Tanaha 1954).

At early stages of leaf growth, weight increases are associated with elongation. After the completion of elongation, the weight continues to increase because of an accumulation of proteins and starch and an increase in cell wall materials such as hemicellulose. The leaf weight decreases at later stages of growth because proteins, sugars, and starch are translocated to upper leaves.

1.4.3. Leaf growth of a crop

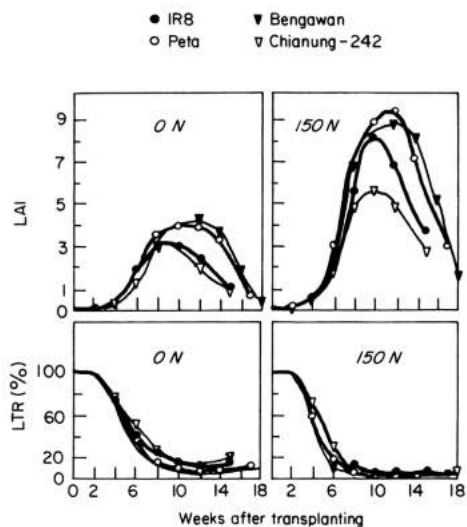
The leaf growth of a rice crop, as a whole, can be measured in terms of the weight of whole leaves per unit of ground area, and of leaf area of whole leaves per unit of ground area. Because leaves intercept incident solar radiation, leaf area index is widely used in the research of crop photosynthesis and growth analysis.

Leaf area index (LAI) is defined as:

$$\text{LAI} = \frac{\text{sum of the leaf area of all leaves}}{\text{ground area of field where the leaves have been collected}}. \quad (1.1)$$

The same unit must be used for both leaf area and ground area. Even though a leaf has two surfaces, it is customary to measure only one. In crops such as wheat, all the exposed green tissues, including leaf blades, leaf sheaths, and culms, are measured for LAI. In rice, however, it is common to measure only the area of leaf blades because photosynthesis by sheaths and culms is negligible. LAI values imply the magnitude of leaf area relative to ground area. Thus, $\text{LAI} = 2$ means that a crop has a leaf area twice as large as the ground area. If all the leaves are arranged flat in one plane parallel to the ground with no dead space, the leaves of a crop with $\text{LAI} = 1$ covers the ground surface completely. But all the leaves are neither flat nor in the same plane. Hence, LAI values greater than 1 are needed to cover the ground surface. LAI increases as growth advances and reaches a maximum at around heading when the rice plant has its 5 largest leaves. After heading, however, LAI declines as the lower leaves die (Fig. 1.22).

1.22. Leaf area index (LAI) and light transmission ratio (LTR) of 4 varieties under 0 and 150 kg N/ha at successive growth stages, 1967 dry season (Yoshida and Ahn 1968).



A rice crop can attain maximum LAI values of 10 or greater at heading time. The critical LAI value at maximum crop photosynthesis is about 5–6.

Because LAI is the sum of the area of whole leaves, it can be analyzed as follows:

$$\begin{aligned} \text{LAI} &= \text{average leaf size} \times \text{number of leaves per shoot} \\ &\quad \times \text{number of shoots per hill (or plant)} \\ &\quad \times \text{number of hills (or plants) per unit of ground area.} \end{aligned} \quad (1.2)$$

In agronomic practice, spacing and nitrogen application are the two major factors influencing leaf area growth under most conditions. Spacing determines the number of hills per unit of ground area, and both nitrogen application and spacing affect average leaf size, number of leaves per shoot, and number of shoots per hill. In addition, tillering capacity of a variety modifies the influence of spacing and nitrogen application.

Several techniques are available for estimating leaf area (Yoshida et al 1976): 1) use of electronically operated area meter, 2) blueprint-gravimetric method, and 3) leaf length-width measurement. Recent advances in electronics have produced an instrument to accurately measure the area of any irregular shape. The leaf length-width measurement is the easiest among the three and it uses a correction factor (K). The leaf area is given as:

$$\text{Leaf area (cm}^2\text{)} = K \times \text{length (cm)} \times \text{width (cm)} \quad (1.3)$$

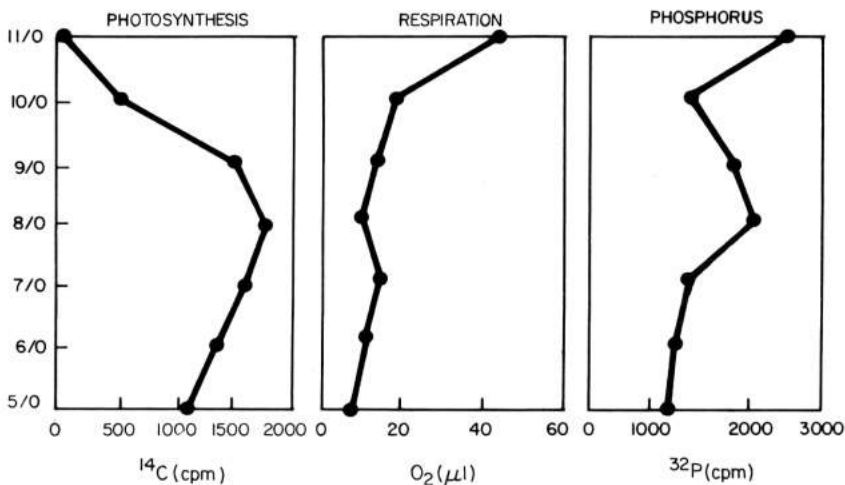
The correction factor used for rice leaves ranges from 0.67 to 0.80, depending on variety and growth stage. The value of 0.75, however, can be used for all growth stages except the seedling stage and maturity.

1.4.4. Functions of individual leaves

a. Physiologically active centers. The rice plant at any given growth stage is composed of leaves of physiologically different ages and this suggests that those leaves are different in their contribution to the growth of the whole plant.

Accumulation of ^{32}P in plant tissues is usually considered an indication of high metabolic activity. When ^{32}P is absorbed through the roots of solution-cultured rice plants, an accumulation is found in the topmost leaf and the third and fourth leaves (Fig. 1.23). In the topmost leaf that is still elongating, a ^{32}P accumulation is associated with a high respiratory rate. This leaf, however, is low in photosynthetic activity and depends on the lower leaves for assimilates. In other words, the topmost elongating leaf is dependent on the lower leaves. The third or fourth fully developed leaf from the top has the highest photosynthetic activity among the leaves and exports assimilates to upper leaves. These photosynthetically active leaves are considered the most important for growth of the whole plant and are called *physiologically active centers* (Tanaka 1961a). Any leaf serves as a physiologically active center at some point in the plant's life cycle. Since new leaves develop upward as lower leaves die, the physiologically active centers move upward as growth advances. Thus, the physiologically active centers may be 7/0 leaf during the tillering stage, move to 9/0 and 10/0 leaves after panicle primordia initiation, and to 10/0 and 11/0 leaves during milky stage.

b. Division of work among leaves. Leaves are different not only in age but in position relative to panicles or roots. Physical distance appears to control the direction of assimilate movement. At the milky stage, the flag leaf, 12/0, exports assimilates mainly to panicles, whereas the lowest leaf, 8/0, exports a large amount of assimilates to the roots (Table 1.7). Thus, grain growth appears to be largely dependent on the upper leaves, and root activity is maintained by assi-



1.23. Distribution of ^{32}P , photosynthetic activity, and respiration of individual leaves of the rice plant (Tanaka 1960).

Table 1.7. Fate of ^{14}C assimilated by leaves of different positions at milky stage.^a

Plant parts	Position of leaves	Assimilating leaves		
		12/0	10/0	8/0
Panicles	—	2562 ^b	370	60
Leaf blades	12/0	26,124	160	106
	11/0	—	130	66
	10/0	—	46,560	50
	9/0	—	34	40
	8/0	—	—	51,360
Internodes	Panicle–12/0	620	240	114
	12/0–11/0	376	70	112
	11/0–10/0	24	70	40
	10/0–9/0	16	70	40
Roots	—	—	—	444

^a Tanaka (1958). ^bCounts per minute per 10-mg sample.

lates sent by the lower leaves. This relationship, however, should not be taken as the fixed assignment of individual leaves. There is evidence in other plants that the division of work among leaves is flexible (King et al 1967, Rawson and Hofstra 1969). If, for some reason, the lower leaves are not properly functioning or die, the upper leaves may supply assimilates to the roots.

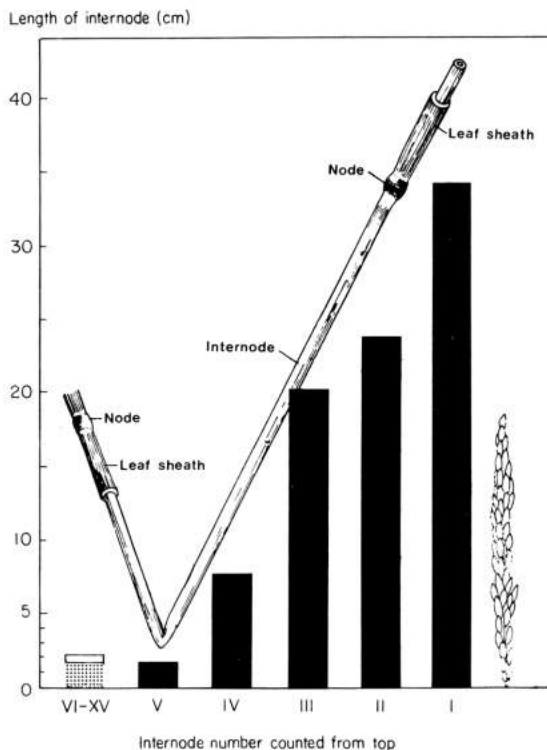
c. Function of leaf sheath. The leaf sheath contributes very little to photosynthesis but it performs other important functions. Until internode elongation starts at around panicle primordia initiation, the culm remains very small, about 1 cm long, and the leaf sheath supports the whole plant. Even after the completion of internode elongation, the leaf sheath contributes to the breaking strength of the shoot by 30 – 60% (Chang 1964). Thus, it functions as a mechanical support to the whole rice plant. In addition, it serves as a temporary storage site for starch and sugar before heading (Murayama et al 1955, Togari et al 1954). The accumulated carbohydrate in the leaf sheath and culm translocates into the grains after heading.

The estimated contribution of the accumulated carbohydrate to the grain carbohydrate normally ranges from 0 to 40%, depending on the rate of nitrogen application and growth duration (see Chapter 7). The accumulated carbohydrate also serves as a carbohydrate source for developing tiller buds. In contrast with the leaf sheath, leaf blades of healthy rice plants do not accumulate starch; those of plants infected with tungro virus accumulate an appreciable amount of starch, which can be easily demonstrated by the iodine reaction (Ling 1968).

1.5 CULM

1.5.1. Morphology

The culm is composed of a series of nodes and internodes (Fig. 1.24). It is enclosed within the sheath before heading, and a small portion of the culm right below the panicle becomes exposed after heading.

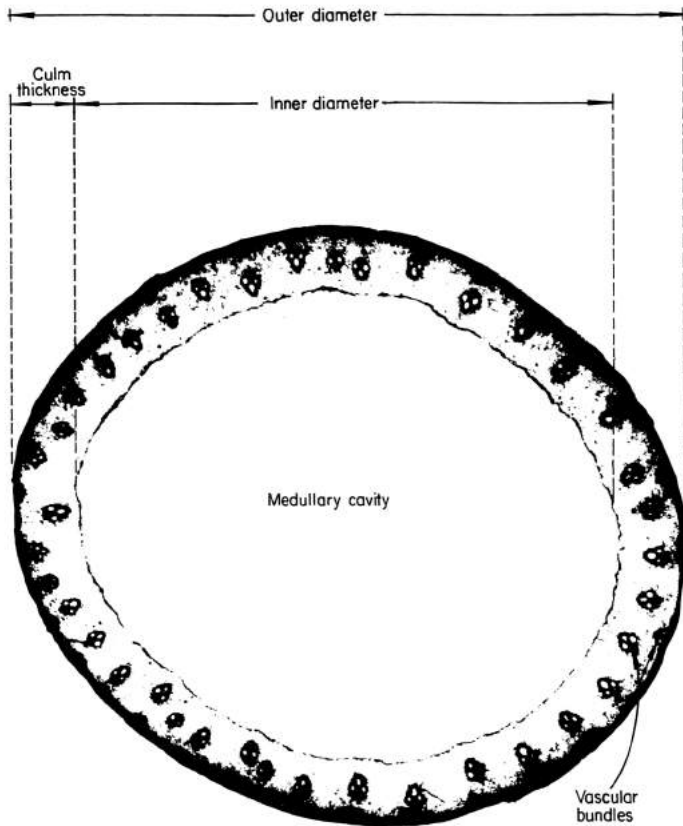


1.24. The culm, node, and internode of the rice plant (adapted from Hoshikawa 1975).

The total number of nodes on the main culm is equal to the number of leaves developed on the culm plus two, which account for nodes for the coleoptile and panicle. Thus, if a variety develops 15 leaves on the main culm, it has 17 nodes. Only a few internodes at the top elongate; the rest are short and thickened into a solid section. The uppermost internode is the longest, and the internodes decrease in length as their distance from the plant base decreases. The total of unelongated internodes accounts for only a few centimeters. An elongated internode is conveniently considered as one whose length exceeds 5 mm. The number of elongated internodes (ranging from 3 to 8, averaging around 5) varies with variety and environment. After heading, the sum of the lengths of elongated internodes accounts for a large fraction of plant height.

The outer diameter of internodes, about 2–6 mm, varies with internode position, kind of shoot (main culm or tillers), and environmental conditions.

In cross section (Fig. 1.25), the internode has a large hollow space called the *medullary cavity*, whose diameter is the inner diameter of the internode. Many large vascular bundles are found in the middle portion of the internode tissue. In addition, many small vascular bundles are located near the epidermis. In the lower elongated internodes, fourth or fifth from the top, many air spaces may be found between the vascular bundles (Fig. 1.26).

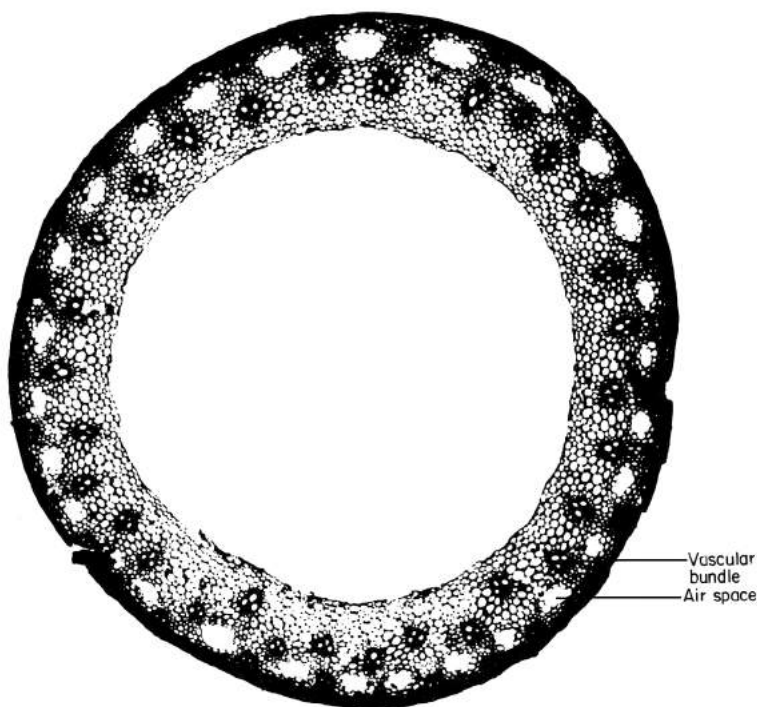


1.25. Cross section of an upper internode

Several plant height characteristics are measured in agronomic investigations: plant height, culm height, and crop height. Plant height refers to the longest distance between the plant base and the tip of the highest leaf (or panicle, whichever is longer). Rice leaves, usually bent, are stretched along the culm axis for plant height measurement. Culm height is the length between the plant base and the panicle necknode. It is considered a more meaningful measure than plant height when lodging resistance is to be examined. Crop height may be defined as the length between the ground surface and the highest point of the crop canopy.

1.5.2. Internode elongation

Internode elongation is closely associated with growth duration (Hosoda and Iwasaki 1960, Vergara et al 1965). In early- and medium-maturing varieties, it usually starts around panicle primordia initiation. In late-maturing varieties, it starts before panicle primordia initiation. In photoperiod-sensitive varieties, extended photoperiod increases the number and total length of internodes. In photoperiod-insensitive varieties, it has no influence on internode elongation.



1.26. Air space in a lower internode.

Unusual environments, such as deep seeding and deep water, induce internode elongation even at early growth stages. Seed placement 2 cm deep in soil does not induce internode elongation but the placement deeper than 3 cm may induce elongation of the first and second internodes (Sekiya 1953).

In deepwater and floating rices, internode elongation occurs in response to increased water depth. The maximum observed rate of internode elongation is 25 cm/day but about 2–10 cm/day is more common (Vergara et al 1976).

1.5.3. Culm characteristics related to lodging

Physically, lodging can be examined in terms of the bending moment and the breaking strength of the culm and sheath (Chang 1964). The bending moment is the product of shoot weight and the height of the main axis (culm height). After heading, the panicle weight increases as the grains grow, and hence the bending moment increases. If other things are equal, a tall variety has a greater bending moment than a short variety because it has a greater culm height.

The shoot's breaking strength is greatly affected by 1) length of lower internodes, 2) strength or stiffness of the elongated internodes, and 3) strength and tightness of the leaf sheath.

Lodging usually results from the bending or buckling of the 2 lowest internodes, which have elongated more than 4 cm. The strength of elongated internodes

is affected by mechanical strength, chemical composition, and plant nutritional status. The mechanical strength is related to culm thickness and tissue strength. Partly a varietal character, mechanical strength is modified by growing conditions. Increased nitrogen applications, which are essential for high yields, cause elongation of the lower internodes, making the crop more susceptible to lodging. Lodging decreases grain yield drastically, particularly when it occurs right after heading and when panicles are brought in contact with standing water. The beneficial and ill effects of heavy applications of nitrogen present a serious dilemma.

Among organic and inorganic constituents of the culm, holocellulose and potassium content are highly correlated with breaking strength, but silica content is not related to culm stiffness (Kono and Takahashi 1961a, c). Before heading, large amounts of starch accumulate in the culm and sheath. The starch was believed to contribute to the shoot's stiffness (Sato 1959). A later examination, however, showed no correlation between starch content and breaking strength (Kono and Takahashi 1961a).

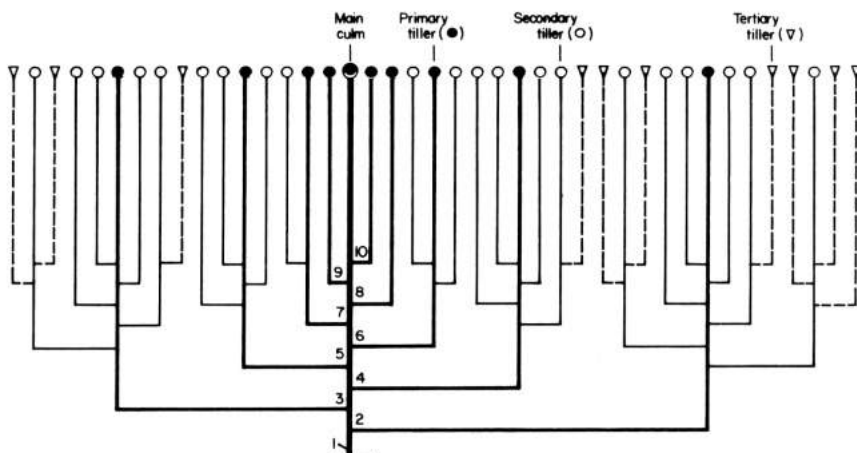
The culm's mechanical strength is increased by potassium applications, which increase its thickness (Noguchi 1940) and maintain high turgor pressure in the cells (Kono and Takahashi 1961b). Where lodging is a serious problem, balanced fertilization is essential for achieving high yields. The presence of the living leaf sheath accounts for about 30–60% of the shoot's breaking strength. Because lodging normally occurs somewhere in the lowest two internodes, the leaf sheaths enclosing these internodes must be stiff. These are sheaths of the lower leaves during the ripening period. It is important, therefore that cultural practices be directed toward preventing the lower leaves from early withering. In spite of work done on lodging resistance, the only successful approach to increasing lodging resistance has been to develop short varieties. Short varieties, however, are not always lodging resistant (Chandler 1969) because other characteristics such as culm thickness, tissue strength, and rate of senescence of lower leaves modify the breaking strength of the shoot.

1.6. TILLERING

1.6.1. Tillering pattern

Tillers are branches that develop from the leaf axils at each unelongated node of the main shoot or from other tillers during vegetative growth. When the fifth leaf on the main culm emerges, the first leaf of the tiller comes from the axil of the second leaf on that culm. Similarly, when the sixth leaf on the main culm emerges, the first leaf of the tiller comes from the axil of the third leaf on that culm. Thus, the n th leaf on the main culm and the first leaf of the tiller that emerges from the axil of the $(n-3)$ th leaf grow synchronously. This rule applies not only to the main culm but to all the tillers.

On the main culm, the coleoptile and the first leaf normally do not produce tillers; tillering usually starts from the second leaf. On each tiller the prophyll develops before the first leaf emerges. The prophyll, corresponding to the coleop-



1.27. Tillering pattern of rice.

tile on the main culm, lacks a blade and is similar to the sheath in structure. The prophyll, which is white, is enclosed within the leaf sheath on the main culm and is not visible. It is the first leaf that can be seen when a new tiller comes out. Tillers may or may not emerge from the prophyll node.

When the 13th leaf on the main culm emerges, and if tillers come from all except the prophyll nodes, there should be a total of 40 tillers: 9 primary, 21 secondary, and 10 tertiary (Fig. 1.27). The number of tillers shown in Figure 1.27 gives the theoretical maximum under specified conditions. In reality, however, all the tiller buds do not necessarily develop into tillers. Some may remain dormant. Spacing, light, nutrient supply, and other environmental and cultural conditions affect tillering. For example, phosphorus deficiency or deep planting impairs tillering. In transplanted rice, about 10–30 tillers may be produced at conventional spacing, but only 2–5 may form in direct-seeded rice.

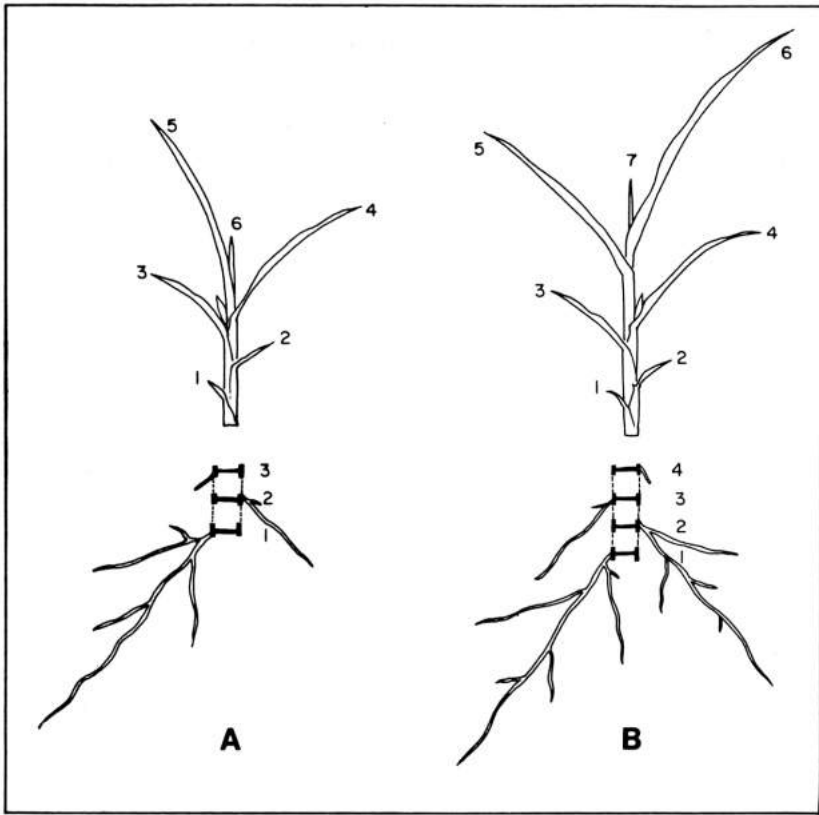
1.6.2. Synchronous growth of a tiller, a leaf, and roots

A tiller and roots emerge from the same node at the same time. When the sixth leaf emerges, a tiller and roots start emerging from the third node (Fig. 1.28). Similarly when the seventh leaf emerges, a tiller and roots come from the fourth node. If roots of a seedling are removed when the seventh leaf is about to emerge and the plant is placed in culture solution, new roots will come only from the fourth node.

1.7. ROOTS

1.7.1. Morphology

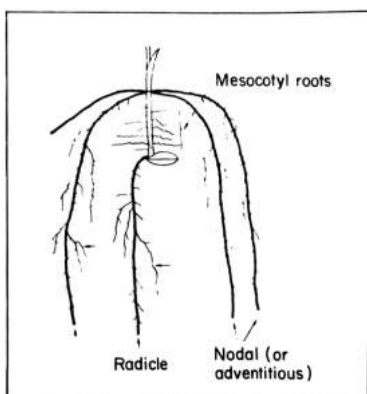
Rice develops a radicle (seminal root), mesocotyl roots, and nodal (or adventitious) roots (Fig. 1.29).



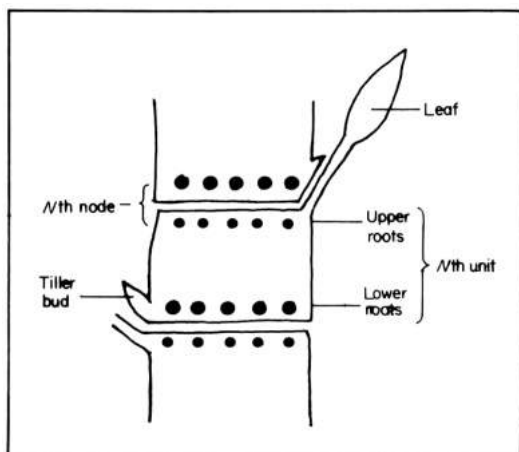
1.28. Synchronous growth of a tiller, a leaf, and roots of a rice plant (adapted from Fujii 1974).

After germination, one radicle emerges and elongates to a maximum length of about 15 cm; it functions until the seventh-leaf stage. Mesocotyl roots emerge from the axis between the node of the coleoptile and the base of the radicle. Mesocotyl roots develop only under such conditions as deep seeding or when the seed is treated with chemicals.

The rice root system is basically composed of nodal roots. Each node usually develops about 5–25 roots. When the development of root, leaf, and tiller is examined, it is more convenient to regard an internode rather than a node as a unit (Fig. 1.30). A leaf and thin roots emerge from the upper region of the internode whereas a tiller and thick roots develop from the internode's lower region. Roots developing directly from the culm's nodal regions are called primary roots. The diameter of the primary roots ranges from 0.5 mm to greater than 1 mm. As growth advances, the primary roots develop branched secondary roots, which in turn develop tertiary roots, and so on. Under lowland conditions, rice is known to develop sixth-order branched roots. The root diameter becomes successively



1.29. Three kinds of rice roots (Hoshikawa 1975).

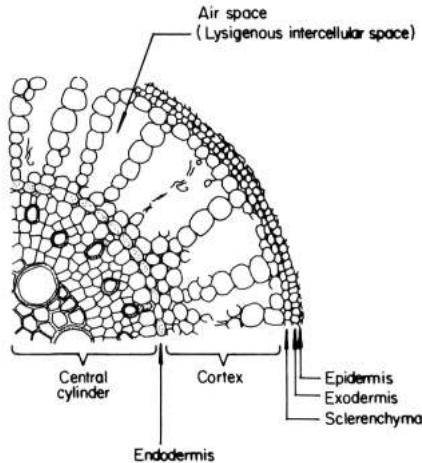


1.30. Structural unit of root, leaf, and tiller (Kawata et al 1963).

smaller (ranging from 1,000 to 40 μm) as the order of branching increases.

The formation of root hairs is greatly affected by the root environment. Aerobic conditions in upland soils favor root hair formation (Kawata and Ishihara 1959, 1961, Kawata et al 1964); the reductive conditions of flooded soils impair it. Rice root hairs are about 5–10 μm in diameter and about 50–200 μm long. Most rice varieties reach a maximum rooting depth of 1 m or deeper in soft upland soils. In an anaerobic environment, such as flooded soils with impaired water percolation, rice roots seldom exceed a maximum depth of about 40 cm. Actual root depth found in the field is controlled not only by genetic ability but also by environmental conditions. Total root length increases as the shoot grows. At heading, it is about 2–3 km/plant when plants are grown singly in a root box. In an upland field, the total root length ranges from 15 to 34 km/m² of soil surface. Specific root length varies from 10 to 1,000 m/g dry weight. Thick roots are shorter per unit dry weight than thin roots. The average length of rice roots is about 300 m/g dry weight, which corresponds to a root with a diameter of 0.2 mm.

1.31. Cross section of a matured rice root (adapted from Hoshikawa 1975).



One characteristic of rice roots is the presence of large air spaces in mature roots (Fig. 1.31). These air spaces are connected with those in the culms and leaves, providing an efficient air passage system from shoot to root.

Root age can be visually classified into different groups based on formation of rootlets, as shown in Table 1.8 (Inada 1967). Young roots without rootlets are normally milky white in color. As age advances, a larger portion of a root near the base successively turns yellow, pale brown, brown, and dark brown in color. The tip portion of a growing root, however, usually remains milky white.

1.7.2. Root-shoot relationships



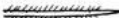
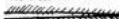
Weight growth of the root is closely related to weight growth of the whole plant. This relationship is called allometry or relative growth.

Root dry weight is related to total dry weight of the plant by the following formula:

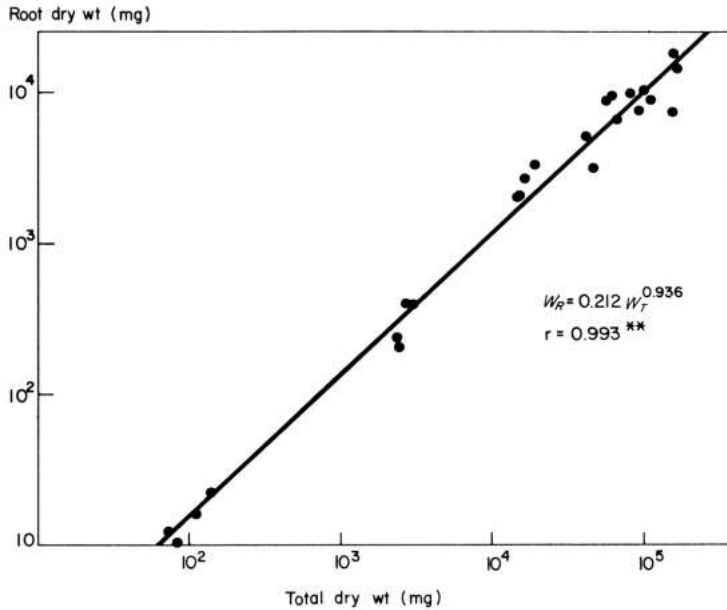
$$W_R = H W_T^h, \tag{1.4}$$

$$W_R = H W_T^h,$$

Table 1.8. Visual classification of rice roots.^a

Grouping	Rootlet formation (%)	Av length (cm)	Age of roots (days)
I 	Rootlet: none	5– 7	< 3
II 	Rootlet: ca. 50%	10–20	3–7
III 	Rootlet: ca. 80%	15–30	7–14
IV 	Rootlet: over 90%	> 30	>14

^a Adapted from Inada (1967).



1.32. Relationship between total dry weight and root dry weight of 4 rice varieties (IRRI 1978).

where W_R is root dry weight, W_T is total dry weight (i.e., shoot dry weight plus root dry weight), and H and h are constants. Equation 1.4 can be converted into a logarithmic form:

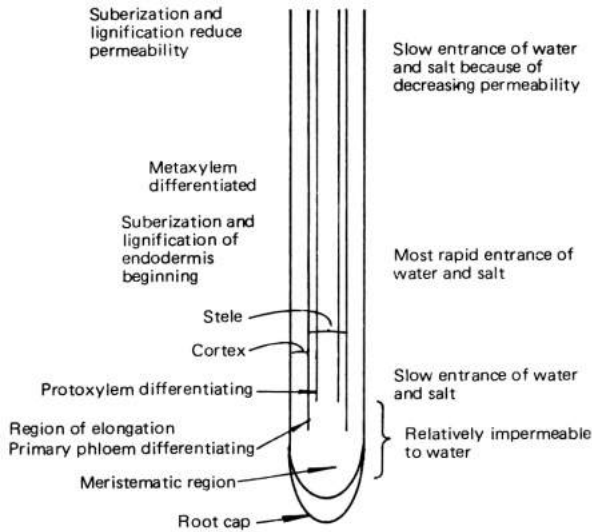
$$\text{Log } W_R = \text{log } H + h \text{ log } W_T. \quad (1.5)$$

Thus, $\log W_R$ is a linear function of $\log W_T$. The above relationship has been tested for different rice varieties under different environmental conditions. One such study gives the following formula:

$$W_R = 0.212 W_T^{0.936} \quad (1.6)$$

where the weight is expressed in milligrams (Fig. 1.32). Thus, when the plants are small (substitute 1 for W_T), W_R/W_T is about 0.2; W_R/W_T value approaches 0.1 as the plant grows larger (substitute 10^5 for W_T). In other words, the ratio of root dry weight to total dry weight ranges from about 0.2 at the seedling stage to about 0.1 at heading.

The above relationship between root and total dry weight gives an estimate of root mass left in the soil if shoot weight is known. For instance, when a crop produces a shoot dry weight of 3 t/ha at heading, a root dry weight of about 330 kg/ha is left in a *recoverable form* in the soil. Since it is known for other cereal crops that a considerable amount of organic substances is released into the soil from roots as root exudates (Barber and Martin 1976), the actual amount of



1.33. Diagram of a young root, showing relation between anatomy and absorbing regions for water and salt (from *Plant and Soil Water Relationships* by P. J. Kramer, Copyright © 1969 by McGraw-Hill, Inc. Used with the permission of McGraw-Hill Book Company).

organic matter left in the soil and attributable to root growth should be much higher.

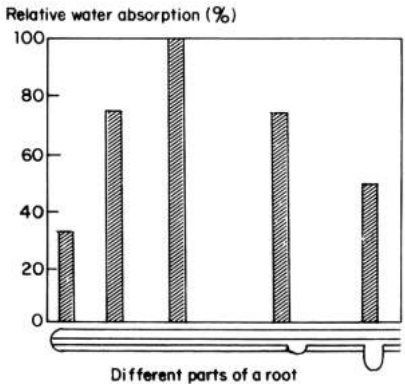
1.7.3. Water and nutrient uptake by single roots

The tip of a single root is relatively impermeable to water and the region some distance away from the tip toward the proximal end also has a low permeability to water due to suberization. The entrance of water and salt is most rapid between the above two low permeable regions of a root (Fig. 1.33).

Along the axis of a single rice root, the meristematic region is about 0.25 mm from the tip; branched roots are recognizable at 30–40 mm; and considerable suberization occurs at about 40–50 mm. Suberization is more intense in regions further away from the tip (Kawata and Lai 1968). Water absorption is most active between the root tip and the site of branched roots (Fig. 1.34).

1.7.4. Water and nutrient uptake by old and new roots

When half of the roots of a rice plant are cut at the base around panicle initiation time and the plant is placed in nutrient solution for about 10 days, new roots will emerge to replace those lost. The capacity of these new roots to absorb water and nutrients can be examined if they are placed in separate nutrient containers (Okajima 1960).



1.34. Relative water absorption rate of different parts of a single rice root (Kawata and Lai 1968).

As shown in Table 1.9, old roots took up about 60% of the water and nutrients absorbed by the plant. Even if water and nutrient uptake is expressed on a dry root weight basis, the capacity of the old roots is greater. This higher capacity may be partly attributed to the tissue's low nutrient and high sugar content, which favor active nutrient uptake. The new roots, however, have a higher oxidizing capacity than the old roots.

1.7.5. Water and nutrient uptake by the root system

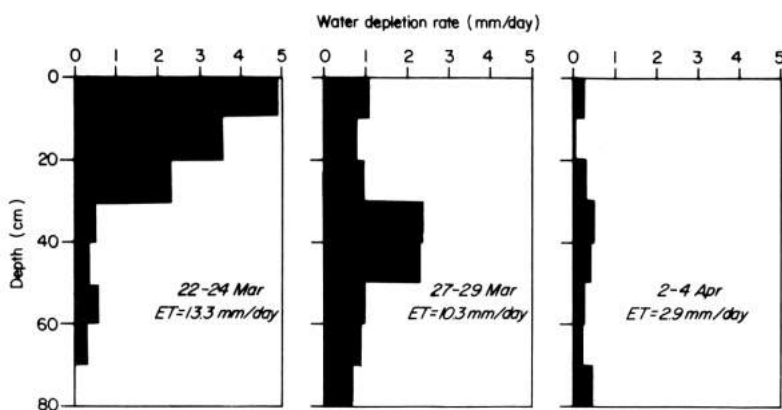
Water shortages are frequently a limiting factor for crop growth in upland fields and in rainfed lowland fields.

When water is supplied uniformly to all the soil profiles, the shallow layers are depleted of water first. Plants then take water from increasingly greater depths (Fig. 1.35). The rate of water absorption from a given soil volume is proportional

Table 1.9. Absorption of water and nutrients by old and new roots.^a

	Roots			Amt. absorbed ^b			
	Dry wt (g)	No.	Max. root length (cm)	H ₂ O (ml)	N (mg)	P (mg)	K (mg)
Old	1.75	157	33	155 (64)	14.0 (62)	4.5 (63)	9.8 (63)
New	1.32	175	25	86 (36)	8.5 (38)	2.5 (37)	5.7 (37)
Total				241	22.5	6.8	15.5

^a Okajima (1962). ^bFigures in parentheses indicate percentages of the total.



1.35. Water extraction patterns after the irrigation on 21 Mar 1978 (IRRI 1979).

to the effective total root length if other conditions are held constant (Gardner 1960, 1964).

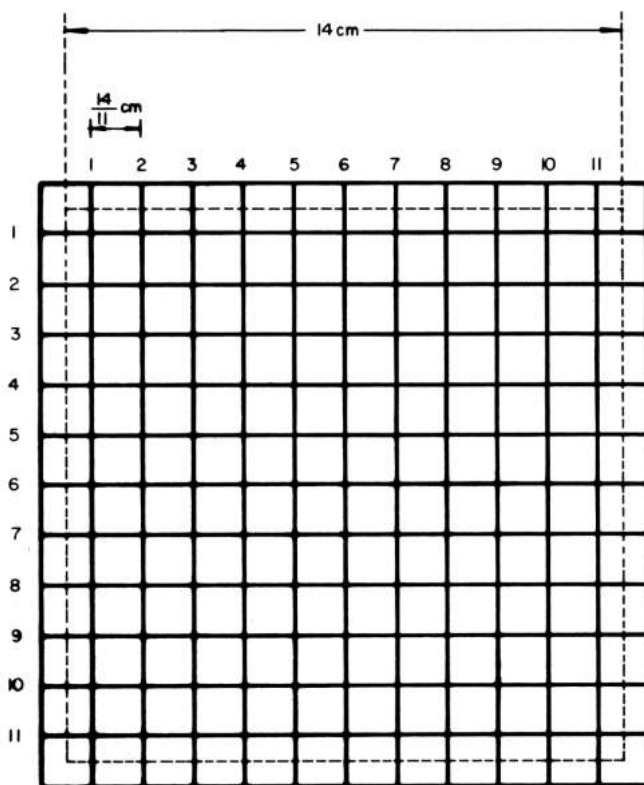
The high rate of water absorption results in a more rapid decrease in soil water potential in the shallow layers. Since the rate of water absorption is also proportional to soil water potential if other things are the same, the water absorption from the shallow layers will decrease. At this time, more water is available to the roots in the deeper soil profiles, and, hence, more water will be absorbed from these layers.

In the mathematical model presented by Gardner (1960), the root was considered an infinitely long cylinder of uniform radius and water-absorbing properties. That is an approximation of the plant's root and may not always apply to the real root. For greater accuracy, the root length should be corrected for root hairs and for degree of suberization.

The total root length is also related to the plant's capacity to absorb a nutrient. For corn plants grown in culture solution, the rate of phosphate uptake was proportional to the total root length (Jungk and Barber 1974). Thus, the capacity of the plant to absorb water and nutrients is closely related to the total length of the root system.

1.7.6. Measurement of root length and root density

Measurement of total root length, even in a small sample, is difficult and tedious because roots can reach great lengths in even small volumes of soil. In 1966, Newman devised an elegant technique by which the total root length can be measured with relative ease. Newman's method, as it is popularly used, uses a grid over which a root is randomly spread (Marsh 1971). Consider a grid with a total area of $14 \times 14 \text{ cm}^2$ and with a regular distance of $14/11 \text{ cm}$ between lines (Fig. 1.36). It is expected that the longer the root that is spread on the grid, the more intercepts it will make with the straight lines. Thus, the number of intercepts can be



1.36. A line grid for indirect measurement of total root length in complex line patterns (adapted from March 1971).

used to estimate the length of the root. Knowing the number of intercepts, the total root length is given as:

$$R = \frac{\pi N A}{2H} \quad (1.7)$$

where R = the total length of root,

N = the number of intercepts between the root and the straight lines,

A = the area of the square or rectangle, and

H = the total length of the straight lines.

In Fig. 1.36 there are 11 horizontal and 11 perpendicular straight lines. Thus, the equation 1.7 becomes:

$$R = \frac{3.14 \times N \times 14 \times 14 (\text{cm}^2)}{2(14 \times 11 + 14 \times 11) (\text{cm})}$$

$$= \frac{43.96 \times N}{44} (\text{cm}) \approx N (\text{cm}) . \quad (1.8)$$

In other words, the number of intercepts gives an estimation of the total root length in centimeters. This method can also be used for estimating the length of any irregular shape of lines.

Root length per unit volume of soil is called root density:

$$\text{Root density} = \frac{\text{Total root length (cm)}}{\text{Volume of soil where the roots have been collected (cm}^3\text{)}} \quad (1.9)$$

Thus, the root density has a dimension of cm^{-2} . It is used as a measure of root growth in a field-grown crop. The root density of rice crops ranges from less than 1 cm^{-2} in a deep soil horizon to more than 30 cm^{-2} around the plant base.

1.7.7. Root characteristics related to drought resistance

The rice root system can be studied using several techniques: 1) root box, 2) core sampling in the field, and 3) monolith. Since drought occurs when there is an imbalance between water absorption and transpiration, greater root growth can help the plant perform better under a limited water supply. The root-shoot ratio of rice varieties can be studied by the root box technique. The ratios range from 0.05 to 0.3 at heading, and average about 0.1. Under drought conditions, the soil starts drying from the surface but the deep soil horizon may remain wet and able to supply water to the plant's roots. Consequently, deep root portions may be more meaningful than shallow root portions when the drought resistance of a variety is to be examined. For this reason, the deep root-shoot ratio is considered a better measure for drought resistance in the field. The deep root-shoot ratio of rice varieties is defined as the weight, in milligrams, of roots that are deeper than 30 cm/gram shoot. It ranges from less than 10 to greater than 80 mg/g.

Table 1.10. Vertical root density distribution of 7 rice varieties grown on an upland field, IRRI, 1977.^a

Variety	Depth (cm)							
	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80
Lowland								
IR20	14.4	2.8	0.9	0.4	0.1			
IR2035-117-3	22.7	5.8	0.8	0.1	0.1			
IR442-2-58	16.8	7.1	1.2	0.3	0.1			
Upland								
OS4	12.6	1.4	0.8	0.9	0.8	0.5	0.5	0.2
Moroberekan	11.8	2.3	0.9	0.8	0.6	0.8	0.4	0.2
Salumpikit	16.2	5.5	1.9	1.4	0.8	0.6	0.3	0.1
20 A	19.8	2.6	0.9	0.8	0.9	0.9	0.6	0.4

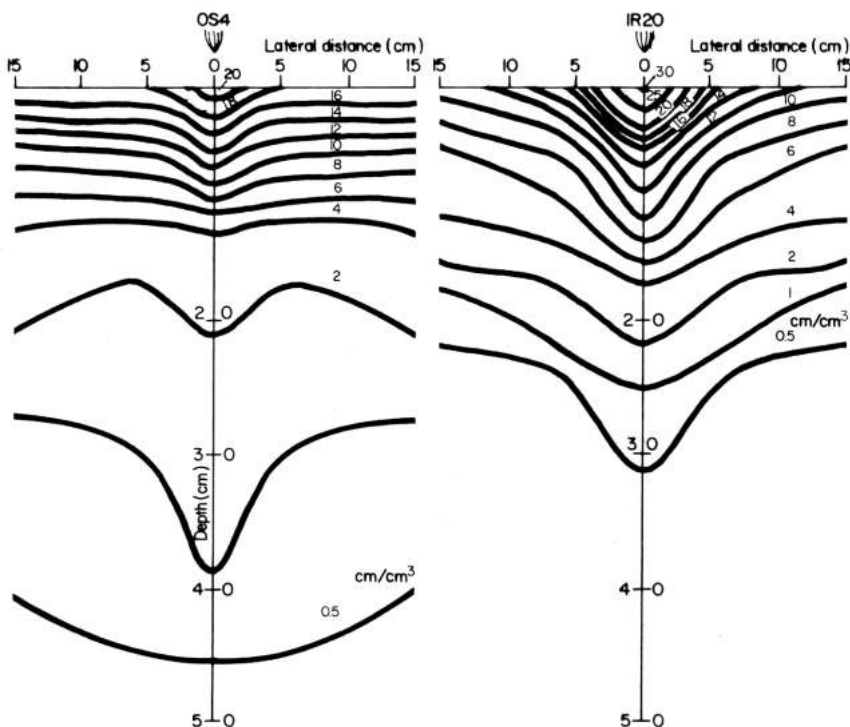
^aIRRI (1978).

When shallow-rooted lowland and deep-rooted upland varieties are grown in the field, there is not much difference between their root densities down to 30 cm beneath the soil surface. The differences are greater in the soil horizons below 30 cm (Table 1.10). This justifies the use of deep root-shoot ratios in the root box technique.

In the field, rice roots grow and extend vertically and laterally. IR20, a shallow-rooted, high-tillering variety, has a very high root density around the plant base but the root's growth, both vertically and laterally, is limited (Fig. 1.37). On the other hand, OS4, a deep-rooted, low-tillering variety, has a well-spaced lateral root distribution and its roots penetrate deeper than those of IR20. Such differences may in part account for the differences in drought resistance between the two varieties.

1.8. PHASIC DEVELOPMENT FROM VEGETATIVE TO REPRODUCTIVE GROWTH STAGES

The rice plant initiates panicle primordia when certain physiological and environmental conditions are met. Panicle primordia on top of the culm can be seen under a microscope about 30 days before heading. Although the duration from panicle



1.37. Iso-root density diagram of rice varieties OS4 and IR20 grown in the field (IRRI 1978).

primordia initiation to heading is slightly affected by variety and weather conditions, it is considered almost constant, about 30 days under most conditions. Variations in length of time from germination to heading are attributed to variations in duration from germination to panicle primordia initiation. Thus, early-maturing varieties initiate panicle primordia earlier than late-maturing varieties.

1.8.1. Response to photoperiod

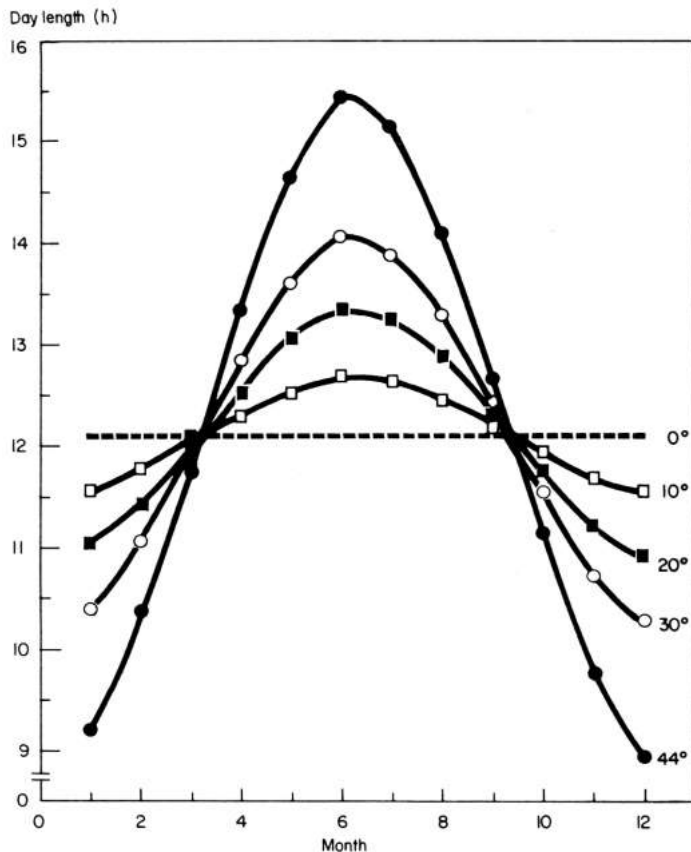
a. Introduction. The length of a day, defined as the interval between sunrise and sunset, is known as *photoperiod*. The response of the plant to photoperiod is called *photoperiodism*.

Rice is basically a short-day plant. It initiates panicle primordia in response to short photoperiods. Panicle primordia may be initiated late or they may not develop when the plant is subjected to long photoperiods. Strictly speaking, however, the rice plant responds to *nyctoperiods* or the length of night. Under natural conditions, a short day implies a long night because a day cycles every 24 hours. Thus, the term *short day* can still be used without any practical confusion.

Rice is now being grown in northeastern China at 53°N, in Central Sumatra on the equator, and in New South Wales, Australia, at 35°S. Day length varies widely with latitude and with season for a given latitude (Fig. 1.38). At a latitude of 44°N, which is close to the practical northern limit for rice cultivation in Japan, day length varies from 9 hours to 15 hours 30 minutes. At the equator, however, it varies from only 12 hours 6 minutes to 12 hours 8 minutes, the difference being only 2 minutes.

At the early stages of research on photoperiodism, the small seasonal differences in day length in the tropics were thought to be unimportant in controlling plant behavior. Later work, however, demonstrated that tropical plants might be more sensitive than temperate plants to small differences in day length (Chang, J.H. 1968). Rice provides a good example. In Malacca, Malaysia, at a latitude of 2°N, the difference between the maximum and the minimum day lengths is only 14 minutes: The variety Siam 29 differentiates this small difference in day length: it takes 329 days to flower when planted in January and only 161 days when planted in September (Dore 1959). Historically, the northerly movement of rice cultivation in the temperate regions has been made possible by selecting varieties that are early maturing, more tolerant of low temperatures, and less sensitive to day length.

Light as low as several to 100 lx may delay initiation of flower primordia. Electric lights installed near the fields may delay flowering. There is some evidence that civil twilight in the morning can delay flowering, while that in the evening may or may not. Civil twilight is defined as the interval between sunrise or sunset and the time when the true position of the center of the sun is 6° below the horizon. At this time stars and planets of the first magnitude are just visible and darkness forces the suspension of normal outdoor activities. The duration of civil twilight varies with locality and time of year; it is about 21–32 minutes long at latitudes from 0° to 40°N (Smithsonian Meteorological Tables 1963). The intensity of light during this time ranges between about 10 and 4 lx.



1.38. Variations in daylength at different northern latitudes.

b. Basic vegetative phase. The vegetative growth stage is divided into the basic vegetative phase (BVP) and the photoperiod-sensitive phase (PSP).

Because the very young plant is insensitive to photoperiod, the early growth stage that must occur before floral initiation can be triggered by short days has been termed the BVP. The length of the BVP ranges from 10 to 63 days; a BVP longer than 100 days has not yet been found in rice varieties. One simple way to estimate the BVP is to subtract 35 days from the growth duration (days to flower) at the optimum photoperiod, i.e., the shortest growth duration. This assumes that the period from the initiation of panicle primordia to flowering is 35 days (Vergara and Chang 1976).

c. Photoperiod-sensitive phase. After the BVP, the plant enters the PSP during which floral initiation can be triggered by short days. The PSP of photoperiod-insensitive varieties is less than 30 days; that of sensitive varieties, longer than 31 days.

Optimum photoperiod and *critical photoperiod* are terms commonly used to characterize the PSP. Optimum photoperiod is the day length at which the duration from sowing to flowering is at a minimum. The optimum photoperiod of most varieties is about 9–10 hours. A longer or shorter photoperiod delays flowering, the delay depending upon the sensitivity of the variety. Critical photoperiod is the longest photoperiod at which the plant will flower or the photoperiod beyond which it cannot flower. The critical photoperiod of most varieties ranges from 12 to 14 hours.

The length of the PSP is usually determined by subtracting the shortest growth duration (growth duration at the optimum photoperiod) from the longest growth duration (growth duration at the critical photoperiod) of the variety. Since many varieties remain vegetative for a long time if grown under long-day conditions, experiments are usually terminated after 200 days, and the PSP of the variety is given the value of 200⁺. Under continually long photoperiods, some varieties have been reported to remain vegetative even after 12 years of growth.

The length of the PSP is a measure of the variety's sensitivity to photoperiod. The shorter the critical photoperiod, the longer the PSP. A short optimum photoperiod is also associated with long PSP (Vergara and Chang 1976).

d. Classification of rice varieties by photoperiodic reactions. Agronomic terms such as early, medium, late, aus, or aman are useful only in particular regions

Table 1.11. Photoperiodic reaction of some selected rice varieties and breeding lines.^a

Sensitivity to photoperiod	Variety	Days to flowering at photoperiod ^b of				PSP (days)	BVP (days)	Date of sowing ^c
		10	12	14	16			
Insensitive	IR12-178	89	89	^d	91	2	54	Dec. 1968
	Fujisaka 5	67	64	71	^d	7	29	July 1962
	Norin 20	49	48	48	59	11	13	
	IR8	101	100	109	112	12	65	March 1970
	Tainan 3	89	89	97	114	25	54	Jan. 1964
Weakly sensitive	IR22	69	73	101	102	33	34	March 1970
	IR20	76	76	103	112	36	41	March 1970
	IR5	93	101	130	134	41	58	March 1970
	C4-63	72	81	110	123	51	37	July 1967
	Peta	70	85	125	145	75	35	May 1963
Strongly sensitive	Siam 29	61	112	^e	^e	200 ⁺	26	Jan. 1964
	Latisail	55	84	^e	^e	200 ⁺	20	March 1972
	Podiwi A-8	76	136	^e	^d	200 ⁺	41	July 1962
	Puang Nahk 16	68	90	^e	^e	200 ⁺	33	May 1963
	Raminad St. 3	69	121	^e	^e	200 ⁺	34	May 1964

^aAdapted from Vergara and Chang (1976). ^bThe plants received 10 hours of natural light from 0700 to 1700 hours. The light intensity in the darkrooms was 400 lx and the temperature, 20°C. ^cDate of test. Variations in growth duration can occur because of differences in greenhouse temperature during growth. ^dNot tested. ^eNo panicle initiation after 200 days of growth.

where the climates are similar. The classification of rice varieties by photoperiodic reactions is more rational and should be applicable in a wider range of climates. The following practical grouping is suggested (Vergara and Chang 1976).

Reaction to photoperiod	Characteristics
Insensitive	Very short PSP (less than 30 days) and BVP varying from short to long
Weakly sensitive	Marked increase in growth duration when photoperiod is longer than 12 hours; PSP may exceed 30 days but flowering occurs under any long photoperiod
Strongly sensitive	Sharp increase in growth duration with increased photoperiod; no flowering beyond critical photoperiod; BVP usually short (not more than 40 days)

It should be kept in mind that there is no sharp dividing line between the photoperiod-sensitive and photoperiod-insensitive varieties, and any definition would be based on arbitrary criteria.

Table 1.11 lists the photoperiodic reactions for some selected rice varieties and breeding lines. To illustrate a continuous variation in photoperiod sensitivity, the varieties or lines are listed in increasing order of length of PSP.

Although the PSP and BVP are shown in Table 1.11, they can be calculated for the variety Peta as follows:

$$\begin{aligned}
 \text{BVP} &= \text{shortest growth duration} - 35 \\
 &= 70 - 35 \\
 &= 35 \text{ days}
 \end{aligned}
 \tag{1.10}$$

$$\begin{aligned}
 \text{PSP} &= \text{longest growth duration} - \text{shortest growth duration} \\
 &= 145 - 70 \\
 &= 75 \text{ days}
 \end{aligned}
 \tag{1.11}$$

Optimum photoperiod: 10 hours

Critical photoperiod: 16 hours

e. Agronomic implications of photoperiodism. Photoperiod-insensitive varieties can flower and ripen throughout the year provided irrigation water is available. Thus, the use of photoperiod-insensitive varieties makes the planning of rice cultivation more flexible and more suitable to the multiple cropping systems characteristic of progressive agriculture.

On the other hand, the photoperiod sensitivity of rice varieties continues to be a useful characteristic under certain environments. Floating rice is planted early in the season when the soil can still be worked. It matures when the annual flood waters recede, about 180–200 days after sowing. A variety with such a long growth period must be photoperiod sensitive. So far, there is no known tropical variety that has a long growth period and is insensitive to photoperiod (Vergara and Chang 1976).

Table 1.12. Yield of traditional tropical rices in relation to transplanting time.^a

Variety	Yield ^b (kg/ha)				
	July	August	September	October	November
Bangkhen 293	229	3478	4791 ^b	3386	2435
Luang Tawng 101	67	2455	4121	3098	2234
Nang Mon S-4	155	2222	2971	2010	1174
Puang Nahk 16	4136	4104	4769	3492	2388
Jao Luang 11	158	1791	3571	2120	2681
Khao Dok Mali 105	66	1219	3031	3020	1820
Bai Lod 104	388	1758	3519	2241	2019
Khao Pak Maw 17	265	1537	3820	2187	1528

^a Takahashi et al (1967). ^b Italic figures indicate highest yields.

Photoperiod sensitivity may function as a safety mechanism when the onset of the rainy season is considerably delayed (Oka 1958). In most of tropical Asia, the onset of the rainy season is unpredictable and varies from year to year, whereas its end is fairly fixed. Thus, when planted late, a photoperiod-sensitive variety may still mature at its usual time regardless of shortened growing periods. On the other hand, a photoperiod-insensitive variety requires a specific growing time before flowering, and hence, maturity. Thus, such a variety will suffer from water stress at later growth stages after the rain ceases.

Most traditional rice varieties in the tropics are sensitive to photoperiod, have long maturity periods, and are tall. When they are grown with high levels of applied nitrogen, they tend to lodge at later growth stages, and their grain yields are extremely low. When these varieties are planted later than usual, they have a shorter growth duration and usually are shorter in height, and consequently, have increased lodging resistance.

Table 1.12 shows the results of delayed-planting experiments using photoperiod-sensitive varieties. The September transplanting, 2 months later than usual, gave the highest yield for all varieties. *Delayed planting* of photoperiod-sensitive traditional indica rice varieties prevented excessive growth and lodging, and resulted in high grain yields.

1.8.2. Response to temperature

a. The temperature summation concept. Temperature summation is a summation of daily mean temperatures over a certain period of growth or development. When the temperature drops to a certain level, growth or development may stop. Temperatures below this threshold are considered ineffective.

Two ways of calculating temperature summation have been used for rice (Asakuma 1958, Copeland 1924, Nagai 1962):

$$\text{Temperature summation} = \Sigma (\text{Daily mean temperature}) \quad (1.12)$$

$$\text{Temperature summation} = \Sigma (\text{Daily mean temperature} - \text{threshold temperature}). \quad (1.13)$$

The temperature summation in equation 1.13 is computed only for days when daily mean temperature is greater than the predetermined threshold temperature. Different threshold temperatures (ranging between 5° and 15°C) are used for different crops. The temperature summation is also called heat units, heat sum, or degree-days (Chang, J.H. 1968, Lowry 1967).

The concept of temperature summation presupposes that the growth or development of a plant is linearly related to temperature or the total amount of heat to which it is exposed. For example, if it takes 100 days from germination to flowering at an overall daily mean temperature of 20°C, temperature summation is 2,000 degree-days (20°C × 100 days). It follows then that the same plant will take 80 days to flower at 25°C (2,000 degree-days/25°C). It must be kept in mind that a linear relationship between developmental rate and temperature is an essential empirical basis for the use of temperature summation.

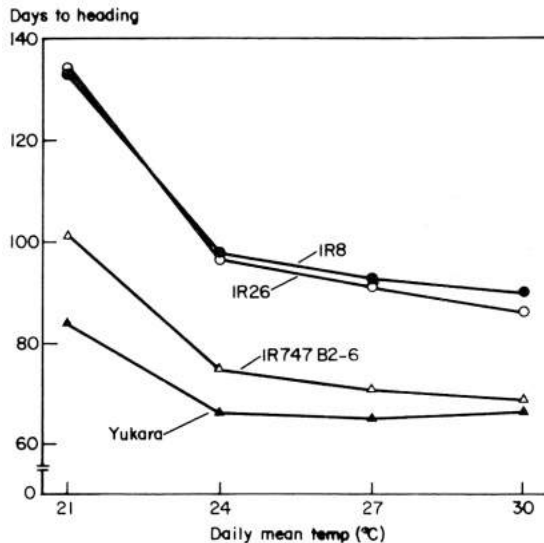
For more than 200 years, plant ecologists, climatologists, and crop scientists have used temperature summation to relate temperature to crop duration and productivity. For example, temperature summation was used to examine whether rice should be introduced into Hokkaido, northern Japan, where summer is short and, therefore, temperature determines the crop species to be grown (Nagai 1962). Often temperature and crop productivity are well correlated because there is a close association between temperature and solar radiation. Solar radiation, however, is the primary climatic determinant for crop productivity. Since it is more direct and rational to examine the relationship between solar radiation and crop productivity, several refined crop productivity models based on photosynthesis and respiration have been proposed (Monteith 1972).

b. Response of rice varieties to temperature. Temperature summation varies with the maturity of a variety; early-maturing varieties have smaller temperature summations than late-maturing ones. Temperature summation from sowing to heading for selected Japanese varieties ranges from about 1,000 to 3,000 degree-days depending on varieties, latitudes, and planting seasons (Toriyama et al 1969). Ripening requires an additional 700–800 degree-days (Ishizuka et al 1973, Komoda 1958). Consequently, from sowing to maturity, a rice crop requires about 2,000–4,000 degree-days, which corresponds to 80–160 days when grown at a mean temperature of 25°C.

Generally, a crop planted in early spring in the temperate region requires a larger temperature summation because early-spring temperatures are too low to be effective. Similarly, a variety adapted to a warm climate, when planted in cool regions, requires a larger temperature summation because it has a high threshold temperature. The estimated threshold temperatures for some Japanese varieties range from 9° to 18°C (Asakuma 1958). If the threshold temperature is subtracted from the daily mean temperature, the temperature summation for the sowing-to-heading period ranges from about 600 to 1,000 degree-days, depending on variety.

The relationship between temperature and growth duration can be examined experimentally by growing photoperiod-insensitive varieties in temperature-controlled facilities. In recent years, growth chambers and the phytotron have

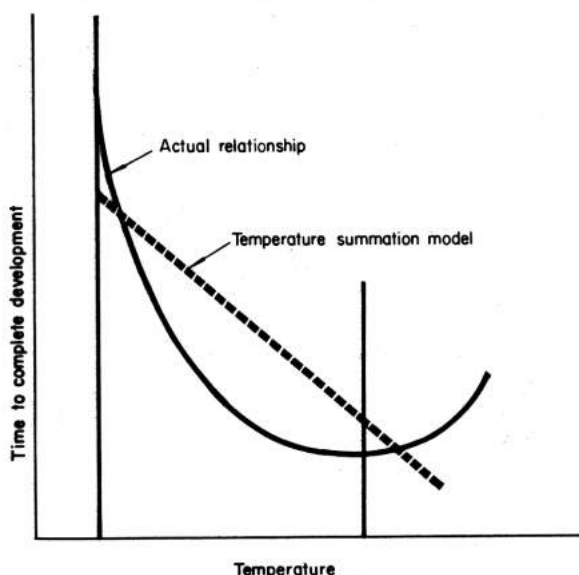
1.39. The relationship between temperature and days to heading for 4 photoperiod-insensitive varieties grown in temperature-controlled glasshouses (IRRI 1975).



become commercially available and are being used for many such studies.

The responses of four photoperiod-insensitive varieties to constant temperatures are shown in Figure 1.39. There are clear varietal differences in the number of days to heading for each temperature in terms of temperature summation or heat requirement. Yukara, a variety from northern Japan, has a much lower temperature summation value than IR8 and IR26, both tropical varieties. The shape of the response curves is basically the same and typical for many other crops. Within a daily mean temperature range of 21°–30°C, the number of days to heading is not linearly related to temperature. When temperature drops from 24° to 21°C, there is a sharp increase in days to heading. For example, the number of days to heading for IR26 increases from 96 days at 24°C to 134 days at 21°C. In other words, a temperature drop by 1°C causes a 13-day delay in heading. When the temperature is increased above 24°C, however, days to heading decreases to 91 days at 27°C and to 86 days at 30°C. In other words, a temperature rise of 1°C above 24°C shortens the number of days to heading by less than 2 days. These results appear to indicate that temperatures above 24°C are much less effective than those below 24°C, suggesting the existence of a *ceiling temperature*. This *idling effect* of high temperature on growth duration is similar to that observed in the field. When IR747B2-6 is grown in the field throughout the year at Los Baños, Philippines, where monthly mean temperatures change from 25.3°C in January to 29.4°C in May, it matures in 95 days regardless of planting time.

A generalized relationship between temperature and length of time required to complete development is shown in Figure 1.40. The curve indicates a temperature below which the plant will not grow. Also, there is an intermediate optimum temperature that permits the most rapid development. Above the optimum,



1.40. Relationship between development time and mean temperature for the period, as compared with the temperature summation model for the relationship (from *Weather and Life* by Lowry, W. P., 1969. Used with the permission of Academic Press).

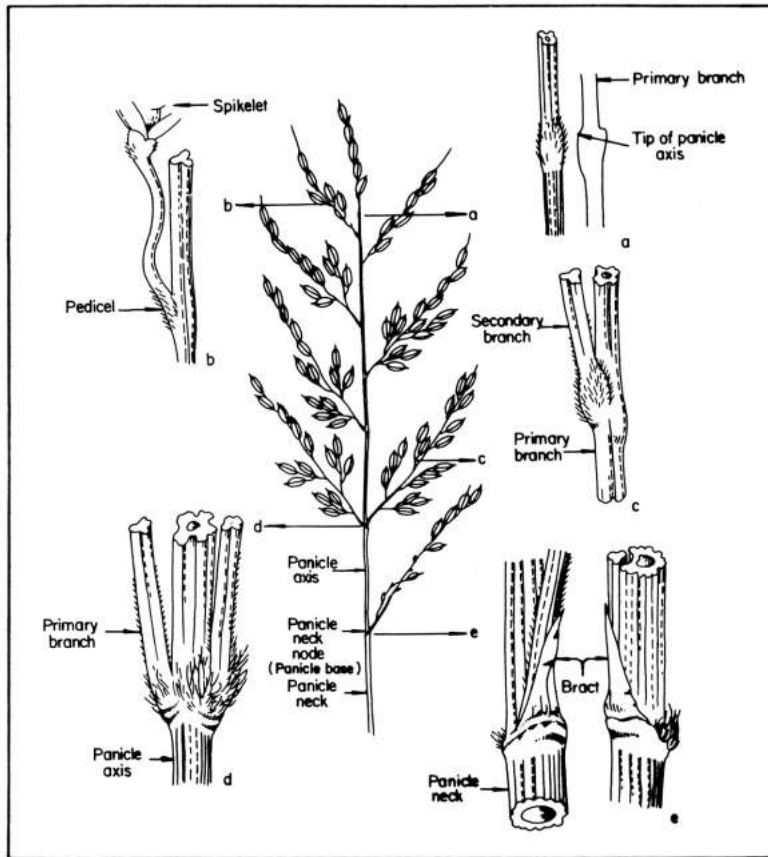
adverse temperatures cause a lengthening of the time required for development. The actual response of the plant to temperature is curvilinear while the temperature summation concept assumes a linear relationship.

The foregoing example indicates that there is no linear relationship between temperature and growth duration. This nonlinearity seriously limits the use of temperature summation.

The entire growth process from germination to maturity includes many component physiological and biochemical processes. Some processes may be temperature insensitive, others may be linearly dependent on temperature, and still others may be logarithmically dependent on temperature. Thus, the implicit assumption of the temperature summation concept that growth rate or developmental rate is a linear function of temperature is an oversimplification.

Temperature control of growth duration in photoperiod-insensitive varieties is understood on the basis of the following:

- (i) A rise in temperature increases the rate at which leaves emerge.
- (ii) The number of developed leaves on the main culm before heading is fairly constant for a given variety.
- (iii) As a result of (i) and (ii), the number of days from sowing to heading is fairly constant under a given temperature regime.
- (iv) A rise in temperature increases the rate of grain filling after flowering.



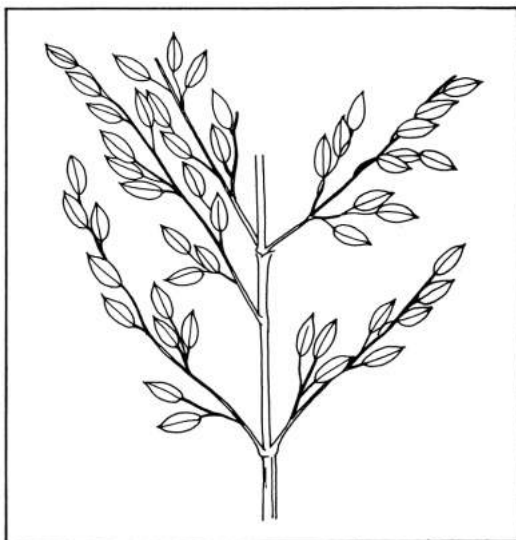
1.41. Component parts of a panicle (adapted from Hoshikawa 1975).

1.9. PANICLE

1.9.1. Morphology

The major elements of a panicle are the base, axis, primary and secondary branches, pedicel, rudimentary glumes, and spikelet.

The panicle axis extends from the panicle base to the apex. It has 8–10 nodes at 2- to 4-cm intervals from which primary branches develop. In turn, secondary branches develop from the primary branches. Pedicels develop from the nodes of the primary and secondary branches, on top of which spikelets are positioned (Fig. 1.41). Usually only one primary branch comes from the panicle base but under favorable conditions, such as sunny weather or fertile soils, two or three primary branches may emerge from the panicle base. A panicle with twin or triplet primary branches on the panicle base is referred to as a *female panicle* (Fig. 1.42). The female panicle is an instance of a shortened internode between the primary



1.42. Female panicle with twin rachis-branches on a neck node (Matsushima 1970).

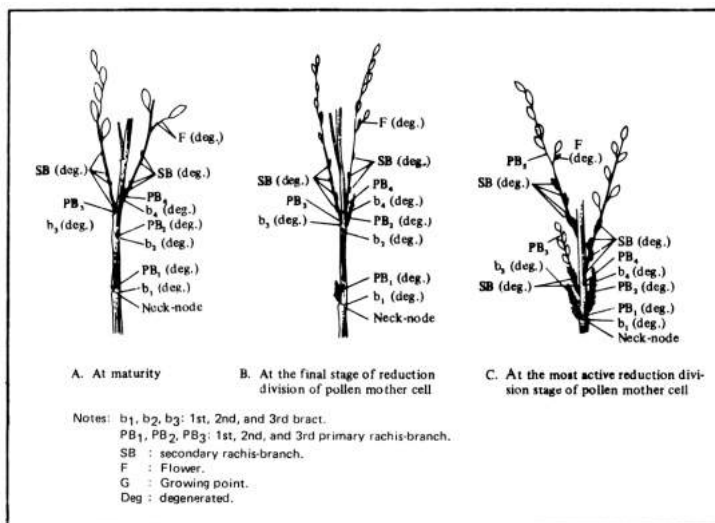
branches on the panicle axis. An ample supply of nitrogen at the neck-node differentiation may produce high percentages of female panicles. Thus, the formation of female panicles indicates good growing conditions at the neck-node differentiation.

When a panicle is carefully examined at maturity, many degenerated vestigial organs can be recognized: spikelets, primary branches, secondary branches, bracts, and the growing point (Fig. 1.43). These organs degenerate between spikelet differentiation and the end of reduction division while differentiation occurs during the preceding period, neck-node differentiation to spikelet differentiation (see next section). The environmental conditions at each period have a profound influence on organ differentiation and degeneration. The spikelet number observed at maturity is the difference between the differentiated and the degenerated.

1.9.2. Outline of panicle development before heading

The initiation of panicle primordium starts about 30 days before heading; it corresponds to the time when the fourth leaf from the top begins to elongate.

Panicle development and growth start with the neck-node differentiation and end when the pollen is fully matured. Table 1.13 shows the sequential steps of panicle development. The total duration of panicle development varies with variety and weather and ranges from 27 to 46 days. The duration of panicle development is shorter in early-maturing varieties than in late-maturing varieties. Under normal weather conditions and for medium growth duration varieties, however, the total duration of panicle development is about 33 days. The results in Table 1.13 were obtained from studies in japonica rice in Japan. Since there is no



1.43. Vestiges of degenerated organs on an adult panicle and their degenerating processes (Matsushima 1970).

fundamental difference between japonica and indica rices and since temperature regimes during panicle development are similar in both the tropics and temperate regions, the developmental stages described in Table 1.13 also apply to tropical rices.

When a young panicle has grown about 1 mm long, it can be seen with the naked eye or through a magnifying glass. Agronomists often refer to this stage as *panicle initiation* for nitrogen topdressing. The duration from panicle initiation to heading is about 23–25 days in both temperate and tropical regions.

1.9.3. How to determine the developmental stages of a growing panicle

For a precise study of the stages of panicle development, samples are sectioned and examined under a microscope. The technique requires specialized knowledge and skill. The following methods, however, provide simple means by which the developmental stages can be identified (Matsushima 1970).

a. Leaf number index. When the number of leaves to be developed on the main culm is constant, the leaf number can be taken as a measure of the plant's physiological age. This applies to photoperiod-insensitive varieties and to crops of the same rice variety grown under the same environmental conditions.

Since different varieties may have different total numbers of leaves on the main culm, the leaf number per se cannot be used as a reliable measure of the physiological age of plants of all varieties. The leaf number index corrects for such variation:

$$\text{Leaf number index} = \frac{\text{number of leaves developed by a particular time}}{\text{total number of leaves to be developed}} \times 100 \quad (1.14)$$

Table 1.13. Duration of each development stage for a panicle or a spikelet.^a

Developmental stages ^b	Duration (days)	
	1953 ^c	1954 ^d
Differentiating stage of the neck node	2.0	2.0
Increasing of bracts stage	1.0	1.0
Duration of differentiation of bracts	3.0	3.0
Early differentiating stage of primary rachis-branches	1.5	1.0
Middle differentiating stage of primary rachis-branches	2.0	2.0
Late differentiating stage of primary rachis-branches	2.2	1.0
Duration of differentiating stage of primary rachis-branches	5.7	4.0
Early differentiating stage of secondary rachis-branches	1.2	1.0
Late differentiating stage of secondary rachis-branches	2.0	1.5
Duration of differentiating of secondary rachis-branches	3.2	2.5
Initial stage of spikelet differentiation	1.0	1.0
Early differentiating stage of spikelets	3.0	3.0
Middle differentiating stage of spikelets	1.0	1.2
Late differentiating stage of spikelets	4.0	3.2
Duration of differentiation of spikelets	9.0	8.4
Differentiating stage of pollen mother cell	2.5	1.8
Reduction division stage	2.0	1.8
Early stage of extine formation	1.2	1.6
Extine formation stage	3.3	2.5
Early ripe stage of pollen	2.0	2.0
Ripe stage of pollen	5.5	5.0
Total	37.4	32.6

^aMatsushima (1970). ^bThe topmost spikelets were used. ^cUnusual weather. ^dNormal weather.

For example, when a 14-leaf and a 18-leaf variety have developed 6 leaves on the main culm, their leaf number indexes are 43 and 33, respectively.

The leaf number indexes are related to the developmental stages of a growing panicle (Table 1.14). Such relationship holds only for *terminal spikelets* and for *16-leaf varieties*. The neck-node differentiation occurs when the leaf number index is around 77, or when the plant has developed 12.3 leaves. The spikelet differentiation stage comes at a leaf number index of around 90, or when the plant has 14.4 leaves.

Table 1.14. Developmental stages and morphological characteristics.^a

Developmental stages	Morphological characteristics		
	Leaf no. index	Exsertion of <i>n</i> th leaf counted from the top	Panicle length
1. Necknode differentiation stage	76–78	4th leaf	
2. Branch differentiation stage			
a. Primary branch differentiation stage	80–83	3rd leaf	
b. Secondary branch differentiation stage	85–86		0.5–0.9 mm
3. Spikelet differentiation stage			
a. Early stage	87	2nd leaf	1.0–1.5 mm
b. Middle stage	88–90		1.5–3.5 mm
c. Late stage	92		3.5–15.0 mm
4. Pollen mother cell differentiation stage	95	Flag-leaf	1.5–5.0 cm
5. Reduction division stage of pollen mother cell	97		5.0–20.0 cm
6. Extine formation stage	100		Full length
7. Ripe pollen stage	100		Full length

^a Modified from Matsushima (1970).

When a variety has more or less than 16 leaves on the main culm, its leaf number index must be corrected for a deviation from 16 so that Table 1.14 can be used for varieties of any leaf number. The correction factor is calculated as:

$$\text{Correction factor (C.F.)} = (100 - \text{leaf number index}) \times \frac{16 - \text{total number of leaves}}{10} \quad (1.15)$$

Calculation of the corrected leaf number index then becomes:

$$\text{Corrected leaf number index} = \text{leaf number index} + \text{C.F.} \quad (1.16)$$

Example:

Total number of leaves on main culm: 14

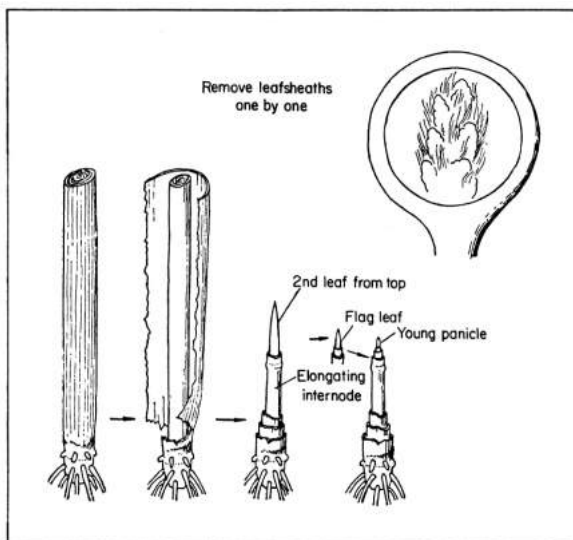
Plant age: 12.6 leaf stage

Leaf number index: $12.6/14 = 90$

Correction factor: $(100 - 90) \times \frac{16 - 14}{10} = 2$

Corrected leaf number index = leaf number + C.F.
 $= 90 + 2$
 $= 92$

The leaf number index can be converted into leaf number counted from the flag leaf as shown in Table 1.14.



1.44. Examination of a young panicle by removing leaf sheaths (adapted from Hoshikawa 1975).

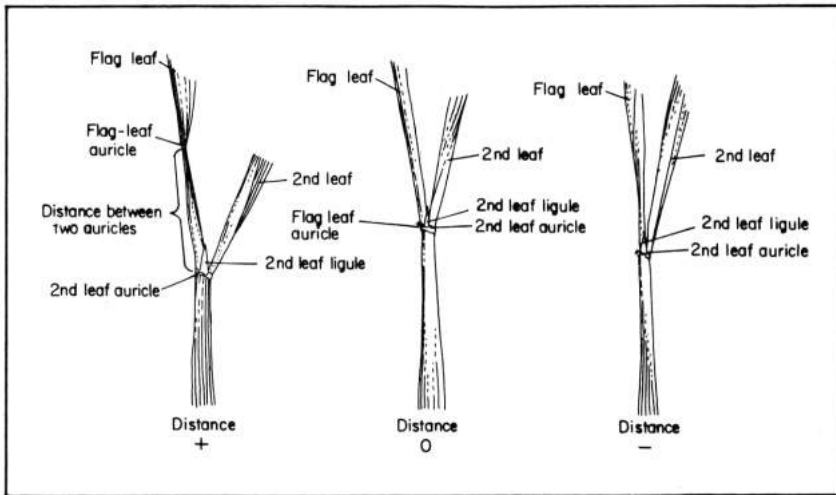
b. Length of young panicle. The young panicle can be seen with the naked eye for the first time at the early stage of differentiation of the secondary rachis-branches. The panicle at that time is about 0.5–0.9 mm long. Table 1.14 shows the relationship between panicle length and developmental stage. A panicle that has grown 1.0 mm, has already entered the spikelet differentiation stage.

The young panicle is usually examined in the following way. Starting at about 30 days before the estimated heading date, several large tillers from 2 or 3 average-sized hills are cut from the plant's base every 3 days. Since the leaf sheaths envelop the culm very firmly, a sewing needle is used to split and strip the sheaths one by one (Fig. 1.44). The flag leaf, recognized as a little white cone, should be stripped off carefully with the tip of the needle. Inside is the young panicle. At the 1-mm panicle stage (panicle initiation), the young panicle has white hairs and is easily distinguished from a leaf. A magnifying glass makes the examination easier.

The difference between the initiation of panicle primordia and the agronomic panicle initiation stage is about 7–10 days.

c. Distance between the auricles of the flag leaf and the penultimate leaf. The distance between the flag leaf auricle and the penultimate leaf (2nd leaf) auricle provides a useful means by which to identify the reduction division stage, one of the stages most vulnerable to environmental stresses.

When the flag leaf auricle has emerged from the sheath of the penultimate leaf and is located above the penultimate leaf auricle, the distance is given a plus (+) sign. When the flag leaf auricle is positioned at the same height as that of the



1.45. How to read the distance between the auricle of the flag leaf and that of the immediate lower leaf (Matsushima 1970).

penultimate leaf, the distance is zero (0). And when the flag leaf auricle is still in the sheath of the penultimate leaf, the distance is given a minus (-) sign (Fig. 1.45).

The most active reduction division stage starts when the distance between the auricles is -3 cm and ends when the distance is +10 cm. In other words, when the flag leaf auricle appears from the sheath of the penultimate leaf, the panicle undergoes the most active period of reduction division.

1.10. HEADING AND ANTHESIS

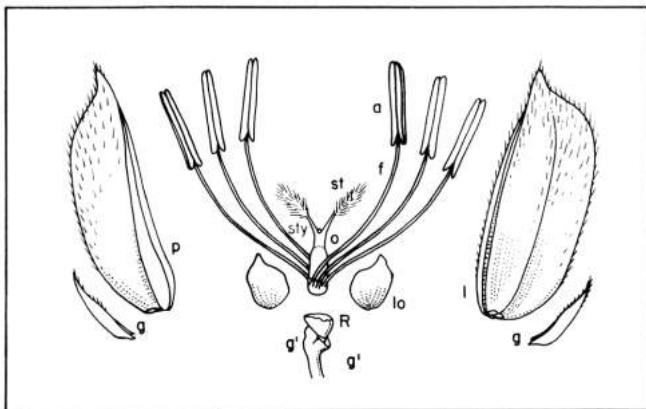
1.10.1. Morphology of a spikelet

The spikelet is borne on the pedicel, a short stalk that is an extension of the panicle axis and the primary or secondary branch (Fig. 1.46).

There are two short rudimentary glumes at the upper end of the pedicel. A pair of sterile lemmas and the rachilla are located between the rudimentary glumes and the spikelet. The flower is enclosed in the lemma and palea, which may be either awned or awnless.

The flower consists of the pistil, stamens, and lodicules. The components of the pistil are the stigmas, styles, and ovary. The stigma is plumose, on to which pollen grains are shed. The ovary is thick, smooth, and bears two styles.

There are six well-developed stamens, composed of anther and filament. Two small, oval, thick, and fleshy bodies, called the lodicules, are situated at the base of the ovary. The lodicules become distended with water and assist in separating the lemma and palea at flowering.



1.46. A spikelet of rice (adapted from Nagai 1962). g = sterile lemmas, g' = rudimentary glume, R = rachilla, l = lemma, p = palea, lo = lodicule, o = ovary, st = stigma, sty = style, a = anther, f = filament.

1.10.2. Heading

After the flag leaf emerges about 18 days before heading, the panicle grows fast and moves upward in the flag leaf sheath as the internodes elongate. About 6 days before heading, the flag leaf sheath thickens — an indication that a panicle is enclosed. The 6 days are called the booting stage.

Elongation of the second internode from the top is completed 1 or 2 days before heading. Then the topmost internode elongates rapidly and pushes up the panicle. As a consequence, the panicle is exerted from the flag leaf sheath. Heading means panicle exertion. In general, panicle exertion is fast and complete in japonica rices, but slow and incomplete in some indica rices. Low temperatures aggravate poor panicle exertion.

Within a plant, some tillers usually head earlier than the main shoot. The date of heading differs not only within a plant but also among plants in the same field. It usually takes 10–14 days for all the plants in a field to complete heading. For convenience, heading date is defined as the time when 50% of the panicles have exerted.

1.10.3. Anthesis (flowering)

Anthesis refers to a series of events between the opening and closing of the spikelet, lasting about 1–2.5 hours. At the beginning of anthesis, tip portions of the lemma and palea begin to open, filaments elongate, and anthers begin to exert from the lemma and palea. As the spikelet opens wider, the tip of the stigma may become visible. The filaments elongate further to bring the anthers out of the lemma and palea. The spikelet then closes leaving the anthers outside.

Anther dehiscence usually occurs just before or when the lemma and palea open; consequently, many pollen grains fall onto the stigma. For this reason, rice is a self-pollinated plant.

When the filaments elongate further, the anthers are positioned just above or droop over the lip of the lemma and palea, and pollen grains are released into the air. These pollen grains may be blown by the wind to the stigmas of other spikelets. Since self-pollination precedes cross-pollination, the percentage of the latter is usually less than 1.

Pollen grains are viable for only 5 minutes after emerging from the anther, whereas the stigma can be fertilized for 3–7 days. Pollen grains are more sensitive to high temperatures than is the stigma. When treated with hot water at 43°C for 7 minutes, they lose viability. The stigma remains active under the same conditions. This differential response to high temperature is used for emasculation in hybridization.

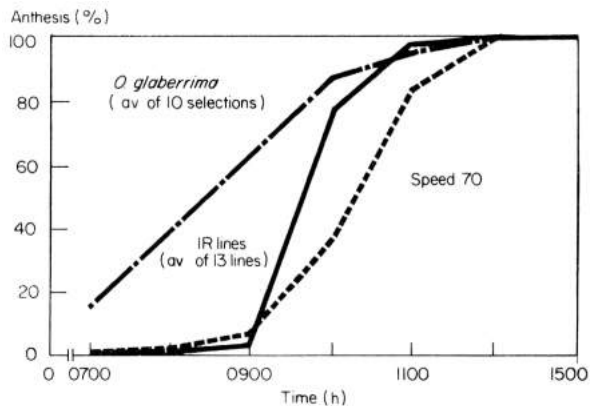
When a portion of the panicle has exerted, anthesis will occur, starting with the spikelets at the tip of upper panicle branches. Hence, the date of anthesis is the same as the date of heading. The date of anthesis of individual spikelets varies with the positions of the spikelets within the same panicle. Spikelets on the upper branches have anthesis earlier than those on the lower branches; within a branch, a spikelet at the tip flowers first.

It takes 7–10 days for all the spikelets within the same panicle to complete anthesis; most of the spikelets complete anthesis within 5 days. Within the same field it takes 10–14 days to complete heading because panicle exertion varies within tillers of the same plant and between plants in the same field. Hence, it takes about 15–20 days for all the spikelets of a crop to complete anthesis.

The time of day when anthesis occurs varies with weather conditions. Under normal weather conditions in the tropics, most rice varieties (*O. sativa*) begin anthesis at about 0800 and end at about 1300 hours. When temperatures are low, anthesis may start late in the morning and continue into the late afternoon. On rainy days, pollination may occur without the opening of the lemma and palea.

There is a marked difference in anthesis time between *O. sativa* and *O. glaberrima* (Fig. 1.47). For instance, at 0900 hours, about 60% of the spikelets in

1.47. Anthesis time of *O. sativa* and *O. glaberrima* selections (IRRI 1978).



O. glaberrimas flowered but less than 5% in *O. sativa* had anthesis (IR lines and Speed 70).

Pollen tubes start elongating after germination. Fertilization is normally completed 5–6 hours after anthesis; then the fertilized ovary develops into brown rice.

1.1.1. RIPENING

1.1.1.1. Ripening and senescence

The ripening period is characterized by grain growth — increase in size and weight, changes in grain color, and senescence of leaves.

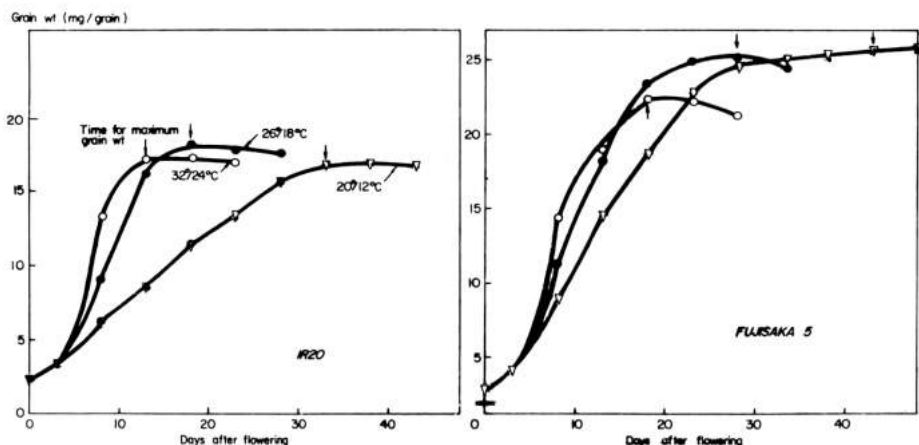
At the early stages of ripening, the grains are green; they turn yellow as they mature. The texture of the grains changes from a milky, semifluid state to a hard solid. On the basis of such changes the ripening period is subdivided into milky, dough, yellow ripe, and maturity stages.

Before heading, a considerable amount of starch and sugar accumulates in the culms and leaf sheaths. This accumulated carbohydrate is translocated to the grains during ripening. Leaf senescence starts from the lower leaves and extends upward as the plant matures. Leaf senescence is faster in indica than in japonica rices and in warm regions than in cool regions. In cool regions, some leaves remain green even at maturity.

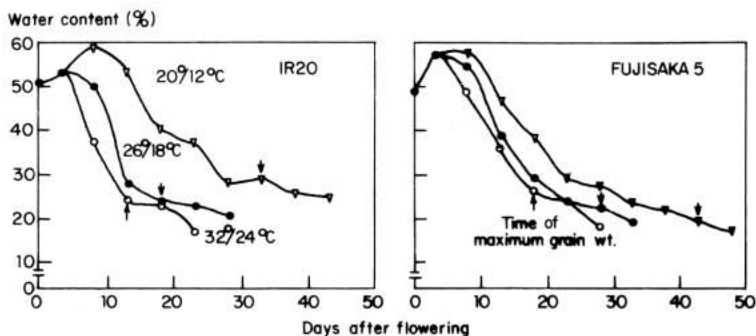
The relationship between rate of leaf senescence and grain filling is complex. In some cases, faster leaf senescence results from a faster translocation of carbohydrates and proteins from leaves to grains, which in turn may be related to faster grain filling. In other cases, faster leaf senescence indicates unfavorable weather or soil conditions.

1.1.1.2. Growth of single grains

The process of grain growth is quantified by the increase in dry weight and the



1.48. Growth of single grains IR20 and Fujisaka 5 at different temperatures (Yoshida and Hara 1977).



1.49. Changes in the water content at successive stages of growth of 2 varieties of rice under 3 temperature regimes (Yoshida and Hara 1977).

decrease in water content. The rate of grain growth is faster and the grain filling period is shorter at higher temperatures (Fig. 1.48). The duration of grain filling, defined as the number of days required to reach maximum weight, is 13 days at a mean temperature of 28°C, and 33 days at 16°C for IR20, an indica rice. Fujisaka 5, a japonica rice, takes a little longer to ripen: 18 days at a mean temperature of 28°C and 43 days at 16°C. Comparable figures for a field crop are much greater than those for a single grain because time of heading and anthesis vary among panicles and among spikelets within the same panicle. Hence, the crop, as a whole, takes a longer time to ripen than does a single grain. The final grain weights attained at high and low temperatures are about the same for IR20, suggesting that IR20 is well adapted to high temperatures during ripening. In Fujisaka 5, however, the final grain weight at 28°C is about 15% less than that at 16°C. Thus, high temperatures appear to have some detrimental effect on Fujisaka 5. Their detrimental effect is much more conspicuous in wheat (Sofield et al 1974).

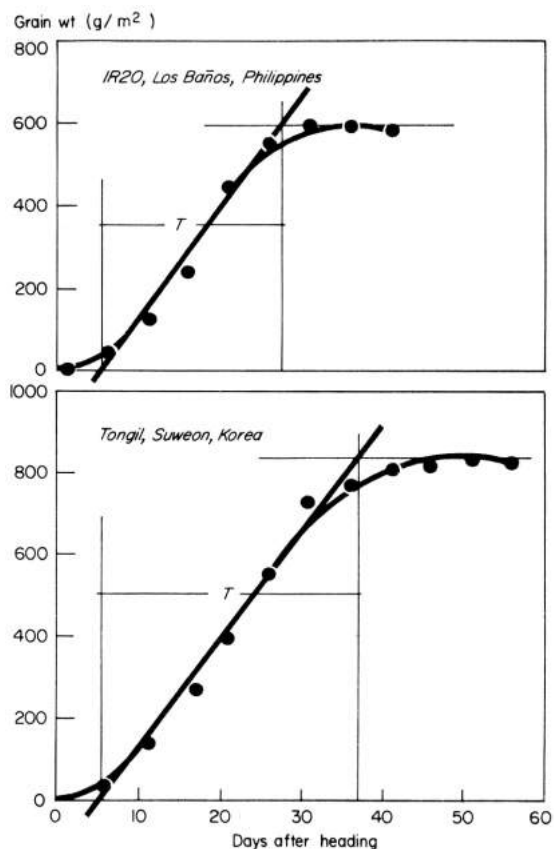
During the initial phases of grain filling, the water content of the grains is about 58% and it declines to about 20% or less at maturity (Fig. 1.49). As temperatures increase, water content decreases faster.

1.11.3. Grain growth of a field crop

Grain growth of a field crop is initially slow, enters a linear phase where the growth rate is fast, and then slows down toward maturity (Fig. 1.50).

Agronomically, the duration of ripening is from the date of heading to the time when the maximum grain weight is attained. The time of harvest is usually determined by past experience, grain color, and leaf senescence. The length of ripening, predominantly affected by temperature, ranges from about 30 days in the tropics to 65 days in cool temperate regions such as Hokkaido, Japan, and New South Wales, Australia (Tanaka and Vergara 1967).

In crop physiology, the effective grain-filling period (T) or the period of physiological maturity is defined as shown in Figure 1.50. The length of T is considered more meaningful for grain growth than the length of the agronomic



1.50. Grain growth of rice at 2 locations. T is the effective grain tilling period (IRRI 1978).

ripening period because most of the dry grain weight is attained during the effective grain-filling period. Effective grain filling lasts about 23 days for IR20 at Los Baños, Philippines, and 33 days for Tongil at Suweon, Korea. The rates of increase in grain weight are almost identical at the two locations, i.e., about 26–27 g/m² per day. The grain growth rate is only slightly less than the maximum crop growth rate normally achieved during the vegetative growth stage, i.e., about 30 g/m² per day.

1.12. YIELD AND YIELD COMPONENTS

1.12.1. Yield

Rice yield is usually reported as rough rice (paddy) at 14% moisture content, except in a few countries, such as Japan and Korea, where yield is expressed in terms of brown rice or sometimes in terms of polished rice. A conversion factor of 1.25 is usually used when brown-rice yield is converted to rough-rice yield.

1.12.2. Harvest index and grain-straw ratio

A common way of examining rice grain yield is to measure the total dry weight and dry grain yield, and then compute the ratio of these two, as shown below:

$$\begin{aligned}\text{Harvest index (H.I.)} &= \frac{\text{economic yield}}{\text{biological yield}} \\ &= \frac{\text{dry grain yield}}{\text{total dry weight}}\end{aligned}\quad (1.17)$$

$$\therefore \text{Dry grain yield} = \text{H.I.} \times \text{total dry weight.} \quad (1.18)$$

Equation 1.18 indicates that grain yield can be increased by either increasing total dry matter production or by increasing the harvest index. The total dry weight is a measure of a crop's photosynthetic performance and the harvest index is a measure of the economically useful fraction of the biological yield. The total dry weight of a good rice crop is around 10–20 t/ha, depending on variety, management, and environment. The harvest index is about 0.3 for traditional tall varieties and 0.5 for improved, short varieties. As a result, grain yield usually ranges between 3 and 10 t/ha per crop unless the crop lodges. The grain-straw ratio, similar to the harvest index and extensively used in the past, is a ratio of dry grain yield to dry straw weight:

$$\text{Grain-straw ratio} = \frac{\text{dry grain yield}}{\text{dry straw weight}} \quad (1.19)$$

The grain-straw ratios of rice crops range from about 0.5 for traditional, tall varieties to about 1.0 for improved, short varieties.

1.12.3. Yield components

A second method for examining yield performance is to break the yield into its components:

$$\begin{aligned}\text{Grain yield (t/ha)} &= \text{panicle number/m}^2 \times \text{spikelet number/panicle} \\ &\quad \times \% \text{ filled spikelets} \times 1,000\text{-grain weight (g)} \times 10^{-5}\end{aligned}\quad (1.20)$$

$$\begin{aligned}&= \text{spikelet number/m}^2 \times \% \text{ filled spikelets} \\ &\quad \times 1,000\text{-grain weight (g)} \times 10^{-5}.\end{aligned}\quad (1.21)$$

In equation 1.20, the spikelet number includes filled, partially filled, and unfertilized spikelets. The filled spikelet is called grain. The percentage of filled spikelets is a ratio of the number of grains to the total number of spikelets.¹ The 1,000-grain weight is the average weight, in grams, of 1,000 grains.

¹There is some confusion in the terminology of yield components. The following are considered synonyms when yield components are discussed:

spikelet number/panicle and grain number/panicle
total spikelet number/m² and total grain number/m²
% filled spikelets and % filled grains

Table 1.15. The model yield components of IR8 in the cloudy wet season and in the sunny dry season.^a

Component	Wet season	Dry season
Panicle number per m ²	250	375
Spikelet number per panicle	100	100
Total number of spikelets per m ²	25,000	37,500
Filled spikelets (%)	85	85
1,000-grain wt (g)	29	29
Expected grain yield (t/ha)	6.16	9.24

^a Chandler (1969).

The model yield components of transplanted IR8 are shown in Table 1.15. To produce a yield of 6 t/ha in the cloudy wet season, the required number of spikelets per square meter could be obtained if plants are spaced at 20 × 20 cm (i.e., 25 plants/m²), and each plant produces 10 panicles with 100 spikelets/panicle. Under most weather conditions, 85% filled spikelets is normally expected and the 1,000-grain weight is usually a stable varietal character.

Since equation 1.20 is a kind of arithmetic computation and since each component, particularly the first three, is dependent on others, one cannot increase each yield component at his discretion. For instance, when the number of panicles per square meter is increased by using a high plant density, the number of spikelets per panicle is decreased. A comparison of direct-seeded rice and transplanted rice gives a good example of such a relationship (Yoshida and Parao 1972). It is relatively easy to obtain from direct-seeded rice 600 panicles/m², which is twice the number normally obtained from good transplanted rice. The number of spikelets per panicle, however, is much smaller for the direct-seeded rice. As a result, the total number of spikelets per square meter may be about the same for rice grown under the two cultivation systems.

Maximum yield is predetermined by the potential of a variety and the environment. A computation of yield components would be meaningful for designing a blueprint of the target yield and examining the defects of a given crop if a comparison is made with a crop that has already achieved a good yield under a similar environment.

Each yield component is determined at a particular stage in the plant's life (Matsushima 1970). In the transplanting rice cultivation, the number of panicles per square meter is largely dependent on tillering performance, which is largely determined by 10 days after the maximum tiller number stage. In the direct-seeding system, however, the number of panicles per square meter is largely dependent on seeding rate and percentage of emergence. The number of spikelets per panicle, on the other hand, is determined during the reproductive growth stage. Early in the reproductive growth, the maximum number of spikelets is determined by the differentiation of branches and spikelets. After spikelet differentiation, some spikelets may degenerate. The number of spikelets observed at heading or at

maturity is the difference between the number of differentiated primordia and the number that degenerate.

The percentage of filled spikelets is determined before, at, and after heading. Unfavorable weather conditions, such as low or high temperatures at about reduction division stage and anthesis, may induce sterility. Unfavorable weather conditions during ripening may hamper continued growth of some spikelets, resulting in unfilled spikelets.

The 1,000-grain weight is a stable varietal character because the grain size is rigidly controlled by the size of the hull. Hence, grain cannot grow to a size greater than that permitted by the hull no matter how favorable weather conditions and nutrient supply are. The size of the hull, however, is subject to slight modifications by solar radiation during the 2 weeks before anthesis.

In summary, weather conditions, cultural management, and nutrient supply greatly influence each yield component. Understanding their interrelationships is a key to improvement in rice yield.

2

CLIMATIC ENVIRONMENT AND ITS INFLUENCE

2.1 RICE-GROWING REGIONS

Because the rice plant is highly adaptable to its environment and because man has succeeded in modifying that environment, rice can now be grown in many different locations and under a variety of climates. Rice is grown in northeastern China at latitude 53°N; in central Sumatra on the equator; and in New South Wales, Australia, at 35°S. It is grown below sea level in Kerala, India; at or near sea level in most rice-growing areas; and at elevations above 2,000 m in Kashmir, India, and Nepal. It can be grown under upland conditions, under moderately submerged conditions, and in 1.5–5 m water.

Oryza sativa, the dominant rice species, is believed to have originated somewhere in Southeast Asia. Today, it is cultivated in Asia, Africa, Europe; North, Central, and South America; and Oceania. Production statistics reveal that Asia is not only the *home area* of *O. sativa* but also the major rice-growing area of the world (Table 2.1). However, *O. sativa* is a newly introduced crop on the other continents, including Africa where *O. glaberrima*, the other cultivated species of *Oryza*, originated. The indica rices are widely grown in tropical regions such as Southeast Asia; japonica rices, which are adapted to cooler areas, are largely grown in temperate countries such as central and northern China, Korea, and Japan. Both indica and japonica rices can also be grown in subtropical regions such as Taiwan.

Table 2.1. World riceland, yield, and production, 1974–1976^a

Region/ country	Production		Area		Yield	
	(10 ³ t)	% of world total	(10 ³ ha)	% of world total	(t/ha)	% of world total
<i>East Asia</i>	150,701	43.8	40,047	28.5	3.8	152
China, Peoples Rep.	121,500	35.3	34,567	24.6	3.5	140
China, Rep.	3,422	1.0	785	0.5	4.4	176
Japan	15,512	4.5	2,756	2.0	5.6	224
Korea, North	3,633	1.1	727	0.5	5.0	200
Korea, Rep.	6,634	1.9	1,212	0.9	5.5	220
<i>Southeast Asia</i>	68,843	20.0	32,328	23.0	2.1	84
Burma	9,038	2.6	5,016	3.6	1.8	72
Indonesia	22,862	6.6	8,557	6.1	2.7	108
Cambodia	1,367	0.4	1,050	0.7	1.3	52
Laos	919	0.3	682	0.5	1.3	52
Malaysia	1,982	0.6	777	0.6	2.6	104
Philippines	6,092	1.8	3,555	2.5	1.7	68
Thailand	15,153	4.4	8,401	6.0	1.8	72
Vietnam, Soc. Rep.	11,430	3.3	4,290	3.0	2.7	108
<i>South Asia</i>	91,764	26.7	52,266	37.3	1.8	72
Bangladesh	17,859	5.2	10,040	7.2	1.8	72
India	66,314	19.3	38,739	27.6	1.7	68
Nepal	2,481	0.7	1,247	0.9	2.0	80
Pakistan	3,782	1.1	1,671	1.2	2.3	92
Sri Lanka	1,328	0.4	569	0.4	2.3	92
<i>West Asia & North Africa</i>	4,282	1.2	1,098	0.8	3.9	156
North Africa	2,349	0.7	466	0.3	5.0	200
West Asia	1,933	0.5	632	0.5	3.1	124
<i>Sub-Sahara Africa</i>	5,313	1.5	4,055	2.9	1.3	52
West Africa	2,697	0.8	2,346	1.7	1.1	44
Central and East Africa	2,616	0.8	1,709	1.2	1.5	60
<i>Europe</i>	3,790	1.1	881	0.6	4.3	172
<i>Latin America</i>	13,316	3.9	7,199	5.1	1.8	72
Brazil	7,640	2.2	5,288	3.7	1.4	56
Others	5,676	1.7	1,911	1.4	3.0	120
<i>USA and Oceania</i>	5,563	1.6	1,135	0.8	4.9	196
USA	5,111	1.5	1,057	0.7	4.8	192
Oceania	452	0.1	78	0.1	5.8	232
<i>World</i>	343,834	100	140,280	100	2.5	100

^a Palacpac (1978).

Geographers define the tropics as the region between the Tropic of Cancer (23.5°N) and the Tropic of Capricorn (23.5°S). It is commonly said that the tropics is where winter never comes, implying that the temperature remains high throughout the year. However, at high altitudes the weather is cool and the common definition no longer holds. Thus, it would be more meaningful to define the tropics in terms of temperature. One such definition proposed by Koppen in 1936 uses the threshold monthly mean temperature for the coldest month of the year (Trewartha 1968). The monthly mean temperature of 18°C for the coldest month is used for a climatic boundary of the tropics.

Another temperature-based definition, proposed in 1945 by the plant ecologist Kira, uses a heat index — a summation of monthly mean temperature. The heat index, which involves the minimum temperature for plant growth as a threshold temperature, is defined as:

$$W = \sum (t_i - 5) \quad t_i \geq 5, \quad (2.1)$$

where t_i is the monthly average temperature in centigrade, and the heat index (W) is for 12 months. The subtropics and tropics are defined as regions where the heat index value is greater than 180° and 240°C, respectively. When such classification is applied to the subtropics and tropics, the heat index can be converted to the annual mean temperature because monthly mean temperatures in these regions are always higher than the threshold temperature. For instance, an annual mean temperature of 20°C gives:

$$W = \sum (t_i - 5) = (20 - 5) \times 12 = 180°. \quad (2.2)$$

Similarly, an annual mean temperature of 25°C gives a heat index value of 240°C. Thus, heat index values of 180° and 240°C correspond to annual mean temperatures of 20° and 25°C, respectively. This modification defines the tropics as the region where annual mean temperature is above 25°C.

Vegetation characteristics can also be considered as a convenient basis by which to identify the tropics, subtropics, and temperate regions of Asia. In Asia, an annual mean temperature of 20°C is considered as the northern limit for vegetation that includes palm (palmae) and screw-pines (pandanus), and 25°C is the northern limit for dipterocarps (Dipterocarpaceae).

Karachi, Pakistan (25°N), and New Delhi, India (28°N), are north of the Tropic of Cancer but have annual mean temperatures of 25.8°C and 25.3°C, respectively. Hence, they have a tropical climate by Kira's definition. By Koppen's definition, however, New Delhi does not have a tropical climate because the monthly mean temperature for the coldest months (December, January, and February) is below 18°C.

2.2. EFFECTS OF CLIMATE

The average rice yields in rice-growing countries range from less than 1 to more than 6 t/ha. There are a number of biological, environmental, and socioeconomic

Table 2.2. Climatic influence on rice production.

	Temperate	Tropics
Crop period	Temperature	Rainfall
Productivity	Sunlight	Sunlight
Stability	Temperature	Rainfall
	Rainfall	Typhoons
	Sunlight	
	Typhoons	

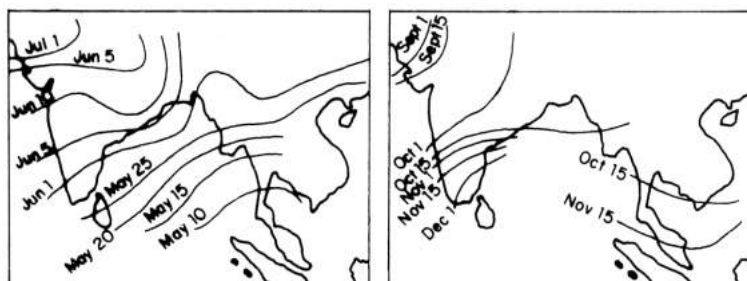
reasons for the large differences in rice yield. Low yields are associated with upland rice, rainfed lowland rice, deepwater rice, and the poor socioeconomic conditions in the tropics, whereas high yields are associated with irrigated lowland rice and the good socioeconomic conditions in the temperate regions.

Temperature, solar radiation, and rainfall influence rice yield by directly affecting the physiological processes involved in grain production, and indirectly through diseases and insects. In the field, these factors are often difficult to separate from one another.

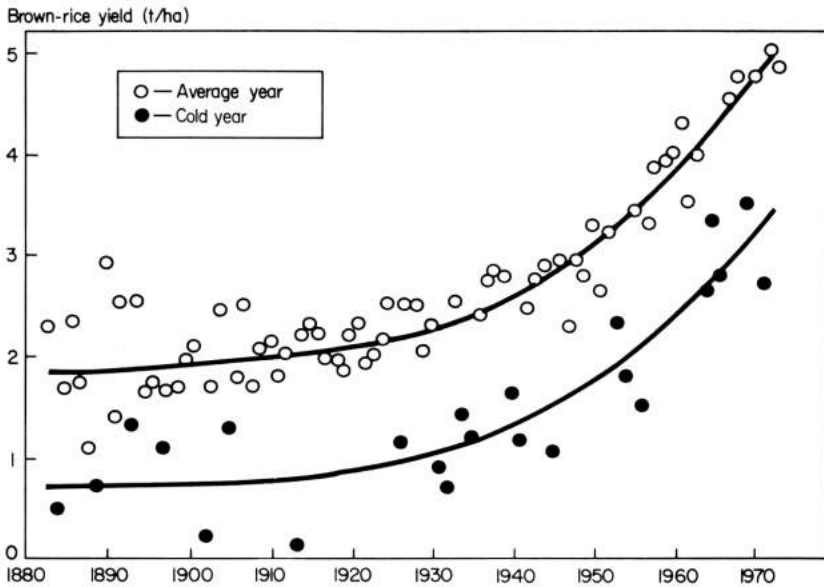
From a crop physiologist's point of view, crop period, productivity, and stability are important aspects of rice cultivation. Climatic factors affect each of them in different ways (Table 2.2).

In the temperate regions, irrigated rice cultivation starts when spring temperatures are between 13° and 20°C; the crop is harvested before temperatures drop below 13°C in the autumn. In the tropics where temperature is favorable for rice growth throughout the year and irrigation is not available in most places, cultivation starts with the rainy season. The average dates of the onset and withdrawal of the monsoons are known for particular regions of South Asia (Fig. 2.1). The starting time and duration of rainfed rice cultivation is largely determined by these two dates.

In both the tropics and the temperate regions, rice yield per hectare is primarily determined by the level of incident solar radiation. In the tropics, when adequately



2.1. Average dates of the onset (left) and withdrawal (right) of the southwest monsoon, and the dates of the start of the northeast monsoon over Indo-China and Malaya (right) (from Tropical Climatology by S. Nieuwolt. Copyright © John Wiley 1977. Reprinted by permission of John Wiley & Sons, Ltd.).



2.2. Effect of technical improvement on average brown-rice yields in Hokkaido, Japan, during the past 90 years (Satake 1976).

managed, the dry season crop usually produces higher yields than the wet season crop because it receives more sunlight.

Stability of crop yields is affected by several factors. In Hokkaido, which is the northern limit of rice cultivation in Japan, low temperatures frequently cause crop failure. Between 1880 and 1970, 22 crops were affected by cool summer temperatures (Fig. 2.2). In addition, low sunlight associated with excessive rainfall during ripening causes low yields. Too little or too much rainfall at any stage of rice growth can cause partial or total crop failure. In Thailand, more than 15% of the cropped area totally failed because of either drought or flood during 8 of the 58 years from 1907 to 1965 (Table 2.3). In 24 of the 58 years, more than 10% of the cropped area was not harvested at all.

In both the tropics and the temperate region, typhoons are unavoidable hazards. One way to minimize crop damage by typhoons is to shift crop seasons so that ripening proceeds when typhoons are least frequent.

2.3. TEMPERATURE

2.3.1. Physical aspects

Average temperatures for a month or a year are computed from daily mean temperatures, which are usually calculated by averaging the daily maximum temperature plus the daily minimum temperature.

Table 2.3. Total rice areas, percentage of damaged area, and the cause of damage in Thailand (1907–1965).^a

Year	Cultivated area (10 ³ ha)	Harvested area (10 ³ ha)	Totally failed area ^b (%)	Rice production (10 ³ t)	Cause of damage
1917	2223	1757	21.0	2989	Flood
1919	2479	1404	43.4	2270	Drought
1928	2722	2386	16.3	3882	Drought
1929	3036	2445	19.5	3875	Drought
1936	3258	2226	31.7	3380	Drought
1942	4379	2876	34.3	3854	Flood
1945	3762	2847	24.3	3572	World War
1954	5557	4524	18.6	5709	Drought
1957	5075	4287	15.5	5570	Drought

^a Isrankura (1966). ^b $\frac{\text{cultivated area} - \text{harvested area}}{\text{cultivated area}} \times 100$.

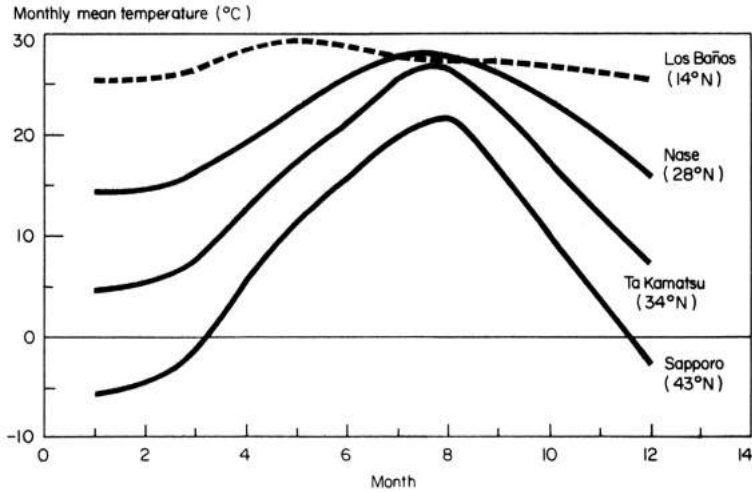
In studies using controlled temperature facilities, such as the phytotron and growth chambers, daily mean temperature is normally a weighted mean of day and night temperatures:

$$\text{Weighted daily mean temperature} = \frac{D \cdot t_D + N \cdot t_N}{24} \quad (2.3)$$

where D = daytime in hours,
 t_D = temperature during daytime,
 N = nighttime in hours, and
 t_N = temperature during nighttime.

The monthly mean temperatures vary with latitudes, as shown in Figure 2.3. Generally, the annual mean temperature decreases, and seasonal variation increases with increasing latitude. One major characteristic of the tropical climate is seasonal uniformity in temperature. At Los Baños, Philippines, for example, monthly mean temperatures range from 25.3°C in January to 29.4°C in May, the difference being only 4.1°C.

Diurnal temperature variation ranges from about 5° to 20°C, or even greater between the daily maximum and daily minimum. The main factor governing the diurnal variation is *continentality* (Fig. 2.4). All marine locations display very small diurnal changes because the surrounding water has a large value of specific heat and serves as a buffer to minimize temperature changes. Diurnal changes increase rapidly with distance from the sea. The maximum values for diurnal changes are found in the dry tropics at about 15°–25° latitude.



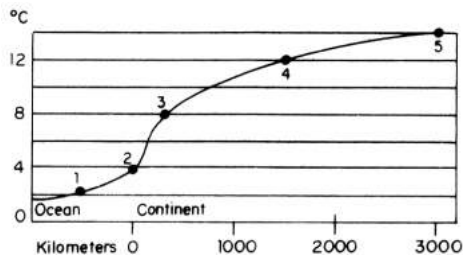
2.3. Monthly mean temperatures at 4 places of different latitudes in Asia.

An important characteristic of tropical and temperate climates is obtained by comparing seasonal variations and diurnal changes in temperature. In the temperate regions, the annual range exceeds the daily range; in the tropics, the daily range is greater than the annual range. At Los Baños, Philippines, the diurnal temperature variation ranges from 7.1°C in December to 11.0°C in April, compared with a maximum variation of 4.1°C in the year's monthly mean temperatures. At Singapore, the annual temperature range is about 2.2°C, while the diurnal range reaches 6.2°C. This characteristic of the tropical climate is described by the well-known saying: the nights are the winter of the tropics.

Temperature always goes down as elevation increases. The decrease of temperature attributable to altitude is about 0.6°C/100 m in the lowest 1.5 km of the atmosphere (Lockwood 1974). Thus temperature at any elevation in the tropics may be estimated by the following formula:

$$\text{Temperature at high elevations} = \text{Temperature at sea level} - 0.6 h, \quad (2.4)$$

2.4. Change in the amplitude of daily temperature (°C) variation with distance from the ocean. Latitude about 40°N; elevations not over 500 m. Numerals indicate locations of stations. Station 1 is an island. Station 2 is at the coast (from an Introduction to Climate by G. T. Trewartha 1968. Copyright © 1968 by McGraw-Hill, Inc. Used with the permission of McGraw-Hill Book Company.)



where temperature is in degrees centigrade, and h is the altitude above sea level in hectometers. For example, if a monthly mean temperature at sea level is 30°C, the corresponding temperature at 1,000 m above sea level would be 24°C. While the above equation gives an easy way to estimate temperature at a given elevation under most conditions, it must be used with caution because the local variations of the temperature drop with elevation are sometimes quite large.

2.3.2. Critical low and high temperatures

Extreme temperatures are destructive to plant growth and, hence, define the environment under which the life cycle of the rice plant can be completed.

The critically low and high temperatures, normally below 20°C and above 30°C, vary from one growth stage to another (Table 2.4). These critical temperatures differ according to variety, duration of critical temperature, diurnal changes, and physiological status of the plant.

Subjecting the rice plant to temperatures below 20°C at about the reduction division stage of the pollen mother cells usually induces a high percentage of spikelet sterility (Satake 1969). Differences among rice varieties in response to low temperatures at this stage have been clearly demonstrated. When Norin 20, a susceptible variety, was held at 15°C for 4 days, 51% of the spikelets were sterile. Hayayuki, a tolerant variety, under the same conditions produced only 5% sterile spikelets.

Temperatures as low as 12°C will not induce sterility if they last for only 2 days, but will induce about 100% sterility if they last for 6 days.

Low temperature-induced sterility is normally attributed to low night temperatures. High day temperatures, however, appear to alleviate the effects of low night temperatures (see Table 2.7). When the plant was subjected to a constant night

Table 2.4. Response of the rice plant to varying temperatures at different growth stages.^a

Growth stage	Critical temperature ^b (°C)		
	Low	High	Optimum
Germination	10	45	20–35
Seedling emergence and establishment	12–13	35	25–30
Rooting	16	35	25–28
Leaf elongation	7–12	45	31
Tillering	9–16	33	25–31
Initiation of panicle primordia	15	—	—
Panicle differentiation	15–20	38	—
Anthesis	22	35	30–33
Ripening	12–18	30	20–25

^aAdapted and modified from Yoshida (1977a). ^bRefers to daily mean temperature except for germination.

temperature of 14°C for 9 days at the reduction division stage of pollen mother cells, a day temperature of 14°C induced 41% sterility. The percentage sterility was, however, decreased to 12% when the day temperature was raised to 26°C.

In northern temperate regions where the summer is short, farmers raise rice seedlings in a plastic-protected nursery where the temperature can be maintained higher inside than outside. In this way they can start rice cultivation in the early spring when air temperatures are still below the critical limit for germination and rooting. Seedlings are then transplanted when the air temperature reaches above 13–15°C.

Upland-grown rice seedlings have higher starch and protein content, and thus have higher rooting capacity than lowland-grown seedlings. Therefore, rice seedlings raised in protected upland nursery beds can be transplanted when the daily mean temperature is about 13.0°–13.5°C, but seedlings raised in lowland nursery beds can be transplanted only when the daily mean temperature rises to 15.0°–15.5°C (Yatsuyanagi 1960).

The foregoing examples illustrate the complexity of temperature effects on growth and development at different stages of the life cycle. Hence, care must be taken to interpret critical temperatures, such as those shown in Table 2.4.

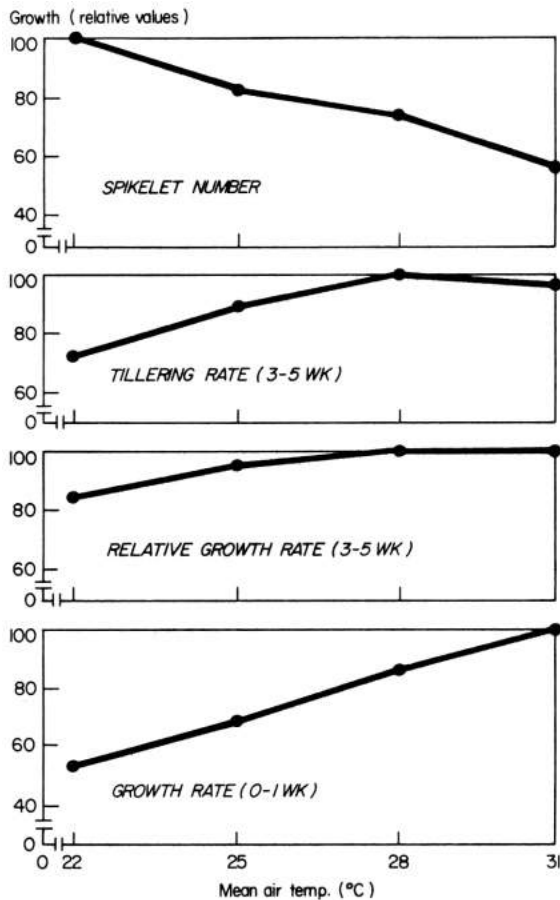
2.3.3 Effects of moderate temperature on growth and yield

Within the critical low and high temperatures, temperature affects grain yield by affecting tillering, spikelet formation, and ripening. There is usually an optimum temperature for different physiological processes and these vary to some degree with variety. Therefore, the results of an experiment depend on the variety used and on whether the range of temperatures studied is above or below the optimum.

Temperature greatly influences the growth rate just after germination (Fig. 2.5). Within a temperature range of 22°–31°C, the growth rate increases almost linearly with increasing temperatures. The temperature quotient, Q_{10} , is customarily used to assess temperature effects on rates of growth and differentiation. Q_{10} is defined as:

$$Q_{10} = \frac{\text{Rate at } (t + 10)^\circ\text{C}}{\text{Rate at } t^\circ\text{C}} \quad (2.5)$$

Thus, Q_{10} is the increase in rate when temperature rises by increments of 10°C. The use of Q_{10} assumes that rates of differentiation and growth are expected to obey the Arrhenius relation, i.e., to increase logarithmically with temperature. For many plant processes, Q_{10} is between 2 and 3 within a moderate temperature range. For the postgermination growth of rice, Q_{10} is about 2 but the relation between growth rate and temperature is linear, not logarithmic. Q_{10} normally decreases with increasing temperature. Respiration of the rice plant increases with increasing temperatures up to 32°C, above which it declines (Fig. 2.6). Between 19° and 25°C, the Q_{10} of the respiration is close to 2, but it becomes much less in the high temperature range from 25° to 32°C.

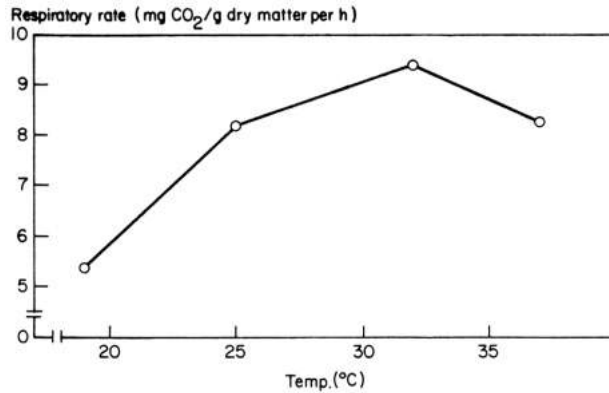


2.5. Effects of temperature on growth of IR8 in a controlled environment (Yoshida 1973).

At later stages (3–5 weeks after sowing), temperature only slightly affects the tillering rate and the relative growth rate, except at the lowest temperature studied (22°C).

The effect of temperature on tillering is affected by the level of sunlight or illumination in an artificially lighted growth room. Basically, higher temperatures increase the rate of leaf emergence, and provide more tiller buds. Under low light conditions, some of the tiller buds may not develop into tillers because of a lack of carbohydrate necessary for growth. Under these conditions, low temperatures may produce more tillers. When light is adequate, however, higher temperatures increase tiller number (Yoshida 1973a).

During reproductive stage, the spikelet number per plant increases as the temperature drops. Thus, the optimal temperature appears to shift from high to low as growth advances from the vegetative to the reproductive stages.

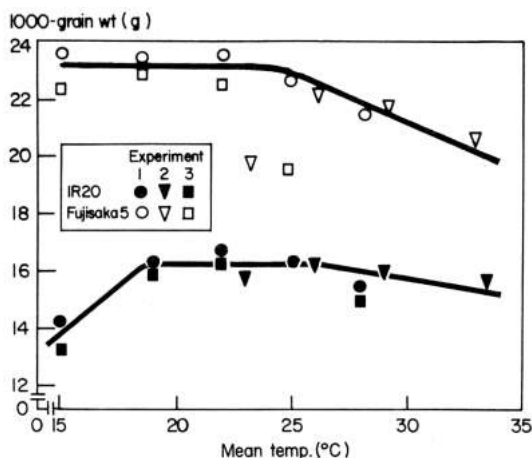


2.6. Effect of temperature on respiratory rate of the rice plant (average of 4 varieties, 30-day-old plants grown in culture solution) (adapted from Tanaka et al 1966).

The mean optimum temperature for ripening of japonica rice in Japan is reported as about 20°–22°C (Aimi et al 1959, Matsushima et al 1957, Matsushima and Tsunoda 1958). This optimum temperature agrees with the results of a statistical analysis of the effects of climatic factors on rice yield (see equation 6.1). The temperature during ripening appears to affect the weight per grain. The 1,000-grain weight of the same variety is almost constant under different environments and cultural practices. However, the 1,000-grain weight of the same variety varied from about 24 g at a mean temperature of 22°C in the 3-week period after heading to 21 g at a mean temperature of 28°C in Kyushu, southern Japan (Murata 1976).

In the tropics, a daily mean temperature as high as 29°C is not detrimental to ripening when solar radiation is high. Yields of 8–10 t/ha are obtained at Los Baños, Philippines, when rice crops ripen in April and May, 2 months characterized by high temperatures and high solar radiation. This suggests that indica varieties are better adapted to high temperatures, while japonica varieties require low temperature for better ripening. A controlled-temperature experiment showed that the optimum daily mean temperatures for grain filling range from 19° to 25°C for IR20, an indica rice, and from 16° to 22°C for Fujisaka 5, a japonica rice (Fig. 2.7). Note that there is no sharp optimum temperature for grain filling, but there is a range of optimum temperatures.

As discussed in Chapter 1, the length of ripening is inversely correlated with daily mean temperature. Thus, persistent cloudy weather conditions will be more detrimental to grain filling under high temperatures because of a shorter ripening period. In fact, a combination of high temperatures and low light can seriously impair ripening (Table 2.5). Since grain weight (W) and percentage of filled spikelets (F) are both affected by light and temperature, the overall effect of the light-temperature interaction on grain filling can be assessed by computing the ripening grade ($W \times F$).



2.7. Relationship between 1,000-gram weight and mean temperature for 2 rice varieties (Yoshida and Hara 1977).

2.3.4. Air vs water temperature

Lowland rice, grown in flooded soils and varying water depths, is inevitably affected by water temperature.

The basic principle governing which temperature, air or water, affects rice growth more is the position of the growing point with respect to water depth (Tsunoda and Matsushima 1962).

Until the initiation of panicle primordia, the growing points of leaves, tillers, and panicles are under water, and water temperature affects growth and develop-

Table 2.5. Effect of light and temperature on grain growth of IR20 and Fujisaka 5 rices.^a

Light ^b	Temperature ^c	Grain wt ^d (W) (mg)	Filled spikelets (F) (%)	Ripening grade ^e (W × F)
<i>IR20</i>				
Low	Low	15.5	65	1014 (71)
Low	High	14.8	62	910 (64)
High	Low	16.3	87	1423 (100)
High	High	16.0	86	1370 (96)
<i>Fujisaka 5</i>				
Low	Low	22.0	86	1890 (90)
Low	High	20.4	84	1718 (82)
High	Low	23.0	91	2102 (100)
High	High	21.9	92	2013 (96)

^a Yoshida and Hara (1977). ^bLow: 36 cal/cm² per day PAR (photosynthetically active radiation), High: 114 cal/cm² per day PAR.

^cLow: 23/15°C, High: 32/24°C. ^dLSD value at 5% level is 0.2 for both varieties. ^eFigures in parentheses indicate relative values with 100 as the maximum.

ment. Leaf elongation and plant height growth, however, are affected by both air and water temperatures, presumably because they are completed in an aerial environment.

As the growing panicles reach above the water surface around reduction division stage and, thereafter, the effects of water temperature decrease; eventually air temperature becomes dominant in controlling panicle growth and ripening (Tsunoda and Matsushima 1962, Matsushima et al 1964c). Thus, the effects of air and water temperatures on grain yield and yield components vary with growth stage (Matsushima et al 1964b). At early growth stages, the water temperature affects yield by affecting the panicle number per plant, spikelet number per panicle, and the percentage of ripened grains. At later stages air temperatures affect yield by affecting the percentages of unfertilized spikelets and percentages of ripened grains.

The effects of water temperature are determined by both the magnitude of temperature and water depth. Under most conditions, water temperature is higher than air temperature, and increasing the water depth extends the duration during which water temperature controls panicle growth. Thus, when air temperature goes down below the critical level, increasing the water depth about 15–20 cm at the reduction division stage is an efficient method of protecting the rice plant against sterility caused by low air temperature (Nishiyama et al 1969).

2.3.5. Low-temperature stress

a. Occurrence of low-temperature problems. Depending on growth stages, injury to rice may occur when the daily mean temperature drops below 20°C. Cool injury can occur not only in the temperate regions but also at high altitudes and in dry season crops in the tropics. Countries reporting cool injury on rice include Australia, Bangladesh, China, Colombia, Cuba, India, Indonesia, Iran, Japan, Korea, Nepal, Pakistan, Peru, Sri Lanka, USA, and USSR.

b. Types of cool injury. Common cool injuries are failure to germinate, delayed seedling emergence, stunting, leaf discoloration, panicle tip degeneration, incomplete panicle exertion, delayed flowering, high spikelet sterility, and irregular maturity. Among them, high spikelet sterility, delayed heading, and irregular maturity are common in many countries.

c. Stunting at seedling stage. Stunting, a reduction in plant height, is a common symptom of cool injury in seedlings and is highly correlated with weight growth of both shoot and root. In flooded fields, stunting is caused by cold water brought about by either cool weather conditions or cold reservoirs. Tolerance for cold water is particularly important in areas such as California, USA, where rice seeds are broadcast into about 15 cm of cold standing water.

A wide range of varietal differences is found in cold water tolerance at the seedling stage. When shoot length and percentage of survival were taken as measures for cold tolerance and when those of a U.S. variety, Caloro, were taken as 100, the relative performance of 19 U.S. varieties ranged from 35 to 110 for shoot length and from 26 to 110 for percentage of survival (Table 2.6). A further

Table 2.6. Cold water tolerance of United States rice varieties.^a

Variety	Crop intro- duction no.	Location	Grain type	Maturity group ^b	Length, % of Caloro	Survival, % of Caloro
Caloro	1561-1	California	Short	Midseason	100.0	100.0
Calady 40	9202	California	Medium	Midseason	109.6	91.2
Mochi Gomi	9051	California	Glutinous	Midseason	96.6	88.2
Calrose	8988	California	Medium	Midseason	91.1	95.5
Colusa	1600	California	Short	Early	89.1	64.6
Arkrose	8310	Arkansas	Medium	Midseason	88.9	91.2
Cody	8642	Ark. & Mo.	Short	Early	78.2	100.0
Fortuna ^d	1334	Southern	Long	Midseason	73.7 ^c	79.4
Early Prolific ^d	5883	Southern	Medium	Early	72.4 ^c	90.0
Rexoro	1779	La., & Texas	Long	Late	67.4 ^c	91.2
Lacrosse	8985	Southern	Medium	Early	65.7 ^c	86.7
Nato	8998	Southern	Medium	Early	65.7 ^c	82.4
Century Patna 231	8993	Southern	Long	Early	61.2 ^c	73.5
Texas Patna	8321	La., & Texas	Long	Late	60.0 ^c	85.3
Gulfrose	9416	Southern	Medium	Early	58.0 ^c	90.0
Bluebonnet 50	8990	Southern	Long	Midseason	57.2 ^c	110.0
Texas Patna 49	8991	La., & Texas	Long	Late	51.8 ^c	58.6 ^c
Zenith	7787	Southern	Medium	Early	48.9 ^c	54.3 ^c
Nira ^d	2702	Southern	Long	Midseason	46.6 ^c	60.0 ^c
Bluebonnet ^d	8322	Southern	Long	Midseason	34.6 ^c	25.7 ^c

^a Ormrod and Bunter (1961). ^b Maturity group in the location in which the variety is principally grown. ^c Indicates that the variety is less tolerant than Caloro when comparisons are made by LSD (5%). ^d Varieties no longer commercially used in the US.

test of 36 varieties from 8 countries, including Japan and Korea, showed ranges from 24 to 112 for shoot length and 15 to 122 for percentage of survival. Although, it is clear that there is a wide range of varietal differences, cold water tolerance at the seedling stage is not related to cold tolerance at the reduction division stage.

d. Delayed heading. In regions where summers are short, cool weather conditions may delay growth and, hence, heading. Under such conditions, the rice crop may ripen at lower temperatures than the usual and may not complete grain filling before the temperature drops below the critical level for ripening. Raising seedlings in a plastic-covered nursery in early spring and transplanting right after the temperature rises to 13°–15°C is one way of providing more warm days and a greater chance to complete grain filling. There are some degrees of varietal difference in the ability to grow fast under cool weather conditions (Tsunoda, K. et al 1966).

e. Low temperature-induced sterility. Rice is most sensitive to low temperatures (15°–20°C) at the young microspore stage after reduction division. It is less sensitive just before and at the leptotene stage of reduction division, about 10–11 days before anthesis. This information has been obtained from a very precise work using uniform, single plant material grown in the phytotron (Satake 1976).

Table 2.7. Effect of day and night temperatures at 2 critical stages on spikelet sterility and anthesis.^a

Duration of low-temperature treatment (days)	Day temperature ^b	Night temperature ^c	Spikelet sterility (%)		Flowered spikelets (%) heading
			Booting stage	Heading time	
3	26	20	2.2%	10.7%	53.3%
		14	8.2	9.2	5.0
		8	11.6	7.2	5.0
	20	20	4.2	9.8	8.3
		14	7.3	8.2	5.0
		8	15.5	8.0	8.3
	14	20	5.9	6.7	11.0
		14	11.2	8.3	0.7
		8	23.0	5.7	0.3
	6	20	3.7	9.9	95.0
		14	6.4	19.4	36.7
		8	22.5	41.6	13.3
6	26	20	6.1	11.5	91.7
		14	6.6	15.5	18.3
		8	28.0	37.4	1.7
	20	20	7.0	14.6	38.3
		14	25.8	21.1	7.0
		8	74.8	48.3	1.3
	14	20	4.4	12.1	100.0
		14	12.1	38.7	73.3
		8	48.8	71.9	75.0
	9	20	7.4	8.5	98.3
		14	14.4	32.3	76.7
		8	52.5	73.0	16.7
9	26	20	12.9	35.4	93.0
		14	41.3	55.6	24.0
		8	76.0	85.8	2.7

^a Shibata et al (1970). ^b 8 hours. ^c 16 hours.

Other experiments dealing with field crops, however, indicate that rice is most sensitive to low temperatures at 14–7 days before heading, depending on variety and weather conditions (Sasaki and Wada 1973). For practical purposes, 14–7 days before heading, commonly referred to as the *booting stage*¹, is considered the most sensitive stage to low temperatures. The second most sensitive stage is heading or flowering.

¹More specifically it refers to the stage when the distance between auricles of flag leaf and penultimate leaf is about 0 cm.

When the rice plant is subjected to low temperatures for 3 days, it is more sensitive at the booting stage than at heading, as indicated by the higher percentages of sterility (Table 2.7). When the low temperatures are continued for 6–9 days, however, heading is as sensitive as, or even more sensitive than, booting.

As mentioned earlier, spikelet sterility appears to be affected by both night and day temperatures. This can be demonstrated by the cooling index concept (Uchijima, T. 1976). Cooling index (Q) is defined as:

$$Q = (20 - \bar{\theta}_0) N \text{ (degree-day)} \quad (2.6)$$

where 20 = critical low temperature limit ($^{\circ}\text{C}$)

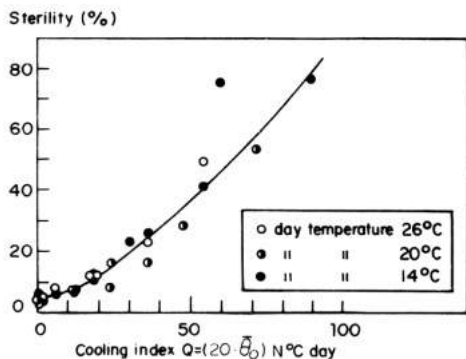
$\bar{\theta}_0$ = weighted daily mean temperature ($^{\circ}\text{C}$),

N = number of days when $\bar{\theta}_0 \leq 20$, and is computed only for days when $\bar{\theta}_0 \leq 20$.

A close correlation between the cooling index and percentage of sterility (Fig. 2.8) was obtained from an analysis of spikelet sterility attributed to low temperatures at booting (Table 2.7). That implies that the day and night temperatures equally affect the incidence of spikelet sterility at booting.

Clear varietal differences are reported for the tolerance for low temperature-induced sterility (Sasaki and Wada 1973). At 14°C for 5 days, tolerant varieties Hayayuki and Akage suffer about 40% spikelet sterility, whereas susceptible varieties Yukara and Shinei suffer about 80–100% spikelet sterility.

In general, japonica varieties are more tolerant of low temperatures than indica varieties. A recent work, however, reveals that some indica varieties are as tolerant as or even more tolerant of low temperatures at booting than some of the most cold-tolerant japonica varieties (Table 2.8). At IRRI, 6 cold-tolerant indica varieties were screened from 12,200 varieties and selections (IRRI 1977). These were compared with three japonica varieties known to be cold tolerant in northern Japan. At 12°C for 4 days, the percentages of fertility of these varieties ranged from 20 to 72%. The distance between auricle of flag-leaf and that of the penultimate leaf at the most sensitive stage varied from -7 cm to $+10$ cm.



2.8. Relationship between cooling index and sterility (Uchijima, T. 1976).

Table 2.8. Cold tolerance ^a of some japonica and indica varieties at booting stage. ^b

Variety		Country of origin	Distance between the auricle of flag leaf and that of penultimate leaf at the most sensitive stage (cm)	Fertility (%)
Indica	Leng Kwang	China	+10	72
	Thangone	Laos	-3	60
	C-21	Philippines	0	45
	Silewah	Indonesia	-6	70
	Pratao	Brazil	0	20
	Dourado A.	Brazil	-3	30
Japonica	Somewake	Japan	-1	45
	Sorachi	Japan	-7	45
	Hayayuki	Japan	-6	60

^a At 12°C for 4 days. ^b Satake (unpublished).

2.3.6. High-temperature stress

a. Occurrences of high-temperature problems. High temperatures cause high percentages of spikelet sterility in dry season crops in Cambodia, Thailand, and India; in the first rice crop in Pakistan; and in the regular crops in Iran and tropical African countries. High percentages of spikelet sterility occur if temperatures exceed 35°C at anthesis and last for more than 1 hour.

Table 2.9. Symptoms of heat stress and varietal differences. ^a

Growth stage	Symptoms	Susceptible varieties
Vegetative	White leaf tip	IR26, Calrose, BKN6624-46-2
	Chlorotic bands and blotches	
	White bands and specks	
	Reduced tillering	
Reproductive	Reduced height	IR24, Calrose
	White spikelets, white panicles	
Anthesis	Reduced spikelet numbers	C4-63G, H4, Calrose, Pelita I/1, Basmati-370, BKN6624-46-2
	Sterility	
Ripening	Reduced grain-filling	TN1, IR24, IR26, H4, Fujisaka 5, C4-63C, Pelita I/1

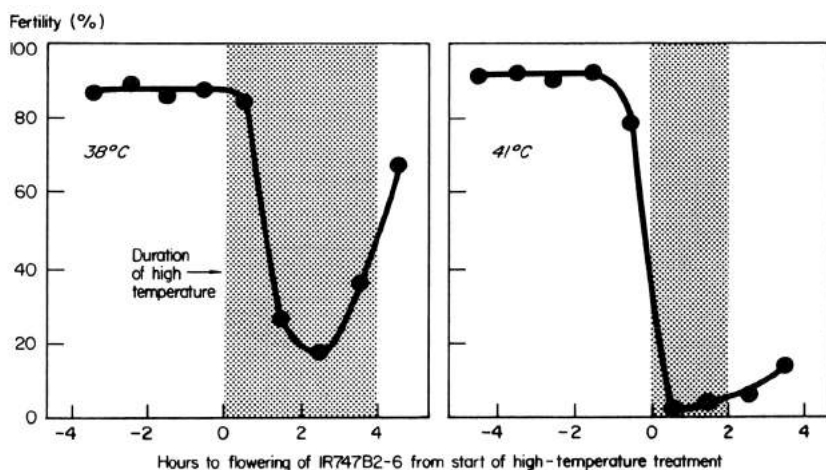
^a IRRI (1975).

b. Types of high-temperature injury. When rice is exposed to temperatures higher than 35°C, injuries occur according to growth stages (Table 2.9). Furthermore, clear varietal differences affect high temperature tolerance at different growth stages. A variety may be very tolerant of high temperatures at one growth stage but susceptible at another. The geographic origin of rice varieties is not related to susceptibility to heat stress. A selection from Thailand, BKN6624-46-2, is much more susceptible to high temperatures at the vegetative and anthesis stages than a Japanese variety, Fujisaka 5.

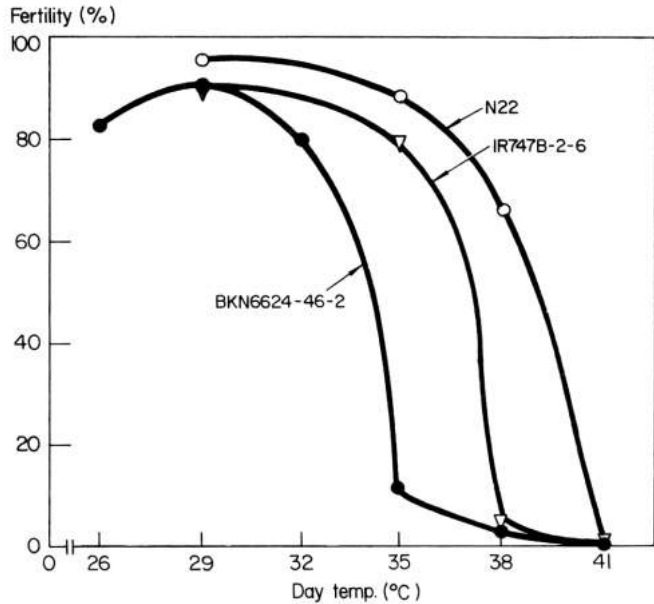
When rice is grown in a heated glasshouse during winter in the temperate regions, white leaf tips, chlorotic bands and blotches, and white bands and specks often develop on the leaves. These symptoms are very similar to those caused by high temperatures during cloudy weather.

c. High temperature-induced sterility. Rice is most sensitive to high temperatures at heading and next most sensitive at about 9 days before heading. One or two hours of high temperature at anthesis has a decisive effect on the incidence of sterility (Fig. 2.9). High temperatures before or after anthesis have much less effect on sterility.

Clear differences exist in the tolerance of rice varieties for high temperature-induced sterility (Fig. 2.10). At 35°C, N22, an upland rice from India, has higher than 80% spikelet fertility, whereas BKN6624-46-2, a lowland selection from Thailand, has about 10% spikelet fertility. If defined as the temperature when spikelet fertility decreases below 80%, the critical temperature is estimated from Fig. 2.10 as 36.5°C for N22, 35°C for IR747B2-6, and 32°C for BKN6624-46-2. Thus, the difference in the critical high temperatures between heat-tolerant N22 and heat-susceptible BKN6624-46-2 is more than 4°C.



2.9. Fertility of the spikelets that flowered in the hours before, during, and after high temperature treatments (Satake and Yoshida 1978).



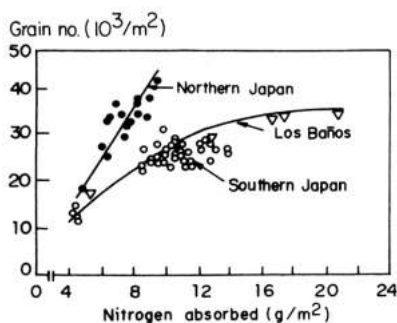
2.10. Fertility of the spikelets that flowered at different day temperatures (Satake and Yoshida 1978).

2.3.7. Interaction between temperature and nutrient supply

a. Number of spikelets per square meter and amount of nitrogen absorbed. Under most conditions, the major determinant of rice yield is total number of spikelets per square meter. There is a good correlation between the number of spikelets per square meter and total nitrogen uptake at heading: as the amount of nitrogen absorbed by the crop by heading increases, the number of spikelets per square meter increases (Fig. 2.11). The efficiency of nitrogen use in producing spikelets is higher in northern than in southern Japan, and data obtained from Los Baños, Philippines, are similar to those from the latter. That suggests that a cool climate favors higher nitrogen efficiency.

A minicrop experiment in the phytotron indicates that number of spikelets per square meter increases as temperature decreases at a given level of nitrogen, and this effect is most significant at the highest level of nitrogen (Table 2.10). However, the efficiency was higher at lower temperatures and lower nitrogen levels. Thus, temperature appears to be a major climatic factor that affects the efficiency at which nitrogen produces spikelets.

b. Low temperature-induced sterility and nitrogen. Nitrogen fertilization affects sterility caused by low temperatures at the reduction division stage. When temperatures are above or far below the critical, nitrogen supply has little effect on sterility. At moderately low temperatures (16°C), however, the percentage sterility increases with an increasing nitrogen supply (Fig. 2.12).



2.11. Relationship between grain number and amount of nitrogen absorbed by heading (Yoshida et al 1972. Data for Japan are adapted from Murayama 1967).

Table 2.10. Effects of temperature on spikelet number and efficiency of nitrogen to produce spikelets (minicrop experiment in the phytotron).^a

Day/night temperature (°C)	Spikelets (10 ² /m ²)			Spikelets (no./mg N absorbed)		
	150 N ^b	100 N	50 N	150 N	100N	50 N
35/27	278	280	244	1.4	2.0	2.9
32/24	299	308	275	1.6	2.2	3.0
29/21	376	313	288	2.1	2.3	3.3
26/18	482	409	326	2.2	2.5	3.2

^a IRRI (1978). ^b Kg N/ha.

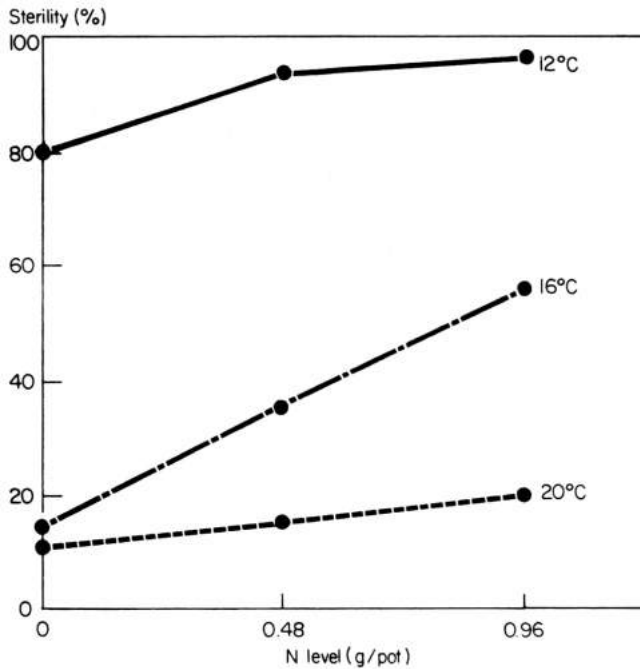
c. Low temperature-induced sterility and phosphorus. The adverse effects of high nitrogen under low temperatures during the reproductive stage can be alleviated by increasing the amount of phosphate applied (Fig. 2.13). This experiment confirms a common observation in northern Japan that the effect of phosphorus on rice yield is more significant in cool than in warm years (Ishizuka 1971).

2.4. SOLAR RADIATION

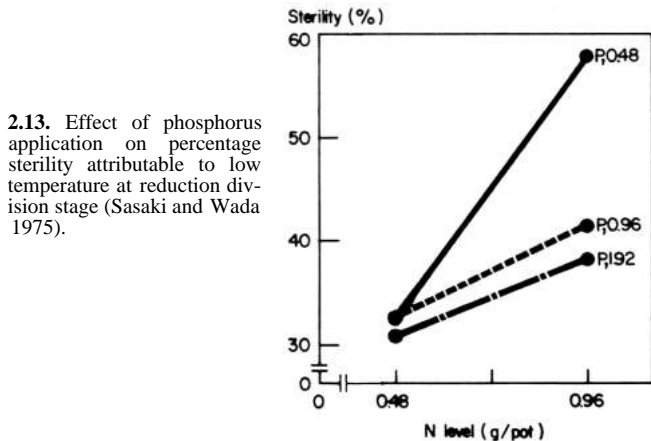
2.4.1. Physical aspects

Most of the radiant energy from the sun has a wavelength between 0.3 and 3 μm , often referred to as short-wave radiation. The earth emits radiation with wavelengths ranging from 3 to 50 μm , which is referred to as long-wave radiation.

Solar radiation penetrating the earth's atmosphere is reflected, absorbed, and scattered by clouds, gases, and aerosols in the form of soil and salt particles, smoke, insects, and spores. The reflection and scattering occur at all angles, and the downward component is usually referred to as diffuse sky radiation. Thus, incoming solar radiation takes the forms of direct radiation and diffuse sky radiation. The sum of these two is called global radiation or simply incident solar radiation.



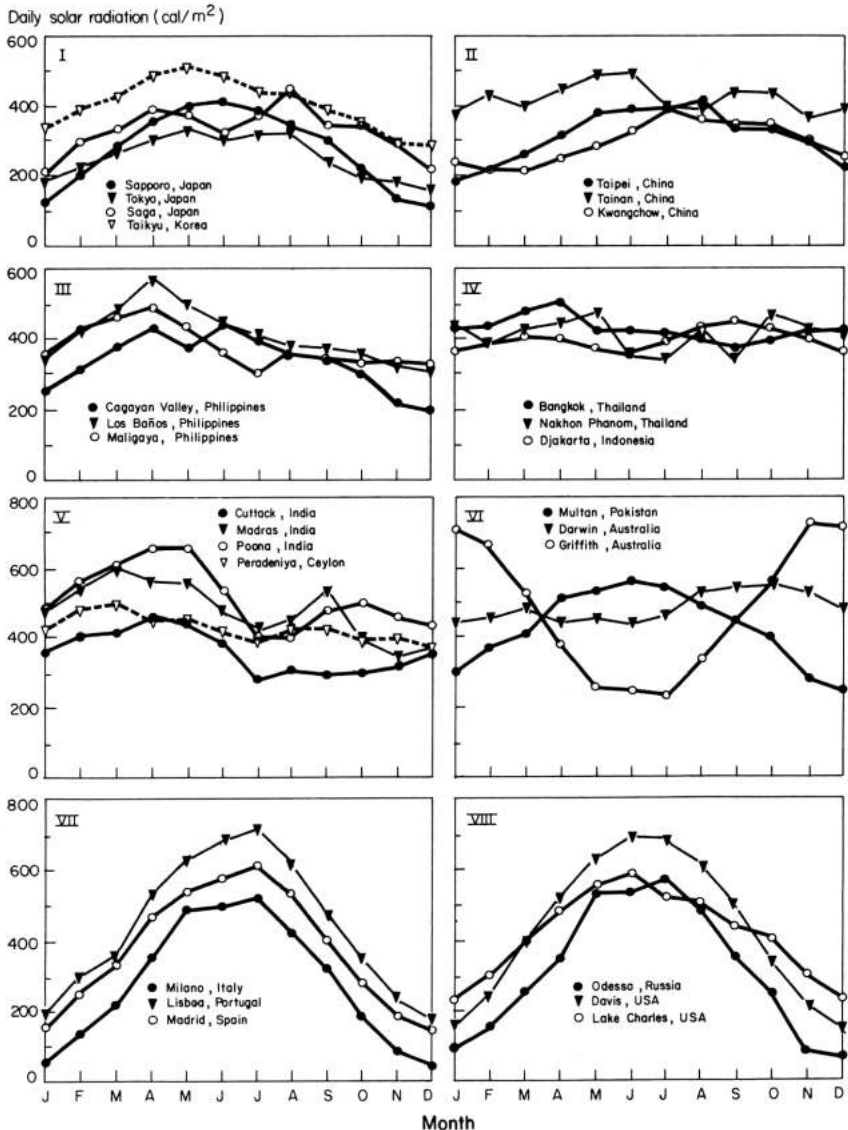
2.12. Effect of nitrogen on percentage sterility attributable to low temperature at meiotic stage (Sasaki et al 1973).



2.13. Effect of phosphorus application on percentage sterility attributable to low temperature at reduction division stage (Sasaki and Wada 1975).

Photosynthesis in green leaves uses solar energy in wavelengths from 0.4 to 0.7 μm , often referred to as photosynthetically active radiation (PAR) or simply light. The ratio of PAR to total solar radiation is close to 0.50 in both the tropics and the temperate regions (Monteith 1972), and represents a weighted mean between the fractions for direct radiation and diffuse sky radiation.

Outside the earth's atmosphere, a surface normal to the sun's rays receives energy at a mean rate of approximately 2 cal/cm^2 per minute, known as the solar constant. The amount of solar radiation received at any location on the earth's surface is a modification of the solar constant by two factors: the geometry of the earth with respect to the sun; and the absorption, reflection, and scattering in the atmosphere. As a consequence, the actual maximum radiation received at the



2.14. Solar radiation in some of the world's major rice-growing areas (Yoshida 1978).

earth's surface ranges from about 40% of the solar constant in humid regions to nearly 80% in arid regions where the cloud cover is sparse. The maximum solar radiation recorded under cloudless skies at noontime is 1.57 cal/cm² per minute (Monteith 1977).

The most commonly used unit of solar radiation in agriculture is the calorie per square centimeter per day (cal/cm² per day). Physicists and plant scientists, however, use other units, such as kilojoule per square meter per second and watt per square meter for solar radiation and other radiant energy in artificially lighted environments. The following lists the relationships between the different units.

$$\begin{aligned} 1 \text{ cal/cm}^2 \text{ per min} &= 1 \text{ langley/min} \\ &= 697 \text{ J/m}^2 \text{ per s} & (\text{J} = \text{Joule}) \\ &= 697 \text{ W/m}^2 & (\text{W} = \text{Watt}) \end{aligned}$$

$$\begin{aligned} 1 \text{ kJ/m}^2 \text{ per s} &= 1 \text{ kW/m}^2 = 1.43 \text{ cal/cm}^2 \text{ per min} & (\text{k} = \text{kilo} = \times 10^3) \\ 1 \text{ GJ/m}^2 &= 23.9 \text{ kcal/cm}^2 & (\text{G} = \text{giga} = \times 10^9) \end{aligned}$$

The annual income of solar radiation in the tropics ranges from about 8 GJ/m² on the margins of the subtropical deserts to about 5 GJ/m² in wet equatorial regions.

The monthly mean solar radiation at 26 sites in 15 rice-growing countries range from 50 cal/cm² per day in December at Milano, Italy, to 700 cal/cm² per day or higher in June or July at Lisboa, Portugal, and Davis, California, USA, or from November through January at Griffith, Australia (Fig. 2.14). Most places, however, appear to receive about 300 cal/cm² per day or more during the rice-ripening period.

2.4.2. Solar radiation requirement at different growth stages

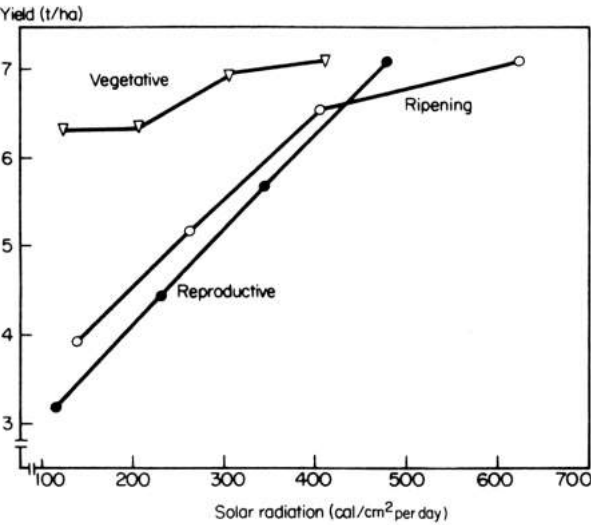
The solar radiation requirements of a rice crop differ from one growth stage to another (Table 2.11). Shading during the vegetative stage only slightly affects yield and yield components. Shading during the reproductive stage, however, has a pronounced effect on spikelet number. During ripening it reduces grain yield considerably because of a decrease in the percentage of filled spikelets. A quantitative relationship between yield and solar radiation at different growth stages is shown in Fig. 2.15. Solar radiation at the reproductive stage has the greatest effect on grain yield; that at the ripening stage, the next highest effect; and that at the vegetative stage, an extremely small overall effect.

Solar radiation of 300 cal/cm² per day during the reproductive stage makes yields of 5 t/ha possible. Less solar radiation during ripening is required to achieve the same yield level. Thus, the effect of solar radiation is apparent only when grain yield is higher than 5 t/ha. When grain yield is below that, sunlight per se may not have any direct significance. Since that conclusion was obtained with a 95-day variety, yield could be even higher with the same level of solar radiation and a medium growth-duration variety. Thus, the right variety and good management could achieve a yield of about 5 or 6 t/ha during the tropical wet season.

Table 2.11. Effect of shading at different growth stages on yield and yield components of IR74782-6.^a

Sunlight (%)	Grain yield (t/ha)	Harvest index	Spikelets (no./m ²)	Filled spikelets (%)	1000-grain wt (g)
<i>Vegetative stage</i>					
100	7.11	0.49	41.6	88.9	20.0
75	6.94	0.48	40.6	89.9	19.9
50	6.36	0.51	38.3	89.5	19.9
25	6.33	0.51	38.1	84.3	19.8
<i>Reproductive stage</i>					
100	7.11	0.49	41.6	88.9	20.0
75	5.71	0.47	30.3	87.8	20.3
50	4.45	0.40	24.4	89.4	19.5
25	3.21	0.36	16.5	89.4	19.1
<i>Ripening stage</i>					
100	7.11	0.49	41.6	88.9	20.0
75	6.53	0.49	41.1	81.1	20.0
50	5.16	0.44	40.6	64.5	19.5
25	3.93	0.38	41.7	54.9	19.1

^aYoshida and Parao (1976).



2.15. Effect of solar radiation at different growth stages on grain yield of IR747B2-6 (Yoshida and Parao 1976).

In the tropics, solar radiation is higher in the dry than in the wet season. Consequently, the dry season yield is usually higher. The excessively cloudy weather during the wet season is often considered a serious limiting factor to rice production in monsoon Asia. This conclusion is true when yields higher than 6 t/ha

are to be achieved. It is, however, inadequate if we refer to the current yield levels when the national average yield is still about 2 t/ha in most Southeast Asian countries.

2.4.3. Solar energy use

When solar radiation is incident on a well-developed rice crop, about 20% of the total radiation is reflected into the sky (Murata et al 1968, Kishida 1973). Of the reflected radiation, only about 10% is photosynthetically active radiation (PAR); the rest is in the near far red region. In other words, about 3–5% of PAR is lost by reflection at the canopy surface (Fig. 2.16) (Kanda 1975). Taking 5% for the loss attributed to reflection, about 90% of PAR will be absorbed by the leaves and about 5% will be transmitted to the ground.

Photosynthetic efficiency of a rice crop can be estimated by:

$$\text{Photosynthetic efficiency} = \frac{\text{chemical energy captured by a crop}}{\text{solar energy received}} \quad (2.7)$$

In practice, however, there are several ways of computing the photosynthetic efficiency. First, chemical energy can be estimated in terms of net gains or gross. Second, solar radiation may be expressed in terms of total incident radiation, PAR, or absorbed PAR. The simplest and most widely used measurement uses net gains for the numerator and total incident radiation for the denominator:

$$\begin{aligned} \text{Photosynthetic efficiency } (E_{\mu}) &= \frac{\text{net gains of chemical energy}}{\text{total incident solar radiation}} \\ &= \frac{K \times \Delta W}{\Sigma S} = \frac{K \times \Delta W}{(\bar{S}) \times T} \times 10^{-4}, \quad (2.8) \end{aligned}$$

where K = heat of combustion (cal/g),

ΔW = dry matter increase (g/m²),

ΣS = total amount of incident solar radiation (cal/m²),

\bar{S} = average daily incident solar radiation (cal/cm² per day), and

T = number of days.

The measured E_{μ} values vary with growth stages, ranging from 0.52% at a LAI of 0.36 to 2.88% at a LAI of 4.10, for example. The measured maximum E_{μ} value for rice is 3.7% (Murata et al 1968). In the more comprehensive 5-year experiment of the Japanese International Biological Program (IBP), however, the highest E_{μ} for each year ranged from 2.83 to 3.32% with a mean value of 3.00% (Kanda 1975). For the entire growing period, the 5-year mean E_{μ} is 1.25% for total dry matter. If grains alone are considered, E_{μ} becomes 0.48% (Table 2.12). The theoretical maximum E_{μ} is estimated at 5.3% (Loomis and Williams 1963). In the IBP experiment, the highest E_{μ} (4.53%) was recorded for maize (Kanda 1975).

When 1 is substituted for T in the equation 2.8, ΔW becomes dry matter increase per square meter per day, which is crop growth rate. Thus, crop growth rate

Table 2.13. Heat of combustion for different parts of the rice plant.^a

Plant part	Heat of combustion (cal/g)
Leaf blade	4036
Leaf sheath	3569
Root	3177
Panicle	3978
Dead leaf	3611
Whole plant	3718

^a Mean values calculated from Murata et al (1968).

go in our attempts to increase crop yields. Several scientists used different methods of estimating maximum potential rice yields using different assumptions (Evans 1972, Murata and Matsushima 1975, IRRI 1977).

An estimate of the maximum potential rice yield is given by the product of the maximum photosynthetic net production per day or per unit of incident solar radiation and the number of effective days for grain production.

There are two basic methods for estimating maximum photosynthetic net production. Method 1 estimates the gross production by examining the efficiencies of component processes in the energy flow of canopy photosynthesis and subtracts the respiration losses to obtain the net production (Murata and Matsushima 1975). Method 2 is more empirical and much simpler. It uses the recorded maximum photosynthetic efficiency of rice crops (IRRI 1977). Both methods implicitly assume that the sink size is not limiting to grain production and that all the photosynthates are carbohydrate and contribute to grain carbohydrate.

Method 1

Assumptions:

- (a) The period for yield production is 40 days after heading.
- (b) The average daily solar radiation is 400 cal/cm² per day of which 45% is photosynthetically active.
- (c) Of the photosynthetically active radiation, 5.5% is lost by reflection at the canopy surface and another 10% through absorption by inactive tissues.
- (d) Eight photons are required to reduce 1 molecule of carbon dioxide, corresponding to an efficiency of 26% in energy conversion,
- (e) The loss due to light saturation in the upper leaves is 17% at 400 cal/cm² per day.
- (f) The conversion factor for dry matter is 3,900 cal/g.
- (g) The respiration loss is the sum of 1.5% of dry weight/day (1.5 kg/m² in this case) and 25% of the gross photosynthesis.
- (h) The ratio of husk weight to the dry grain weight is 20%.

Calculation:

Maximum grain yield

$$\begin{aligned}
 &= (400 \times 10^4 \times 0.45 \times 0.945 \times 0.90 \times 0.26 \times 0.83 \times 0.75 \\
 &\quad - 1500 \times 0.015 \times 3900) \times 40/3900 \\
 &= 1640 \text{ g/m}^2 \text{ (dry weight)} \\
 &= 19.1 \text{ t/ha (brown rice at 14\% moisture content).} \\
 &= 23.8 \text{ t/ha (rough rice at 14\% moisture content).}
 \end{aligned} \tag{2.11}$$

Method 2. The equation 2.8 can be rewritten as:

$$W = \frac{E_\mu \times T \times \bar{S}}{K} \times 10^4, \tag{2.12}$$

where T is the effective grain-filling period discussed in Chapter 1.

Assumptions

(a) The effective grain-filling period is 35 days for temperate regions and 25 days for the tropics.

(b) Two E_μ values are used: 3.5% represents the high efficiency and 2.5%, the moderately high efficiency; 3.3% is the highest recorded E_μ in Japanese IBP trials (Kanda 1975).

(c) The heat of combustion for the grain is 4,000 cal/g.

(d) The ratio of husk weight to the dry grain weight is 20%.

(e) The contribution of the carbohydrate stored before flowering is negligible when the maximum potential yield is to be achieved.

Calculation:

When appropriate corrections are made for weight ($\times 10^{-6}$), area ($\times 10^4$), husk ($\times 1/0.8$), and moisture content ($\times 1/0.86$), grain yield will be computed as:

$$\begin{aligned}
 \text{Grain yield at} \\
 \text{14\% moisture content} &= \frac{E_\mu \times T \times \bar{S}}{K} \times 10^4 \times \frac{10^4}{10^6} \times \frac{1}{0.8} \times \frac{1}{0.86}.
 \end{aligned} \tag{2.13}$$

The results of the calculation are shown in Figure 2.17.

In method 1, E_μ can be computed as:

$$E_\mu = \frac{1,640 \times 3,900}{400 \times 40 \times 10^4} = 0.04 = 4.0\%. \tag{2.14}$$

The E_μ value of 4.0% is higher than the maximum recorded value of 3.3% for rice.

Substituting 4.0% for the E_μ value in equation 2.13 gives 20.4 t/ha when T is 35 days and 23.2 t/ha when T is 40 days. Thus, methods 1 and 2 give basically similar estimates of the maximum potential yield. That implies that the efficiencies of component processes along the flow of energy are well integrated into a single E_μ value. An important assumption in the foregoing estimates is that high photo-

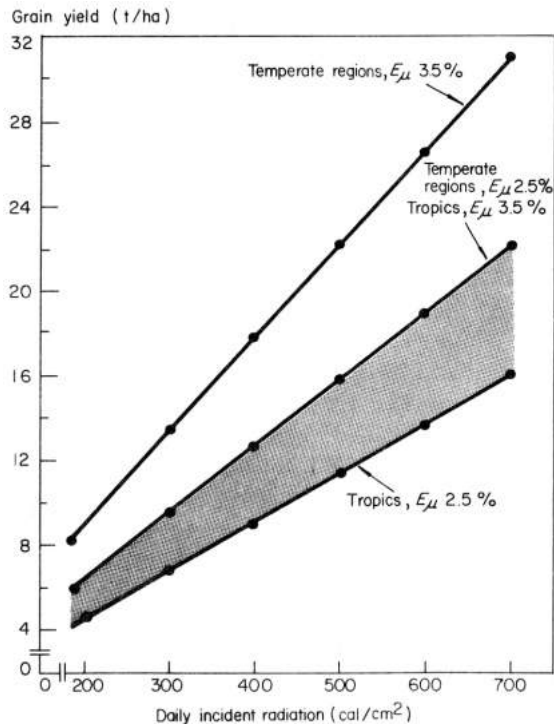
synthetic efficiency recorded for a short period during the vegetative growth stage should continue during ripening when senescence occurs.

Figure 2.17 shows a linear relationship between incident solar radiation and potential yield. This is because the same E_{μ} value is used at all levels of incident solar radiation. However, E_{μ} value is expected to decrease with increasing level of incident solar radiation. As a consequence, the relationship between incident solar radiation and potential yield would likely be curvilinear but not linear. However, information as to how E_{μ} relates to incident solar radiation in rice is lacking. Therefore, the potential yields calculated by equation 2.13 are likely to be underestimates at lower levels of incident solar radiation and overestimates at higher levels.

The estimated potential yield shown in Figure 2.17 indicates that the temperate region, where the effective grain-filling period is longer, is more productive than the tropics on per-crop yield basis. The estimated maximum yields may be compared with recorded maximum yields: 13.2 t/ha in Japan with an estimated solar radiation of 400 cal/cm² per day and 11.0 t/ha at IRRI with an estimated solar radiation of 550 cal/cm² per day.

At IRRI and with good management, about 6 t/ha is normally obtained in the wet season when incident solar radiation is about 300 cal/cm² per day during ripening

2.17. Relation between potential yield and incident radiation during the grain-filling period of rice (IRRI 1977).



period. When the rice crop was given carbon dioxide enrichment before flowering to increase spikelet number per square meter but was kept under normal atmospheric conditions after flowering, it yielded 7.7 t/ha (Yoshida 1976). Thus, the recorded maximum yields are close to the estimated potential yields.

2.5 RAINFALL AND FIELD WATER RELATIONSHIPS

Under rainfed rice culture and where temperatures are within the critical low and high ranges, rainfall is perhaps the most limiting factor in rice cultivation. When irrigation is provided, however, growth and yield are determined largely by temperature and solar radiation. Because of the unpredictable variation in frequency and amount of rainfall for a given location over time, it is extremely difficult to find a simple relationship between annual rainfall and grain yield. At best, only the probable occurrence of drought can be predicted based on long-term records. Furthermore, it is difficult to generalize on the water requirement of rice because of variations in topography, soil characteristics, and length of the crop-growing period among different locations, and because local practices affect the amount of water necessary for land preparation. Currently, however, rainfed rice cultivation is limited to areas where the annual rainfall exceeds 1,000 mm.

2.5.1. Transpiration and growth

Transpiration is the loss of water in the form of vapor from plant surfaces. The plant will wilt or die unless water is supplied to compensate for the water lost by transpiration. Transpiration occurs mainly through stomates and to a much lesser extent through the cuticle. Thus, the transpiration is controlled primarily by the opening and closing of stomates.

Transpiration may increase the rate of upward movement of salt in the plant or it tends to cool the leaves because 590 calories is removed per 1 gram of water. Yet, these may not be absolutely essential for plant life. Thus, transpiration is usually considered an unavoidable evil, unavoidable because of the structure of leaves and evil because it often results in water deficits and injury by desiccation (Kramer 1969).

The amount of water lost through transpiration is directly related to amount of growth. The transpiration ratio is the number of grams of water transpired per gram of dry matter produced. It varies with soil moisture, climate, variety, growth stage, and growth duration of the plant. It ranges from 171 to 766 g/g but it is generally around 250-350 g/g (Matsushima 1962, Yoshida 1975c). The transpiration ratio implies that dry matter production is proportional to the amount of water transpired by the plant. When calculated for grain production, the transpiration ratio of an early-maturing variety is only one-third that of a late-maturing variety (Matsushima 1962). Thus, the former uses water for grain production more efficiently than the latter.

Transpiration is, however, only part of total water loss by a field-grown rice crop. Water is lost through evaporation from soil or water surfaces and through percolation.

Table 2.14. Water requirement of an irrigated rice crop.^a

By water loss	
Transpiration	1.5–9.8 mm/day
Evaporation	1.0–6.2 mm/day
Percolation	0.2–15.6 mm/day
Range of total daily loss	5.6–20.4 mm/day
By field operation	
Seed nursery	40 mm
Land preparation	200 mm
Field irrigation	1000 mm
Total	1240 mm/crop

^aKung (1971).

2.5.2. Water requirements

The water requirements of irrigated rice in 43 locations in China, Japan, Korea, the Philippines, Vietnam, Thailand, and Bangladesh are summarized in Table 2.14.

Water is lost from irrigated rice during the crop season, through transpiration, evaporation, and percolation. Water losses through percolation are the most variable. The total water loss shown in Table 2.14 ranges from 5.6 to 20.4 mm/day, but most of the observed values for total water loss range from 6 to 10 mm/day. Thus, on the average, about 180–300 mm water/month is needed to produce a reasonably good crop of rice.

In field operation, a total of 1,240 mm is an average water requirement for an irrigated rice crop. The same figure is obtained if the assumptions are made that the crop duration is 5 months, monthly water requirement is 200 mm, and land preparation requires 200 mm water. If land preparation takes more than 30 days, however, as much as 500–600 mm of water may be required.

Several different units are used in discussing the water needs of field crops:

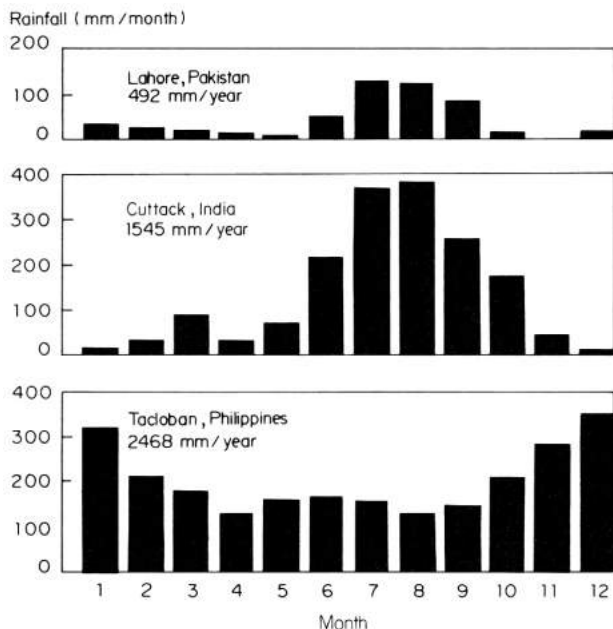
$$\begin{aligned} 1 \text{ liter/ha per second} &= 8.64 \text{ mm/day} \\ &= 86.4 \text{ m}^3/\text{ha per day} \end{aligned}$$

$$1 \text{ md/day} = 0.116 \text{ liter/ha per second} = 10.0 \text{ m}^3/\text{ha per day}.$$

2.5.3. Water gains — precipitation

Precipitation (rainfall plus snow) is the primary source of water in agriculture. Rainfed rice depends mainly on current rainfall, whereas water is supplied to irrigated rice through a *storage* system, which collects precipitation and stores it for later use.

The amount and pattern of rainfall varies widely from one place to another, and from year to year. At the moment, there is no way to predict the amount and pattern of rainfall for a given region with sufficient accuracy. What we know is *average rainfall* based on long-term records.



2.18. Monthly rainfall at 3 rice-growing areas in Asia.

The rainfall patterns of three Asian rice-growing regions illustrate the basic patterns of rainfall distribution (Fig. 2.18):

- Lahore, Pakistan, represents a semiarid climate. The annual rainfall is about 500 mm/yr, much less than the water requirement of a rice crop. Hence, rice is grown only when irrigation is provided. Deccan Heights in the Indian subcontinent has a similar climate.
- Cuttack, India, has a typical dry and wet monsoon climate. Only one monsoon brings most of the rainfall, and the wet season is distinct from the dry. Rainfed rice cultivation is started in June and the crop is harvested in November or December. Most rice-growing regions in South and South-east Asia have this type of climate. The duration of the rainy season and the amount of rainfall, however, vary with location.
- Tacloban, Philippines, receives rain from two monsoons (northeast and southwest). As a consequence, rainfall is fairly evenly distributed throughout the year, and no regular dry season occurs. Under this type of climate, rice can be grown throughout the year but harvesting and drying may pose some problems.

These basic rainfall patterns could be further classified into subgroups. For example, Kawaguchi and Kyuma (1977) proposed 9 climatic groups for tropical Asia while Oldeman and Suardi (1977) considered 17 climatic zones related to cropping patterns in Asia. For individual rainfall data, the reader is advised to refer to handbooks of climatology or reports from local weather stations.

2.5.4. Water losses: evapotranspiration and percolation plus seepage

In lowland rice fields, water losses largely result from transpiration, evaporation, and percolation plus seepage. Transpiration is the loss of water through plant surfaces and evaporation is the loss of water from free water surfaces. The combined water losses through transpiration and evaporation are referred to as evapotranspiration.

Transpiration losses increase with leaf area index (LAI) and reach a plateau at a LAI of 3.5–4.0. At this plateau, the transpiration loss on sunny days is about 6 ± 2 mm/day (Kato et al 1965a), and that accounts for about 90% of the evapotranspiration losses (Kato et al 1965b). Evaporation is high at early growth stages, when the LAI is small, and accounts for most of the evapotranspiration losses. As LAI increases, evaporation decreases and transpiration accounts for most of the evapotranspiration losses.

Evapotranspiration is related to meteorological factors and will be discussed in detail in the succeeding section. Percolation, seepage, and surface run-off, largely controlled by edaphic factors such as topography and soil characteristics, are highly location specific. In sloping areas, water may move by gravity from a high to a low level. In upland fields, evapotranspiration, percolation, and surface run-off are the major forms of water loss.

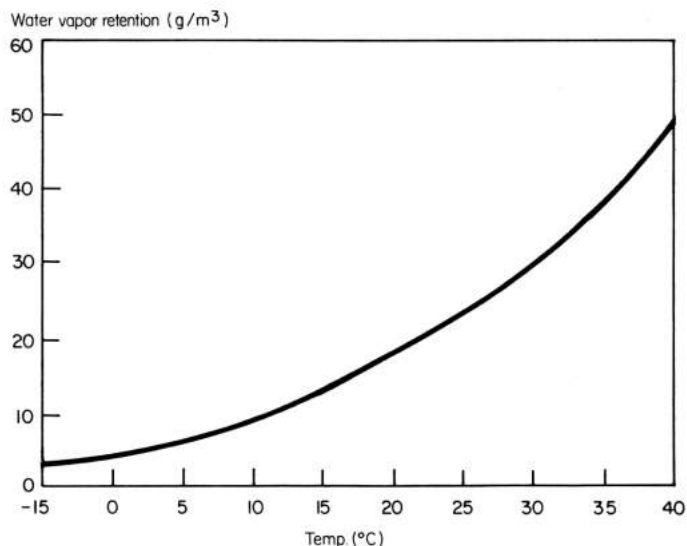
Percolation occurs in a vertical direction. Water is lost through seepage by its horizontal movement through a levee. In practice, percolation and seepage are combined and taken as a measure of the water-retaining capacity of a field.

Percolation is largely affected by topography, soil characteristics, and the depth of the water table. In extreme cases, percolation plus seepage ranges from almost nil on heavy soils to greater than 100 mm on sandy soils. Rice grown on sandy soils in Japan requires, on the average, about three times more water than rice grown on clay soils (Fukuda and Tsutsui 1968). Because of topography and soil characteristics, the percolation-plus-seepage loss is relatively high in Japan and rather low in many other rice-growing countries. For example, a percolation-plus-seepage loss of 20 mm/day is considered desirable for productive rice fields in Japan, but considered exceptionally high in other countries.

The surface water-storage capacity is determined by the levee's height in lowland fields and by the slope and roughness of the soil surface in upland fields. Surface runoff or overland flow occurs when rainfall intensity exceeds the surface storage capacity and the percolation-plus-seepage rate or infiltration rate. In lowland fields, the effective daily rainfall is defined as being not less than 5 mm and not more than 50 mm (Fukuda and Tsutsui 1968). In upland fields, however, the upper limit of effective daily rainfall should be much less because the loss due to surface runoff would be greater.

2.5.5. Evapotranspiration

As explained before, the term *evapotranspiration* includes evaporation from both water and plant surfaces. The phase change implied by the evaporation is physically identical wherever it takes place.



2.19. Variations in the capacity of air at different temperatures for water vapor.

For evaporation from a surface to continue there are several physical requirements. First, there must be a supply of energy to provide the quite large latent heat of vaporization, which varies with temperature; it is about 590 cal/g at around 15°C and 580 cal/g at 30°C.

Second, the vapor pressure in the overlying air must be less than that at the evaporating surface since evaporation (a net transfer of water vapor) is zero if there is no gradient in vapor pressure. The gradient in vapor pressure is controlled by the capacity of the air to take up more water vapor and the degree of turbulence in the lower atmosphere necessary to replace the saturated air near the evaporating surfaces. The turbulence is caused by winds or by convectional currents. While winds are not particularly stronger in the tropics than in other regions, convection is frequent.

The air's capacity to retain water vapor increases rapidly with temperature (Fig. 2.19). Warm tropical air masses can, therefore, take up more water vapor than cold ones. The actual amount also depends on the air's relative humidity — the lower it is, the more favorable are the conditions for further evapotranspiration. The dry tropics have, therefore, very high rates of evapotranspiration.

Third, water must be available for evaporation, this being a limiting factor under dry conditions.

2.5.6. The concept of potential evapotranspiration

The term *potential evapotranspiration*. (PE), originally proposed by Thornthwaite (1948), was defined as the water lost by vegetation if the soil is never water deficient. PE was more explicitly defined by Penman (1948) as the amount of

water transpired in a unit of time by a short green crop of uniform height, which completely shades the ground and is never short of water. Penman preferred to use the term *potential transpiration* for PE. The Penman concept suggests that PE represents the maximum possible evaporative loss from a vegetation-covered surface. The actual evapotranspiration, however, may exceed PE when there is a supply of advected energy (Chang 1968, Ward 1975). Advection is known as the *oasis effect* and may occur where a moist area is surrounded by or adjacent to hot, dry land. Under such conditions, sensible heat will be transferred to the moist area and its evapotranspiration rate will be increased.

In a humid climate, such as during the rainy season in monsoon Asia, advected energy is probably negligible and, hence, the PE defined by Penman may apply to actual evapotranspiration. In an arid or semiarid climate, the existence of large amounts of advected energy renders the concept of PE inexact and unrealistic.

Pruitt (1960) developed the notion of *potential maximum evapotranspiration* to allow for the situation in which advected energy is an important factor in determining evapotranspiration rates.

More recently, van Bavel (1966) developed an equation relating PE to net radiation, ambient air properties, and surface roughness. As an improvement over the Penman equation, the proposed model contains no empirical constants or functions. The van Bavel equation is applicable to a wide range of weather conditions, under which advection of sensible heat to the evaporating surface occurs. Thus, the refinement of both theoretical and experimental treatments of PE has caused the meaning of PE to change, and caution should be taken when using the term.

2.5.7. Pan evaporation

Up to the present, different kinds of pans — size, design, and installation — have been used to measure the evaporation rate from a free water surface (Chang 1967, Ward 1975). The data obtained from using these pans are quite different. For instance, a small-sized pan gives a higher evaporation rate than a large-sized pan under the same weather conditions. Hence, extreme care must be exercised when interpreting pan evaporation data collected from different sources.

To eliminate the effects of pan design and installation on evaporation rates, the World Meteorological Organization (WMO) adopted the U.S. Weather Bureau Class A pan as the interim standard for the International Geophysical Year. Since that time, the class A pan has been widely accepted in many countries.

The U.S. Weather Bureau Class A pan is a cylinder 120.7 cm (47.5 inches) in inside diameter and 25.4 cm (10 inches) deep. It is constructed of galvanized iron or monel metal, preferably the latter, in areas where the water contains large amounts of corrosive substances. The evaporation pan is placed on a wooden platform with the bottom approximately 10 cm above the ground so that air may circulate beneath the pan. The site should be fairly level, sodded, and free of obstructions; the grass should be frequently watered. The pan should be filled to a level 5 cm below the rim, and refilled when the water has evaporated 2.5 cm.

Under most conditions, a decrease in the water depth is recorded every morning and the pan is refilled to the specified level. The measurement is corrected for rainfall. The evaporation rate is for the day previous to the measurement.

The ratio of field evaporation to pan evaporation is called crop coefficient or pan factor. The crop coefficient value of irrigated rice obtained from the use of a U.S. Weather Bureau Class A pan is reported to be 0.86 during the wet season in northern Australia (Chapman and Kininmonth 1972).

2.5.8. Simplified energy balance method

Application of the law of energy conservation to the streams of heat energy arriving at, entering, and leaving the earth's surface leads to an equation of energy balance at the earth's surface where the energy conversion occurs (Davies and Robinson 1969):

$$R_n = E + H + G + ph, \quad (2.15)$$

where R_n = net radiation,

E = energy used for evapotranspiration,

H = sensible heat,

G = soil-water heat flux, and

ph = energy used for photosynthesis.

Under most conditions, the net storage of heat by soil-water and the energy captured by photosynthesis are small, and thus the equation (2.15) can be reduced to:

$$R_n = E + H. \quad (2.16)$$

For freely transpiring, well-covered surfaces with no water shortage in the root zone, evapotranspiration may use most of the net radiation, and sensible heat may approach zero. This evapotranspiration rate gives the maximum, which may be similar to Penman's potential transpiration or Thornthwaite's potential evapotranspiration. Thus, the potential evapotranspiration (PE) is given by:

$$PE = \frac{R_n}{L}, \quad (2.17)$$

where L is the latent heat of vaporization (590 cal/g). The net radiation can be directly measured with a net radiometer or can be estimated from solar radiation data.

For a paddy field, the ratio of net radiation to total incoming short-wave radiation varies from 0.70 at the early growth stages to 0.55 at ripening, with a mean value of 0.62 (RGE 1967a). Thus, the average net radiation of a rice crop can be estimated by:

$$R_n = 0.62 \times S. \quad (2.18)$$

Combining equation 2.17 with 2.18 gives the complete equation for potential evapotranspiration (Yoshida 1979).

$$\begin{aligned}
 PE &= \frac{R_n}{L} = \frac{0.62 \cdot S}{L} = 0.0017 (0.62 \cdot S) \\
 &= 0.0105 \cdot S \text{ (mm/ } T \text{)},
 \end{aligned}
 \tag{2.19}$$

where S is expressed in calories per square centimeter per T , and T can be day, week, or month. This equation implies that the potential evapotranspiration is about 1 mm/100 cal. incident solar radiation.

Even under flooded conditions, however, sensible heat is not negligible (RGE 1967b). When loss of energy by sensible heat is taken into account, equation 2.19 is modified into:

$$E_R = \frac{0.82 \cdot R_n}{L} = 0.0086 \cdot S \text{ (mm/ } T \text{)}, \tag{2.20}$$

where E_R is a realistic estimate of evapotranspiration from a paddy field after the crop has been established.

Although the above energy balance equation has been derived in a very simplified manner, estimated potential evapotranspiration agrees well with direct measurements of evapotranspiration and agronomic experiments.

Agricultural engineers at the International Rice Research Institute (IRRI) measured evapotranspiration (ET) from a 400-m² field with minimized seepage loss and obtained the following empirical formula:

$$ET = 0.15 + 0.01072 \cdot S. \tag{2.21}$$

The first term of equation 2.21 was the average percolation and seepage rate during the measurement (IRRI 1965). Good agreement between equations 2.19 and 2.21 may support the common belief that the ET of flooded rice is essentially equal to potential evapotranspiration.

The potential evapotranspiration computed from equation 2.19 correlates well with the observed U.S. Weather Bureau Class A pan evaporation rate at IRRI, Los Baños, Philippines:

$$PE = 0.93 \times \text{pan evaporation}. \tag{2.22}$$

Agronomic experiments on irrigation requirements in IRRI's fields indicate that about 7 mm water/day is necessary after the stand establishment to achieve the maximum dry season yield (IRRI 1970). The same conclusion can be obtained from estimates of evapotranspiration and percolation plus seepage in the following way: Given a value of 14,964 cal/cm² for April 1970, the daily evapotranspiration is obtained by equation 2.20:

$$E_R = \frac{0.0086 \times 14,964}{30} = 4.4 \text{ mm/day}. \tag{2.23}$$

For IRRI fields, the best estimate of the daily percolation plus seepage is about 3 mm for the dry season. Thus, the total water consumption (evapotranspiration + percolation plus seepage) in an IRRI field becomes 7.3 mm/day, which agrees well with the agronomic field experiments.

2.5.9. The Penman equation

The Penman method for estimating PE combines the turbulent transfer and the energy balance approaches (Chang 1967; Penman 1948, 1956; Ward 1975). It requires observations on net radiation, temperature, humidity, and wind speed.

There are three basic equations, the first of which is a measure of the drying power of the air. This increases with an increasing saturation deficit, indicating that the air is dry and with high windspeeds:

$$E_a = 0.35 (e_a - e_d) (0.5 + u_2/100) \text{ (mm/day)} \quad (2.24)$$

where E_a = aerodynamic term of evaporation,
 e_a = saturation vapor pressure at
the mean air temperature (mm Hg),
 e_d = actual vapor pressure in air (mm Hg), and,
 u_2 = wind speed at a height of 2 m above
the ground surface (miles/day).

The second equation provides an estimate of the net radiation available for evaporation and heating at the earth's surface:

$$R_n = A - B \text{ (mm/day)} \quad (2.25)$$

where A is the short-wave incoming radiation and B is the long-wave outgoing radiation, as estimated in the following expressions:

$$A = (1 - r) R_a (0.18 + 0.55 n/N) \text{ (mm/day)} \quad (2.26)$$

$$B = \sigma T_a^4 (0.56 - 0.09 \sqrt{e_d}) (0.10 + 0.90 n/N) \text{ (mm/day)}, \quad (2.27)$$

where R_a = theoretical radiation intensity at the ground
surface in the absence of an
atmosphere expressed in evaporation units,
 r = the reflection coefficient of
the evaporation surface,
 n/N = ratio of actual/possible
hours of bright sunshine,
 σ = Stefan-Boltzman constant,
 T_a = mean air temperature ($^{\circ}\text{K}$), and
 e_d = as in equation 2.24.

The equations 2.24 and 2.25 can be combined when appropriate assumptions are made:

$$E = \frac{\Delta/\gamma \cdot R_n + E_a}{\Delta/\gamma + 1} \text{ (mm/day)} \quad (2.28)$$

where Δ = slope of the saturation vapor
pressure curve for water at
the mean air temperature mm Hg/ $^{\circ}\text{C}$, and

γ = constant of the wet and dry bulb
psychrometer equation (0.49 mm Hg/°C).

The equation 2.28 is the final form of the Penman equation.

The quantity E will vary according to the value assigned to the reflection coefficient r in the equation 2.26. Thus, if r is 0.25, E will represent the PE from a short green crop; if r is 0.05, E will represent the evaporation from open water. The net radiation (R_n) can be measured directly with a net radiometer. If solar radiation data are available, the net radiation of a rice crop can be estimated by equation 2.18.

The ratio, Δ/γ , is dimensionless, and is a factor that makes allowance for the relative significance of net radiation and evaporativity in total evaporation. For example, at 10°, 20°, and 30°C, the Δ/γ values are 1.3, 2.3, and 3.9, respectively. Thus, during summer months when evaporation totals are high, the net radiation term is given more weight than the evaporativity term. Furthermore, in humid areas R_n is usually greater than E_a so R_n tends to be the dominant term in the equation.

A systematic comparison of the Penman method with seven other methods indicated that only the Penman estimates correlate closely with pan evaporation data throughout the year in Thailand (Juntharasi 1977).

2.5.10. The Thornthwaite method

Thornthwaite's formula for estimating potential evapotranspiration uses lysimeter and watershed observations of water losses in the central and eastern US (Thornthwaite 1948, Thornthwaite and Mather 1955, 1957). Physically, it is based on the high correlation between temperature and solar radiation. His formula reads:

$$E = 1.6 b(10 t/I)^a \quad (2.29)$$

where E = potential evapotranspiration in centimeters,

t = monthly mean temperature in °C,

a = cubic function of I ,

b = correction factor for actual day length
of hours and days in a month, and

I = annual heat index.

The annual heat index (I) is the sum of 12 monthly heat indices (i):

$$i = (t/5)^{1.514} .30 \quad (2.30)$$

To evaluate a , the following equation is used:

$$a = 6.75 \times 10^{-7} \times I^3 - 7.71 \times 10^{-5} \times I^2 + 1.792 \times 10^{-2} \times I + 0.49239. \quad (2.31)$$

Because it requires only monthly mean temperatures, Thornthwaite's method probably has been most extensively used to compute potential evapotranspiration

for many regions. It has also been used to estimate the potential evapotranspiration and water balance of rice crops in monsoon Asia (Maruyama 1975).

A fundamental defect of Thornthwaite's method is the degree of correlations between temperature and the energy available for evaporation, depending on weather conditions. Thornthwaite's method fits areas where the climates are similar to those in central and eastern US.

2.5.11. The van Bavel method

Van Bavel (1966) modified the Penman equation in such a way that it contains no empirical constants or functions, and is not restricted to grass or to any other specified set of surface conditions other than unrestricted water supply.

For practical purposes, the van Bavel equation takes the following form:

$$E_o = \frac{\Delta/\gamma H + L B_v d_a}{\Delta/\gamma + 1} \quad (\text{mm/h}) \quad (2.32)$$

where E_o = potential evaporation,

Δ/γ = the same as in equation 2.28,

H = approximated by net radiation (cal/cm^2),

L = latent heat of vaporization (cal/g),

B_v = transfer coefficient for water

vapor ($\text{g}/\text{cm}^2/\text{min}$ per mb), and

d_a = vapor pressure deficit at elevation Z_a (mb).

The van Bavel method of estimating PE is perhaps the most comprehensive approach that has ever been attempted. It is applicable to a wide range of environments where advection is present. The ratio of measured vs computed evapotranspiration varies from 0.87 to 1.05 with a weighted mean of 0.96. This disagreement, however, appears to be within instrumental and measurement errors over a range in daily evaporation from 3 to 12 mm.

2.5.12. Water balance

Knowing water gains and losses, we can calculate the balance between the two. Water balance can be examined at the root zone for a given field, or it can be viewed on a much larger scale, such as a hydrologic cycle, as illustrated in Figure 2.20.

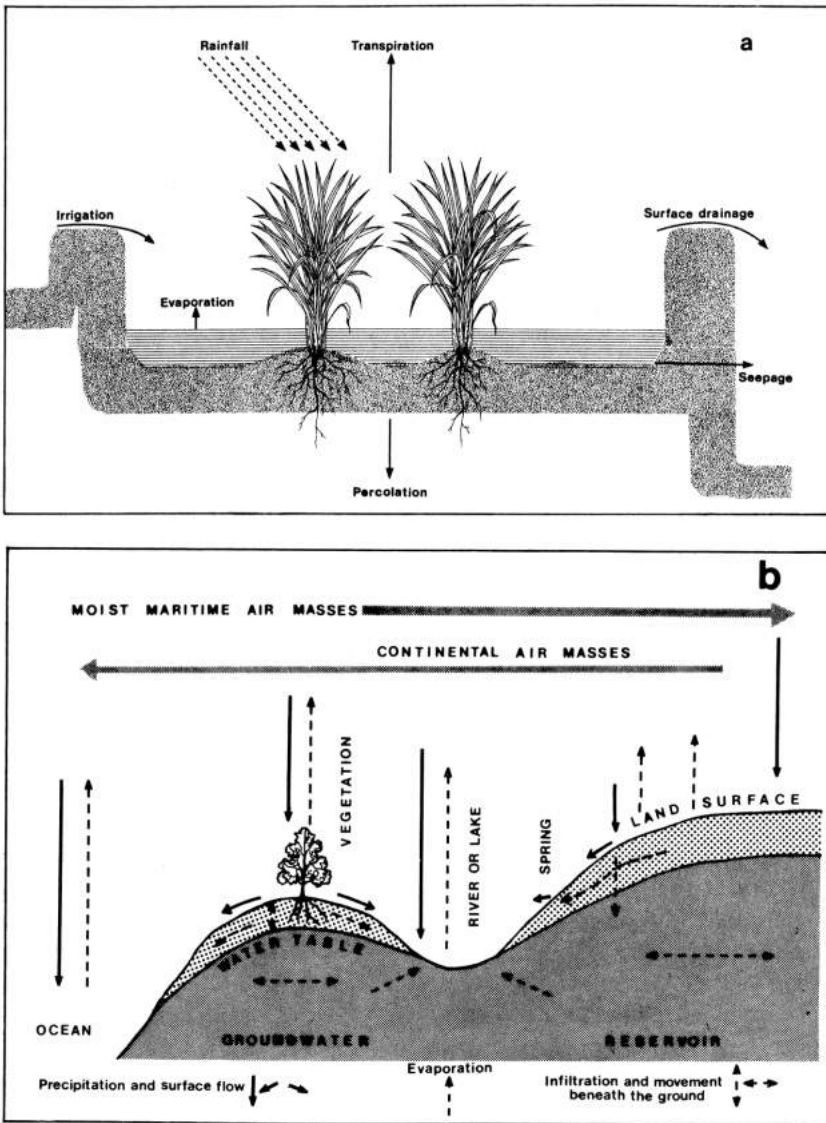
In its simplest form the water balance states that, in a given volume of soil, the difference between income (W_{in}) and outgo (W_{out}) during a certain period is equal to the changes in storage (ΔW) of the soil during the same period:

$$\text{Income} - \text{outgo} = \Delta \text{ storage}$$

or

$$W_{in} - W_{out} = \Delta W \quad (2.33)$$

where ΔW can be changes in soil moisture in upland fields or changes in water depth in irrigated lowland fields.



2.20a. The water balance of a root zone for lowland rice. b. Some major relationships between the hydrologic cycle, waters on the land, and the air-mass cycle (from *An Introduction to Climate* by G. T. Trewartha 1968. Copyright © 1968 by McGraw-Hill, Inc. Used with the permission of McGraw-Hill Book Company).

Under most conditions,

$$W_{in} = P + I, \quad (2.34)$$

where P is rainfall and I , irrigation. On sloping topography, surface runoff or

overland flow from fields at a higher level can also be taken as a component of W_{in} .

At the same time, water may be withdrawn from the soil (W_{out}) by evapotranspiration (E), percolation and seepage (P & S), and runoff or overland flow.

Under the simplest situation and disregarding runoff or overland flow, the water balance can be formulated as:

$$\Delta W = P + I - E - P \text{ \& } S. \quad (2.35)$$

This equation states the law of mass conservation with respect to water.

To compute ΔW , however, the rooting depth of a crop and the soil moisture characteristics in the field must be known. Unfortunately, very little is known of the rooting depth of rice in the field. To estimate water requirements or the irrigation interval, however, knowledge of the water storage capacity of the soil is not necessary. If the initial moisture conditions of the soil are specified, the water requirement or irrigation need can be obtained from:

$$\Delta W = O$$

or

$$P + I = E + P \text{ \& } S. \quad (2.36)$$

The initial condition could be the water depth set up for irrigated lowland rice, or the field moisture capacity for upland crops. In equation 2.36, ($P + I$) is the amount of water required to maintain the initial condition. E can be estimated by various methods as discussed in the preceding sections and (P & S) can be measured directly or its estimated value can be obtained for representative soils. For example, the average percolation and seepage rates for paddy soils in the Philippines are estimated at 2 mm/day for the wet season and 4 mm/day for the dry (Wickam and Singh 1978). Thus, the total monthly water requirements of a rice crop in the Philippines average about 180 mm for the wet season and about 270 mm for the dry (Table 2.15). These estimates agree with experimental results on irrigation needs. Monthly water requirements for rice are about 200 mm. The average total requirement for 1 rice crop is about 1,200 mm, assuming that the crop duration is 5 months and that land preparation requires 200 mm water.

Under rainfed conditions and disregarding (P & S), the equation 2.35 can be reduced to:

$$\Delta W = P - E \quad (2.37)$$

The equation 2.37 may be regarded as a *climatic water balance*; it gives a rough estimate of water shortages or excesses (Fig. 2.21). Wet season is the time when rainfall exceeds evapotranspiration. At Los Baños, Philippines, January to April is the dry season and June to December is the wet season. May is a transition period. The wet season thus defined agrees well with the crop period for the rainy-season rice crop.

Water deficit or drought occurs at unpredictable times. From 1967 to 1971, a monthly water deficit occurred three times during the wet season — July 1967,

2.21. Monthly balance of precipitation minus evapotranspiration at Los Baños, 1967–1971 (Yoshida 1978).

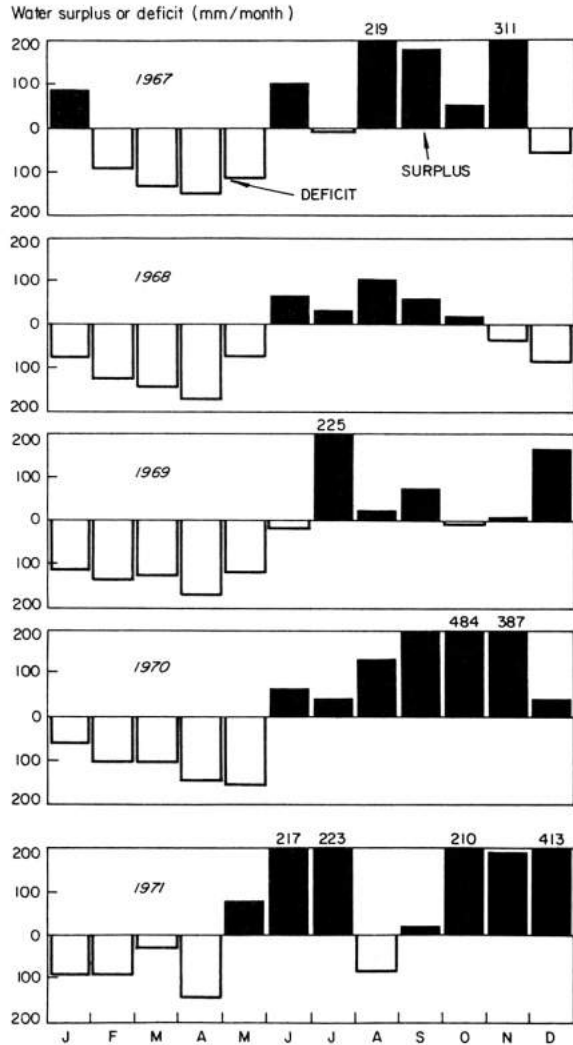


Table 2.15. Average water requirement of a paddy field in the Philippines.^a

	Wet season	Dry season
Daily solar radiation ^b (cal/cm ²)	367	463
Daily evapotranspiration (mm)	4	5
Seepage and percolation (mm/day)	2	4
Daily total (mm)	6	9
Monthly total (mm)	180	270

^aYoshida(1979). ^bAverage values for wet season (July–November) and dry season (January–May).

October 1969, and August 1971. Thus, the rainfed rice, even in monsoon Asia, is exposed to frequent water shortages — the major reason for unstable rice production in the rainfed rice regions.

2.5.13. Effect of water deficit on growth and yield

Water stress at any growth stage may reduce yield. The most common symptoms of water deficit are leaf-rolling, leaf-scorching, impaired tillering, stunting, delayed flowering, spikelet sterility, and incomplete grain filling.

The rice plant is most sensitive to water deficit from the reduction division stage to heading. Three days of drought at 11 days and at 3 days before heading reduces yield significantly by causing a high percentage of sterility (Table 2.16). Once sterility occurs, there is no way for the plant to compensate. On the other hand, water deficits during the vegetative stage may reduce plant height, tiller number, and leaf area, but yield will not be affected by the retarded growth if water is supplied in sufficient time to permit the plant's recovery before flowering.

2.5.14. Effect of water excess on growth and yield

Depending on topography and rainfall patterns, low-lying areas may be subjected to different water depths and to different durations of high water. These areas may be tentatively divided into the following categories (Vergara et al 1976):

a. Deep-water areas. The water is between 150 cm and 400 cm deep and usually remains in the field for 3-4 months. Special varieties known as *floating rice* are planted in these areas. Large areas of floating rice are found in Bangladesh, northeast India, and Thailand.

b. Flood areas. Flood areas include the margins of deep-water areas, low-lying areas, and tidal swamps. The water is less than 150 cm deep and usually remains in the field for several months. Tall indica varieties, known as *flood rice*, are commonly used.

Table 2.16. Effects of drought on yield and yield components of rice^a

Drought treatment (days from heading)	Yield (g/hill)	Panicles (no./hill)	Sterility (%)	Filled spikelets (%)	1000-grain wt (g)
-55	18.0	11	11	70	21.8
-51	16.8	11	9	66	22.0
-43	19.5	11	14	65	21.5
-35	20.0	12	11	60	20.5
-27	17.0	11	12	54	20.2
-19	15.7	11	34	52	20.8
-11	6.5	10	62	29	21.6
- 3	8.3	10	59	38	20.9
+ 5	16.5	11	10	59	21.9
+13	20.5	10	7	66	22.5
No stress	22.7	10	15	65	21.9

^aMatshushima (1962).

Table 2.17. Yield of variety Jaya under 3 levels of submergence (25, 50, 75% of crop ht) at each of the 3 growth phases during aman (Jul–Nov) and boro (Jan–Apr). 1973–74.^a

Plant growth stage	Ht of plant submerged (%)	Relative grain yield (%)	
		1973 (aman)	1974 (boro)
Control (continuous submergence 5 ± 2 cm)		100	100
Seedling establishment to maximum tillering	25	82	75
	50	75	62
	75	68	58
Maximum tillering to flowering	25	81	74
	50	71	64
	75	72	56
Flowering to maturity	25	79	71
	50	76	66
	75	70	50

^a Adapted from Pande (1976).

c. Submerged areas. The water level and duration are variable but the plants are usually completely submerged. In some areas submergence occurs almost every year. In many lowland rice fields submergence occurs only during typhoons or unusually heavy, continuous rains.

Attention is currently focused on improving rice varieties adapted to flood areas by incorporating the elongation genes of floating rice into improved semi-dwarf high-yielding varieties. These new varieties, called *deepwater rices*, can remain short when the water is shallow and grow tall in response to increased water depths (Jackson et al 1972).

A large portion of the rainfed lowland rice area falls into the category of submerged areas, where partial submergence is the common problem. When a rice crop is submerged to different degrees at different growth stages, the grain yield decreases in different proportions. For example, with 25% plant height submergence at tillering, yield decreases by 18% in aman and 25% in boro; with 75% submergence at ripening, yield decreases by 30% in aman and 50% in boro (Table 2.17). The yield-decreasing effects of partial submergence could be attributed to impaired tillering and decreased area of photosynthetic leaf surface. To overcome the adverse effects of partial submergence on grain yield, varieties with intermediate plant height (about 110–130 cm, taller than semidwarfs and shorter than traditional tall varieties) are replacing semidwarf varieties in shallow water areas that are subject to occasional floods.

2.6. ANNUAL PRODUCTIVITY IN TEMPERATE REGIONS AND THE TROPICS

In temperate regions, one or two rice crops can be grown annually. In the tropics, three to four crops a year are possible, provided irrigation is available. Thus, rice

Table 2.18. Annual productivity of rice in temperate regions and in the tropics.^a

Location	Crop Season	Yield (t/ha)
Hokkaido, Japan (43°N)	May-October	6.5
Kagawa, Japan (34°N)	March-July	5.5
	July-October	5.4
		10.9
Okinawa, Japan (27°N)	January-June	6.2
	June-August	4.9
	September-November	4.2
		15.3
Los Baños, Philippines (14°N)	January-May	8.5
	May-July	4.9
	July-October	5.9
	October-December	4.4
		23.7

^a Yoshida (1977a).

yield can be compared in two ways: on a per-crop basis and on an annual-production basis.

The maximum recorded yield per crop in Japan was 10.5 t brown rice/ha, which is equivalent to 13.2 t rough rice/ha (Agricultural Policy Study Commission 1971). In the tropics, rice variety IR24 yielded 11.0 t/ha in the dry season in Los Baños, Philippines (IRRI 1973), and IR8 produced 10.7 t/ha at Battambang, Cambodia (Hirano et al 1968). The highest recorded rice yield in India is 17.8 t/ha in Maharashtra State (Suetsugu 1975). Thus, on a yield-per-crop basis, tropical areas are no less productive than the temperate regions. In terms of annual rice production, the tropics has a distinctly greater potential than the temperate regions.

In Hokkaido, Japan, where only 1 crop a year is grown, about 6.5 t/ha was obtained in a normal year (Table 2.18). In this region, low temperature is often a major cause of crop failure; hence, rice yield is unstable depending on weather conditions.

In southern Japan, 2 crops yielded a total of about 11 t/ha in 1 year. In Okinawa, the southernmost part of Japan, a field experiment recorded 15.3 t/ha from 3 crops. And, in the Philippines, about 24 t/ha were recorded for 4 crops a year.

These data clearly indicate that the potential annual rice productivity is much higher in the tropics than in the temperate regions. In practice, however, continuous rice cropping may not be advisable because of severe disease and insect problems. However, the tropical environment for rice cultivation at any time of the year provides great flexibility in planning rice production.

3

MINERAL NUTRITION OF RICE

3.1. SOIL SUBMERGENCE AND RICE NUTRITION

An ample water supply is probably the greatest advantage of soil submergence for irrigated rice. Unstable production of rainfed lowland and upland rice crops is largely attributed to water shortages.

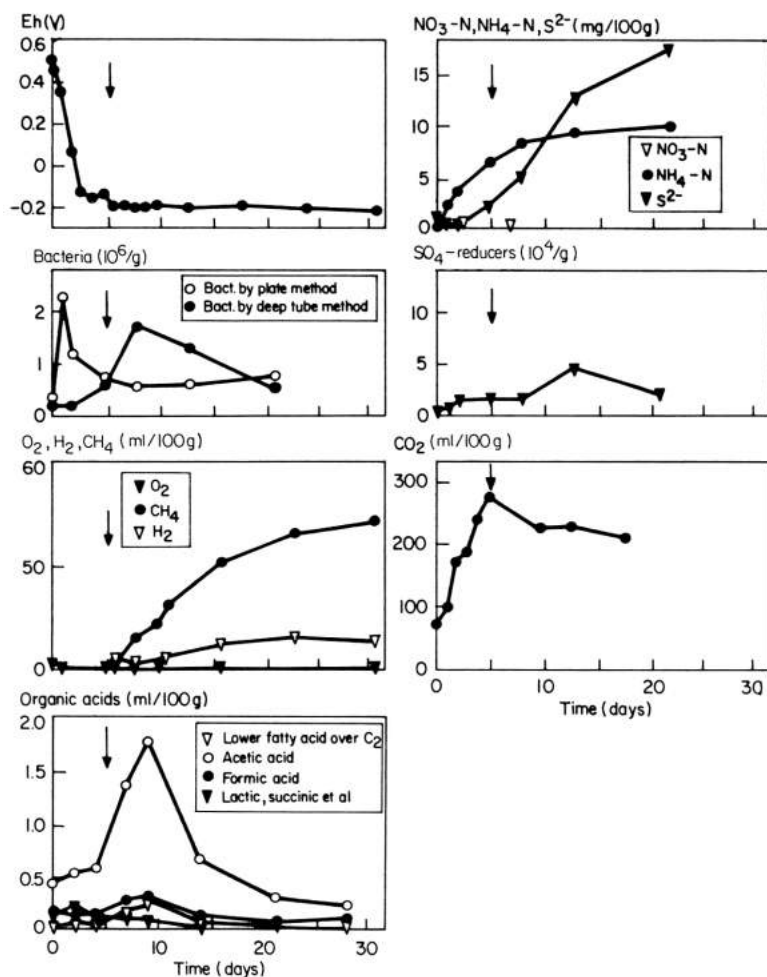
Submergence creates a unique environment for rice's growth and nutrition. The root environment during submergence is characterized by a lack of oxygen and subsequent series of reductive changes; the exchange of gases between soil and air is markedly curtailed.

Within a few hours after submergence, microorganisms use up the oxygen present in the water or trapped in the soil (Fig. 3.1). After the disappearance of the molecular oxygen, carbon dioxide and organic acid levels increase sharply. The amounts of methane and molecular hydrogen increase gradually because of the anaerobic microbial activity.

To avoid suffocation of root tissues in submerged soils, the rice plant has developed special tissues through which air is transported from shoot to root. This subject will be discussed in the succeeding section.

In submerged soils, ammonia is the major form of nitrogen available for rice. Although relatively low concentrations of ammonia are toxic to many upland crops, rice tolerates and uses ammonia efficiently at relatively high concentrations.

An increase in the availability of phosphate is an obvious benefit of soil submergence. Thus, the application of phosphate is less vital to lowland rice than to upland rice and other upland crops. Phosphate applications, however, are



3.1. Course of microbial metabolism in waterlogged paddy soil during incubation in syringe at 35°C. Before an arrow: facultative anaerobic metabolism; after an arrow: strictly anaerobic metabolism (Takai and Kamura 1966).

important when soils have a high capacity to fix phosphate, when temperature is unfavorably low for rice growth, and where little or no phosphate fertilizer has been applied in the past.

Concentrations of phosphorus, potassium, iron, manganese, and silicon increase in the soil solution after soil submergence. The concentration of zinc, however, decreases. The increase in ferrous iron concentration is often excessive, inducing iron toxicity in rice.

Under upland conditions, weeds, particularly those having the C-4 pathway, grow vigorously and compete with rice for light and nutrients. Submergence curtails weed growth (Tanaka, I. 1976).

Table 3.1. Direct and indirect evidences for transport of molecular oxygen from shoot to root in plants.^a

Measurement or observation	Plant species
Deposit of brown ferric iron compounds on root surface	Rice (<i>Oryza sativa</i> L.) <i>Salicornia herbacea</i> L. <i>Arachis hypogaea</i>
Oxidation of pigments	General
thionin	Rice
leucomethylene blue	Rice
a-napththylamine	Rice
Esculin	Rice
Bacterial luminescence on root surface in dark	Rice
Chemiluminescence	Pumpkin (<i>Cucurbita</i> spp.)
Oxygen concentrations in root tissues as affected by removal of shoot, root cortex and by oxygen tension in root medium	Rice
Polarographic measurement of oxygen diffused from roots	Rice Barley (<i>Hordeum vulgare</i> L.) Bog plants and rice 12 nonaquatic species
Transport of isotopic oxygen from shoot to root	Rice and barley Broad bean (<i>Vicia faba</i> L.) Rice, corn (<i>Zea mays</i> L.), barley

^a Yoshida and Tadano (1978).

3.2. ADAPTATION TO SUBMERGED SOILS

3.2.1. Oxygen transport

The most direct evidence for oxygen transport from shoot to root has been obtained through the use of isotope oxygen (^{15}O and ^{18}O). When isotope oxygen is fed to the shoot, the same oxygen can be recovered from the root. There is much other direct and indirect evidence for the transport of molecular oxygen in rice and other plant species (Table 3.1).

Microscopic examinations of the rice plant have established the presence of well-developed air spaces in leaf blade, leaf sheath, culm, and roots. These air spaces constitute an efficient air-passage system in rice. The system of transporting oxygen from shoot to root in rice is about 10 times more efficient than that in barley and 4 times more efficient than that in corn (Jensen et al 1967).

The rice plant develops air spaces in the culm even in upland conditions. The rice plant grown in submerged soils, however, develops more and larger air spaces (Table 3.2). Thus, the presence of air spaces in rice is controlled by both genetics and environment. The air spaces may be considered as many small pipes each with one end connected to the leaf sheaths and the other to the roots.

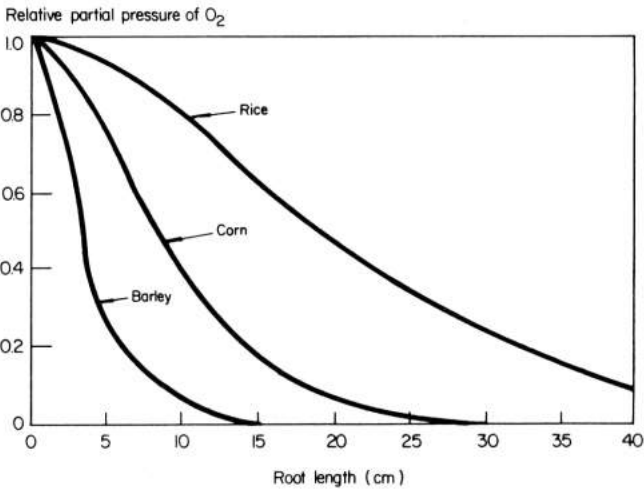
Table 3.2. Development of air space in the culm of variety IR36 grown under upland and lowland conditions.^a

	Number			Mean diameter (mm)		
	3rd ^b	4th	5th	3rd	4th	5th
Upland	0	4	21	—	0.09	0.10
Lowland	5	26	28	0.15	0.22	0.23

^a IRR I (1979). ^b Internode position from the top.

Air enters the rice plant through the leaf blade and leaf sheath stomates and moves downward to the nodes at the plant base. Oxygen is supplied to tissues along the air path and moves further downward into the roots where it is used for respiration. Finally, the air diffuses outward from the plant roots into the surrounding soil.

When oxygen moves downward from shoot to root and from the basal part of the root to the root tip, a certain amount of oxygen may leak out laterally or may be consumed by tissues along the pathway. Thus, partial oxygen pressure in the root tissue is expected to decrease with an increase in the distance between the root tip and the root base. At about 40 cm from the root base, partial oxygen pressure drops to about one-tenth the partial pressure at the root base (Fig. 3.2). Because oxygen is essential for cell division and enlargement at the root tip, root elongation slows or ceases when the partial oxygen pressure drops considerably. Thus, in an anaerobic environment where root elongation is totally dependent on oxygen from



3.2. Relative partial pressure of oxygen at the root tip as a function of root length (Jensen et al 1967).

the shoots, the longest roots are much shorter than those in an aerobic environment.

A quantitative measurement of oxygen diffused from root surfaces can be made by polarography. Along the root axis, the maximum rate of oxygen diffusion is observed within about 1 cm of the apical region (Armstrong 1964, 1967). Recently, large varietal differences in the amount of oxygen released from the roots have been found. These differences are closely related to differences in the tolerance for straighthead disease, which is attributed to hydrogen sulfide toxicity (Joshi et al 1975).

Generally, oxygen transport from shoot to root is considered a physical diffusion of air through the air-passage system within the tissues. Mitsui (1965), however, proposed an enzymatic excretion of oxygen in rice roots. He suggested that rice roots possess a glycolic acid pathway in which glycolic acid is successively oxidized to carbon dioxide. The energy liberated during this oxidation can not be stored as adenosine triphosphate (ATP) and is transferred to the formation of hydrogen peroxide. The hydrogen peroxide thus produced is decomposed by catalase into molecular oxygen and water. Whether a physical diffusion or an enzymatic excretion operates in the rice plant needs further examination.

3.2.2. Root oxidizing power

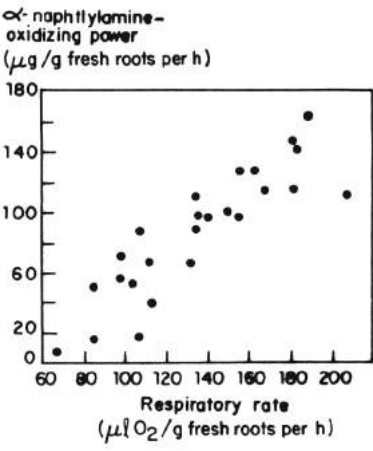
Oxygen diffusion from rice roots constitutes an important part of the roots' oxidizing power. For example, ferrous iron and hydrogen sulfide can be oxidized by molecular oxygen diffused from root surfaces. In addition, rice roots are able to oxidize certain pigments, such as *a*-naphthylamine and *o*-dianisidine. These pigments are only slowly oxidized by molecular oxygen but are easily oxidized by peroxidase in the presence of hydrogen peroxide (Matsunaka 1960; Kawata and Ishihara 1965). Young roots oxidize *a*-naphthylamine better than old roots. Along the root axis, the maximum oxidation is observed about 4–5 cm from the root tip, except in the apical region 0.5 cm from the root tip (Nomoto and Ishikawa 1950).

The oxidation of *a*-naphthylamine is controlled by the amount of hydrogen peroxide rather than by peroxidase activity per se. The *a*-naphthylamine test measures the ability of plant tissues to produce hydrogen peroxide. Old roots may have higher peroxidase activity than young roots but a lower oxidizing power because a smaller amount of hydrogen peroxide is produced. In some bog species, the roots' oxidizing activity is nine times greater than can be accounted for by oxygen diffusion from the roots. Thus, enzymatic oxidation is the principal mechanism for the high oxidizing activity (Armstrong 1967).

The *a*-naphthylamine oxidizing power of rice roots is well correlated with the respiratory rate (Fig. 3.3); therefore, it is used as a quick test to diagnose the metabolic activity of rice roots (Yamada et al 1961).

3.2.3. Reduction of the rhizosphere and development of special roots

The rhizosphere of rice plants becomes reductive from about panicle initiation



3.3. Relationship between respiratory rate and α -naphthylamine-oxidizing power of rice roots (Yamada et al 1961).

through heading (Alberda 1954, Mitsui and Tensho 1953). At this time, rice plants usually develop a fine, highly branched root mat in the soil surface or soil-water interface (Alberda 1954, Fujii 1974, Kawata et al 1963). Since oxygen, either carried by flowing water or generated by the photosynthesis of blue-green algae, is abundant in these regions, it is postulated that the root mat serves as *respiration roots* (Alberda 1954). As such, they absorb oxygen from the water and send it to other root systems located in the anaerobic soil horizons. This role of the root mat, however, has not yet been critically examined.

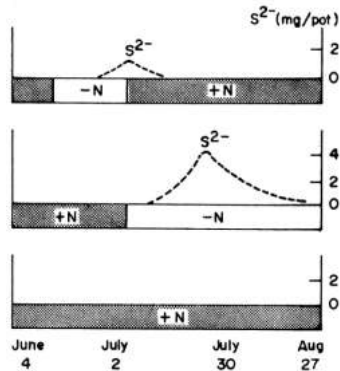
The formation of a root mat is closely related to water percolation and redox potential. No root mat is formed when flooding and drainage are alternated every 2 days and the redox potential is kept high (Table 3.3). Plants grown in solution

Table 3.3. Effect of water environments on percentage of root mat formation originated from each root unit. ^a

Treatment	Root unit ^b (%)			Eh ₇ of soil (mV)	
	9th	10th	11th	3 cm deep	10 cm deep
Flooded (no percolation)	16.7	14.3	4.5	-135	-155
Percolated (2.5 cm/day)	4.7	8.2	9.0	-118	-128
Midsummer drainage	4.4	3.0	4.5	-183	-123
Alternate flooding and drainage	0	0	0	+115	+120

^a Soezima and Kawata (1969). ^b Includes roots from the lower region of the *n*th node and those from the upper region of (*n* - 1)th node. Figures indicate percentages of root number originated from each root unit in relation to the total root number.

3.4. Relation between time of nitrogen application and production of S^{2-} in media (Okajima 1958).



culture with ammonium nitrogen produce a root mat but those grown with nitrate nitrogen do not (Soezima and Kawata 1969).

The reduction of the rice rhizosphere is not necessarily related to particular growth stages but is largely dependent on nitrogen nutrition (Fig. 3.4). Appreciable amounts of hydrogen sulfide can be found in the culture solution when a rice plant becomes nitrogen deficient. No hydrogen sulfide is found when the plant receives ample nitrogen regardless of the growth stage. In the field, however, rice absorbs large quantities of nitrogen, depletes available soil nitrogen, and grows vigorously at around panicle initiation. As a consequence, rice tends to be lower in nitrogen content afterwards. Therefore, the beginning of rice rhizosphere reduction tends to coincide with panicle initiation to heading.

3.2.4. Anaerobic respiration

The existence of an oxygen transport system from shoot to root in rice and other bog plants suggests that these plants avoid suffocation of root tissues in anaerobic root environments. While there is some evidence of anaerobic respiration in rice (John et al 1974, John and Greenway 1976), it appears to be of minor importance.

The cells of excised rice roots are highly sensitive to oxygen deficiency. When excised rice roots are exposed to a nitrogen atmosphere for 4–5 hours, destructive changes take place in the tissue's cellular organelles (Vartapetian 1973). The respiratory rate of excised roots declines very rapidly in a nitrogen atmosphere, while intact roots maintain a respiratory rate as high as in an aerobic atmosphere. The respiratory rate of excised roots in an aerobic atmosphere is as high as that of intact roots (Arikado 1959). Apparently, rice roots have only a slight tolerance for oxygen deficiency but avoid suffocation when they are connected to shoots.

3.2.5. Iron-excluding power

In submerged soils, ferric iron is reduced to the ferrous form. As a consequence, the level of ferrous iron in the soil solution may increase to 300 ppm or higher. Although rice benefits from increases in ferrous iron, it is often injured by

excessive levels in the soil solution. A physiological disorder attributable to iron toxicity occurs in acid sandy, acid sulfate, and acid organic soils.

Rice roots have three functions to counteract iron toxicity (Tadano 1976, Tadano and Yoshida 1978):

- (a) Oxidation of iron in the rhizosphere, which keeps iron concentrations low in the growth media.
- (b) Exclusion of iron at the root surface, which prevents the iron from entering the root.
- (c) Retention of iron in the root tissue, which decreases the translocation of iron from root to shoot.

When the concentration of iron in the culture solution is low, its absorption by the rice plant is not directly related to water absorption. However, when the concentration is high, the iron content in the shoot is increased proportionately with increases in water absorption, and the total amount of iron absorbed also increases. That indicates that iron absorption by mass flow is an important mechanism when the concentration is high in the rooting media.

Respiratory inhibitors that normally retard the absorption of nutrients such as ammonia and phosphate, also retard iron absorption from a culture solution containing low concentrations of iron. However, at high iron concentrations, respiratory inhibitors, such as KCN, NaN_3 , and DNP, decrease the rate of respiration but increase iron absorption (Table 3.4). The iron-excluding power shown in Table 3.4 is calculated as:

$$\text{Iron-excluding power} = \frac{a-b}{a} \times 100 (\%), \quad (3.1)$$

where a is the amount of iron, in milligrams, contained in the same volume of culture solution as that of water absorbed by the plant, and b is the amount of iron, in milligrams, actually absorbed by the plant.

The iron-excluding power of a healthy rice plant is 87%, meaning that 87% of the iron that has reached the root surface, along with the water absorbed by the plant, is not *absorbed* or *excluded*. A pretreatment of rice roots with respiratory inhibitors decreases the iron-excluding power. Thus, the iron-excluding power of rice roots appears to be associated with the roots' metabolic activity. That suggests that iron toxicity in rice can be caused by high levels of ferrous iron in soil solution and also by the decreased metabolic activity of roots.

3.3. NUTRIENT AVAILABILITY IN SOIL

3.3.1. Transport of soil nutrients to plant roots

Two major theories have been proposed to explain how soil nutrients can be made available to plant roots: contact exchange and soil solution.

The contact exchange theory proposed by Jenny and Overstreet (1938) postulates that a close contact between root surfaces and soil colloids allows a direct

Table 3.4. Effect of respiratory inhibitors on the iron-excluding power of rice roots and translocation percentage of iron.^a

Inhibitor	Concn of inhibitor (M)	Respiratory rate ($\mu\text{l O}_2/100\text{mg dry roots per hour}$)	Water absorption (ml/plant)	Iron absorption (mg/plant)	Iron-excluding power ^b (%)	Trans-location percentage of iron ^c
None	—	39.3	49	1.93	87	19.1
KCN	10^{-4}	26.6	36	3.34	69	21.3
	10^{-3}	2.6	30	5.73	36	34.6
NaN_3	10^{-4}	5.2	24	4.51	37	44.3
	10^{-3}	1.1	23	5.23	24	44.7
DNP	10^{-5}	35.5	51	5.45	64	16.5
	10^{-4}	2.8	27	5.69	30	23.4

^a Tadano (1976). ^b Iron-excluding power (%) = $(a - b)/a \times 100$: where a is the amount of iron in milligrams contained in the same volume of culture solution as that of water absorbed by the plant and b is the amount of iron in milligrams absorbed by the plant.

^c Translocation percentage of iron = the amount of iron translocated to the shoot relative to the total amount of iron absorbed by the plant.

exchange of H^+ released from plant roots with cations from soil colloids. This process may occur to some extent but the degree of its importance in nutrient transport is questioned (Mengel and Kirkby 1978).

The soil solution theory, now widely accepted, proposes that soil nutrients are dissolved into solution and transported to root surfaces by both mass-flow and diffusion. Mass-flow occurs when there is a gradient in the hydraulic potential, the sum of gravitational and pressure potential, and nutrients move along with water flow from higher to lower hydraulic potential. The amount of nutrients reaching the root is thus dependent on the rate of water flow or the plant's water consumption and the average nutrient concentration of the water.

Diffusion occurs when there is a gradient in the ion concentration between the root surface and the surrounding soil solution. The ions move from the concentrated to the diluted region. The rate of diffusion is governed by Fick's first law, which states that the rate of diffusion is proportional to the gradient in concentration between the two regions:

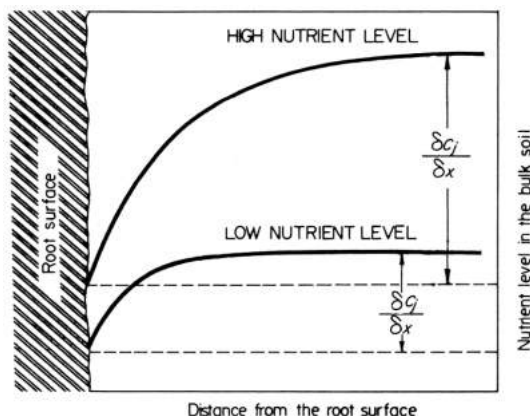
$$J_j = -D \frac{\partial C_j}{\partial x} \quad (3.2)$$

where J_j = diffusive flux or flow of species j (mol/cm^2 per s),

D = diffusion coefficient of species j (cm^2/s), and

$\frac{\partial C}{\partial x}$ = gradient in concentration of species j in the x -direction (mol/cm^4).

If two soils of different nutrient levels are considered, the soil with the higher level has the steeper concentration gradient and, therefore, the diffusion rate to the



3.5. Nutrient-depletion pattern at the immediate vicinity of the root for a soil with a high nutrient level and one with a low nutrient level in the bulk soil (Mengle and Kirkby 1978).

root surface is greater (Fig. 3.5). The higher nutrient level in the soil solution also gives a higher concentration at the root surface, causing a more rapid uptake rate. The larger gradient allows this uptake rate to be maintained.

The relative importance of mass-flow and diffusion in nutrient transport in the soil (Barber 1962) can be illustrated by the following computation. The computation assumes that the phosphorus concentration in the soil solution is 0.5 ppm and the transpiration ratio is 300 g/g. The critical phosphorus concentration in rice tissue is 2,000 ppm (0.2%). The transpiration ratio is the number of grams of water transpired per gram of dry matter produced. Thus, the amount of phosphorus that is available to the root surface from the soil solution is:

$$0.5 \times \frac{300}{1,000} = 0.15 \text{ mg P / 300 g H}_2\text{O} . \quad (3.3)$$

If this amount of phosphorus is absorbed by 1 g of dry rice tissue, the phosphorus concentration in the tissue will be:

$$\begin{aligned} 0.15 \text{ mg P} \times 1,000 &= 150 \text{ mg P / 1,000 g dry weight} \\ &= 150 \text{ ppm P} . \end{aligned} \quad (3.4)$$

Thus, mass-flow can only account for less than one-tenth (150 ppm/2,000 ppm) of the phosphorus content necessary for normal growth. It follows that diffusion is the dominant process for transport of phosphorus in soil solution.

A similar calculation can be made for potassium. Assume that the potassium concentration in the soil solution is 80 ppm K, and the critical potassium concentration in rice tissue is 1.5%. Then, the potassium concentration in rice tissue that can be accounted for by mass-flow will be:

$$\begin{aligned} 80 \times \frac{300}{1000} \times 1,000 &= 24,000 \text{ ppm K} \\ &= 2.4\% \text{ K} . \end{aligned} \quad (3.5)$$

Table 3.5. Composition of soil solution.^a

Growth stage	Concn (ppm)				
	NH ₄ -N	P ₂ O ₅	K ₂ O	CaO	SO ₃
Tillering	54	1.4	100	370	672
Panicle initiation	8.0	1.1	62	375	412
Heading	0.2	trace	19	295	384

^aData were taken from No. 5 plots on 11 Jun, 14 Jul, and 15 Aug in Table 2 (Tanaka 1961b).

Thus, mass-flow alone can account for the amount of potassium needed for normal growth.

The relative importance of mass-flow and diffusion in the transport of a nutrient from the soil solution to root surfaces depends on concentrations of that nutrient in both soil solution and plant tissue. A generalized relationship between the ion concentration in the soil solution and the concentration within plant tissues is discussed elsewhere (Barber 1962).

3.3.2. Nutrient concentrations in the soil solution and culture solution

To see how rice grows in soil solution, a solution culture pot was connected to a soil culture pot so that the leachate in the latter flowed through a drainage hole to the former (Tanaka 1961b). The solution was cycled twice a day. Rice growth in the soil culture was normal but that in the culture solution was poor and the plants appeared to be phosphorus deficient. The chemical composition of the leachate at three growth stages is shown in Table 3.5, and can be compared with the chemical

Table 3.6. Composition of culture solution.^a

Element	Concn of element in solution (ppm)
N	40
P	10
K	40
Ca	40
Mg	40
Mn	0.5
Mo	0.05
B	0.2
Zn	0.01
Cu	0.01
Fe	2

^aYoshida et al (1976).

composition of the culture solution commonly used for rice (Table 3.6). The comparison indicates that the leachate had adequate concentrations of all nutrients except phosphorus. Analysis at maturity supported the observation that phosphorus was extremely deficient in the plants grown in the leachate (Table 3.7).

A later experiment, however, demonstrated that rice can grow normally even at 0.1 ppm P in the culture solution provided a much larger pot is used (Tanaka 1962). This experiment indicated that rice can absorb phosphorus from a solution with 0.1 ppm P and, hence, the concentration in the leachate can not be considered limiting to rice growth; the total supply of phosphorus plays an important role.

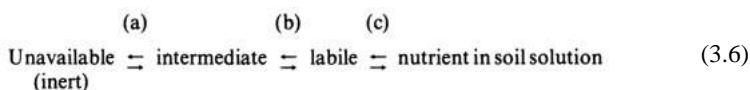
The above two experiments lead to the following points:

- The soil can replenish phosphorus in the soil solution as plants absorb it. This process increases the total supply of phosphorus even though the concentration itself is low.
- In a well-mixed solution culture, the total supply of phosphorus is determined by pot size, the phosphorus concentration in culture solution, and the renewal frequency of the culture solution. To meet the plant's phosphorus requirement, the pot size must be large at low concentrations of phosphorus, or, if it is small, the phosphorus concentration must be high. If, however, the pot size is small and the concentration is low, the renewal frequency of the culture solution must be increased.

3.3.3. Dynamics of nutrient availability

The important point in the above discussion is the maintenance of an adequate concentration gradient between root surfaces and the soil solution. It follows that the ability of the soil to maintain an adequate concentration in the soil solution is critically important.

For most nutrients, an idealized reaction sequence can be formulated in terms of transfer rates between forms (Bache 1977):



The equilibrium (a) between the unavailable and intermediate forms is established slowly, perhaps over many decades. The intermediate forms are the long-term reserves that can be replenished slowly from inert forms or, more rapidly, by fertilizer reactions with soil minerals. Some examples of intermediate forms are potassium ions in clay interlayers and phosphate ions in dicalcium phosphate crystals. The equilibrium (b) between intermediate and labile forms is established over a shorter time period, perhaps a few months to a year. Labile nutrient (loosely held) is a fraction of a soil nutrient that comes to equilibrium with the solution rapidly, within hours in laboratory experiments and perhaps longer in the field. The amount of the labile pool is usually measured using a radioactive isotope such as ^{32}P . If the soil contains a sufficient labile pool of a nutrient, it is able to maintain an adequate concentration by releasing the nutrient into the soil solution

Table 3.7. Growth and composition of the rice plant grown in soil and in soil leachate.^a

	Dry wt (g/pot)			Nutrient content in leaves (%)				
	Panicles	Leaves	Roots	N	P ₂ O ₅	K ₂ O	CaO	SiO ₂
Soil-grown	105	75	13	0.74	0.19	4.5	0.90	5.7
Solution-grown	20	23	7	0.61	0.05	3.4	0.62	4.0

^a Data were taken from No. 5 plots in Table 5 (Tanaka 1961b).

in response to the plant's absorption. In general, the labile pool represents the major component of the quantity factor while the nutrient concentration of the soil solution is the intensity factor. Nutrient absorption by plant roots is directly dependent on the concentration of the soil solution (intensity factor), which in turn is regulated by the labile pool (quantity factor). Introduction of the quantity-intensity concept into the dynamics of nutrient availability has proved useful in understanding the relationship between nutrient uptake and soil nutrients. Further details on the dynamics of nutrient availability are discussed elsewhere (Bache 1977, Mengel and Kirkby 1978).

3.4. NUTRIENT ABSORPTION

3.4.1. Active ion absorption

In their pioneering work on ion absorption by the fresh water algae *Nitella clavata* and the roots of young barley seedlings, Hoagland and his associates demonstrated that plant cells can absorb ions from a low-concentration solution (external) into a high-concentration solution (cell sap) (Hoagland 1944, Epstein 1972). Such uphill ion transfer does not occur spontaneously; the cells must expend energy to make the ions move against the concentration gradient. The necessary energy must be supplied by respiration within the tissues. The term *active absorption* or *active transport* is used to refer to such energy-requiring ion movement.

If active ion absorption requires energy supplied by respiration, any factors that affect the supply of the substrate necessary for respiration and the rate of respiration would affect the rate of ion absorption. Evidence is cited below in support of active ion absorption (Epstein 1972).

a. Accumulation ratio. The concentration of an ion may become far greater in the cells than in the external solution. This is often called *accumulation*. The ratio of the ion concentration within the cells to that of the external solution — accumulation ratio — is about 1,000 or higher for potassium and chloride. A ratio as high as 10,000 is not uncommon. The accumulation ratio tends to increase as the external concentration decreases.

b. Temperature. The temperature coefficient (Q_{10}) for ion absorption is about 2 or higher, indicating that ion absorption is dependent on metabolic activity.

c. Oxygen. The absorption of many ions is affected by oxygen tension in the

root medium — an indication of respiration dependence. Rice is highly adaptive to anaerobic environments. Although anaerobiosis inhibits ion uptake of adapted rice plants, this inhibited uptake is at least equal to uptake by nonadapted plants with continuous aeration (John et al 1974).

d. Metabolic inhibitors. Various metabolic inhibitors such as fluoride, iodoacetate, cyanide, and DNP decrease ion absorption.

DNP permits respiratory electron flow to proceed but blocks formation of ATP from ADP. Since ATP is probably the direct source of energy for ion absorption, the fact that DNP decreases the rate of ion absorption indicates that energy is required for active ion absorption.

e. Carbohydrate. Barley roots low in sugar content absorb more potassium from a solution to which sugar has been added than from a control solution lacking sugar.

f. Light. Accumulation of chloride, bromide, and nitrate by the green algae *Nitella clavata* depends on light as an energy source.

3.4.2. Energetics of active ion absorption

The amount of energy required for active ion absorption can be estimated by the following formula (Epstein 1972):

$$\Delta G^{\circ} = RT \ln \frac{C_2}{C_1} , \quad (3.7)$$

where ΔG° = free energy change,

C_1 = concentration of an ion in the external solution
(in a strict sense, the concentration
should be replaced by activity),

C_2 = concentration of an ion in the cells,

R = gas constant (1.99 cal/mol per °K), and

T = absolute temperature (°K).

At a temperature of 20°C and an accumulation ratio of 10,000, we get

$$\begin{aligned} \Delta G^{\circ} &= 1.99 \times 293 \times 2.303 \log (10^4) \\ &= 5,371 \text{ cal/mol.} \end{aligned} \quad (3.8)$$

This is comparable to the amount of energy released by 1 mol ATP when it hydrolyzes to inorganic phosphate and ADP, i.e., about 7,000 cal/mol standard-free energy at pH 7.0 and 25°C.

3.4.3. Effects of hydrogen sulfide and temperature on nutrient absorption

a. Hydrogen sulfide. Hydrogen sulfide, one of the common toxic substances produced in highly reductive soils, is a well-known inhibitor of the iron- and copper-carrying redox enzyme.

When rice roots are in contact with hydrogen sulfide in culture solution, leaves wilt depending on the concentration and the duration of contact. If the contact is

Table 3.8. Effect of H₂S concentration and contact period on the wilting of rice seedlings.^a**A) Long contact with H₂S solution.**

Av concn of S (ppm)	Wilted leaves (%) after contact of							
	0 h	24 h	43 h	48 h	66 h	90 h	139 h	288 h ^b
2.7	0	0	17	39	67	72	83	85
1.7	0	0	22	22	61	62	62	64
1.3	0	0	6	6	22	27	21	41
0.7	0	0	0	0	0	5	0	29
0.4	0	0	0	0	11	9	7	42
0.07	0	0	0	0	0	0	0	42
0.00	0	0	0	0	0	0	0	0

B) Short contact with H₂S solution (2.9 ppm S).

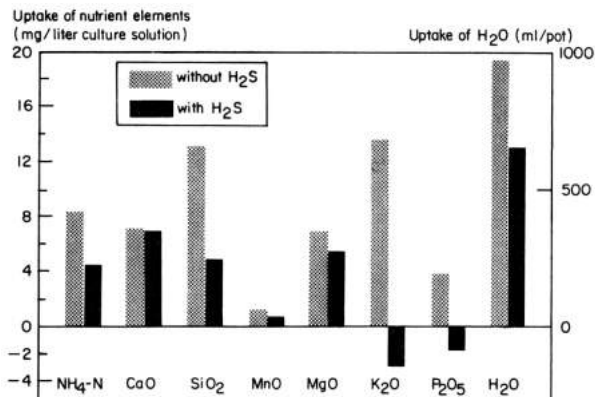
Contact period	Wilted leaves (%) after contact was discontinued for			
	24 h	48 h	96 h	240 h
0.5 h	0	0	0	0
1.0 h	0	0	0	0
2.0 h	0	0	0	10
Contact continued				
240 h	0	0	60	67
Check	0	0	0	0

^a Mitsui (1960). ^b Contact discontinued after 90 h.

sufficiently long, leaves will wilt even at a concentration of 0.07 ppm. As the concentration increases, wilting occurs after a much shorter period of contact (Table 3.8).

Hydrogen sulfide inhibits nutrient uptake with a short period of contact and before the wilting becomes visible (Fig. 3.6). The inhibition is not the same for different nutrients. The percentage decrease in uptake ranges from 3% for CaO to 143% for P₂O₅. Actually, concentrations of K₂O and P₂O₅ in culture solution increase with hydrogen sulfide treatment, which implies that these nutrients have slower uptake rates than water. The inhibition of nutrient absorption by hydrogen sulfide appears to follow the order: P₂O₅ > K₂O > SiO₂ > NH₄ - N ≥ MnO > H₂O > MgO > CaO. Other respiratory inhibitors (sodium cyanide, sodium azide, and butyric acid) also retard nutrient uptake in a manner similar to that of hydrogen sulfide.

Besides inhibiting nutrient uptake, hydrogen sulfide enters the roots, moves into the shoot, and disturbs growth and translocation. Hydrogen sulfide retards translocation of carbohydrates, nitrogen, and phosphorus from the basal part of the culm to the growing organs. The accumulation of those nutrients in the culm may



3.6. Uptake of H₂O and other nutrient elements as influenced by H₂S (Mitsui 1960).

stimulate late tillering and result in disturbed growth patterns (Okajima et al 1958).

b. Temperature. Low temperatures decrease the respiratory rate and retard nutrient uptake. The percentage reduction in nutrient uptake caused by low temperatures is not the same for different nutrients (Table 3.9). The inhibitory effects of low temperatures on nutrient uptake follows the order: P₂O₅ > H₂O > NH₄-N > SO₄ > K₂O > MgO > CaO. Note that this order resembles that for the inhibitory effects of hydrogen sulfide on nutrient uptake.

High temperature also retards the absorption of NH₄-N, P₂O₅, and K₂O by rice (Baba et al 1953).

3.4.4. Selective ion absorption

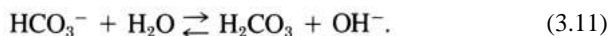
Changes in the solution pH provide information about the plant's relative rate of absorption among different ionic species. When a rice plant absorbs a cation from solution, a hydrogen ion is released from the roots to maintain electrical neutrality in the solution:



As a consequence, the solution pH goes down. When an anion is absorbed from the solution, a bicarbonate ion is released from the roots:



The bicarbonate ion combines with a hydrogen ion to form undissociated carbonic acid, freeing a hydroxyl ion:



Thus, the solution pH rises.

As shown in Table 3.10, the rice plant absorbs NO₃⁻ faster than it does Ca²⁺; as a result, the solution pH increases. The rice plant absorbs NH₄⁺ faster than it does

Table 3.9. Effect of soil temperature on nutrient uptake by the rice plant.^a

Temperature	Nutrient uptake (mg/150 seedlings per 48 h)							
	P ₂ O ₅	SO ₃	Cl	NH ₄ -N	K ₂ O	MgO	CaO	H ₂ O
30°C (A)	39.0	16.5	22.3	19.3	38.1	8.7	4.9	73.8
16°C (B)	21.8	12.0	25.0	13.2	28.4	7.7	5.7	49.1
B/A x 100	56	71	112	68	79	88	116	67

^a Takahashi et al (1955).

SO₄²⁻, and the solution pH decreases sharply.

When NH₄⁺ and NO₃⁻ are available, the rice plant prefers NH₄⁺, and the solution pH decreases. Later, however, the solution pH increases as NO₃⁻ is absorbed.

The relative absorption rate of cations by the rice plant appears to follow the order:

$$\text{NH}_4^+ > \text{K}^{++} > \text{Mg}^{2+} > \text{Ca}^{2+} \quad (3.12)$$

Among anions, it appears to be:

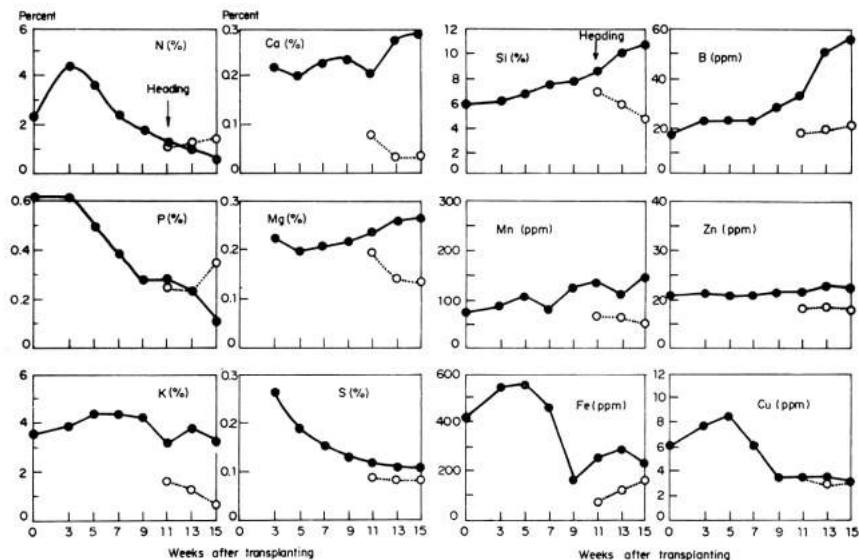
$$\text{NO}_3^- > \text{H}_2\text{PO}_4^- > \text{Cl}^- > \text{SO}_4^{2-}. \quad (3.13)$$

Fertilizers are sometimes classified as *physiologically acid* and *physiologically basic*. Physiologically acid fertilizers refer to those that would make soil acidic as a result of the plant's selective absorption of a fertilizer component. Ammonium sulfate and ammonium chloride are physiologically acid. Calcium nitrate is physiologically basic.

Table 3.10. Changes in solution pH caused by selective absorption of ions by the rice plant.^a

Nutrient	Solution pH		
	Initial	2nd day	5th day
Ca(NO ₃) ₂	5.83	8.55	9.18
CaCl ₂	5.85	5.85	6.40
CaSO ₄	5.89	5.70	5.40
CaH ₄ P ₂ O ₈	4.20	5.21	5.23
NH ₄ NO ₃	5.82	3.05	5.45
NH ₄ Cl	5.83	3.00	2.85
(NH ₄) ₂ SO ₄	5.81	2.85	2.55
NH ₄ H ₂ PO ₄	5.00	3.05	3.00
KCl	5.83	4.60	4.40
MgCl ₂	5.83	5.63	4.90

^a Ishizuka and Tanaka (1969).



3.7. Nutrient contents of a rice crop (variety IR8) at different stages of growth. IRRI, 1968 dry season (Yoshida unpublished).

3.4.5. Nutrient uptake at different growth stages

Changes in the nutrient content of the rice plant at different growth stages in both temperate regions and the tropics have been repeatedly studied. The studies demonstrate that nutrient uptake is affected by climate, soil properties, amount and type of fertilizers applied, variety, and method of cultivation (Ishizuka 1965, 1971, Tanaka et al 1964). Nevertheless, the changes in nutrient content at various stages in the life history of the rice plant are strikingly similar.

The nitrogen, phosphorus, and sulfur contents in the vegetative parts are generally high at early growth stages and decline toward maturity (Fig. 3.7). In contrast, the silicon and boron contents are low at early stages and increase steadily toward maturity.

The contents of nitrogen and phosphorus are generally higher in the panicles than in the straw (leaves plus culm), whereas those of potassium, calcium, magnesium, silicon, manganese, iron, and boron are higher in the straw. Sulfur, zinc, and copper contents are about the same in both straw and panicle.

3.4.6. Nutrient removal

The total nutrient uptake by a crop is affected by the percentages of nutrients in the dry matter and the dry-matter production (kg/ha). The total uptake ranges from 30–40 g/ha per crop for copper to 890–1,018 kg/ha per crop for silicon (Table 3.11). Uptake of silicon is far greater than that of any other nutrient. Since the rice plant absorbs such large quantities of silicon, it is sometimes referred to as a silicicolous plant.

Table 3.11. Nutrient content and total uptake in 2 rice varieties at maturity. IRRI, 1968 dry season.^a

Nutrient	Nutrient content in		Amount of nutrients removed by 1 crop (kg/ha)		Amount of nutrients removed by 1 t rice	
	Straw	Panicle	Total	Panicle	Total	Panicle
<i>IR8</i>						
N	0.60%	1.27%	164	116	18.9 kg	13.3 kg
P	0.09	0.42	46	38	5.17	4.37
K	3.07	0.68	309	62	35.5	7.13
Ca	0.29	0.04	27.3	3.74	3.14	0.43
Mg	0.27	0.14	34.8	13	3.99	1.49
S	0.094	0.078	14.7	7.12	1.69	0.82
Cl	1.06	0.13	97.8	12	11.2	1.38
Si	8.14	2.57	890	235	102	27.0
Fe	470 ppm	111 ppm	4.79	1.01	551 g	116 g
Mn	108	49	1.32	0.45	152	52
B	55	24	0.66	0.22	76	25
Zn	24	18	0.35	0.16	40	18
Cu	3	3	0.04	0.03	6	3
<i>Peta</i>						
N	0.62 %	1.07 %	143	68.5	23.5 kg	11.2 kg
P	0.18	0.20	34.4	12.8	5.65	2.10
K	2.43	0.27	308	17.3	50.6	2.84
Ca	0.23	0.044	29.7	2.82	4.88	0.46
Mg	0.21	0.12	32.2	7.68	5.29	1.26
S	0.10	0.075	16.8	4.80	2.76	0.79
Cl	1.06	0.18	117	11.3	19.2	1.86
Si	8.23	3.04	1018	195	167	32.0
Fe	256 ppm	158 ppm	4.08	1.01	670 g	166 g
Mn	111	41	1.59	0.26	261	43
B	55	24	0.81	0.15	133	25
Zn	22	15	0.36	0.10	59	16
cu	2	2	0.03	0.01	5	2

^a The grain yields of IR8 and Peta were 8.70 and 6.09 t/ha, respectively (Yoshida, unpublished).

IR8, an improved variety, has a higher harvest index than Peta, a tall, traditional variety. This characteristic is reflected in the partitioning of nutrients between panicle and straw. In IR8, the panicles remove 71% nitrogen and 83% phosphorus, whereas in Peta they remove 48% nitrogen and 37% phosphorus. The panicles of IR8 and Peta remove only 20% and 6% potassium.

The nutrients necessary to produce 1 t rough rice in the tropics are about 19–24 kg nitrogen with a mean value of 20.5 kg nitrogen, 4–6 kg phosphorus with a mean value of 5.1 kg phosphorus, and 35–50 kg potassium with a mean value of 44.4 kg potassium (Table 3.12). Similar information is also available for moderate and high yielding crops in Japan (Table 3.12).

Despite a large difference in yield, the removal of nitrogen, phosphorus, and potassium is quite similar between moderate and high yielding crops. A compari-

Table 3.12. Nutrient removal by rice crops in the tropics and Japan.

	Yield (t/ha)	Nutrient removal (kg/t rough rice)		
		N	P	K
Tropics (IRRI)				
IR8 ^a	8.70	18.9	5.2	35.5
Peta ^a	6.09	23.5	5.7	50.6
Av of 3 varieties × 4 crops ^b	4.74	19.0	4.3	47.0
Mean		20.5	5.1	44.4
Japan ^c				
Japan No. 1 contest winner (Mr. Kitahara, 1958)	12.80	15.2	3.4	21.7
Av of 14 agr. exp. sta.	5.34	17.0	3.8	22.2
Mean		16.1	3.6	22.0

^a From Table 3.11. ^bTanaka et al (1964). ^cCalculated from Yamazaki (1966) using a factor of 1.25 to convert brown-rice yield to rough-rice yield.

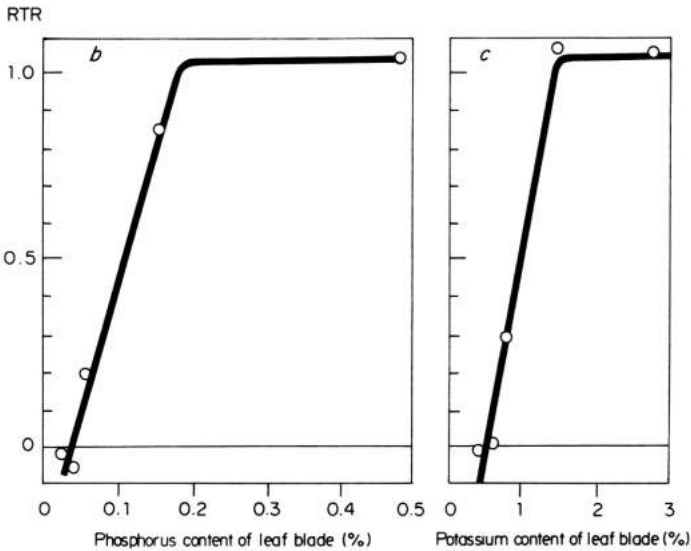
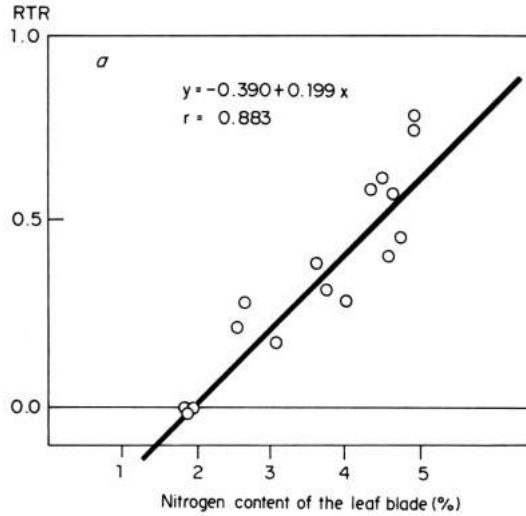
son of the data obtained in the tropics and Japan indicates that lower amounts of nutrients are absorbed in Japan to produce the same yield. The reason for such difference is difficult to explain. One major reason for the difference in nitrogen removal can be seen in the harvest index. A crop with a higher harvest index should require less nitrogen because less nitrogen is retained by the straw. A luxurious absorption of potassium by rice crops grown in the IRRI field may account for the difference in potassium. Dividing 1 t rough rice by the nutrient removal values gives the efficiencies of absorbed nutrients, i.e., kilogram rough rice per kilogram nutrient absorbed. The nitrogen-removal value for the tropics is about 20 kg and, hence, the efficiency of nitrogen use is about 50 kg rough rice/kgN. Similarly, the efficiency of nitrogen use for Japan is about 62 kg rough rice/kg N. Thus, the efficiency of nitrogen use appears to be 20% higher in Japan than in the tropics.

The foregoing discussion indicates that nutrient removal by a rice crop increases almost proportionately as rice yield increases, and provides an empirical relationship between yield and nutrient requirements.

3.5. MINERAL NUTRITION AND TILLERING

Tillering is a characteristic of the rice plant, particularly that of transplanted rice. Each node of a shoot — main culm and tillers — has a tiller primordium. Whether

3.8a. Relation of relative tillering rate (RTR) with nitrogen content of the leaf blade (Yoshida and Hayakawa 1970). b. Relationship between RTR and phosphorus content of the leaf blade (Yoshida and Hayakawa 1970). c. Relationship between RTR and potassium content of the leaf blade (Yoshida and Hayakawa 1970).



the primordium develops into a tiller depends on such factors as the nutritional status of the plant, the supply of carbohydrate, and the light and temperature conditions. Tillering is highly impaired by nitrogen or phosphorus deficiency. Hence, the nutrient status of the plant should be related to tillering performance.

Because there is always a tiller primordium at each node of a shoot, the increase in tiller number per unit time should be proportional to the total number of tillers present (Yoshida and Hayakawa 1970):

$$\frac{dN}{dt} = rN, \quad (3.14)$$

where N is number of tillers, t is time, and r is a constant. The solution for the equation 3.14 is:

$$r = \frac{\log_e N_2 - \log_e N_1}{t_2 - t_1} = \frac{2.303 (\log_{10} N_2 - \log_{10} N_1)}{t_2 - t_1} \quad (3.15)$$

The constant r is called the *relative tillering rate* (RTR) on the analogy of the relative growth rate. Equation 3.14 can be rewritten as:

$$\text{RTR} = \frac{dN}{dt} \times \frac{1}{N} \quad (3.16)$$

Thus, RTR can be considered the mean tillering rate per tiller and used as a quantitative measure for the relationship between mineral nutrition and tillering. As shown in Figure 3.8a and b, the RTR is closely correlated with nitrogen, phosphorus, and potassium content in the leaf blades. Tillering stops when nitrogen content in the blade becomes 2.0%, phosphorus 0.03%, and potassium 0.5%.

The tillering rate increases linearly with an increasing nitrogen content of up to 5%. With phosphorus, the tillering rate increases up to about 0.2%, above which an increase in phosphorus has no effect on tillering. Similarly, potassium content as high as 1.5% increases the tillering rate.

The critical phosphorus concentration for tillering appears to be affected by temperature. Tiller number per square meter increases with an increasing phosphorus content of up to 0.35% in rice crops grown in Hokkaido, Japan, where low temperatures prevail (Shiga et al 1976). Such a high phosphorus requirement can be a reason why phosphate applications are particularly beneficial in cool years in Hokkaido.

An examination of tillering is one useful way to examine the growth status of a rice crop. When tillering is retarded by a nutrient shortage, growth parameters such as leaf area and dry weight also decrease (Table 3.13). The table also illustrates that any nutrient whose content is below optimum level limits overall growth even though other nutrients are present in sufficient quantities.

3.6 MINERAL NUTRITION AND PHOTOSYNTHESIS

Nutrient content is related to the photosynthetic activity of leaves because essential nutrients are directly or indirectly involved in photosynthesis and respiration. For example, nitrogen is a constituent of proteins which, in turn, are constituents of protoplasm, chloroplasts, and enzymes. Phosphorus as inorganic phosphate, an energy-rich phosphate compound, and a coenzyme, is directly involved in photosynthesis. Potassium is involved in opening and closing the stomata that control carbon dioxide diffusion into green tissues, a first step in photosynthesis (Fujino 1967, Fischer and Hsiao 1968). Potassium is also essential in activating enzymes such as starch synthetase (Nitsos and Evans 1969).

The relative photosynthetic rate of leaf blades is positively correlated with their nutrient content (Fig. 3.9). The critical nutrient contents for a high leaf photo-

Table 3.13. Effects of nutrient supply in culture solution on leaf area, tiller number, dry weight, and nutrient contents in rice.^a

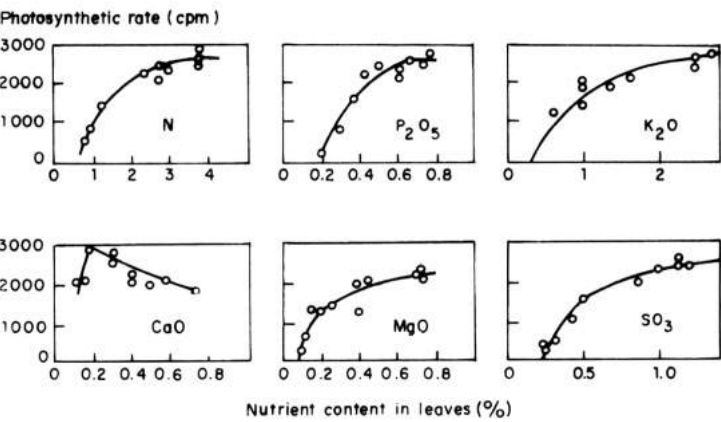
Nutrient supply	Weeks after transplanting				
	2	4	6	8	10
<i>Leaf area (cm²/pot)</i>					
Complete	312	2280	4616	5734	6008
Low N	266	951	1405	1926	2206
Low P	207	834	1298	1377	1701
Low K	223	832	1230	2943	3980
<i>Tiller number (no./pot)</i>					
Complete	5.3	41.0	65.0	65.3	58.3
Low N	3.8	21.0	26.7	34.0	23.0
Low P	3.8	21.0	32.7	31.0	29.3
Low K	3.8	31.0	54.0	53.5	52.5
<i>Dry wt (g/pot)</i>					
Complete	1.45	15.6	49.6	81.4	133.0
Low N	1.17	7.33	18.5	27.8	39.6
Low P	1.13	6.41	15.4	27.7	36.6
Low K	1.21	5.63	16.9	33.3	51.3
<i>Nitrogen content (% in leaf blades)</i>					
Complete	<u>4.64^b</u>	<u>3.33</u>	<u>2.37</u>	<u>2.03</u>	<u>1.96</u>
Low N	<u>4.32</u>	<u>2.66</u>	<u>1.90</u>	<u>1.66</u>	<u>1.64</u>
Low P	4.57	4.15	3.51	3.15	3.03
Low K	4.83	4.18	3.19	3.36	3.47
<i>Phosphorus content (% in leaf blades)</i>					
Complete	<u>0.60</u>	<u>0.38</u>	<u>0.23</u>	<u>0.13</u>	<u>0.18</u>
Low N	0.63	0.53	0.45	0.43	0.33
Low P	<u>0.23</u>	<u>0.08</u>	<u>0.05</u>	<u>0.03</u>	<u>0.03</u>
Low K	0.68	0.50	0.25	0.25	0.25
<i>Potassium content (% in leaf blades)</i>					
Complete	<u>2.8</u>	<u>2.8</u>	<u>2.3</u>	<u>2.1</u>	<u>1.9</u>
Low N	2.9	2.5	1.9	1.8	1.9
Low P	2.8	2.4	2.4	1.9	1.6
Low K	<u>2.0</u>	<u>1.0</u>	<u>0.6</u>	<u>0.5</u>	<u>0.5</u>

^a Yoshida and Hayakawa (unpublished). ^b Underlines indicate nutrient content of the complete versus a particular nutrient to be compared.

synthetic rate are estimated at 2% for N, 0.4% for P₂O₅, 1% for K₂O, 0.4% for MgO, and 0.5% for SO₃.

Because of its importance in rice, the relationship between nitrogen and photosynthesis has been studied by many scientists (Table 3.14).

In general, leaf photosynthetic rate is correlated linearly or curvilinearly with leaf nitrogen or protein content. The shape of the mathematical form may depend



3.9. Relationship between nutrient content of leaves and photosynthetic activity (Tanaka 1961).

Table 3.14. Nitrogen nutrition and photosynthetic rate of single leaves in the rice plant^a.

Authors	Year	Result ^b
Ishizuka & Tanaka	1958	Curvilinear relation between ¹⁴ CO ₂ assimilation by leaf and N% in leaf blade; 2% N gives maximum assimilation.
Mitsui & Ishii	1938	P _n is linearly correlated with N% between 3 and 6% N.
Mitsui & Ishii	1939	P _n is linearly correlated with N content per leaf area.
Murata	1961	Topdressing of N increased P _n and N content per leaf area.
Osada	1967	P _n is linearly correlated with protein-N%, protein-N content per leaf area and SLW.
Takano & Tsunoda	1971	P _n is linearly correlated with protein-N content per leaf area but not with protein-N%.
Takeda	1961	Quadratic relation between P _n and N content per leaf area. Different light-photosynthesis curves for low and high N content per leaf area.
Tsuno, Inaba, & Shimizu	1959	P _n is linearly correlated with N%.
Yoshida & Coronel	1976	P _n is linearly correlated with N content per leaf area and with leaf conductance.

^a Modified from Yoshida and Coronel (1976). ^b N_n, nitrogen; P_n, net photosynthetic rate; SLW, specific leaf weight.

on the techniques used for measuring the photosynthetic rate, range of experimental conditions, physiological status of the plant, and degree of fitness.

The photosynthesis of single leaves can be described by the fundamental equation:

$$\text{Flux (gross photosynthesis)} = \frac{\text{potential difference}}{\text{resistance}} = \frac{C_a - C_c}{\text{resistance}}, \quad (3.17)$$

where C_a = the concentration of carbon dioxide in the air and C_c = the concentration of carbon dioxide at the carboxylating surface.

The resistance in equation 3.17 is composed of boundary layer (r_a), stomatal (r_s), mesophyll (r_m), and carboxylating (r_c) resistance. When they are connected in series, the total resistance is given by:

$$\text{Resistance} = r_a + r_s + r_m + r_c \quad (3.18)$$

The boundary-layer resistance is related to leaf size and shape and wind velocity. Nitrogen nutrition may affect any other resistance or all other resistances at the same time.

When rice plants are subjected to a nitrogen deficiency, the stomatal resistance of leaves, particularly that of the lower leaves, increases sharply, indicating that the stomates are closed to a considerable degree. This increased stomatal resistance is associated with a decrease in photosynthetic rate. Thus, the leaf photosynthetic rate is highly correlated with leaf conductance, a reciprocal of stomatal resistance (Fig. 3.10). Since stomatal resistance is the first critical step in carbon dioxide diffusion in leaf photosynthesis, the linear relationship between the leaf photosynthetic rate and leaf conductance may be interpreted as evidence of the effects of nitrogen nutrition on leaf photosynthesis via stomatal control.

3.7 NITROGEN

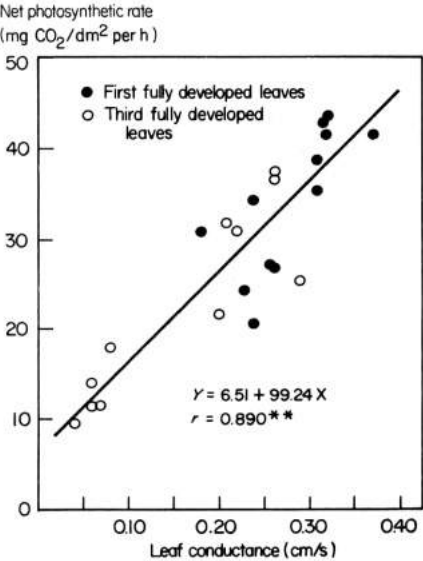
3.7.1 Occurrence of deficiency

Nitrogen is the most important nutrient for rice, and its deficiency occurs almost everywhere unless nitrogen is applied as a fertilizer.

Fertilizer-requirement trials conducted throughout Japan indicate clearly that lowland rice responds better to nitrogen applications than to applications of phosphorus and potassium (Table 3.15). Yet, lowland rice depends more on soil fertility than on fertilizers. When neither compost nor nitrogen fertilizer is applied, the yield index of lowland rice is 78, whereas the indices of upland rice, barley, and wheat are less than 40. The dependence of lowland rice on soil fertility is best illustrated by a Japanese saying: "Grow paddy with soil fertility, grow barley with fertilizers."

3.7.2. Forms of nitrogen

In solution culture, rice can absorb and use ammonia-N, nitrate-N, urea-N, and amino acid-N. Ammonia is the major and stable form of nitrogen in submerged



3.10. Relationship between leaf conductance and net photosynthetic rate of rice leaves (Yoshida and Coronel 1976).

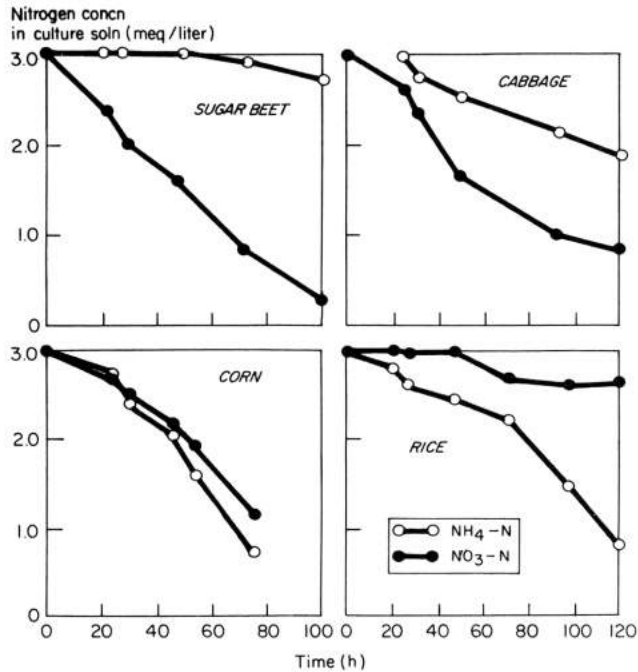
soils; nitrate is the major form in upland soils. Although relatively low concentrations of ammonia are toxic to many upland crops, relatively high concentrations are tolerated and used efficiently by rice.

Studies to determine the relative effectiveness of ammonia and nitrate as nitrogen sources for rice often encounter difficulty with changes in the pH of the culture solution. The changes result from the selective absorption of ammonia or nitrate, as illustrated in 3.4.4. The secondary effect of pH changes, such as iron

Table 3.15. Average response of lowland rice, upland rice, barley, and wheat to the application of nitrogen, phosphorus, and potash in Japan. ^a

Crop	Compost	Yield index ^b				Trials (no.)
		No fertilizer	PK	NK	NP	
Lowland rice	Without	78	83	95	96	1,161–1,185
	With	80	84	96	96	456–466
Upland rice	Without	38	51	84	75	117–126
	With	58	70	91	95	18
Barley and wheat	Without	39	50	69	78	822–841
	With	48	59	88	95	392–408

^a Imai and Imaizumi (1956). ^b The figures are indices taking the yield of the complete-fertilizer plot as 100.



3.11. Selective absorption of ammonia and nitrate from ammonium nitrate in culture solution (Tadano and Tanaka 1976).

deficiency at higher pH values, sometimes makes it difficult to draw a conclusion with confidence.

At early growth stages and with up to 200 ppm N, rice grows better with ammonia than with nitrate, whereas cucumbers grow better with nitrate (Oji and Izawa 1974). Upland crops such as Azuki bean, radish, sugar beet, and soybean use nitrate better than they do ammonia even at 14 ppm N (Tadano and Tanaka 1976). After panicle initiation and at 100 ppm N, which is unusually high for this growth stage, nitrate is a better nitrogen source for rice than ammonia. At 20 ppm N, however, ammonia is as good as nitrate (Tanaka et al 1959). Therefore, at realistic levels of nitrogen concentration in the soil solution, ammonia appears to be better than or as good as nitrate throughout the rice plant's entire growth cycle.

Rice absorbs ammonia in preference to nitrate from a solution that contains both. Excised roots from rice seedlings absorb ammonia 5 to 20 times faster than nitrate, depending on the solution pH (Fried et al 1965). With intact plants, rice also absorbs ammonia faster than nitrate, whereas the opposite is true with sugar beets (Fig. 3.11). Although rice prefers ammonia, it does not accumulate free ammonia in leaf tissues (Table 3.16); surplus ammonia is converted into asparagine. Cucumbers, however, accumulate in plant tissue considerable quantities of free ammonia, along with alanine and serine (Oji and Izawa 1974).

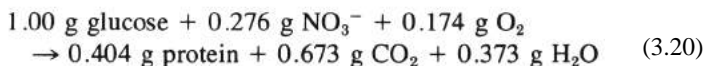
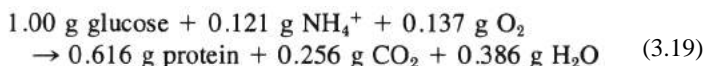
Table 3.16. Free ammonia content in tissues of rice and cucumber 0–7 days after treatment with ammonium nitrogen in culture solution.^a

Plants	Plant parts	NH ₄ -N concn in culture solution (ppm)	Free ammonia (mg N/g fresh wt)			
			0 day	3 days	5 days	7 days
Rice	Roots	20	0.03	0.04	0.03	0.04
		200	0.03	0.14	0.18	0.28
	Leaves	20	0.02	0.05	0.03	0.04
		200	0.02	0.14	0.10	0.17
Cucumber	Roots	20	0.00	0.01	0.04	0.02
		200	0.00	0.08	0.15	0.11
	Leaves	20	0.02	0.04	0.01	0.02
		200	0.02	0.29	0.35	0.53

^a Oji and Izawa (1974).

On the other hand, rice tissues accumulate nitrate when the nitrate concentration of the solution is high, whereas cucumber tissues do not (Table 3.17). That suggests that rice has a lower capacity than cucumber to reduce nitrate to ammonia. This capacity may limit the over-all rate of nitrogen assimilation and, hence, growth in rice.

In bioenergetics, the assimilation of nitrate requires more energy than that of ammonia because nitrate must be reduced to ammonia. Stoichiometric relationships for protein synthesis from both ammonia and nitrate can be given by the following equations (Penning de Vries and van Laar 1977):



In higher plants, including rice, most of the nitrate reduction occurs in green leaves under light. At high light intensities, where the rate of carbon dioxide diffusion limits the over-all rate of photosynthesis, the energy required for the nitrate reduction can be supplied by surplus energy produced by the photochemical reaction in photosynthesis (see Chapter 5; Penning de Vries 1975b). In this case, the nitrate reduction proceeds free of cost, without consuming assimilates to generate the required energy. At low light intensities, however, the CO₂ reduction (dark reaction) and nitrate reduction are probably competitive (Penning de Vries

Table 3.17. Nitrate content in tissues of rice and cucumber 0–7 days after treatment with nitrate nitrogen in culture solution.^a

Plants	Plant parts	NO ₃ -N concn in culture solution (ppm)	Nitrate content (mg N/g fresh wt)			
			0 day	3 days	5 days	7 days
Rice	Roots	20	0.03	0.83	0.52	0.83
		200	0.03	0.88	0.69	1.09
	Leaves	20	0.02	0.27	0.26	0.42
		200	0.02	0.33	0.45	0.67
Cucumber	Roots	20	0.01	0.46	0.35	0.33
		200	0.01	0.61	0.61	0.78
	Leaves	20	0.01	0.15	0.01	0.00
		200	0.01	0.42	0.22	0.15

^a Oji and Izawa (1974).

1975b). Under such condition, the rate of nitrate assimilation into organic nitrogen appears to slow down in rice (Dikshoorn and Ismunadji 1972).

Ammonia appears to suppress manganese absorption at near-neutral pH (Table 3.18), but manganese absorption increases with increasing pH. At pH 6 and 7, the manganese content of leaves and roots is much lower with ammonia than with nitrate.

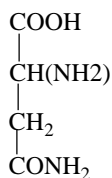
Table 3.18. Effect of solution pH and source of nitrogen on manganese content of the rice plant.^a

Nitrogen source	pH	Dry wt (g/plant)	Mn content (ppm)		(a)/(b)
			Leaves (a)	Roots (b)	
NH ₄	3.5	13	70	20	3.5
	4	36	80	20	4.0
	5	41	460	200	2.3
	6	44	610	560	1.1
	7	19	680	2200	0.3
NO ₃	3.5	24	90	30	3.0
	4	39	290	30	3.6
	5	39	830	280	3.0
	6	24	1000	3310	0.4
	7	9	1380	6260	0.2

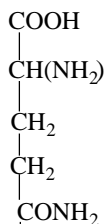
^a Tanaka and Navasero (1966a).

3.7.3. Asparagine and glutamine

A wide range of free amino acids and amides is found in rice tissues. The kinds and quantities of these free amino acids and amides depend on plant parts, growth stages, nitrogen sources, climatic environments, and assay techniques. Two kinds of free amide are normally present in rice leaf tissues: glutamine can be found regardless of nitrogen nutrition while asparagine can be found only when the rice plant is provided with ample nitrogen. The chemical formulas are:



Asparagine



Glutamine

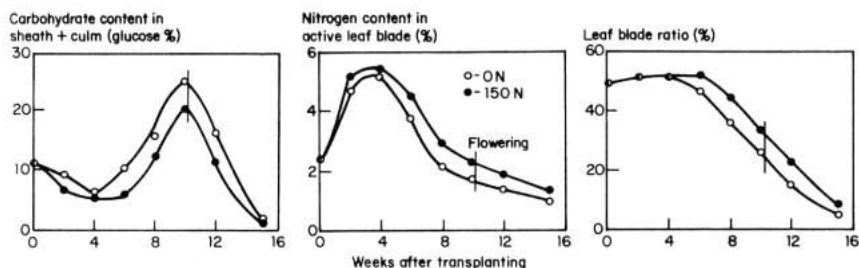
Asparagine appears to serve for the temporary storage of excess nitrogen when excessive ammonia has been absorbed. Hence, the presence or absence of asparagine in leaf tissues may indicate the need for nitrogen. An asparagine test using simplified paper chromatography has been proposed to determine the need for nitrogen topdressing at panicle initiation (Ozaki 1955).

3.7.4. Nitrogen nutrition and carbohydrate metabolism

When absorbed into the roots, ammonia is usually combined with α -oxoglutarate to produce glutamate. Glutamic dehydrogenase catalyses this reaction and contains zinc. Once glutamate is formed, the amino group in glutamate can be transferred to other oxoacids (keto-acids) by transamination.

Photosynthesis produces carbohydrates, some of which are translocated to the roots. In rice, the amount of sucrose translocated per day is about 5–10% of the root dry weight (Yoshida, T. 1968). This sucrose eventually provides α -oxoglutarate and other oxoacids which, in turn, are combined with ammonia or amino groups to form various amino acids. In this way nitrogen nutrition and carbohydrate metabolism are interrelated.

When more ammonia is absorbed, more carbohydrate is consumed to provide α -oxoglutarate. As a consequence, less carbohydrate is accumulated in the plant. When ammonia absorption is decreased, surplus photosynthates accumulate as starch and sugars, mainly in the leaf sheath and culm. Thus, a low starch or carbohydrate content in the leaf sheath plus culm is associated with a high nitrogen content and a high weight proportion of leaf blade to leaf sheath plus culm. An example of this relationship is shown in Figure 3.12. When the rice plant absorbs nitrogen actively at early growth stages, photosynthetic products are preferentially used for protein synthesis and production of leaf blades. As a result, the carbohydrate content of the leaf sheath plus culm tends to be lower. When



3.12. Carbohydrate content of leaf sheath plus culm, nitrogen content of active leaf blade, and active leaf blade ratio of IR8, 1967 dry season (Yoshida and Ahn 1968).

photosynthetic production increases relative to the absorption rate of ammonia, the nitrogen content decreases and surplus photosynthates accumulate.

The close and inverse correlation between nitrogen nutrition and carbohydrate accumulation suggests that the latter can be used as an indication of nitrogen deficiency. A starch iodine test has been proposed to determine the need for nitrogen topdressing at panicle initiation (Kiuchi 1968).

3.7.5. Partial productive efficiency

One of the central themes in plant nutrition is to find the particular growth stage when supplying a nutrient produces the maximum yield per unit amount of nutrient absorbed.

Partial productive efficiency of nitrogen for grain production is defined as:

$$\text{Partial productive efficiency of nitrogen absorbed at period } (n-1) \text{ to } (n) = \frac{Y(n) - Y(n-1)}{N(n) - N(n-1)}, \quad (3.21)$$

where $Y(n)$ = grain weight of the treatment corresponding to period (n) ,

$Y(n-1)$ = grain weight of the treatment corresponding to period $(n-1)$,

$N(n)$ = total nitrogen uptake of the treatment corresponding to period (n) , and

$N(n-1)$ = total nitrogen uptake of the treatment corresponding to period $(n-1)$.

In other words, partial productive efficiency is the amount of grain produced per unit amount of nitrogen absorbed at a particular growth stage. Thus, the greater the value of partial productive efficiency, the higher the efficiency of nitrogen absorbed to produce grains. Partial productive efficiency of nitrogen for straw is also defined in the same way as for grain.

The solution culture technique provides a convenient means to study partial productive efficiency. In solution culture, the nutrient supply can be controlled

Table 3.19. Design of experiment for study of partial productive efficiency.

Stage	Period ^a	Days (cumulative no.) after transplanting
I	23 Jun– 6 Jul	14
II	6 Jul–15 Jul	23
III	15 Jul–23 Jul	31
IV	23 Jul–31 Jul	39
V	31 Jul– 8 Aug	47
VI	8 Aug–18 Aug	57
VII	18 Aug–30 Aug	69
VIII	30 Aug–15 Sep	85
IX	15 Sep–14 Oct	114

^a Transplanted on 23 June.

easily. In a classical work by Kimura and Chiba (1943), nitrogen was supplied in 9 different ways with respect to growth stages (Table 3.19, 3.20). To produce plants that would contain different amounts of nitrogen, each supply had seven different levels of nitrogen concentration in culture solution (Table 3.21). Thus, altogether there were 63 treatments. The results of the above experiment are summarized in Table 3.22 and Figure 3.13. From these results, several important conclusions can be drawn:

- Nitrogen absorbed at early growth stages is used to produce more straw than grain.
- Nitrogen absorbed at later growth stages is used to produce more grain than straw.
- The partial productive efficiency for both grain and straw is higher when the nitrogen supply is lower.
- There are two peaks in the partial productive efficiency for grain. The first is not related to a particular growth stage but to the amount of nitrogen absorbed

Table 3.20. Supply and withdrawal of nitrogen for each stage.^a

Treatment	Stage								
	I	II	III	IV	V	VI	VII	VIII	IX
a	0	–	–	–	–	–	–	–	–
b	0	0	–	–	–	–	–	–	–
c	0	0	0	–	–	–	–	–	–
d	0	0	0	0	–	–	–	–	–
e	0	0	0	0	0	–	–	–	–
f	0	0	0	0	0	0	–	–	–
g	0	0	0	0	0	0	0	–	–
h	0	0	0	0	0	0	0	0	–
i	0	0	0	0	0	0	0	0	0

^a 0 = supply, – = withdrawal.

Table 3.21. Concentration of nitrogen in culture solution used for different periods.

Treatment	Nitrogen concentration (ppm)						
	23 Jun- 10 Jul	10-13 Jul	13 Jul- 4 Aug	4-13 Aug	13-26 Aug	26 Aug- 3 Sep	3 Sep- 14 Oct
1	1.0	1.5	3.0	3.8	3.0	2.0	2.0
2	1.5	2.1	4.2	5.1	3.9	2.5	2.4
3	2.0	3.0	6.0	6.8	5.0	3.2	2.9
4	2.5	4.2	8.5	9.2	6.5	4.0	3.5
5	3.5	6.0	12.0	12.4	8.4	5.0	4.2
6	5.0	8.5	17.0	16.7	10.8	6.4	5.0
7	7.5	12.0	24.0	22.5	14.0	8.0	6.0

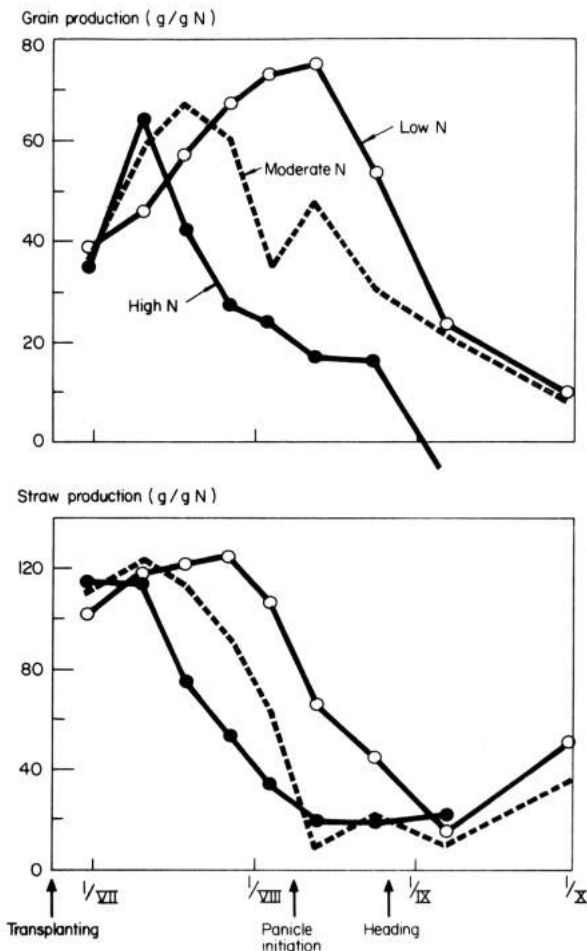
by the plant. It appears when total nitrogen uptake reaches 170 mg N/plant. Thus, the first peak appears at stage II when the nitrogen concentration in the culture solution is high, and it appears at later growth stages when the concentration is low.

- The second peak appears at stage VI (from 19 to 9 days before heading), when the nitrogen concentration is moderate. This corresponds to the time when young panicles are growing actively.
- When the nitrogen concentration is high, there is no second peak. Thus, the most efficient time to supply nitrogen for grain production varies with the level of nitrogen supply.

Table 3.22. Partial productive efficiencies of nitrogen for grain and straw.^a

Treatment	Stage								
	I	II	III	IV	V	VI	VII	VIII	IX
<i>Grain</i>									
1	39	46	58	67	73	75	53	23	10
2	35	41	57	70	69	56	50	41	13
3	37	43	73	65	55	58	38	22	4
4	36	59	67	60	35	47	30	21	9
5	39	64	58	35	23	41	21	12	-45
6	33	62	47	26	22	21	20	21	2
7	35	64	41	26	24	16	16	-6	-
<i>Straw</i>									
1	102	117	121	125	107	66	45	14	50
2	102	126	130	111	86	50	10	26	30
3	108	141	112	97	88	46	5	14	4
4	111	123	113	91	63	10	21	10	34
5	113	122	98	75	62	16	8	-	-
6	116	113	83	58	34	22	28	2	12
7	114	115	74	52	34	19	18	21	-

^a Kimura and Chiba (1943).



3.13. Partial productive efficiency of nitrogen for grain and straw production in rice (drawn from Kimura and Chiba 1943).

If very limited, nitrogen should be supplied at about 20 days before heading. When the supply is moderate, nitrogen may be given twice — at the early growth stages and at about 20 days before heading. When nitrogen is abundant, applications at the early growth stages are most efficient for grain production.

Recall that about 16 kg nitrogen is required to produce 1 t rough rice in Japan and the efficiency of nitrogen for grain production is about 62 kg grain/kg N absorbed (see Section 3.4.6.). These values are quite comparable to those of partial productive efficiency shown in Table 3.22.

3.7.6. Nitrogen topdressing at panicle initiation

Applying nitrogen at about 20 days before heading has a high productive efficiency when the level is moderate or low. This period coincides with the active growth of

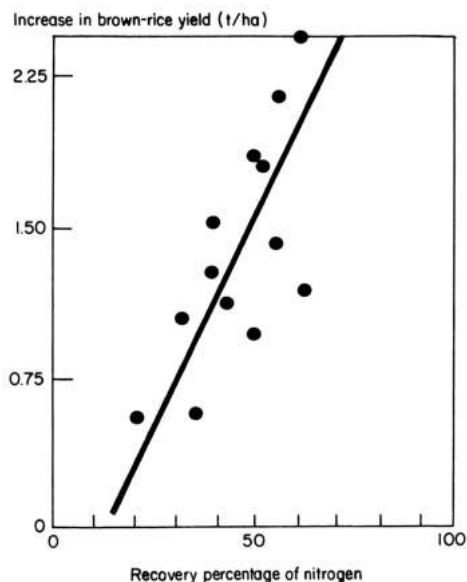
young panicles before heading (see Chapter 1). In practice, nitrogen topdressing is applied at panicle initiation, when the young panicles grow about 1–2 mm long, which is about 23–25 days before heading. The absorbed nitrogen at this time is efficiently used to increase spikelet number and, hence, panicle size. For this reason, topdressing at panicle initiation is called *Ho-goe* in Japanese, implying *panicle fertilizer*.

In farmer's fields, rice leaves usually turn yellow at around panicle initiation, indicating a nitrogen deficiency. Under such conditions, nitrogen topdressing is highly recommended to increase grain yield.

Another effect of nitrogen topdressing on yield could be through active photosynthesis during ripening. Nitrogen absorbed at panicle initiation should help keep leaves green after heading and thereby contribute to active photosynthesis for grain production.

The timing of topdressing also affects the lodging resistance of a crop (Singh and Takahashi 1962). Topdressing at 20 days before heading not only gives the maximum panicle weight but also increases lodging resistance by affecting the length and diameter of internodes, dry matter accumulation in the basal portions, and the breaking strength of shoots.

The capacity of soil to hold applied nitrogen is an important consideration in determining the efficiency of basal versus split applications of nitrogen fertilizer. Recovery percentages of applied nitrogen differ among soils when the fertilizer was placed deeply to minimize nitrogen loss through denitrification (Fig. 3.14). Higher recovery percentages correlate with increases in grain yield attributable to nitrogen applications. Apparently, the applied ammonia is lost through leaching,



3.14. Relationship between yield increase by nitrogen application over no added nitrogen and recovery percentage of the applied nitrogen (Takahashi 1959c).

the degree of which depends on soil properties. Soils with montmorillonite clays tend to have higher recovery rates than those with kaolinite clays or allophane.

For soils with low nitrogen-holding capacity, split applications of fertilizer should result in a higher nitrogen recovery and, hence, a higher yield than a basal application. On the other hand, split applications may not be any better than a basal application in soils where the applied ammonia is well held by clays. In Japan, zeolite, which has a cation exchange capacity of about 80–160 meq/100 g, is applied to increase the soil's nitrogen-holding capacity.

3.7.7. Efficiency of fertilizer nitrogen for grain production

Agronomists usually express the efficiency of fertilizer nitrogen in kilograms of rough rice produced per kilogram of nitrogen *applied*. Physiologists, on the other hand, define the efficiency of nitrogen utilization in kilograms of rough rice produced per kilogram of nitrogen *absorbed*.

These two efficiencies can be related by introducing a third parameter, percentage of nitrogen recovery:

$$\begin{array}{lcl} \text{Efficiency of} & \text{percentage of nitrogen} & \text{efficiency of utilization} \\ \text{fertilizer nitrogen} & = \text{recovery (kg absorbed} & \text{(kg rice/kg absorbed} \\ \text{(kg rice/kg applied N)} & \text{N/kg applied N)} & \text{N)} \end{array} \quad (3.22)$$

The percentage of nitrogen recovery varies with soil properties, methods, amounts, and timing of fertilizer applications, and other management practices. It usually ranges from 30 to 50% in the tropics (Prasad and De Datta 1979). The percentage of nitrogen recovery tends to be high at low levels of nitrogen and when nitrogen is placed deep in the soil or topdressed at later growth stages.

The efficiency of utilization for grain production in the tropics is about 50 kg rough rice/kg nitrogen absorbed, and this efficiency appears to be almost constant regardless of the rice yields achieved. In temperate regions, the efficiency appears to be about 20% higher than in the tropics (see Table 3.12 and Section 3.7.6.).

Using values for the recovery percentage and utilization efficiency obtained for the tropics, the efficiency of fertilizer nitrogen can be calculated as:

$$\begin{aligned} \text{Efficiency of fertilizer nitrogen} &= (0.3 \sim 0.5) \times 50 \\ &= 15\text{--}25 \text{ kg rice/kg applied N.} \end{aligned} \quad (3.23)$$

These values are found in agronomic experiments (Prasad and De Datta 1979).

3.7.8. Grain yield and fertilizer requirements

Grain yield (Y) can be analyzed as yield obtained without fertilizer nitrogen (Y_0) and yield increase obtained by fertilizer application (ΔY_F):

$$\begin{aligned} Y &= Y_0 + \Delta Y_F \\ Y &= Y_0 + (\text{fertilizer efficiency}) \times N_F, \end{aligned} \quad (3.24)$$

where N_F is amount of nitrogen applied (kg/ha), and Y_o represents nitrogen fertility levels in the soil. Y_o varies with soil type and perhaps with variety. Values of 2 t/ha and 3.5 t/ha are assigned to Y_o so that the first value represents the average nitrogen fertility level of paddy fields and the second represents a high fertility level. Yield increases obtained by fertilizer application can be computed from the second term of equation 3.24.

As shown in Figure 3.15, grain yield is determined by soil fertility level, amount of nitrogen applied, and percentage of nitrogen recovery. At $Y_o = 2$ t/ha, 50 kg of fertilizer nitrogen can produce yields of 2.75–3.25 t/ha. To produce 6 t/ha, a minimum of 160 kg N is needed. These computations illustrate the relationship between the target yield and fertilizer requirements.

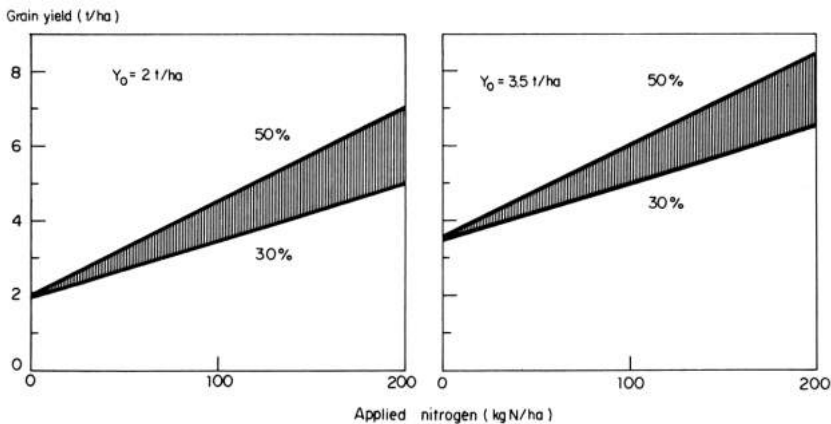
3.8. PHOSPHORUS

3.8.1. Occurrence of deficiency

Phosphorus deficiency occurs widely in soils of low or high pH: acid latosolic soils, acid sulfate soils, calcareous soils, and alkali soils. Ando soils, which have a high capacity to fix applied phosphorus, need much larger amounts of phosphorus than usual. For example, the optimum for acid Ando soils in northern Japan is about 200 kg P_2O_5 /ha; that for calcareous soils at Dokri, Pakistan, about 45 kg P_2O_5 /ha; and that for calcareous soils at Rajendranagar, India, about 80–100 kg P_2O_5 /ha.

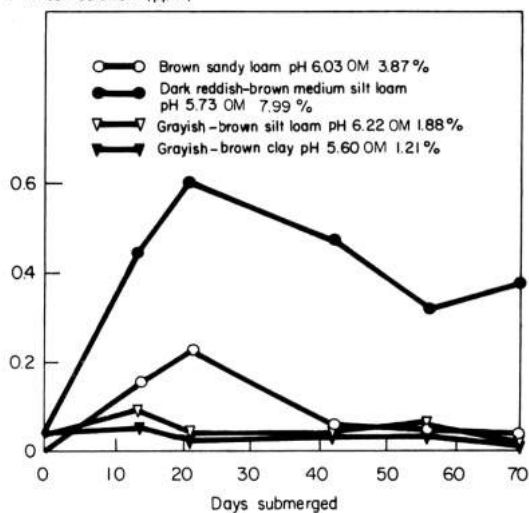
3.8.2. Phosphorus in soil solution

Depending on soil type, submergence increases the concentration of phosphorus in the soil solution from less than 0.05 ppm to about 0.6 ppm and subsequently decreases it (Fig. 3.16). The increase of phosphorus solubility in submerged soils



3.15. Simplified models for relationship between fertilizer nitrogen and rice yield. 30% and 50% are minimum and maximum nitrogen-recovery percentages.

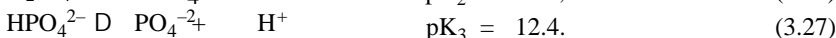
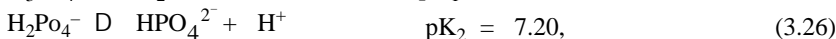
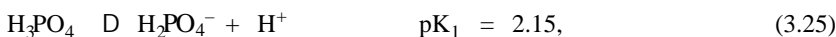
P in soil solution (ppm)



3.16. Changes in concentration of soluble phosphorus with duration of submergence (Ponnamperuma 1965).

may be attributed to a reduction of ferric phosphates to the more soluble ferrous phosphate, and to a displacement of phosphates from ferric and aluminum phosphates by organic anions. The subsequent decrease may be caused by a resorption of phosphate on clay or aluminum hydroxide and an increase in pH (Ponnamperuma 1965).

The ionic species of phosphate in the soil solution is dependent on pH. Orthophosphoric acid dissociates into three forms according to the following equations:



Within a pH range of 4.0–8.0, the principal ionic species present in the soil solution are H_2PO_4^- and HPO_4^{2-} . Relative proportions of H_2PO_4^- and HPO_4^{2-} at different pHs can be calculated by:

$$\frac{K_2}{[\text{H}^+]} = \frac{[\text{HPO}_4^{2-}]}{[\text{H}_2\text{PO}_4^-]} \quad (3.28)$$

Thus, at pH = 7.2, H_2PO_4^- and HPO_4^{2-} are present in equal proportions. At pH = 5, however, H_2PO_4^- is the dominant species and HPO_4^{2-} is almost absent.

3.8.3. Partial productive efficiency

The partial productive efficiency of phosphorus for grain is higher at early growth stages than at later stages (Table 3.23) because phosphorus is needed for tillering

Table 3.23. Partial productive efficiency of phosphorous for grains.^a

Growth period	Partial productive efficiency		
	Low P	Medium P	High P
29 Jun–8 Jul	144	270	193
8 Jul–17 Jul	245	167	300
17 Jul–29 Jul	213	285	197
29 Jul–7 Aug	139	64	51
7 Aug–19 Aug	136	74	30
19 Aug–28 Aug	–1433	27	–21

^a Hayashi et al (1951).

and because the total phosphorus requirement is small relative to nitrogen. Furthermore, if sufficient phosphorus is absorbed at early growth stages, it can be easily redistributed to growing organs. Rice's need for phosphorus at early growth stages advocates for basal application.

3.8.4. Varietal performance on phosphorus-deficient soils

Clear varietal differences in rice's ability to absorb soil phosphorus and in growth and yield on a phosphorus-deficient acid soil in Thailand have been reported (Koyama et al 1973). Varietal differences in grain yield were most remarkable when no phosphorus was applied and progressively decreased when phosphorus application was increased (Fig. 3.17). Variety Dawk Mali 3 grew better and yielded higher when no phosphorus was applied. This was associated with higher phosphorus absorption.

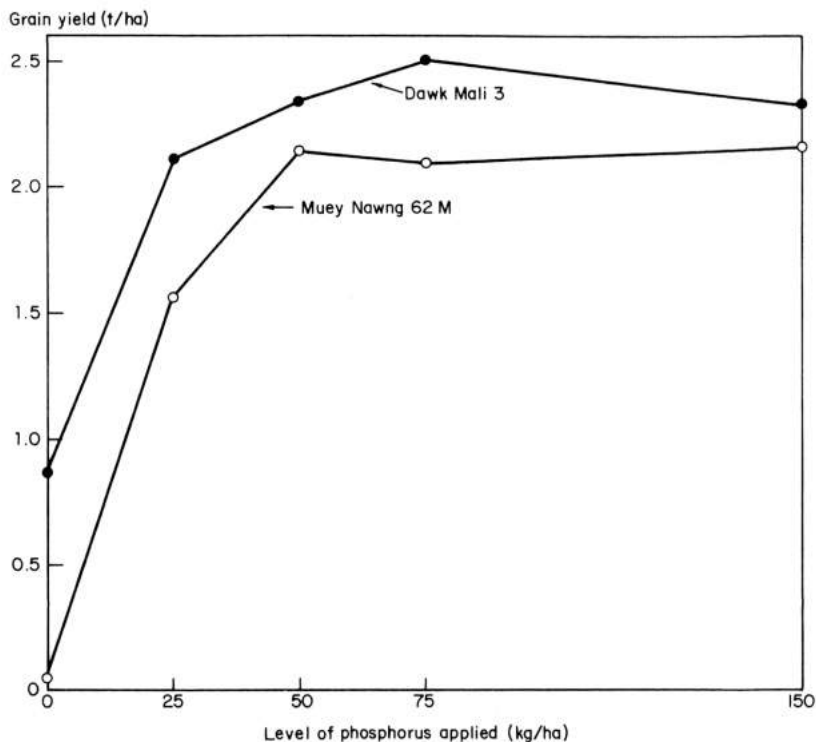
Studies showing varietal differences only in soil culture (pot or field) and not in solution culture experiments led Koyama et al to conclude that varietal differences in the ability to grow better on a phosphorus-deficient acid soil is caused by differences in the ability to extract soil phosphorus. Subsequently, similar varietal differences were observed on a wide range of varieties (Ponnamperuma 1976a).

3.9. POTASSIUM

3.9.1. Occurrence of deficiency

Potassium deficiency occurs to a limited extent in lowland rice. Low potassium content or potassium deficiency is often associated with iron toxicity, which is common on acid latosolic soils and acid sulfate soils.

Potassium deficiency is frequently accompanied by *Helminthosporium* leaf spots, which is a common symptom of *Akiochi* on sandy soils in Japan and Korea. Potassium deficiency also occurs on poorly drained soils, partly because toxic substances produced in highly reductive soils retard potassium uptake and partly because less soil potassium is released under poorly drained conditions.



3.17. Responses of two varieties to different levels of applied phosphorus (drawn from Koyama et al 1973).

3.9.2. Potassium in soil solution

Submergence increases the concentration of potassium in the soil solution. The increases are higher in sandy soils rich in organic matter and are associated with soluble ferrous iron and manganese (Table 3.24). This can be considered one of the benefits of flooding. A disadvantage, however, would be the loss in coarse-textured soils with drainage.

3.9.3. Partial productive efficiency

The partial productive efficiency of potassium for grain is generally high at early growth stages, declines, and becomes high again at later stages (Table 3.25). Since rice requires large quantities of potassium, a sustained supply is necessary up to heading when the reproductive stage is complete. Note that only 20% of the absorbed potassium is translocated to the panicles; the rest remains in the vegetative parts at maturity (see Table 3.11).

3.9.4. Partial replacement of potassium by sodium

Since most of the enzymes requiring univalent cations are not activated by sodium

Table 3.24. Relationship between increase in concentration of K⁺ in the soil solution on submergence and soil properties.^a

Soil no.	pH	Organic matter (%)	Texture	Ex K ⁺ (ppm of soil)	Soluble K ⁺ (ppm)			Soluble Fe ⁺⁺ and Mn ⁺⁺ (ppm)
					Start	Peak	Increase	
25	4.8	4.4	Fine sandy loam	140	7.6	12.5	5.9	230
18	5.6	6.0	Sandy loam	185	6.3	12.7	5.4	90
1	7.4	2.6	Loamy fine sand	100	3.2	5.2	2.0	73
28	4.7	2.9	Clay	165	2.3	7.9	5.6	342
14	4.7	2.3	Clay	108	2.4	6.5	4.1	340
31	6.2	3.4	Clay	160	3.5	6.0	2.5	174
4	6.9	1.8	Clay	60	1.6	1.9	0.3	39

^aPonnamperuma (1965).

(Evans and Sorger 1966), sodium can only substitute for potassium to a limited extent.

Replacement of potassium by sodium is probably possible in less specific processes, such as the maintenance of cell turgor and when potassium is limited. One of the potassium deficiency symptoms in rice is droopy leaves. When sodium chloride is added, however, the leaves remain erect, suggesting that droopy leaves are caused by reduced cell turgidity. Sodium absorption helps maintain the high turgidity responsible for erect leaves (Yoshida and Castañeda 1969).

When potassium is limited, the addition of 1,000 ppm of sodium chloride to the culture solution improves vegetative growth, which eventually results in increased panicle yield (Table 3.26).

The antagonistic effect of sodium on potassium absorption by rice varies with the level of potassium supply. Sodium chloride decreases the potassium content only when the supply of potassium is high, but it has no effect on potassium when the supply is low. This suggests that a relatively high sodium content can benefit rice nutrition under weakly saline conditions and when the potassium supply is limited.

Table 3.25. Partial productive efficiency of potassium for grains.^a

Growth period ^b	Partial productive efficiency		
	Low K	Medium K	High K
12 Jul–22 Jul	0.051	0.082	0.046
22 Jul–1 Aug	0.058	0.082	0.058
1 Aug–11 Aug	0.049	0.065	0.019
11 Aug–21 Aug	0.007	0.014	0.004
21 Aug–31 Aug	0.021	0.007	0.023

^aKiuchi (1952). ^bTransplanting = 12 Jul; heading = 5 Sep.

Table 3.26. Effects of a moderately high concentration of sodium chloride on the growth and potassium requirement of the rice plant at the vegetative growth stage.^a

Potassium supply (ppm)	Dry shoot wt (g)		Nutrient content of shoot (%)			
			K		Na	
	No NaCl	1000 ppm NaCl	No NaCl	1000 ppm NaCl	No NaCl	1000 ppm NaCl
1	9.0	15.7	0.33	0.30	0.14	1.63
2	16.0	21.8	0.56	0.56	0.15	1.76
5	24.2	30.4	0.76	0.77	0.12	1.39
10	31.7	38.5	1.23	0.92	0.10	1.24
50	33.4	36.3	1.18	1.11	0.12	1.37
100	39.9	36.7	1.51	1.34	0.09	1.03
200	47.7	44.2	2.75	1.80	0.10	0.98

^a Yoshida and Castañeda (1969).

3.10. ZINC

3.10.1. Occurrence of deficiency

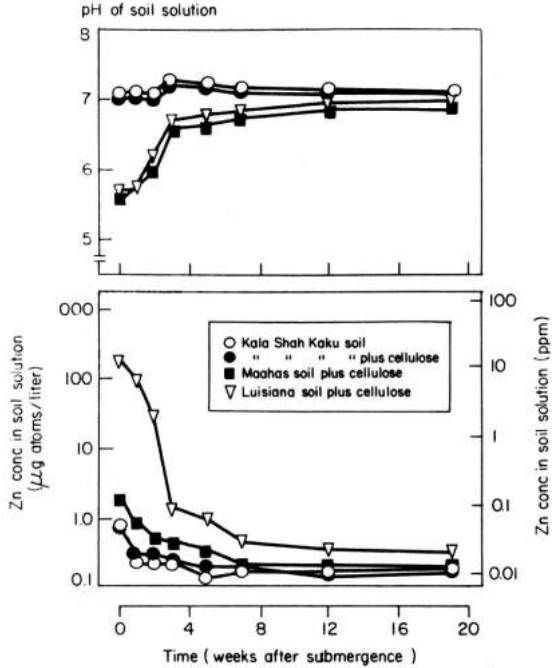
Zinc deficiency of lowland rice occurs widely in near-neutral to alkaline soils, particularly calcareous soils. In a severe case of zinc deficiency, transplanted rice seedlings may die or direct-sown seeds may fail to emerge. In most cases, however, symptoms become visible about 2–3 weeks after transplanting and a spontaneous recovery from the deficiency may occur 6–8 weeks after soil submergence.

3.10.2. Zinc in soil solution

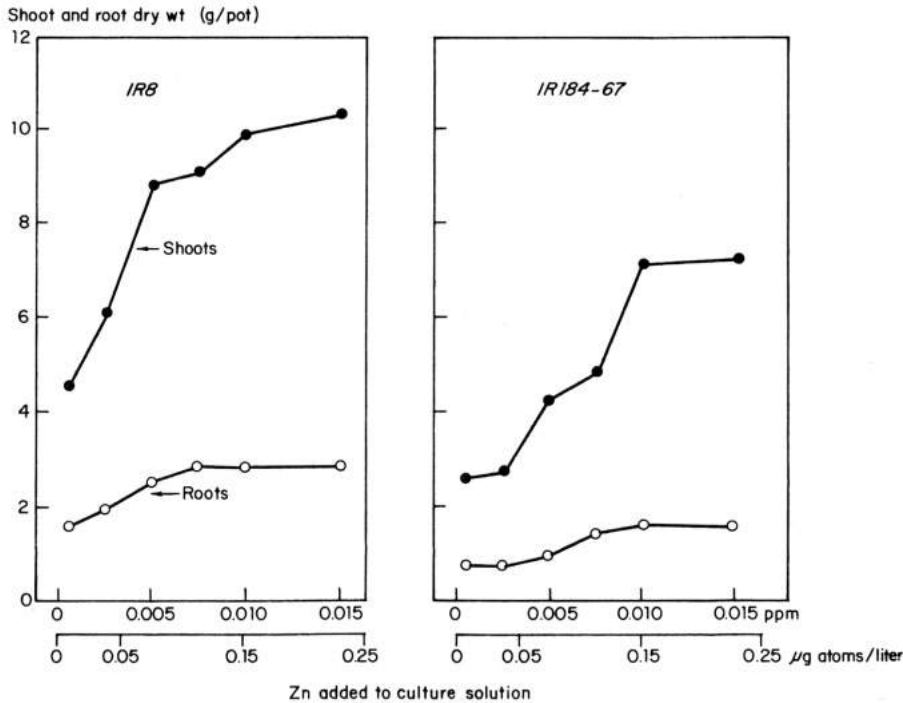
The availability of both soil zinc and applied zinc is much higher in upland soils than in submerged soils (Yoshida 1975c). Soil submergence causes a substantial decrease in the zinc concentration in the soil solution (Fig. 3.18). After prolonged submergence, the zinc concentration tends toward an ultimate value between 0.02 and 0.03 ppm. In a solution culture experiment using 2 varieties, the critical low concentration for zinc deficiency was about 0.01 ppm (Fig. 3.19). Zinc concentrations in the culture solution for other plant species to attain maximum growth range from 0.003 to 0.016 ppm (Carroll and Loneragan 1968).

In Maahas and Luisiana soils, soil pH increases substantially during the first 3 weeks after submergence, during which zinc concentrations fall rapidly. Since the solubility of zinc decreases with increasing pH, decreases in zinc concentration might be predicted; however, factors other than soil pH could be operating. For example, in Kala Shah Kaku soil, where zinc deficiency occurs, a substantial decrease in zinc concentration during the first 2 weeks is not accompanied by any increase in soil pH. The ultimate value of the zinc concentration in the soil solution, however, is considered adequate for healthy plant growth. Thus, zinc

3.18. Changes with time in pH and concentration of zinc in the soil solution of flooded soils (Forno et al 1975).



3.19. Relationship between amounts of zinc added to the nutrient solution and the dry weights of shoots and roots of IR8 and IR184-67 when harvested 37 days after germination (Forno et al 1975).



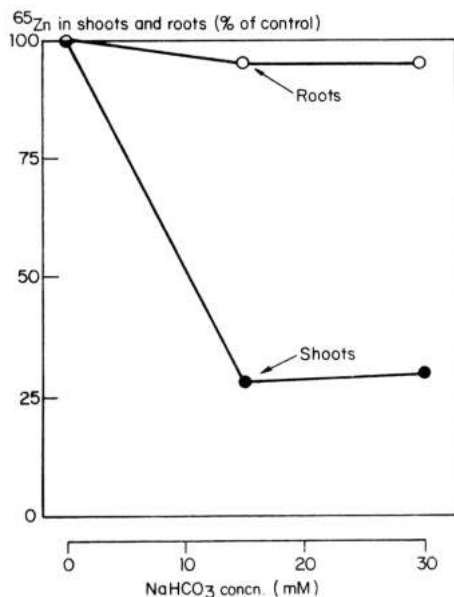
concentrations in the soil solution alone cannot explain why rice suffers from zinc deficiency on Kala Shah Kaku soil.

3.10.3. Effects of bicarbonate and organic acid on zinc absorption

Bicarbonate and organic acid may accumulate to toxic levels in submerged soils depending on soil pH, organic matter content, and soil temperature.

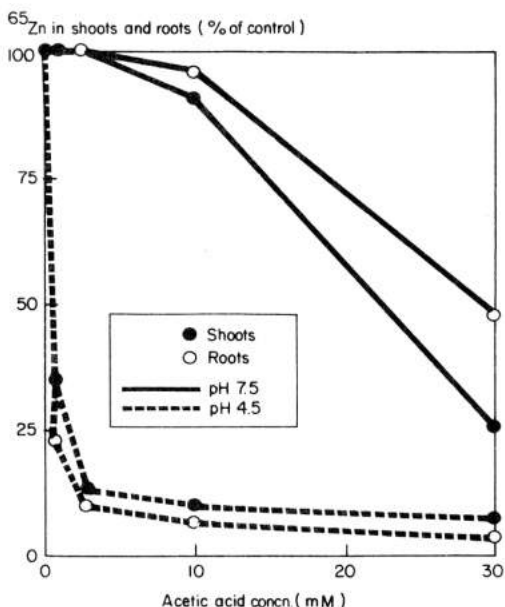
A concentration of 15 or 30 mM HCO_3^- causes a reduction of about 70% in the ^{65}Zn content of the shoots, but only a reduction of about 5% in the roots (Fig. 3.20). These results suggest that the effect of HCO_3^- on zinc transport to the shoots is greater than its effect on absorption by the roots. HCO_3^- has a similar effect on zinc transport from root to shoot in wheat (Forno et al 1975a). In calcareous and other alkaline soils, bicarbonate concentrations exceeding 10 mM are common during 3–6 weeks after submergence. Thus, the inhibitory effect of bicarbonate on zinc absorption is likely to be one of the major causes of zinc deficiency in alkaline soils.

The effect of acetic acid on zinc absorption varies with pH. At pH 4.5, acetic acid at a concentration of only 0.3 mM reduces the ^{65}Zn in the shoots by 70% and in the roots by about 77%. At concentrations of 10 and 30 mM, plants wilt, and the ^{65}Zn activity in the shoot and root tissues is reduced by 94% and 97%, respectively (Fig. 3.21). At pH 7.5, however, additions to the culture solution of acetic acid up to 3 mM have no detectable effect on ^{65}Zn uptake; the effects are small even at a concentration of 10 mM. However, at 30 mM, the ^{65}Zn activity in the roots is reduced by 51%, while that in the shoots is reduced by 75%.



3.20. Effect of NaHCO_3 on the ^{65}Zn absorbed by the rice variety IR8 at pH 7.3 (Forno et al 1975a).

3.21. Effect of acetic acid on the ^{65}Zn absorbed by the rice variety IR8 at pH 4.5 and 7.5 (Forno et al 1975a)



In some problem soils, organic acids may accumulate in concentrations as high as 10–30 mM. The kinetics of organic acids in submerged soils show that they accumulate in much smaller quantities at high temperatures, and decompose more quickly at high temperatures. Thus, whether organic acids could accumulate in quantities large enough to retard zinc uptake depends on temperature regimes.

The inhibitory effects of bicarbonate and organic acids on zinc absorption lead to the hypothesis that, in calcareous soils and other alkaline soils where zinc deficiency occurs, flushes of microbial activity after submergence cause transitory peaks in HCO_3^- and organic acids, which, either separately or together, cause the temporary inhibition of zinc uptake by the rice plant.

3.10.4. Critical plant zinc content

The critical level for zinc deficiency in the rice plant is about 15 ppm (Fig. 3.22). Similar values are reported for upland crops (Thorne 1957, Carroll and Loneragan 1968).

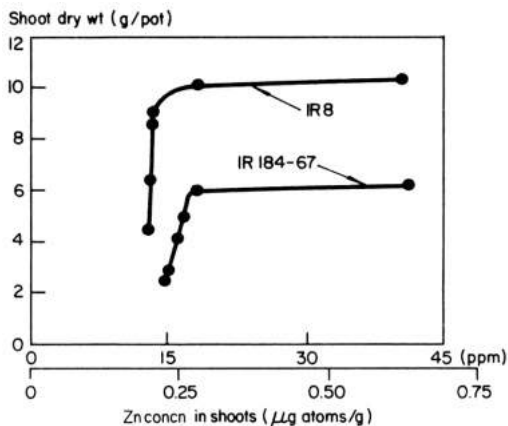
For purposes of diagnosing zinc deficiency, the following criteria have proven useful when combined with visible observations and soil analyses (Yoshida et al 1973):

Zinc content in the whole shoot

- <10 ppm
- 10–15 ppm
- 15–20 ppm
- >20 ppm

Diagnosis

- Definite Zn deficiency
- Very likely
- Likely
- Unlikely



3.22. Relationship between shoot dry weight and the zinc concentration in the shoots of IR8 and IR184-67 (Forno et al 1975).

3.10.5. Varietal performance on zinc-deficient soils

Some rice varieties differ in their ability to grow on zinc-deficient soils. The lines and varieties susceptible to zinc deficiency appear to be less vigorous and low tillering.

In marginal zinc deficiency, the varietal difference may be significant (Table 3.27). On an extremely deficient soil, however, zinc must be applied to the soil to produce profitable yields.

3.11. IRON

3.11.1 Occurrence of deficiency and toxicity

Iron deficiency occurs on neutral to alkaline soils. It is more frequent on upland than on submerged soils. With the same calcareous soil, upland rice may suffer severe iron deficiency while lowland rice may grow normally.

Iron toxicity, on the other hand, occurs only in lowland rice. It is likely to occur on acid sandy, acid latosolic, and acid sulfate soils. Iron toxicity also occurs on

Table 3.27. Effect of zinc application on grain yield of 4 lines in the continuous cropping experiment (IRRI 1970).^a

Line	Grain yield (t/ha)		
	No zinc	Zinc spray	Dipping in 2% zinc oxide
IR1154-243	4.05	4.79	4.56
IR503-103	4.14	4.02	4.14
IR773-112	2.47	4.11	4.44
IR773-118	2.62	2.91	3.34

^aYoshida et al (1973).

some organic soils such as peaty soils.

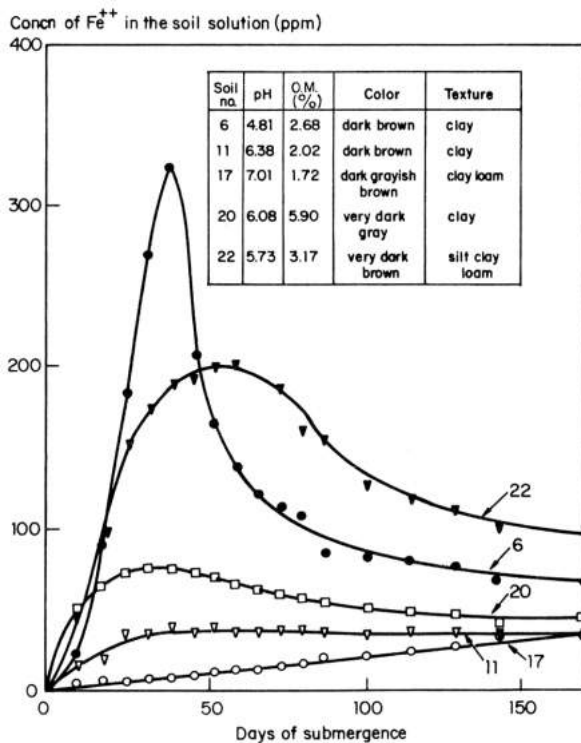
3.11.2. Iron in soil solution

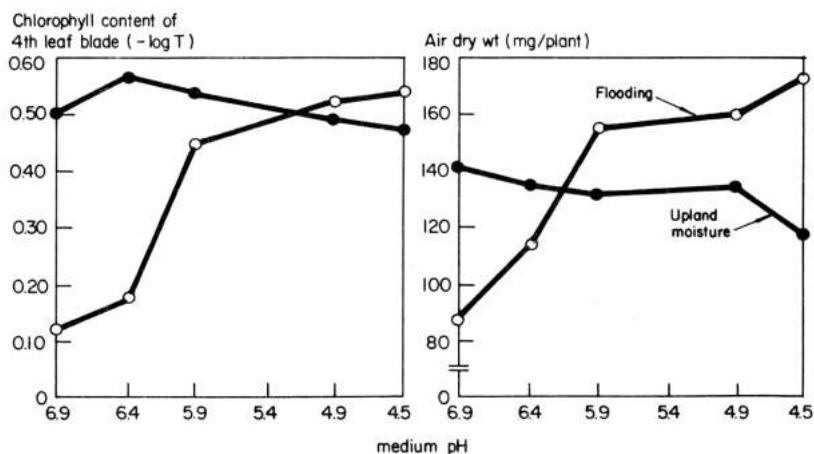
The concentration of ferrous iron in the soil solution increases sharply after submergence (Fig. 3.23). After 4 weeks of submergence strongly acid latosolic soils build up in the soil solution concentrations as high as 300 ppm Fe^{2+} and then show an exponential decrease. After about 6 months of submergence, concentrations are maintained at about 50–100 ppm. The slightly acid soils give maximum concentrations of 50–100 ppm, while slightly alkaline soils low in organic matter may not attain peak concentrations of more than 30 ppm. Such concentrations are still much higher than the concentrations of 2–5 ppm normally used for the culture solution. In general, the concentration of iron in the soil solution is controlled by soil pH, organic matter content, iron content itself, and the duration of submergence.

3.11.3. Iron deficiency

a. High pH-induced iron deficiency. Iron chlorosis commonly occurs on high-pH soils and culture solutions. Iron-deficient plants induced by high pH normally contain high percentages of iron in the roots and low percentages in the shoots.

3.23. Changes in the concentrations of Fe^{2+} in the soil solution of 5 soils (Ponnamperuma 1965).





3.24. Effect of pH and moisture content of synthetic soil media on the chlorophyll content and air dry weight of lowland rice Norin 16 (Takagi 1960).

Impaired translocation of iron from root to shoot in high-pH rooting media is considered one of the causes of iron deficiency (Tanaka and Navasero 1966b).

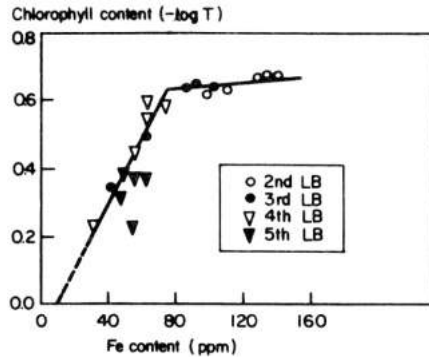
b. Flooding-induced iron deficiency. When rice is grown on a mixture of river sand and bentonite with no organic matter, acute iron deficiency is induced by flooding. Plants grown under upland moisture conditions remain green (Fig. 3.24). This indicates that excess moisture weakens the ability of rice seedlings to absorb iron. At lower pH, however, chlorosis does not occur on the flooded artificial soil. In submerged soils, under most conditions, microbial reduction increases the concentration of ferrous iron in the soil solution, and rice absorbs the iron easily. In the artificial soil there is no reduction and, hence, no increase in the availability of iron. As a consequence, rice suffers from iron deficiency. That suggests that even in natural soils, if soil reduction proceeds slowly due to low temperatures or when an upland field low in organic matter is converted to a paddy field, rice seedlings may suffer from iron chlorosis.

c. Critical plant iron content. Chlorosis is a typical symptom of iron deficiency. It suggests a low chlorophyll content in leaves. In chlorotic leaves, there is a linear relationship between chlorophyll and iron within a range of iron concentrations from 10 to 70 ppm (Fig. 3.25). Thus, the critical iron content in rice leaves is about 70 ppm on a dry matter basis. Similar relationships exist for many other upland crops (Oertli and Jacobson 1960). These results indicate that the internal iron requirement is about the same for rice and other crops.

3.11.4. Iron toxicity

Iron toxicity occurs when the rice plant accumulates iron in its leaves. Its occurrence is associated with a high concentration of ferrous iron in the soil solution (Ponnamperuma et al 1955). The critical iron concentration in the soil solution

3.25. Relationship between chlorophyll content and iron concentrations in the leaf blades (LB) (Takagi 1960).



varies with the pH, and is about 100 ppm at pH 3.7 and 300 ppm or higher at pH 5.0 (Tanaka et al 1966b). Characteristic symptoms of iron toxicity may be observed when the iron content in leaf blades is higher than 300 ppm (Tanaka et al 1966b). High concentrations of iron in the soil solution decrease absorption of other nutrients, such as phosphorus and potassium (Table 3.28).

The production of hydrogen sulfide and ferrous sulfides in flooded soils under highly reduced conditions may contribute to iron toxicity. Hydrogen sulfide and ferrous sulfides lessen the oxidizing capacity of rice roots, thereby increasing the susceptibility of the rice plant to iron toxicity (Tanaka et al 1968, Inada 1966b). Applications of ammonium sulfate increase the incidence of iron toxicity under certain conditions (Inada 1966a).

The plant's nutritional status affects its tolerance for iron toxicity (Table 3.29). Potassium, calcium, magnesium, phosphorus, and manganese deficiencies decrease the iron-excluding power of rice roots. Since calcium, magnesium, and manganese deficiencies do not normally occur in irrigated rice, potassium deserves special attention. Potassium-deficient plants often have a high iron content and exhibit severe symptoms of iron toxicity.

Table 3.28. Effect of iron supply on growth and nutrient content of the rice plant.^a

Iron concn in culture solution (ppm)	Dry wt (g/plant)	Nutrient content			
		Fe (ppm)	N (%)	P (ppm)	K (ppm)
2	6.8	148	3.22	0.35	3.12
75	2.8	341	3.47	0.30	3.06
150	0.9	785	2.96	0.21	2.42
300	0.2	1602	2.52	0.13	1.30

^aIshizuka and Tanaka (1969).

Table 3.29. Absorption and translocation of iron, and iron-excluding power of the rice plants grown in culture solution deficient in various nutritional elements.^a

Status of plant	Iron content (ppm)			Translocation percentage of iron ^b	Iron-excluding power ^c (%)
	Upper leaves	Lower leaves	Culm stem		
Complete	423	732	390	3.5	60
– N	398	830	495	2.5	60
– P	458	864	407	3.7	30
– K	617	983	808	4.5	20
– Ca	544	910	413	4.6	22
– Mg	602	998	480	5.5	27
– Mn	601	826	570	5.4	38

^a Tadano (1976). ^b Amount of iron translocated to the shoot relative to the total amount of iron absorbed by the plant. ^c Defined as formula: $(a - b)/a \times 100$ (%), where *a* is the amount of iron, in milligrams, contained in the same volume of culture solution as that of water absorbed by the plant and *b* is the amount of iron, in milligrams, actually absorbed by the plant.

3.11.5. Varietal performance on iron-deficient and iron-toxic soils

Some degree of varietal difference in the ability to absorb iron appears to exist (Fig. 3.26). When 12 rice varieties were grown on synthetic soil with different moisture regimes and at different pH values, plant color differed greatly, as illustrated by the chlorophyll content of leaves. Variety Tetep showed a consistently high ability to absorb iron from the synthetic soil. Varieties also differ in their tolerance for iron toxicity (Ponnamperuma 1976a).

3.12. MANGANESE

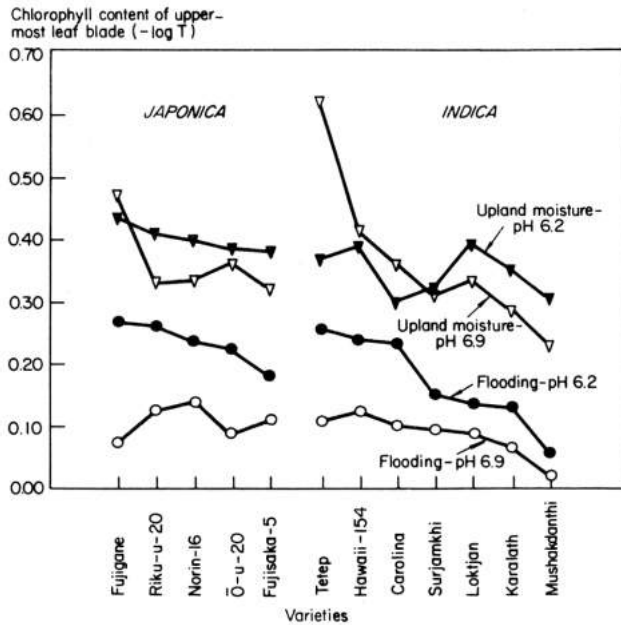
3.12.1. Occurrence of deficiency and toxicity

Manganese deficiency and toxicity seldom occur in field-grown rice. There are, however, reports on manganese deficiency of lowland rice grown on highly degraded paddy soils in Japan (Hashimoto and Kawamori 1951) and manganese toxicity from areas affected by manganese mining (Iwata 1975).

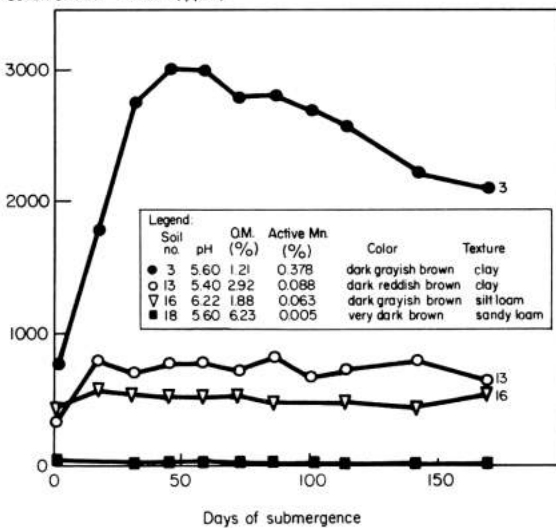
3.12.2. Manganese in soil solution

Concentrations of manganese in the soil solution increase after submergence (Fig. 3.27). Manganese is more readily reduced and rendered soluble than iron. The release of manganese into the soil solution, therefore, precedes that of iron. This increase in availability of manganese is beneficial for rice at a near-neutral pH. In solution culture, 0.1–0.5 ppm Mn is sufficient for maximum rice growth and concentrations higher than 10 ppm are toxic (Ishizuka et al 1961, Tanaka and Navasero 1966a).

3.26. Effect of pH and moisture content of synthetic soil medium on the chlorophyll content of the leaf blades of rice, especially on the difference in the effect between the varieties (Takagi 1960).



Concn of Mn^{++} in soil (ppm)



3.27. Changes in concentration of Mn^{++} in the soil (Ponnamperuma 1965).

3.12.3. Characteristics of manganese nutrition

A comparison between the rice plant's requirement for manganese in solution culture and manganese concentrations in soil solution suggests that a manganese

deficiency is unlikely but toxicity may occur. There are several reasons, however, why manganese toxicity in lowland rice is uncommon (Tadano and Yoshida 1978):

- Rice roots have a high degree of manganese-excluding power. In solution culture, the tissue manganese content increases only four fold with rice plants grown at 300 ppm Mn compared with those grown at 0.1 ppm Mn. It is 109 times for barley and 700 times for radish (Tanaka et al 1975).
- Rice tolerates a high manganese content. The critical tissue content for manganese toxicity is 700 ppm for beans, 1,200 ppm for barley, and 7,000 ppm for rice (Cheng and Quallette 1971).
- Compared with nitrate, ammonia has a retarding effect on manganese uptake (See Table 3.18).
- A high level of iron in submerged soils may counteract an excessive manganese uptake (Ishizuka et al 1961).

In many cases, a high manganese content in rice tissues is frequently associated with high yields, possibly indicating that a high manganese content in the soil is associated with various favorable soil conditions.

3.13. SULFUR

3.13.1. Occurrence of deficiency

Sulfur deficiency is a common nutritional disorder in upland crops but it rarely occurs in lowland rice. Sulfur deficiency of lowland rice has been reported from Mandalay, Burma (Aiyar 1945); the Lower Amazon Basin, Brazil (Wang et al 1976a, b); and South Sulawesi, Indonesia (Mamaril et al 1979). A recent trend in the fertilizer industry to shift from ammonium sulfate to urea and from superphosphate to nonsulfur phosphatic fertilizer may induce more widespread sulfur deficiency in lowland rice.

3.13.2. Sulfate in soil solution

Sulfate is reduced to sulfide in flooded soils. As a consequence, the soil sulfate concentration declines rapidly and is associated with a sulfide accumulation (Fig. 3.28). Thus, the availability of soil sulfur decreases as soil reduction proceeds (Nearpass and Clark 1960).

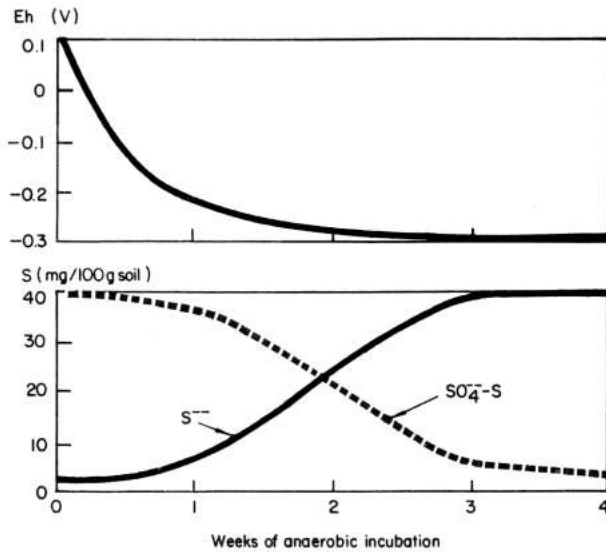
The rate of sulfate reduction in submerged soils depends on soil properties. Concentrations as high as 1,500 ppm SO_4^{2-} in neutral and alkaline soils may be reduced to zero within 6 weeks of submergence (Ponnamperuma 1972).

3.13.3. Natural supply of sulfur

Sources of natural sulfur are soil, irrigation water, and atmospheric precipitation.

a. Soil. Soil contains sulfur in organic and inorganic forms. The *A value*, to assess the available sulfur in submerged soils, is highly correlated with the soil sulfur extractable with Ca (H_2PO_4)₂ or KH_2PO_4 solution (Suzuki 1978). Hence,

3.28. Relationship between Eh and sulfate reduction (Yamane and Sato 1961).



the extraction procedures can be used to estimate the available soil sulfur for lowland rice.

b. Irrigation water. Irrigation water is an important source of sulfur to irrigated rice. The sulfate content in irrigation and river waters ranges from 0.2 ppm in Jari River, Brazil, to 4.7 ppm for the average of river waters in Japan (Table 3.30). If 1,000 mm water is used for a rice crop, 1 ppm S in the irrigation water supplies 10 kg/ha during the entire growth cycle. A little less than 2 kg/ha is required to produce 1 t rice from an improved variety (see Table 3.11). This calculation clearly indicates the importance of sulfur provided by irrigation water.

c. Atmosphere and precipitation. Fumes from active volcanoes, burning trees, and grasses in shifting agriculture, fumes from chemical plants, exhausted gases

Table 3.30. Sulfur content in irrigation and river waters.

Location	Sulfur (ppm)
IRRI, Philippines, irrigation water	2.3
Bulacan, Philippines, irrigation water	3.9
Ngale, Indonesia, irrigation water	0.9
Jari River, Brazil ^a	0.2
Japan, river waters ^b	4.7
Thailand, river waters ^b	1.1
Asia, river waters ^c	2.8
World, river waters ^c	4.1

^a Wang, et al (1976b). ^b Kobayashi, J. (1958).

^c Livingstone (1963).

Table 3.31. Effect of sulfur on dry weight of tops and sulfate-S, organic-S, total-S, and percent dry weight of blade-3 from greenhouse (GH) and outdoor (OD) alfalfa. Means of 5 replications.^a

Sulfate S (mg)	Dry wt				Blade-3					
	Tops		Blade-3		Greenhouse			Outdoors		
	GH (g)	OD (g)	GH (%)	OD (%)	SO ₄ -S (ppm)	Organic-S (ppm)	Total-S (ppm)	SO ₄ -S (ppm)	Organic-S (ppm)	Total-S (ppm)
0	2.1	7.2	20.5	17.6	44	700	750	156	1240	1400
20	22	26	20.9	18.4	49	990	1040	113	1240	1350
40	39	38	20.9	18.8	44	1130	1170	100	1380	1480
80	61	63	21.5	20.6	57	1500	1560	98	1580	1680
120	64	73	21.7	20.8	96	2300	2400	113	1740	1860
160	70	79	20.4	19.5	210	2610	2820	150	2380	2530
320	81	91	20.8	19.6	1250	3430	4690	840	3120	3960
640	75	93	20.9	20.5	1870	3500	5370	1540	3420	4970
1280	78	89	21.3	20.7	2070	3100	5170	1680	3340	5020
2560	70	91	19.8	20.1	2080	3320	5400	1780	3410	5190

^aUlrich et al (1967).

from cars, and burning of disposed materials release sulfur oxide into the atmosphere. The sulfur may be absorbed directly through the leaves, be dissolved in rain water, fall onto the ground, and be absorbed through the roots. Radioactive sulfur has been used to show that the plant can absorb SO₂ through its leaves (Thomas et al 1944).

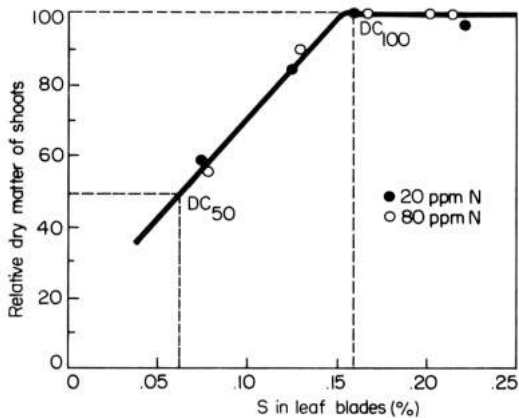
To illustrate the importance of atmospheric sulfur as a sulfur source for plants, alfalfa plants were exposed to unfiltered air and to air filtered through thin beds of activated carbon (Table 3.31). Air-borne sulfur was absorbed by alfalfa, resulting in a significant increase in growth and in the concentration of sulfate S and organic S when the sulfur supply was low.

The amount of sulfur brought by precipitation ranges from 0.1 to 140 kg/ha per year (Fried and Broeshart 1967). The large amount of sulfur in precipitation comes primarily from burned fossil fuels, particularly in industrial centers where SO₂ and other gaseous sulfur compounds are continuously released into the atmosphere. The quantities of sulfur in precipitation in rural areas are usually low.

3.13.4. Critical sulfur content and critical N-S ratio at different growth stages

Two critical levels can be graphically defined (Fig. 3.29): the critical sulfur content and the critical N-S ratio in plant tissues required to obtain maximum dry weight (DC₁₀₀), and the critical sulfur content and the critical N-S ratio in plant tissues to obtain 50% of the maximum dry weight (DC₅₀). The critical sulfur content in straw for the maximum dry weight vanes from 0.16% at the tillering stage to 0.07% at flowering and to 0.06% at maturity (Table 3.32).

3.29. Relationship between relative dry matter of shoots and percentage of sulfur in leaf blades at tillering stage (Yoshida and Chaudhry 1979).



The critical N-S ratio in straw for the maximum dry weight also varies from 23 at tillering to 13 at maturity. The critical N-S ratio required to achieve 50% of the maximum dry weight ranges from 63 at flowering to 40 at maturity. Thus, both critical sulfur content and critical N-S ratios vary with the growth stage of the rice plant.

Since determining the N-S ratio requires extra cost to the single sulfur analysis, the sulfur content in plant tissues is considered a better tool for diagnosing sulfur status in the rice plant.

3.14. SILICON

3.14.1. Occurrence of deficiency

Essentiality of silicon in rice is still open to question. Increased absorption of silicon, however, appears to increase rice's resistance to some environmental

Table 3.32. Critical sulfur contents and N-S ratios at different growth stages. ^a

Growth stage	Critical sulfur (%)				Critical N-S ratio			
	Leaf blades		Straw		Leaf blades		Straw	
	DC ₅₀	DC ₁₀₀	DC ₅₀	DC ₁₀₀	DC ₅₀	DC ₁₀₀	DC ₅₀	DC ₁₀₀
Tillering	0.06	0.16	0.06	0.16	45	29	44	23
Flowering	0.05	0.10	0.04	0.07	52	24	63	23
Harvest	0.04	0.07	0.03	0.06	25	16	40	13

^a Yoshida and Chaudhry (1979). DC₅₀ is the critical sulfur content, or critical N-S ratio, in plant tissue required to obtain 50% of the maximum dry weight. DC₁₀₀ is the critical sulfur content, or critical N-S ratio, in plant tissue required to obtain maximum dry weight.

stresses (Yoshida 1975b).

The application of a silicate slag to degraded paddy soils and peaty soils in Japan and Korea has been found beneficial to rice yields. Yield increases are usually around 10% but may exceed 30% when blast disease is severe.

3.14.2. Silicon in soil solution

Silicon dissolved in an aqueous solution exists as orthosilicic acid, $\text{Si}(\text{OH})_4$. Because silica sol or silica gel derives from the condensation polymerization of orthosilicic acids, orthosilicic acid is sometimes called a *monomer* or a *monomeric* form of silica. The term silica refers to SiO_2 .

The concentration of silicon in the soil solution generally increases with flooding and soils with a high organic matter content give the highest increases (Ponnamperuma 1965). The concentration of silicon extractable with dilute acids shows a more rapid increase with flooding than that of silicon in the soil solution. Readily soluble silicon in the soil is perhaps present as absorbed on or as combined with amorphous aluminum and ferrous hydroxide (Imaizumi and Yoshida 1958, McKealgie and Cline 1963). Soils derived from volcanic ash have high levels of soluble silicon and high silicon-supplying power.

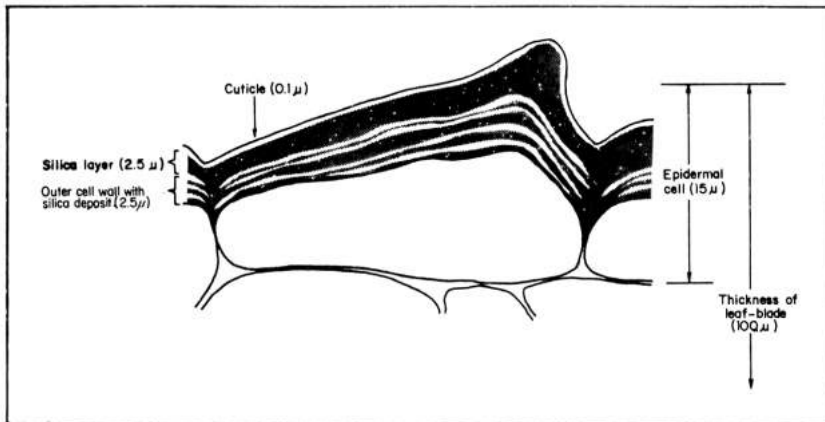
3.14.3. Functions of silicon

The functions of silicon in rice growth are still not clearly understood (Yoshida 1975b).

First, the level of silicon in the plant at which growth is improved by additional silicates is much higher in the field than in solution culture. In the field, an application of silicates is considered beneficial when the silica content of straw is below 11% (Imaizumi and Yoshida 1958). In solution culture, however, the addition of silicon has little effect on vegetative growth when silica content in the leaves is 0.07% (Yoshida et al 1959); it has no effect on rice growth and yield when the silica content of green leaves is above 1.25% (Tanaka and Park 1966). Second, low-silicon plants are susceptible to various kinds of diseases and attacks by insects and mites (Yoshida et al 1962). It is difficult to keep such plants free from these hazards. Third, no direct evidence of the participation of silicon in essential physiological and biochemical processes has yet been found.

Although the results and interpretation of several studies differ, silicon appears to have the following functions in rice growth:

- Increased silicon absorption protects plants against infestations of fungi and insect attacks (Yoshida et al 1962). A thick cuticle-silicon layer (Fig. 3.30) serves as a barrier against fungi, insects, and mites because of its physical hardness. Entomologists have found that the mandibles of rice borer larvae fed on rice plants with a high silicon content were damaged.
- Increased silicon absorption maintains erect leaves (Yoshida et al 1969; Cock and Yoshida 1970). The importance of leaf angle to photosynthesis by a crop canopy is well recognized; erect leaves are desirable in a high yielding rice variety. Although leaf angle is mainly a varietal characteristic, it is affected by



3.30. Schematic representation of the rice leaf epidermal cell (Yoshida 1965).

plant nutrition. In general, nitrogen tends to make rice leaves droopy while silicon keeps them erect. A simulation method estimates that total photosynthesis varies by as much as 36% within a range of leaf angle from 40 to 70°. In other words, the maintenance of erect leaves as the result of silicate application can easily account for a 10% increase in the photosynthesis of the canopy and consequently a similar increase in yields.

- Increased silicon absorption decreases transpiration losses, perhaps through the cuticle, and increases the plant's tolerance for decreased osmotic potential in the rooting medium (Yoshida 1965).

- Increased silicon absorption increases the oxidizing power of rice roots and decreases the excessive uptake of iron and manganese (Okuda and Takahashi 1965; Tadano 1976).

3.14.4. Interrelationship between silicon and nitrogen nutrition

When the amount of nitrogen application is increased, the rice plant becomes more susceptible to diseases and insects and the leaves tend to droop. The silicon content of the rice plant is very much affected by nitrogen applications and, hence, by increased growth (Table 3.33). Increasing the amount of nitrogen application increases grain yield and the total uptake of nitrogen and silicon but decreases the silicon content in the straw. This relationship is more pronounced in pot experiments than in the fields. When the silicon-supplying power of the soil is low and when application of nitrogen is increased to achieve high yields, a similar decrease in silicon content in the rice plant may occur even in the field.

3.14.5. Criteria for determining the need for silicate application

The silica contents of straw in Japan range from 4 to 20% and average 11%. Applications of silicates are normally considered beneficial when the silica content

Table 3.33. Effect of nitrogen application on grain yield and on nitrogen and silica absorption by rice grown on Konosu soil in pots. ^a

Nitrogen level (g/pot)	Grain yield (g/pot)	Nutrient content in straw (%)		Total amount of nutrients absorbed (mg/pot)	
		N	SiO ₂	N	SiO ₂
0	17.3	0.62	13.70	240	2275
1	33.1	0.57	8.80	488	3518
2	54.1	0.57	6.27	819	5274
4	82.8	0.77	6.49	1607	6974

^a Shiroshita et al (1962).

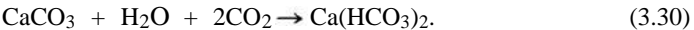
in straw is lower than 11%. A simple soil test is available for the diagnosis (Table 3.34).

The above criteria assume that the beneficial effects of silicate applications on rice yield are attributed to the silicon contained in silicate slags. This assumption, however, may not always be true because these slags contain something other than silicon.

First, silicate slags are as good a liming material as calcium carbonate. A silicate slag applied to soil undergoes the following chemical change:



This is compared with calcium carbonate:



Second, some slags contain about 20% magnesium and about 10% manganese, which may be beneficial to rice growth when soils are deficient in those nutrients. For these reasons, the application of silicate slags may increase rice yields even though the silicon content is high both in the plant and in the soil.

3.15. HYDROGEN SULFIDE

3.15.1. Occurrence of toxicity

A physiological disorder of rice attributed to sulfide toxicity was first reported in Japan by Osugi and Kawaguchi in 1938. Later, *Akiuchi*, a well-known nutritional disorder of rice in Japan, was partly attributed to hydrogen sulfide toxicity. *Akiuchi* occurs mainly on sandy, well-drained, degraded paddy soils low in active iron, and poorly drained organic soils (Baba and Harada 1954, Baba et al 1965, Mitsui 1960, Tanaka and Yoshida 1970).

Straighthead is one of the most destructive diseases of rice in the southern USA. Recent reports suggest that it is caused by hydrogen sulfide toxicity (Allam et al 1972, Allam and Hollis 1972).

Table 3.34. Criteria for predicting slag (calcium silicate) needed for a paddy field.^a

Soil class	SiO ₂ content in rice straw at harvest (on a dry-matter basis) (%)	Available SiO ₂ content in soil (mg/100 g soil)	Rice-yield response to slag application
I	Less than 11	Less than 10.5	A profitable increase with the highest probability
II	11–13	10.5–13	A profitable increase expected in many cases but not in others
III	More than 13	More than 13	No profitable increase expected

^aImaizumi and Yoshida (1958).

3.15.2. Hydrogen sulfide in soil solution

Sulfate is reduced to H₂S in submerged soils (see Fig. 3.1, 3.30). The concentration of free H₂S, however, may be very low because of the formation of insoluble sulfides, chiefly, FeS:



Ferrous sulfides are not toxic to rice; however, free hydrogen sulfide is toxic.

Depending on solution pH, H₂S, HS⁻, and S²⁻ can exist in different concentrations. The relationships between these three species of free sulfides are given in the following equations:

$$p\text{HS}^- = p\text{H}_2\text{S} - p\text{H} + 7.0. \quad (3.32)$$

$$p\text{S}^{2-} = p\text{H}_2\text{S} - 2\text{pH} + 20.9. \quad (3.33)$$

Equation 3.32 can be easily converted to:

$$\frac{[\text{H}_2\text{S}]}{[\text{HS}^-]} = [\text{H}^+] \times 10^7 \quad (3.34)$$

The ratio of H₂S to HS⁻ varies with solution pH from 10 at pH 6.0 to 1 at pH 7.0. Similarly, equation 3.33 is converted to:

$$\frac{[\text{H}_2\text{S}]}{[\text{S}^{2-}]} = [\text{H}^+]^2 \times 10^{20.9} \quad (3.35)$$

It is obvious from equation 3.35 that the concentration of S²⁻ is negligible compared with that of H₂S within pH range from 4 to 8. Thus, H₂S is the most dominant species in the soil pH range usually encountered. HS⁻ can be present in the same quantity as H₂S at pH 7.0; it is negligible at pHs lower than 6.0.

The occurrence of hydrogen sulfide toxicity in rice in flooded soils has been a subject for controversy. There are two approaches by which to determine whether

free hydrogen sulfide can really be present in concentrations toxic to rice in the soil solution of submerged soils.

The first approach is to calculate H_2S concentrations based on the chemical equilibria. As is understood from equation 3.31, the concentration of H_2S increases with a decrease in pH:

$$p \text{ H}_2\text{S} = 2 \text{ pH} - p \text{ Fe}^{2+} - 3.52. \quad (3.36)$$

Similarly, the concentration of Fe^{2+} also increases with a decrease in pH:

$$p \text{ Fe}^{2+} = 2 \text{ pH} - 10.8. \quad (3.37)$$

Combining these two equations:

$$\begin{aligned} p \text{ H}_2\text{S} &= 2 \text{ pH} - (2 \text{ pH} - 10.8) - 3.52 \\ &= 10.8 - 3.52 = 7.28. \end{aligned} \quad (3.38)$$

$$\begin{aligned} [\text{H}_2\text{S}] &= 10^{-7.28} \text{ mol/liter} = \text{constant} \\ &= 5 \times 10^{-8} \text{ mol/liter} = 0.0017 \text{ ppm}. \end{aligned} \quad (3.39)$$

Thus, in the presence of sufficiently large amounts of ferrous iron such as in latosolic soils, the concentration of H_2S is independent of solution pH, and that concentration is far below the critical toxic level (Ponnamperuma 1965). H_2S toxicity, however, may occur in soils low in free iron oxides, such as degraded paddy fields in Japan.

Tanaka et al (1968a) considered the $\text{FeCO}_3 - \text{FeS}$ system in the presence of the high partial pressure of carbon dioxide in submerged soils. High concentrations of both ferrous iron and hydrogen sulfide can be present in the soil solution provided carbon dioxide is produced faster than hydrogen sulfide. FeS is converted to FeCO_3 by carbon dioxide and, as a consequence, free hydrogen sulfide comes into solution. Thus, two theoretical considerations lead to entirely different conclusions.

The second approach is to measure hydrogen sulfide concentrations experimentally. The most common method to measure free hydrogen sulfide in the laboratory is to bubble the incubated soil with nitrogen (Suzuki and Shiga 1953, Yamane

Table 3.35. Free hydrogen sulfide (H_2S) formation in a degraded paddy soil under laboratory conditions.^a

Amount of ferric hydroxide added (g/100 g soil)	H_2S formed (mg S/100 g soil) in soil incubated for				
	4 days	7 days	14 days	21 days	28 days
0	0.31	0.51	0.68	1.03	0.86
0.025	0.28	0.35	0.41	0.39	0.38
0.05	0.25	0.22	0.26	0.20	0.20
0.10	0.15	0.14	0.08	0.13	0.07
0.50	0.06	0.06	0.04	0.05	0.03
1.0	0.02	0.08	0.03	0.03	0.02
2.0	0.02	0.04	0.00	0.03	0.02

^a Shiga (1962).

and Sato 1961) or argon (Connell and Patrick 1969). The evolved hydrogen sulfide can be collected in an appropriate solution and measured by colorimetry or by iodometry. In Table 3.35 free hydrogen sulfide is expressed in milligrams of sulfur per 100 g soil. Assuming that the water content of this system is 200% (which is an overestimation), the estimated concentration of hydrogen sulfide (mg/liter) in the soil solution will be obtained by multiplying the figures in the table by a factor of 5. Free hydrogen sulfide concentrations would then range from 0 to 5.2 ppm, which are quite high compared with the critical concentration of 0.07 ppm. The displacement technique may overestimate the concentration because it pushes the direction of the equilibrium in favor of increasing free hydrogen sulfide. Table 3.35 also indicates that additions of ferric hydroxide markedly decrease the concentration of free hydrogen sulfide in a degraded paddy soil.

The total sulfide concentration can be measured by directly introducing a reacting agent into the soil solution. The concentrations of total sulfide measured by this method ranged from 0.29 to 0.37 ppm in the presence of 300 ppm of ferrous iron at pH 6.5 for a latosolic soil (Tanaka et al 1968a), and from 1.1 to 1.5 ppm in the presence of 100–200 ppm of ferrous iron at pH 6.2 for an Akiuchi soil in Korea (Park and Tanaka 1968).

The most recent technique is to simultaneously measure solution pH and sulfide ions (S^{2-}) with an ion-selective electrode. The concentration of free hydrogen sulfide is calculated by the following formula:

$$pH_2S = 2 \text{ pH} + pS^{2-} - 20.9. \quad (3.40)$$

This technique can be used for in-situ measurement of free hydrogen sulfide in the field (Allam et al 1972). When this method was applied to rice fields in Louisiana, USA, the concentrations of free hydrogen sulfide ranged from 5×10^{-5} to 0.64 ppm with a mean concentration of 0.104 ppm for 53 sites; higher than 0.1 ppm was found in 16 out of 53 sites. These measured concentrations of free hydrogen sulfide were 3 to 10,000 times higher than expected from the theoretical calculation.

3.15.3. Varietal differences in tolerance for hydrogen sulfide toxicity

Rice shows some variation in Akiuchi resistance (Baba 1955, Yamaguchi et al 1958, Shiratori et al 1960). Growth differences in Akiuchi soils are related to the root's capacity for oxidizing hydrogen sulfide and to the degree of starch accumulation in the basal culm. The resistance to straighthead is also related to the oxygen-release capacity of varieties. In a study by Joshi et al (1975), the oxygen-release capacity of 26 varieties ranged from 0.19 to 1.25 $\mu\text{l/min}$. Thus, the tolerance of rice varieties for hydrogen sulfide toxicity appears to relate to the oxygen-release capacity or to the roots' oxidizing power.

3.16. ORGANIC ACID

3.16.1. Occurrence of toxicity

Organic acid toxicity may occur in organic soils and poorly drained soils, and

when large quantities of fresh organic materials such as green manures and straw are incorporated.

3.16.2. Organic acid in soil solution

The concentration of organic acids increases with flooding, reaches a peak, and then decreases to practically nothing (Fig. 3.1, Section 3.31).

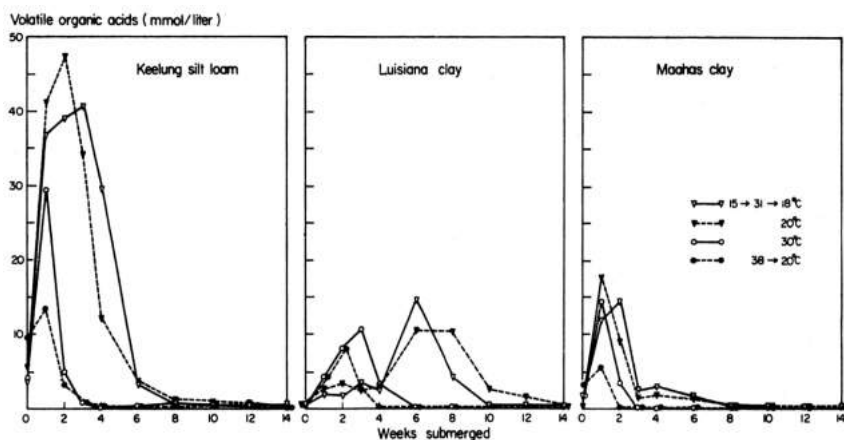
Organic acids such as formic, acetic, propionic, and butyric acids occur in submerged soils. Acetic acid is generally the major organic acid produced (Motomura 1962; Takai and Kamura 1966). Incorporation of organic matter such as green manure, glucose, and straw promotes the production of organic acids in submerged soils (Onodera 1929; Takijima and Sakuma 1961; Motomura 1961, 1962; Ishikawa 1962; Gotoh and Onikura 1971).

Soil temperature has a significant influence on the kinetics of organic acid production. Low temperature leads to a strong accumulation of organic acids (Fig. 3.37; Yamane and Sato 1967; Cho and Ponnampereuma 1971), which suggests that organic acid toxicity is more likely to occur at low temperatures. Low temperatures may also aggravate the harmful effects of organic acids by retarding increases in soil pH. As soil pH decreases, the proportion of injurious undissociated acid increases, as explained in the next section.

3.16.3. Mode of toxicity

High concentrations of organic acids impair root elongation, respiration, and nutrient uptake in rice.

Aliphatic organic acids are toxic to rice at concentrations of 10^{-2} to 10^{-3} M, depending on the kind of acid (Mitsui et al 1959a, Takijima 1963). For monobasic acids, the toxicity increases with increasing molecular weights. The toxicity of polybasic acids and hydroxy acids is much milder than that of the monobasic acids.



3.31. Influence of temperature on the kinetics of volatile organic acids (Ponnampereuma 1976).

Aromatic organic acids are much more toxic to rice than aliphatic organic acids (Takijima 1963). However, the production of aromatic organic acids in submerged soils is not well investigated.

Because organic acids are weak acids, dissociation of the acid is strongly influenced by the solution pH:



A large fraction of the acid exists in the dissociated form at high pHs, while the undissociated form of the acid prevails at low pHs. For example, the dissociation of acetic acid is described as:



$$K_a = \frac{[\text{CH}_3\cdot\text{COO}^-][\text{H}^+]}{[\text{CH}_3\cdot\text{COOH}]} = 1.75 \times 10^{-5} \quad (3.43)$$

or

$$\text{p}K_a = 4.76 \quad (3.44)$$

At pH 4.76, concentrations of the dissociated ($\text{CH}_3\cdot\text{COO}^-$) and the undissociated forms ($\text{CH}_3\cdot\text{COOH}$) become equal.

The relative proportion of the dissociated and the undissociated forms at different pHs can be easily obtained by converting the above formula to:

$$\frac{K_a}{[\text{H}^+]} = \frac{[\text{CH}_3\cdot\text{COO}^-]}{[\text{CH}_3\cdot\text{COOH}]} \quad (3.45)$$

Thus, the ratio varies from 10^{-1} at pH 3.76 to 1 at pH 4.76, to 10 at pH 5.76 and to 10^2 at pH 6.76.

The undissociated form of the acid at low pHs is absorbed by excised roots faster than the dissociated form and appears to be toxic to rice (Tanaka and Navasero 1967). At pH 4, organic acids impair the respiratory rate of rice roots while at pH 7 they do not (Table 3.36). In submerged soils, the soil pH tends to become 6.5 to 6.7 within 3 weeks of submergence (Ponnamperuma 1965). Organic acid toxicity is unlikely to occur at near-neutral pH.

Whether a toxic level of organic acids could accumulate in submerged soils is still an unsettled question.

Mitsui et al (1959b) found the concentration of all organic acids was 4×10^{-3} N in the leachate from pot experiments. They speculated that this concentration could be toxic to rice if all the acids were butyric acid, which is unlikely under most conditions. There is also a suggestion that organic acids could be toxic in neutral submerged soils because the pH of the rice rhizosphere might be much lower than the pH of the rest of the soil (Chandrasekaran and Yoshida 1973).

The kinetics of organic acid formation in the soil solution led Takijima and Sakuma (1961) to conclude that concentrations could be high only for a short time

Table 3.36. Effect of solution pH and organic acid on respiratory rate of rice roots.^a

Treatment	Respiratory rate ($\mu\text{l O}_2/\text{mg per h}$)	
	pH 4	pH 7
No organic acid added	6.52	4.27
Acetic acid (10^{-2} N)	1.49	3.63
Butyric acid (10^{-2} N)	1.45	3.73

^a Tanaka and Navasero (1967)

soon after submergence and that they would affect rice growth only slightly.

Most work on organic acids has been done in the laboratory or the greenhouse, which conditions may differ from the field. Gotoh and Onikura (1971) measured organic acids in soil collected from rice fields supplied with 0–15 trice straw/ha. They took into account the effects of pH values on the proportion of undissociated forms of organic acids in the soil solution. They concluded that the organic acids produced by straw are unlikely to be toxic to rice in southern Japan, where high temperatures prevent their accumulation.

Low soil pH, low soil temperature, high soil organic matter, and incorporation of fresh organic matter favor an accumulation of organic acids and their toxicity to rice. A combination of these factors may induce the toxicity of organic acids in rice under certain circumstances. Furthermore, it is possible for the concentration of organic acids to reach toxic levels around fragments of organic materials.

3.17. IODINE

3.17.1. Occurrence of toxicity

A nutritional disorder of rice is known to occur in some volcanic ash soils in northern Japan when upland fields are converted to lowland fields. The disorder is most conspicuous in the first year after conversion. Known as *reclamation Akagare disease* or Akagare type III (Baba et al 1965), the disorder disappears spontaneously after a few years of rice cultivation. Recent investigations reveal that iodine toxicity is the direct cause of this disease (Tensho 1970, Watanabe and Tensho 1970).

3.17.2. Iodine in soil solution

The chemical transformation of soil iodine is governed by the redox potential (Tensho 1970):



Iodine (I_2) is insoluble in water and is held by soil organic matter under upland conditions. Under lowland (reductive) conditions, iodine is converted to iodide,

which is soluble in water, and the iodide concentration in the soil solution increases. The concentration of iodide in soil solution was found to be as high as 0.7–3 ppm when iodine toxicity symptoms were observed. This concentration is far greater than the 0.05 ppm normally found in river and sea waters. In water culture experiments, iodine toxicity symptoms were induced at a concentration of about 1 ppm (Watanabe and Tensho 1970).

3.17.3. Plant's response to iodine toxicity

Visible symptoms of iodine toxicity begin to appear a few weeks after transplanting, and they are similar to those of zinc deficiency and iron toxicity (see Chapter 4). The alkali soluble iodine content of the affected plants is about 30–40 ppm; healthy plants usually contain less than 10 ppm. Clear varietal differences in tolerance for iodine toxicity have been recorded (Watanabe and Tensho 1970).

3.18. SALINITY

3.18.1. Occurrence of salinity

Salinity is defined as the presence of excessive concentrations of soluble salts in the soil. Major ionic species of salts are sodium, calcium, magnesium, chloride, and sulfate. Among those, sodium chloride is predominant. Salinity occurs in two distinctly different regions: coastal regions and arid and semiarid regions. In the coastal regions, salinity is induced by inundation of sea water; the salinity is often associated with low soil pH. In the arid and semiarid regions, salinity occurs mostly in canal-irrigated areas. Evapotranspiration is very high in the arid and semiarid regions and, as a consequence, water movement is upward, resulting in the accumulation of salts in the root zone. Such saline soils can be easily recognized by the white salt crusts on the soil surface. This type of salinity is often associated with high pH.

In relation to salinity, two soil types are recognized in the arid and semiarid regions.. Saline soils normally refer to soils with pH lower than 8.5 and electric conductivity of the saturation extract greater than 4 mmho/cm at 25°C. Sodic soils are defined in terms of exchangeable sodium percentage (ESP). A soil may be considered sodic if ESP is more than 6, and strongly sodic if the ESP is greater than 15 (Bhumbla and Abral 1978).

3.18.2. Salts in soil solution

Electric conductivity of either the saturation extract or soil solution collected from the root zone is normally measured to quantify the degree of salinity. For rice growing in flooded soils, the two conductivities can be considered comparable. For upland crops and when soil moisture content is about field capacity or below, electric conductivity of the soil solution will be about twice as great as that of the saturation extract (Pearson 1959).

When salinity is moderate, electric conductivity of the saturation extract (ECe) is related to osmotic potential by the following formula:

$$\text{Osmotic potential (in atm)} = 0.36 \times \text{ECe (in mmho/cm)}. \quad (3.47)$$

3.18.3. Physiological nature of salinity injury

When salinity is increased suddenly, water uptake by the plant may be temporarily impaired due to the low osmotic potential of the soil solution. However, the plant is able to reduce the osmotic potential of the cells to avoid dehydration and death. This process is called osmotic adjustment. Both tolerant and sensitive plants seem to adjust osmotically to saline solutions, but still their growth is suppressed in proportion to the osmotic potential of the solution. At present, the physiological causes of growth suppression by salinity are not well understood (Maas and Nieman 1978).

3.18.4. Critical salinity level and varietal difference in salinity tolerance

Rice is very tolerant of salinity during germination but very sensitive at the 1- to 2-leaf stage. Its salt tolerance progressively increases during tillering and elongation and decreases at flowering. Ripening appears to be little affected by salinity. For example, the California variety Caloro germinated at an electric conductivity of 20 mmho/cm, but sprouted seed failed to grow at 4 mmho/cm. Three- and 6-week-old seedlings survived even at 9 and 14 mmho/cm, respectively. The grain yield of Caloro was not appreciably affected by salinity at 4 mmho/cm, but was reduced by 50% at 8 mmho/cm (Pearson 1959, 1961). A considerable degree of varietal difference in salinity tolerance appears to exist. Examples of salt-tolerant varieties are Johna 349, Kala rata, Pokkali, Nonabokra, and Benisail (IRRI 1967, Datta 1972, Ponnampetuma 1977). Available data, however, indicate that the varietal response to different salinity values is complex (Table 3.37). At 4.5 mmho/cm, the relative yield of TN1 or IR8 is as good as or even greater than that of the salt-tolerant variety Nonabokra. At 12.5 mmho/cm, however, the relative yield of Nonabokra is significantly higher than that of either TN1 or IR8.

Table 3.37. Yields^a of 12 rice varieties at 4 levels of salinity.^b

Variety	Electric conductivity of soil solution (mmho/cm)			
	4.5	9.5	12.5	15.5
Patnai	74	71	22	0
Benisail	89	47	39	6
Kumaigare	59	32	9	0
Rupsail	43	38	20	0
Bokra	54	24	2	0
Nonabokra	63	58	35	7
Getu	47	43	18	2
O.C 1393	68	49	4	0
TN1	73	45	8	0
IR8	63	36	16	0
BPI 76	65	49	19	0
SR26B	44	36	3	0

^aYields are relative to control (nonsaline plot) in each variety.

^bComputed from De Datta (1972).

4

NUTRITIONAL DISORDERS

4.1. NUTRITIONAL DISORDERS VS PHYSIOLOGICAL DISEASES

The terms *physiological diseases* or *physiological disorders* were used to refer to nonpathogenic sicknesses of lowland rice in earlier publications (Baba and Harada 1954, Baba et al 1965, Takahashi 1959a, b, 1961). The causes of such physiological diseases were thought to be related to highly reductive soil conditions in paddy fields.

A later investigation revealed that disorders of lowland rice in Asia can be attributed to nutrient deficiencies or toxicities to elements or substances (Tanaka and Yoshida 1970). Thus, the term *nutritional disorders* is preferred for indicating nonpathogenic and nutrient-related disorders. The term *nutritional disorders* has a narrower and more specific meaning than *physiological disorders*. The word *physiological* can imply both nutritional disorders and stresses such as low- and high-temperature stresses.

4.2. OCCURRENCE OF NUTRITIONAL DISORDERS

4.2.1. Cause of nutritional disorders

Nutritional disorders are caused by a nutrient deficiency or toxicity to an element or substance. Under certain circumstances, deficiencies of more than two nutrients or toxicities to more than two elements or substances are compounded. The behavior of nutrients and toxic substances in submerged soils in relation to plant response has been discussed in the preceding chapter.

This chapter focuses on the diagnosis of nutritional disorders. However, before discussing the standard diagnostic techniques, two problems commonly encountered when we attempt to diagnose nutritional disorders will be examined: visible symptoms and nitrogen response.

4.2.2. Visible symptoms

The problem begins when unusual symptoms are observed on the rice plant in the field or when an extension specialist or farmer reports unusual symptoms. The unusual symptoms could be caused by diseases, insects, low or high temperatures, and nutrient deficiencies or toxicities.

Some disease symptoms are easily confused with those of nutritional disorders. Blast, Helminthosporium, Cercospora, and grassy stunt virus are common tropical-rice diseases that produce brown spots on the leaves. It is extremely difficult to differentiate between zinc deficiency and grassy stunt virus in the early stages of symptom development. For this reason, it is advisable to become familiar with disease symptoms and to consult pathologists when pathogenic diseases are suspected.

Unusual symptoms may attract attention when there is a shift from traditional varieties to improved ones. In the Kala Shah Kaku area near Lahore, Pakistan, there was a rice disorder locally known as Hadda or *bronzing* because of a brown discoloration of the leaves. This disorder had been known for many years but the symptoms were quite mild in local traditional varieties grown with little or no nitrogen. The symptoms became pronounced after the introduction of improved varieties, which are normally highly fertilized. It was later learned that the symptoms, due to zinc deficiency, were aggravated by increased applications of nitrogen because the rice plant requires more zinc at high nitrogen levels (Yoshida and Tanaka 1969, Yoshida et al 1970).

The unusual symptoms could also be caused by wrong management practices done by a farmer himself, such as inadequate application of chemicals.

4.2.3. Nitrogen response

Rice yield normally increases when the amount of nitrogen application is increased. If there is little or no yield increase in response to increased nitrogen application, there may be some problem involving variety, soil, or climate. One of the most popularly known examples comes from comparing traditional tall varieties with improved short varieties (Chandler 1968, De Datta et al 1968). Traditional tall varieties fail to yield more in response to increased nitrogen applications mainly because they tend to lodge at high nitrogen levels.

Even after the introduction of improved varieties, a rice crop may not respond to increased nitrogen (Table 4.1). At Dokri, Pakistan, the rice yield increased from 5.6 t/ha to 10.3 t/ha with increased nitrogen rates, whereas at Kala Shah Kaku, the yield decreased from 5.7 t/ha to 4.9 t/ha as nitrogen application was increased up to 134 kg N/ha. This negative response was later found to be due to zinc deficiency (Yoshida et al 1970).

Table 4.1. Fertilizer trial with IR8 at 2 locations in West Pakistan, 1966.^a

N-P ₂ O ₅ -K ₂ O (kg/ha)	Grain yield (t/ha)		
	at Dokri	at Kala Shah Kaku	
0-0-0	5.61	5.74	
0-45-45	7.14	5.48	
34-45-45	8.77	5.15	
67-45-45	9.24	5.57	
101-45-45	9.25	4.90	
134-45-45	10.27	4.94	

^a Yoshida et al (1970).

4.3. DIAGNOSTIC TECHNIQUES

4.3.1. Visible symptoms (Tanaka and Yoshida 1970, Yoshida 1975a)

a. What to observe. Symptoms are one way plants communicate; they are a kind of language. When plants are deficient in a nutrient or suffer toxicity of an element or substance, visible symptoms show up. A systematic method of observing the major plant parts—plant height, tillers, leaves, and roots—is advisable if visible symptoms are used for diagnosing nutritional disorders.

Plant height. Stunted growth is a common symptom for deficiency or toxicity. Unusually tall plants may be induced by Bakanae disease.

Tillers. Reduced tiller number is a common symptom for deficiency or toxicity.

Leaves. Chlorosis, necrosis (brown spots), and orange discoloration are common symptoms of deficiency or toxicity.

The mobility of nutrients within the plant and the position of the leaf on which the deficiency symptoms appear are interrelated. For a nutrient whose mobility is low, symptoms normally appear in upper leaves because the nutrient fails to move from lower to upper leaves where it is needed for active growth. Iron, boron, and calcium are examples of low mobile nutrients. On the other hand, when a nutrient is mobile, symptoms normally appear in the lower leaves. The lower leaves suffer nutrient deficiency because the nutrient is translocated upward. Nitrogen, phosphorus, potassium, and sulfur are examples of mobile nutrients.

Symptoms of element toxicity normally appear in the lower leaves, where the absorbed element accumulates more. Iron, manganese and boron toxicity symptoms appear first in the lower leaves.

There are two kinds of chlorosis: interveinal and uniform. Potassium and magnesium deficiencies cause interveinal chlorosis, whereas nitrogen and sulfur deficiencies produce chlorosis uniformly in the leaves.

Roots. When shoot growth is impaired, root growth is also poor because both are closely connected. Therefore, scanty root growth alone may not mean much.

Root color is affected by age (see Chapter 1) and soil iron content. A root is white when young and actively growing. When it is long and old, and when there is adequate iron in the soil, it is normally brown because of iron oxide deposits on the root surface. When the iron content in the soil is low, however, old roots remain white, pale, or grayish. Under extremely reductive conditions some roots or an entire root system becomes black, suggesting hydrogen sulfide injury. These roots turn brown when they are exposed to air. Roots and the soil mass from flooded soils may have a hydrogen sulfide smell. Hydrogen sulfide can be detected by using a piece of filter paper that has been impregnated with saturated basic lead acetate solution.

b. When to observe symptoms. The early stages of symptom development are the best time for observing visible symptoms. It is of little value to observe plants when the symptoms of the disorder have become so severe that the plants are almost dead.

Zinc deficiency in lowland rice usually appears within 2–3 weeks after transplanting or sowing. Later, the crop may recover spontaneously. When the deficiency is severe, plants may die or the symptoms may persist until flowering or longer. The problem field appears patchy because some plants die early while others survive and grow.

Iron toxicity symptoms may appear on plants grown on sandy soils adjacent to lateritic highlands 1–2 weeks after transplanting. Symptoms may also appear 1–2 months after transplanting and persist until flowering when iron toxicity occurs in peaty or boggy soils.

c. Deficiency symptoms

Nitrogen. Plants are stunted with limited tillers. Except for young leaves which are greener, leaves are narrow, short, erect, and yellowish green. Old leaves die when light straw colored.

Phosphorus. Plants are stunted with limited tillers. Leaves are narrow, short, erect, and dirty dark green. Young leaves are healthy and old leaves die when brown colored. A reddish or purplish color may develop on the leaves if the variety has a tendency to produce anthocyanin pigment.

Potassium. Plants are stunted, but tillering is only slightly reduced. Leaves are short, droopy, and dark green. The lower leaves at the interveins, starting from the tip, turn yellow and, eventually, dry to a light-brown color. Sometimes brown spots may develop on dark-green leaves.

Sulfur. The symptoms are very similar to and almost impossible to visually distinguish from those of nitrogen deficiency.

Calcium. The general appearance of the plant is little affected except when the deficiency is acute. The growing tip of the upper leaves becomes white, rolled, and curled. In an extreme case, the plant is stunted and the growing point dies.

Magnesium. Height and tiller number are little affected when the deficiency is moderate. Leaves are wavy and droopy due to expansion of the angle between the leaf blade and the leaf sheath. Interveinal chlorosis, occurring on lower leaves, is characterized by an orangish-yellow color.

Iron. Entire leaves become chlorotic and then whitish. If the iron supply is cut suddenly, newly emerging leaves become chlorotic.

Manganese. Plants are stunted but have a normal number of tillers. Interveinal chlorotic streaks spread downward from the tip to the base of the leaves, which later become dark brown and necrotic. The newly emerging leaves become short, narrow, and light green.

Zinc. The midribs of the younger leaves, especially at the base, become chlorotic. Brown blotches and streaks appear on the lower leaves, followed by stunted growth. Tillering may continue. The size of the leaf blade is reduced, but that of the leaf sheath is little affected. In the field, uneven growth and delayed maturity are characteristics of zinc deficiency.

Boron. Plant height is reduced. The tips of emerging leaves become white and rolled as in the case of calcium deficiency. The growing point may die in a severe case, but new tillers continue to be produced.

Copper. The leaves appear bluish green, and then become chlorotic near the tips. The chlorosis develops downward along both sides of the midrib; it is followed by dark-brown necrosis of the tips. The new, emerging leaves fail to unroll and appear needle-like for the entire leaf or, occasionally, for half the leaf, with the basal end developing normally.

Low silicon content. Leaves become soft and droopy.

d. Toxicity symptoms

Iron. Tiny brown spots appear on the lower leaves, starting from the tips and spreading toward the bases. These spots combine on interveins. Leaves usually remain green. In a severe case, the entire leaf looks purplish brown.

Manganese. The plant is stunted and tillering is often limited. Brown spots develop on the veins of the leaf blade and leaf sheath, especially on lower leaves.

Boron. Chlorosis occurs at the tips of the older leaves, especially along the margins. Large, dark-brown elliptical spots then appear. The leaves ultimately turn brown and dry up.

Aluminum. The interveinal chlorosis is orangish yellow. In severe cases, the chlorotic portions may become necrotic.

High salt injury. Growth is stunted and tillering reduced. Leaf tips become whitish and, frequently, some parts of the leaves become chlorotic.

Iodine. Small brown spots appear on the tips of lower leaves. These spots spread over the entire leaf, resulting in yellowish-brown or brown discoloration. The affected leaves eventually die.

4.3.2. Plant tissue analysis

The term *plant tissue analysis* usually refers to the inorganic analysis of plant tissues. However, analysis for some organic constituents and assay for enzyme activity have been proposed for the diagnosis of the nutrient status in plant tissues. The iodine test for starch in rice leaf sheaths and a simplified paper chromatography for asparagine in leaf blades are effective in determining a crop's need for nitrogen topdressing at panicle initiation (Kiuchi 1968, Ozaki 1955). An assay for

ribonuclease is useful for diagnosing zinc deficiency in orchard trees (Kessler 1961).

a. Units and expressions used for analytical results. In inorganic analysis, two units are commonly used on a dry weight basis:

Percentage (%): grams nutrient per 100 gram plant material

Parts per million (ppm): milligrams nutrient per kilogram plant material

Thus,

$$1\% = 10^4 \text{ ppm}$$

The expression of chemical form for analytical results varies among reports. In the old literature, analytical results are normally given in the form of oxides such as P_2O_5 and K_2O . In recent years, the trend is to use the elemental forms such as P and K. Under most conditions, convenience dictates which form to use. In greenhouse and laboratory studies, the elemental forms are preferred because they are simpler. Some scientists use milligram atom or microgram atom percent. These expressions may be useful in basic studies where, for example, the element content is related to an enzyme activity. However, they should be avoided in plant tissue analysis for diagnostic purposes and related greenhouse studies.

b. Sampling procedure. In sampling plant materials, problems are often encountered in determining which plant parts to sample, when to sample, and how to replicate the sampling.

The whole shoot, the leaf blades, or the *Y*-leaf (the most recently matured leaf blade) are normally used for tissue analysis in rice (Yoshida et al 1976). In most cases, deficiency or toxicity symptoms appear when plants are young and small; hence, the whole plants (excluding roots) may be sampled for chemical analysis. The grain is generally not suitable for diagnosis because its chemical composition is least affected by the nutrient supply.

The rice leaf sheath functions as a storage organ for potassium, and the potassium content of the leaf blade tends to be maintained at the expense of the leaf sheath. When the plant becomes deficient in potassium, a larger decrease occurs in

Table 4.2. Potassium content in different parts of the rice plant at panicle initiation.^a

Plant part	Position	K content (%) in	
		Normal plants	K-deficient plants
Leaf blade	Upper	2.90	1.51
	Lower	2.88	1.21
Leaf sheath	Upper	3.36	0.90
	Lower	3.68	0.52

^a Matsuzaka et al (1962).

the leaf sheath than in the leaf blade (Table 4.2). Therefore, it would be better to select the leaf sheath for diagnosis.

The most important point in selecting which plant part to sample is knowing the relationship of a nutrient in the selected plant tissue to plant performance such as dry weight or tillering. The sample should be collected when the plants are showing symptoms of a disorder. For example, symptoms of iron toxicity and zinc and phosphorus deficiencies are usually seen 2–4 weeks after transplanting.

In plant tissue analysis, analytical errors are much smaller than sampling errors. Yanagisawa and Takahashi (1964) studied sampling for a field-grown rice crop. The coefficient of variation (CV) for 7 nutrients in the straw ranged from 9 to 21% at maturity (Table 4.3). On the basis of the observed CV, the number of samples that should be taken to give the desired precision at a given CV was computed. In general, if a precision of 10% is desired, it is necessary to randomly collect 10–20 samples from the same field.

c. Soil contamination and sample preparation. Soil contamination is a serious source of errors in plant tissue analysis (Mitchell 1960). How seriously the results of plant tissue analysis could be affected by soil contamination depends on the ratio of a nutrient content in the soil to that in a plant sample and the percentage of soil contamination in the plant sample. For example, the soil-plant nutrient content ratio ranges from 0.5 in phosphorus to 10,000 in titanium (Table 4.4). Assuming that the soil contamination is 0.5% in the sample and the soil-plant nutrient content ratio for a given nutrient is 10, the nutrient content in the sample would be affected by about 5%, as illustrated below:

$$\begin{aligned} C_p \times 0.995 + C_s \times 0.005 &= C_p \times 0.995 + C_p \times 0.05 \\ &= 1.045 \times C_p \end{aligned}$$

where C_p and C_s are nutrient contents in plant and soil, respectively. In other words, when the soil-plant nutrient content ratio is less than 10, a 0.5% soil contamination would not seriously affect the analytical results of the sample. It is not difficult to maintain this degree of cleanliness in routine sample preparation. However, if the soil-plant nutrient content ratio is more than 100, soil contamina-

Table 4.3. Coefficient of variation (CV) for straw analysis for 7 nutrients in a rice crop at maturity.^a

Nutrient	Analytical error (%)	CV of plant samples (%)
N	1.2	17
P ₂ O ₅	2.8	21
K ₂ O	1.0	9
CaO ₂	2.4	10
MgO	5.4	15
MnO	3.8	19
SiO ₂	1.4	9

^aYanagasiwa and Takahashi (1964).

Table 4.4. Estimated average total contents of the constituents of soil fine material and plant dry matter and the soil-plant ratio.^a

Element	Total content (ppm) in		Ratio	Element	Total content (ppm) in		Ratio
	Soil	Plant			Soil	Plant	
P	2,000	4,000	0.5	Mn	2,000	100	20
K	20,000	20,000	1.0	Na	20,000	1,000	20
B	10	10	1.0	Pb	20	1	20
Mo	1	1	1.0	Ni	50	1	50
Ca	30,000	20,000	1.5	Co	20	0.1	200
Zn	100	30	3.3	Fe	50,000	100	500
Cu	50	10	5.0	Cr	200	0.1	2,000
Sr	300	30	10	V	200	0.1	2,000
Mg	20,000	2,000	10	Ti	10,000	1	10,000

^aMitchell (1960).

tion would be a serious problem. For this reason, the analytical values of plant tissues for cobalt and iron are often erratic.

Sampled plants are usually washed with tap water and then, if necessary, with demineralized or distilled water. Cleaning removes contaminants such as soil and dust. At the same time, however, there is a danger that plant constituents such as potassium may be extracted. Hence, excessive washing must be avoided.

Grinding is the final step in sample preparation. In rice, plant material is ground to 1.0- to 2.0-mm particles. Particle size affects the uniformity of the sample material. A small particle size means a smaller portion of a sample can be reliably analyzed. The grinding process is also a source of error in the analysis of some metals, particularly iron and copper. A grinding machine is not advisable for sample preparation in iron analysis.

d. Analytical procedures. The choice of analytical procedures depends on the availability of equipment and the precision required. Table 4.5 summarizes the procedure recommended for routine analysis.

Person-to-person and laboratory-to-laboratory error is difficult to assess but may be quite large. Table 4.6 illustrates the range of errors in a chemical analysis of plant samples when many people analyze subsamples from the same sample bottle. Each analyst used the same analytical procedures and made four determinations on the subsample. The range of errors made by an individual was small but between persons it was quite large, particularly for copper. The data in Table 4.6 were obtained when each analyst knew he was participating in a trial for accuracy. A routine analysis would probably result in larger errors. Furthermore, when different persons or laboratories use different analytical procedures, the errors may be even greater.

To assess the range of errors between persons and laboratories, and to avoid unnecessary confusion from such errors, it is advisable to use standard plant materials for chemical analysis (Bowen 1965).

Table 4.5. Recommended procedures for chemical analysis of rice tissues.^a

Element or constituent	Digestion or extraction	Method of analysis
N	Kjeldahl method	Volumetric
P	Ternary mixture digestion	Colorimetric
Al		
Fe		
Si		
	Ternary mixture digestion or dry ashing	Gravimetric
K	HCL extraction or water extraction	Flame photometric
Na		
Ca	HCL extraction	Atomic absorption spectrophotometer
Mg		
Mn		
Zn		
Cu		
B	HCL extraction	Colorimetric
Cl	Water extraction	Volumetric
Chlorophyll	Acetone extraction	Colorimetric
Sugar	Alcohol extraction	
Starch	Perchloric acid extraction	

^aYoshida et al (1976).

e. Critical concentrations for deficiency and toxicity. The critical contents of various elements for deficiency and toxicity in the rice plant are summarized in Table 4.7. The critical content is subject to modification according to the criteria that define the disorders, the status of other elements or substances in the soil or plant, the growth stages of the plant, the varieties, and the climatic conditions. The critical content obtained from a greenhouse study is sometimes too high and not applicable to field crops. For these reasons, Table 4.7 should be used only as a guide for diagnosis.

Table 4.6. Analysis of standard plant sample by 7 persons.^a

Analyst	K (%)	Mg (%)	Mn (ppm)	Cu (ppm)	Zn (ppm)
A	2.52 ± 0.03	—	17.1 ± 0.2	6.7 ± 0.7	28.4 ± 1.1
B	2.55 ± 0.01	—	18.2 ± 0.5	7.3 ± 1.1	29.0 ± 0.7
C	2.46 ± 0.01	0.178 ± 0.000	17.5 ± 0.0	5.6 ± 0.1	29.4 ± 0.5
D	2.42 ± 0.01	0.121 ± 0.009	20.0 ± 0.0	5.0 ± 0.1	35.0 ± 0.4
E	3.16 ± 0.08	0.176 ± 0.003	15.6 ± 1.3	9.1 ± 2.3	39.7 ± 6.3
F	2.76 ± 0.03	0.162 ± 0.025	14.1 ± 0.9	3.7 ± 0.1	31.3 ± 1.0
G	2.44 ± 0.01	—	17.6 ± 0.1	—	28.9 ± 0.2

^aYoshida et al (1976).

Table 4.7. Critical contents of various elements for deficiency and toxicity in the rice plant.^a

Element	Deficiency (D) or toxicity (T)	Critical content	Plant part analyzed	Growth stage
N	D	2.5%	Leaf blade	Tillering
P	D	0.1%	Leaf blade	Tillering
	T	1.0%	Straw	Maturity
K	D	1.0%	Straw	Maturity
	D	1.0%	Leaf blade	Tillering
Ca	D	0.15%	Straw	Maturity
Mg	D	0.10%	Straw	Maturity
S	D	0.16%	Shoot	Tillering
	D	0.06%	Straw	Maturity
Si	D	5.0%	Straw	Maturity
Fe	D	70 ppm	Leaf blade	Tillering
	T	300 ppm	Leaf blade	Tillering
Zn	D	10 ppm	Shoot	Tillering
	T	>1500 ppm	Straw	Maturity
Mn	D	20 ppm	Shoot	Tillering
	T	7,000 ppm	Shoot	Tillering
B	D	<3.4 ppm	Straw	Maturity
	T	100 ppm	Straw	Maturity
Cu	D	<6 ppm	Straw	Maturity
	T	30 ppm	Straw	Maturity
I	T	30 ppm	Shoot	Tillering
Al	T	300 ppm	Shoot	Tillering

^a Modified from Tanaka and Yoshida (1970).

4.3.3. Soil analysis

a. Available nutrients. The methods of analyzing available nutrients extensively studied for upland soils can be directly applied to upland rice. These methods, however, must be re-examined when applied to lowland rice. As discussed in Chapter 3, the availability of some nutrients increases upon flooding while that of others decreases. Therefore, critical levels of soil nutrients may be different between upland and submerged soils. Table 4.8 lists methods that have been used for analyzing available soil nutrients in lowland rice.

b. Soil pH. The measurement of soil pH is probably the simplest and most informative soil analysis in the diagnosis of nutrient deficiency or toxicity. For example, the visible symptoms of zinc deficiency and iron toxicity are very similar. However, if the pH is measured on air-dried soil samples, the diagnosis becomes easier and more reliable because zinc deficiency is likely to occur on neutral to alkaline soils whereas iron toxicity is more likely to occur on acid soils.

4.4. ASSESSMENT OF THE DIAGNOSIS

4.4.1. Foliar spray technique

When iron deficiency is suspected in the field, 0.1–0.2% of an aqueous solution of ferrous sulfate or ferrous citrate with a small amount of sticker may be applied in a

Table 4.8. Methods for available soil nutrients.^a

Nutrient	Methods of analysis
N	Incubation method
P	Bray-Kurtz No. 2 method
K	Exchangeable form
Si	1N Na-acetate (pH 4.0) extraction
B	Hot water
Cu	DTPA + CaCl ₂ (pH 7.3)
Fe	DTPA + CaCl ₂ (pH 7.3) NH ₄ -acetate (pH 4.8)
Mn	DTPA + CaCl ₂ (pH 7.3)
Mo	0.1 N H ₃ PO ₄ and 3 N NH ₄ H ₂ PO ₄
Zn	NH ₄ -oxalate (pH 3.3) 0.05 N HCl Dithizone + NH ₄ -acetate EDTA + (NH ₄) ₂ CO ₃ DTPA + CaCl ₂ (pH 7.3)

^aKawaguchi and Kyuma (1977) for macronutrients; Randhawa et al (1978) for micronutrients.

band to a chlorotic leaf. Within a week, the band will become green if the chlorosis is due to iron deficiency. For suspected zinc deficiency, 1 or 2 plants may be sprayed with a 0.1% aqueous solution of zinc sulfate or zinc chloride with a small amount of sticker. If the symptoms are due to zinc deficiency, the plant will begin to recover in a week or so.

4.4.2. Greenhouse experiment

A small amount of soil may be collected from the problem field and tested under controlled conditions in the greenhouse for various means of correcting the problem.

Potted conditions in the greenhouse may differ from field conditions. For example, pot experiments in the greenhouse occasionally fail to reproduce symptoms while the problem field suffers severe zinc deficiency. In such a case, the addition of cellulose powder assures the reproduction of zinc deficiency by aggravating the problem (Yoshida and Tanaka 1969).

4.4.3. Field experiment

A final assessment of the diagnosis and the practical means of correcting the problem must be tested at the problem site. Various forms and amounts of chemicals, and methods and times of application can be tested by the field experiment (Yoshida et al 1971, 1973).

The diagnosis is assumed to be correct when the treatment corrects the problem. The cause-effect relationship is thus established. This may not always be true, however. In the alkali soil areas of California, a severe chlorosis called *alkali disease* occurs on water-sown rice. The symptoms are indicative of iron deficiency caused by high pH. In field experiments, the application of ferric sulfate was

effective in curing the chlorosis (Mikkelsen et al 1965). Later experiments, however, revealed that chemically pure ferric sulfate failed to cure alkali disease, whereas commercial ferric sulfate, which contained small amounts of zinc, corrected the problem. In a separate treatment, a small amount of zinc cured the alkali disease (Brandon et al 1972). Now, zinc deficiency is well recognized in the same area where iron deficiency was previously reported though the two may not be completely identical (Mikkelsen and Brandon 1975). The same happened when zinc deficiency of California citrus was studied about 40 years ago (Hoagland 1944).

4.5. CORRECTIVE MEASURES FOR NUTRITIONAL DISORDERS

When the cause or causes of a nutritional disorder is properly identified, cure is the next step. However, detailed discussions of corrective measures are beyond the scope of this book. This section, therefore, will briefly examine the three major approaches to correcting nutritional disorders:

- Agronomic methods
- Soil improvement
- Varietal improvement

4.5.1. Agronomic methods

When the cause of a nutritional disorder is a nutritional deficiency, the problem is usually cured by applying the deficient nutrient. For example, zinc deficiency can be corrected by dipping seedling roots in a 2% ZnO suspension, the foliar application of zinc sulfate, and applying various zinc compounds to the soil. Similarly, sulfur deficiency can be easily corrected by applying various kinds of sulfur-containing materials (Aiyar 1945). An elegant way of correcting sulfur deficiency, however, is to apply ammonium sulfate as a partial replacement for urea (Mamaril et al 1979). The suitability of a particular agronomic technique for a given region depends not only on the effectiveness of the method under given soil conditions but on the availability, price, and cost-benefit ratio of chemicals.

4.5.2. Soil improvement

A toxicity problem is perhaps more difficult to correct than a deficiency problem, particularly when the toxicity is attributed to the inherent soil environment.

When the salt concentration reaches a certain level in the soil, salinity can be cured only by desalinization measures. Hydrogen sulfide injury in sandy, degraded soils can be partially corrected with nonsulfur fertilizers such as urea. However, incorporating hill soils that supply large quantities of ferric iron oxide to the soil is more effective.

4.5.3. Varietal improvement

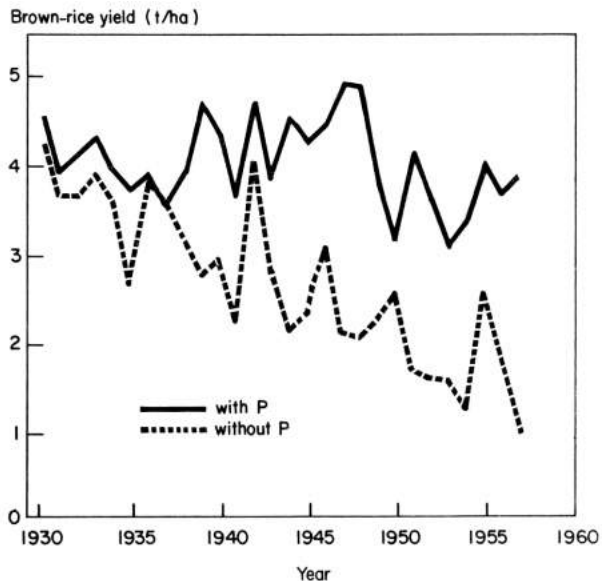
There are some degrees of varietal difference in tolerance for toxicities and deficiencies. Recently, an intensive effort has been made to improve plant toler-

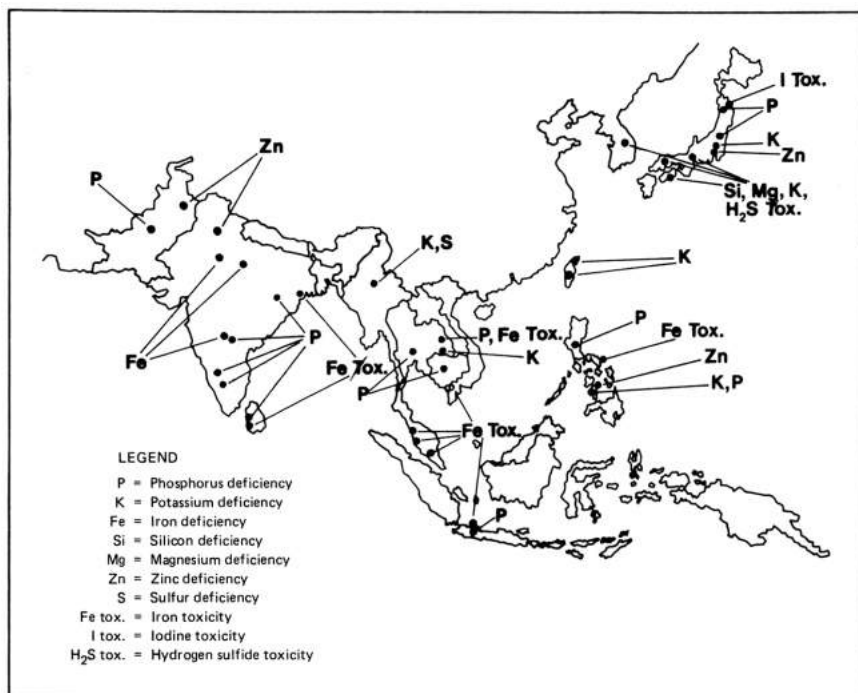
ance for nutritional disorders in various crops (Wright and Ferrari 1976). A similar attempt in rice is under way (Ponnamperuma 1976a, 1977).

To overcome a nutrient deficiency by varietal improvement depends on the assumption that a soil contains a certain amount of the nutrient to be used. One variety may be better able to use a soil nutrient than another. In fact, the contribution of varietal tolerance to rice grain yield was estimated at 0.5–0.8 t/ha for phosphorus deficiency, 0.5–1.5 t/ha for zinc deficiency, and 0.2–0.7 t/ha for iron deficiency at yield levels of 2.5–4.0 t/ha (Mahadevappa et al 1980). When the plant's requirement is large relative to the soil nutrient reserve, however, its differential ability may not contribute much. In theory, once a soil nutrient is depleted, varietal tolerance is no longer effective. This consideration may apply to deficiencies of most nutrients except iron. Iron is a micronutrient for higher plants but it is a macroconstituent of soil. Under such conditions, varietal improvement of the plant's ability to use soil iron is a logical approach to the cure of iron deficiency in plants.

One more point worth considering is to compare gains and losses for the varietal improvement as a means to overcome a nutrient deficiency in the soil. A long-term phosphate experiment indicates that grain yield decreases with time unless the crop receives phosphate fertilizer (Fig. 4.1). When no phosphate is applied, the total soil phosphorus content in both the surface soil and in a furrow slice decreases as a result of the crop's removal of phosphorus. The total soil carbon and nitrogen contents also decrease. Studies on nitrogen fixation by azolla (Watanabe et al 1977) and blue-green algae (Mitsui 1960) show that phosphate application is necessary to increase nitrogen fixation. If an efficient phosphate user (rice variety) is grown without phosphate fertilizer, the nitrogen fixation by azolla and

4.1. Effect of phosphate application on rice yield in the long-term fertilizer experiment, Shiga, Japan. 1930–1957 (Shiga Pref. Agric. Exp. Stn. 1961).





4.2. Nutritional disorders of rice in Asia (Tanaka and Yoshida 1970).

blue-green algae will be minimal and there will be decreases in soil fertility. If phosphate fertilizer is applied, there is no need to improve the rice variety for phosphorus absorption. Varietal difference in phosphorus absorption from soil becomes negligible even at low levels of applied phosphorus (see Fig. 3.17).

Varietal improvement as a means of correcting a toxicity problem is worth trying because correction by other means is often difficult and costly.

4.6. NUTRITIONAL DISORDERS OF RICE IN ASIAN COUNTRIES

Many nutritional disorders of rice have been reported from various rice-growing countries (Table 4.9, Fig. 4.2). These nutritional disorders can be related to soil conditions (Table 4.10).

The following summarizes the soil conditions under which the nutritional disorders may occur. The reader is advised to refer to Chapter 3 for more details.

Flooded soil undergoes reduction, and the concentration of iron may increase to a level high enough to induce iron toxicity. Iron levels in the soil solution are largely determined by the soil pH and the content of readily decomposable organic matter. Low pH and high organic matter content are associated with high iron concentrations.

Table 4.9. Nutritional disorders of rice reported from various rice-growing countries.^a

Country	Physiological disease	Possible cause(s)
Burma	Amiyi-Po	K deficiency
	Myit-Po	P deficiency
	Yellow leaf	S deficiency
Ceylon	Bronzing	Fe toxicity
Columbia	Espiga erecta	?
Hungary	Bruzone	?
India	Khaira disease	Zn deficiency
	Bronzing	Fe, Mn, H ₂ S toxicities
	Yellowing	?
Indonesia	Mentek	Virus disease
Japan	Akiuchi	H ₂ S toxicity, K, Mg, Si deficiencies
	Akagare I	K deficiency (Fe toxicity)
	Akagare II	Zn deficiency
	Akagare III	I toxicity
	Aodachi	?
	Hideri-Aodachi	?
	Straighthead	?
Korea	Akiuchi	H ₂ S toxicity, K, Mg, Si deficiencies?
Malaysia	Penyakit Merah (yellow type)	Virus disease
Pakistan	Pansukh	?
	Hadda	Zn deficiency
Portugal	Branca	Cu deficiency?
Taiwan	Suffocating disease	Virus disease
United States	Straighthead	H ₂ S toxicity
	Alkali disease	Zn deficiency

^aModified from Tanaka and Yoshida (1970).

If a soil is high in active iron, especially when it is also high in easily reducible manganese, it resists the lowering of redox potential, and the iron level remains low. Such soils have a high phosphorus absorption coefficient especially when they are high in active aluminum; phosphorus deficiency therefore tends to develop. If such soils contain a large amount of organic matter, the iron content can be very high and the rice plant may suffer from both phosphorus deficiency and iron toxicity. These disorders occur on soils formed from the early stages of the laterization of basic rocks.

If a soil contains a large amount of easily reducible manganese, manganese toxicity may develop. However, such cases are probably not common because the rice plant tolerates a tissue manganese content as high as 7,000 ppm.

If the active iron content is not high, the soil redox potential falls quickly, the iron concentration in the soil solution rises sharply, and iron toxicity may develop.

Table 4.10. Classification of nutritional disorders in Asia. ^a

Soil	Soil condition	Disorder	Local Name
Very low pH	(Acid sulfate soil)	Iron toxicity	Bronzing
Low pH	High in active iron	Phosphorus deficiency	Akagare Type III
	High in organic matter	Phosphorus deficiency combined with Iron toxicity	
	High in iodine	Iodine toxicity combined with phosphorus deficiency	
	High in manganese	Manganese toxicity ^b	
	Low in active iron and exchangeable cations	Iron toxicity interacted with potassium deficiency	Bronzing Akagare Type I
	Low in bases and silica, with sulfate application	Imbalance of nutrients associated with hydrogen sulfide toxicity	Akiochi
High pH	High in calcium	Phosphorus deficiency Iron deficiency Zinc deficiency	Khaira Hadda Taya-Taya Akagare Type II
	High in calcium and low in potassium	Potassium deficiency associated with high calcium	
	High in sodium	Salinity problem Iron deficiency Boron toxicity ^b	

^a Tanaka and Yoshida (1970). ^b Probably rare.

Since there is a physiological interaction between iron and potassium, a low potassium content in the soil tends to aggravate iron toxicity.

Under reductive conditions, sulfate is reduced to sulfide. If there is little active iron to react with the sulfide, free hydrogen sulfide may exist in the soil solution, damaging the roots and retarding nutrient uptake. As a result, the plant becomes unbalanced in nutrient content and susceptible to *Helminthosporium* infestation.

Low nitrogen supply makes the roots more susceptible to hydrogen sulfide injury and the plants more susceptible to *Helminthosporium*. Potassium-deficient plants are also susceptible to *Helminthosporium*. A low cation exchange capacity is a causative factor in nitrogen or potassium deficiencies at later growth stages if

nitrogen or potassium fertilizers are applied only as basal dressings. Such soils also often have a low active iron content and are called *degraded paddy soils*.

Bronzing, *Akagare Type I*, and *Akiochi* are related. All these disorders occur on sandy or silty soils low in cation exchange capacity and active iron. Small differences in soil characteristics, such as pH, organic matter, potassium content, degree of drainage resulting from physiographic changes, and varietal characters may determine the type of disorder.

Calcareous soils have a pH above 7 and the availability of elements such as phosphorus, iron, and zinc is low, leading to the corresponding deficiencies. Potassium deficiency may also occur if the soil is low in this element.

Soils high in sodium generally have a high pH and total soluble salts. Plants on these soils frequently suffer from a salinity problem and sometimes from iron deficiency and boron toxicity.

In neutral soils, the availability of nutrients is just adequate and deficiencies or excesses of nutrients are unlikely to occur. However, if a soil is low in an essential nutrient, plants may suffer from a deficiency.

On peaty soils, copper deficiency is suspected as a major nutritional problem (Driessen 1978). Copper deficiency is also suspected to cause *Branca* in Portugal. These two problems, however, require further clarification.

In addition to inherently deficient soil environments, a shift in the fertilizer industry from ammonium sulfate to high-analysis nitrogen fertilizers and from superphosphate to concentrated phosphates appears to be triggering the increased incidence of sulfur deficiency in lowland rice.

5

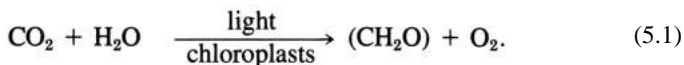
PHOTOSYNTHESIS AND RESPIRATION

5.1. PHOTOSYNTHESIS

5.1.1. Photosynthesis — a review

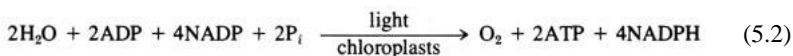
Photosynthesis is a process by which solar energy is captured and converted into chemical energy stored in the form of carbohydrate. About 80–90% of the dry matter of green plants is derived from photosynthesis; the rest (minerals) comes from the soil.

The over-all process of photosynthesis by green leaves is normally described as:

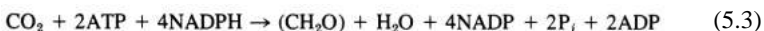


However, photosynthesis can be understood in terms of three partial processes:

- *Diffusion of carbon dioxide to the chloroplasts.* The CO_2 in air (normally around 300 ppm or 0.03% v/v) is transported by turbulence and diffusion to the leaf stomates through which it is diffused to chloroplasts.
- *Photochemical reaction.* The light energy is used to split water, thus producing molecular oxygen, NADPH (reduced nicotinamide adenine dinucleotide phosphate), and ATP (adenosine triphosphate):

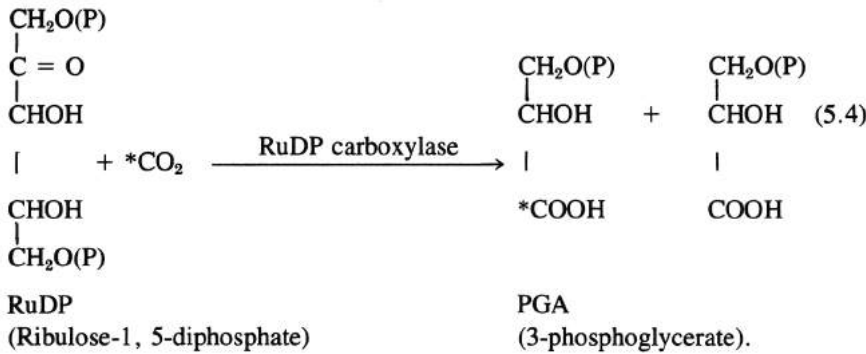


- *Dark reaction.* The NADPH and ATP produced in the light are used to reduce CO_2 to carbohydrates and other compounds.



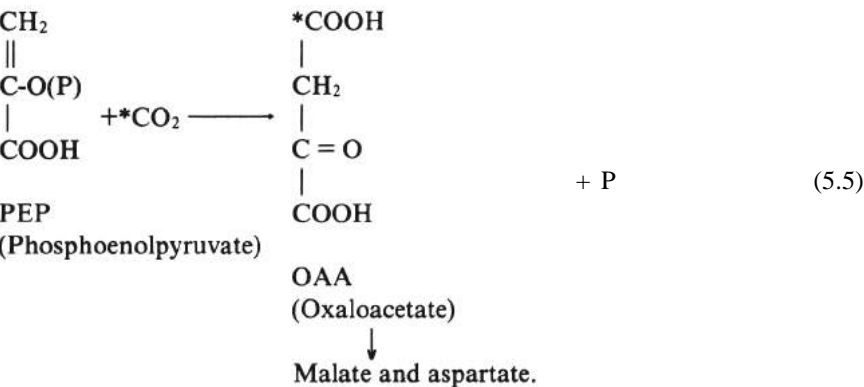
This reaction does not require light and can proceed in darkness.

Carbon dioxide is converted into carbohydrates during photosynthesis by two biochemical processes: C-3 and C-4 pathways (Hatch and Slack 1970, Bjorkman and Berry 1973). In the C-3 pathway, which is often called the Calvin Cycle, carbon dioxide is first incorporated into 3-phosphoglycerate (PGA):

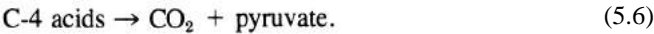


Note that the carbon atom in the CO₂ molecule (marked with an asterisk) is incorporated into the carboxyl group of one PGA molecule. In subsequent reactions, some PGA is converted into carbohydrates and some is used to regenerate RuDP molecules to serve as CO₂ acceptors. PGA is a compound with three carbon atoms per molecule; hence, the pathway is named the three-carbon photosynthetic pathway (C-3 pathway).

In the C-4 pathway, CO₂ is first incorporated into compounds with four carbon atoms:



CO₂ fixation and the formation of C-4 acids, malate and aspartate, occur in the mesophyll cells. The C-4 acids, transported to inner bundle sheath cells, are converted into CO₂ and pyruvate (C-3 compound):



The released CO₂ is fixed again in the Calvin cycle to produce PGA and carbohydrate. The pyruvate returns to the mesophyll cells, where it acquires a phosphate

Table 5.1. Comparison between the C-3 and C-4 plants in photosynthetic performance.

	C-3 plants	C-4 plants	Reference
1. Optimum temperature for photosynthesis	15–30°C	30–45°C	Hatch (1973)
2. Optimum light intensity for photosynthesis	30–50% full sunlight	Full sunlight	Hatch (1973)
3. Photosynthetic rate per unit leaf area	C-4 is about 2 times higher than C-3 under optimal conditions		Hatch (1973)
4. Maximum growth rates under optimal condition	34–39 g/m ² per day	50–54 g/m ² per day	Monteith (1978)
5. Water use efficiency	1.49 mg dry wt/g water	3.14 mg dry wt/g water	Downes (1969)

group from ATP to form PEP, thus regenerating the initial CO₂ acceptor molecule. The over-all efficiency of using CO₂ increased by this additional cycle.

Rice belongs to the C-3 plants. The C-3 pathway operates in most temperate cereal crops such as wheat and barley. Plants adapted to warm climates use the C-4 pathway: sugarcane, maize, sorghum, and millet, and also several important pasture species. The C-4 plants have several advantages for crop production (Table 5.1). The characteristics of the C-4 pathway suggest that the C-4 plants are well adapted to a climate with high temperatures, high light intensity, and limited water supply during the period of active growth.

When photosynthesis occurs, dark respiration is assumed to take place simultaneously. Hence, measured photosynthesis is the difference between true photosynthesis and dark respiration. On the basis of this concept, *gross photosynthesis* refers to the sum of net (measured) photosynthesis and dark respiration:

$$\text{Gross photosynthesis} = \text{net photosynthesis} + \text{dark respiration.}$$

Recently, the discovery of photorespiration has caused confusion in the above concept. However, the term *net photosynthesis* can be used safely because it is the measured net gain in photosynthesis; both dark respiration and photorespiration have been subtracted.

Photorespiration, a characteristic of C-3 plants, has been the subject of intensive research in recent years (Jackson and Volk 1970, Tolbert 1971, Zelitch 1971, 1979). Photorespiration does not produce any ATP and does not provide any useful carbon skeletons for the biosynthesis of new compounds or new tissues. Photorespiration occurs in peroxisomes, whereas dark respiration takes place in mitochondria. Hence, photorespiration is totally different from dark respiration. For these reasons, the classical term *gross photosynthesis* is still useful when growth is considered.

Net photosynthesis is normally measured by CO₂ intake or by O₂ output. Dry weight increases are also often used as estimates of net photosynthesis after appropriate corrections are made for mineral content. The rate of dry weight

change is expressed as (McCree 1974):

$$dW/dt = D - N, \quad (5.7)$$

where D = daytime net total of CO_2 taken up by the plant and
 N = night total of CO_2 evolved by the plant.

When dW/dt is expressed per unit of ground area (g dry matter/ m^2 per day or week), it is called crop growth rate (CGR). The crop growth rate is used as a measure of primary productivity of crops in the field.

5.1.2. Characteristics of rice photosynthesis

Rice is generally believed to have a C-3 photosynthetic pathway (Ishii et al 1977b). There is, however, a report that suggests the operation of both C-3 and C-4 pathways in a salt-tolerant indica variety (Hegde and Joshi 1974).

As a C-3 plant, rice has a high CO_2 compensation point, exhibits photorespiration, and lacks bundle sheath chloroplasts (Table 5.2). Compared with other C-3 species, however, rice has a relatively higher net photosynthetic rate per unit of leaf area. Within *Oryza sativa*, indica rices have a higher optimum temperature than japonica rices. Early papers on rice photosynthesis reported a leaf photosynthetic rate of 10–20 $\text{mg CO}_2/\text{dm}^2$ per hour, while recent papers indicate a rate of 40–50 $\text{mg CO}_2/\text{dm}^2$ per hour. This difference could be attributed primarily to improvements in the measuring technique (Yoshida and Shioya 1976). In early studies on rice photosynthesis, the CO_2 exchange rate was measured by enclosing several cut leaves in a plastic chamber. Later studies, however, use an intact leaf.

The photorespiration rate increases with increasing light intensity, but the rate of photorespiration relative to the rate of CO_2 fixation is higher at lower light intensities. At light intensities lower than 10 klx, photorespiration accounts for 70–90% of CO_2 fixation. At 40 klx, it accounts for 40% (Ishii et al 1977c).

At the moment, lowering the oxygen concentration in air is the most convenient means of reducing photorespiration. A group of plant growth regulators can also reduce photorespiration and increase photosynthetic activity (Zelitch 1979).

When rice was grown in a low-oxygen atmosphere, both photosynthesis and dry matter production increased; grain yield decreased due to an increased percentage of unfertile grains. The percentage spikelet fertility of Tangin Bozu and Hoyoku varieties decreased from 86 and 74% in the 21% O_2 atmosphere to 22 and 46% in the 3% O_2 atmosphere, respectively (Akita and Tanaka 1973). Thus, inhibiting photorespiration by lowering the oxygen concentration did not increase the grain yield.

5.1.3. Crop photosynthesis

Crop photosynthesis in the field is primarily determined by incident solar radiation, photosynthetic rate per unit leaf area, leaf area index, and leaf orientation.

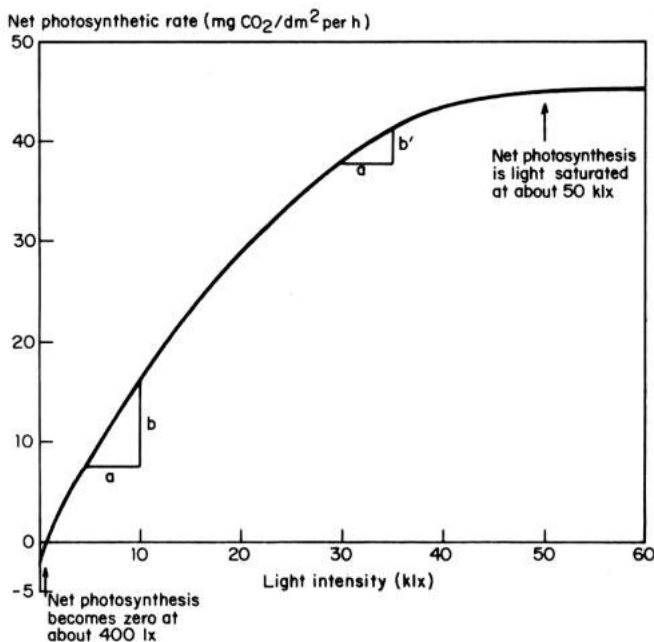
Table 5.2. Some characteristics of rice photosynthesis.

Photosynthetic	characteristics	Measured	results	Experimental	conditions	References
Light	compensation point	400–1,000 lx		25°C, 300 ppm CO ₂		Murata (1961) Ishii et al (1977c)
Temperature	saturation	45–60 Klx		30°C, 300 ppm CO ₂		Murata (1961)
	optimum	20–33°C (for japonica)		300 ppm CO ₂ , 50 klx		Murata (1961); Ishii et al (1977a)
Carbon dioxide	optimum	25–35°C (for indica)		300 ppm CO ₂ , 50 klx		Osada (1964)
	compensation point	55 ppm		25°C, > 10 klx		Ishii et al (1977c)
Net		40–50 mg CO ₂ /dm ² per h		optimum temperature,		Akita et al (1968);
photosynthetic rate				light saturation		Takano and Tsunoda (1971); Yoshida and Shioya (1976)
Biochemical pathway		C-3 pathway				Ishii et al (1977b)
Bundle sheath chloroplasts		None				Akita et al (1969)
Photorespiration		Present				Akita and Miyasaka (1969); Ishii et al (1977a, c)

a. Incident solar radiation. Incident solar radiation in rice-growing regions has been discussed in Chapter 2. High solar radiation is a prerequisite for high rates of photosynthesis.

b. Photosynthetic rate per unit of leaf area. The net photosynthetic rate of rice leaves varies with leaf position, nutritional status, water status, and growth stage. The net photosynthetic rate of active, healthy single leaves is about 40–50 mg CO₂/dm² per hour under light saturation. The net photosynthesis of single leaves reaches maximum at about 40–60 klx, about one-half of full sunlight. Photosynthesis of a well-developed canopy, however, increases with increasing light intensity up to full sunlight and there is no indication of light saturation (Murata 1961).

The light-photosynthesis curve of single leaves indicates that net photosynthesis is zero at a light intensity of about 400 lx (light compensation point), and it increases with increasing light intensity up to about 50 klx (Fig. 5.1). Photosynthetic efficiency, when it is defined as photosynthesis per unit of light energy, is higher at lower light intensities. In Figure 5.1, photosynthetic efficiency is indicated by b for low light intensity and by b' for high light intensity. Obviously, b is much greater than b' . This implies that when the total amount of light energy available for photosynthesis is held constant, the total photosynthesis would be greater if the light is provided to leaves at lower intensities and, hence, for longer durations.



5.1. Light photosynthesis curve of single leaves (schematic).

When the amount of daily incident solar radiation is constant, the intensity of light energy per unit of time weakens as day length increases. Consequently, as the days lengthen, daily photosynthesis increases (Montieth 1965). This long-day effect on photosynthesis is considered an advantage of the temperate climate over the tropical.

c. Leaf area index and leaf orientation. A large leaf area index (LAI) is necessary to intercept incident solar radiation. However, the size of LAI needed to give maximum crop photosynthesis depends on the leaf orientation of the canopy. The leaf orientation affects photosynthesis because it determines the light environment within a canopy. For a comprehensive description of the light environment and rice photosynthesis, the reader is advised to refer to a more specialized paper (Uchijima Z. 1976).

A simplified model will explain the relationship between LAI, leaf orientation, and photosynthesis. The model assumes that decreases in light intensity are due to light absorption by the leaves in a manner analogous to Beer's law.

In their pioneering work on photosynthesis and dry matter production in a plant community, Monsi and Saeki (1953) stated that light absorption by the plant community can be adequately described by Beer's law:

$$\ln \frac{I}{I_o} = -kF \quad (5.8)$$

where I_o = light intensity incident on the leaf canopy;

I = light intensity in the plant community where the LAI is F ;

F = average cumulative total leaf area per unit of ground area,

F is zero at the top of canopy and takes its maximum value at ground level

(a value generally referred to as the LAI); and,

k = foliar absorption coefficient (dimensionless).

k is related to leaf angle or orientation. In rice varieties, k ranges from about 0.4 for erect leaves to about 0.8 for droopy leaves (Hayashi and Ito 1962).

The cumulative leaf area per ground area at which the incident light would be reduced by 95% for erect and droopy rice canopies can be calculated with equation 5.8:

(a) For erect leaves with a k value of 0.4:

$$\begin{aligned} F &= \frac{[\ln (0.05/1.00)]}{(-0.4)} = \frac{[2.303 \log (0.05/1.00)]}{(-0.4)} \\ &= \frac{[-2.303 \log (1.00/0.05)]}{(-0.4)} \\ &= 7.5 \end{aligned} \quad (5.9)$$

(b) For droopy leaves with a k value of 0.8:

$$F = \frac{[\ln (0.05/1.00)]}{(-0.8)} = 3.7 . \quad (5.10)$$

Thus, 95% of the sunlight is absorbed by the leaves in an erect-leaved rice canopy and 5% reaches the soil surface when LAI is 7.5. In a droopy-leaved canopy, a LAI of 3.7 is sufficient to intercept 95% of the sunlight. In other words, erect leaves allow the sunlight to penetrate deeper into the canopy. Because both canopies intercept the same amount of sunlight (95%), and because the erect-leaved canopy requires a greater LAI than does the droopy-leaved canopy, the erect-leaved canopy receives weaker sunlight per unit of leaf area. Consequently, the erect-leaved canopy achieves greater photosynthesis.

Erect leaves allow deeper penetration of incident light because they are oriented with the incident sun beams when the sun is high. For the same reason, erect leaves receive light at lower intensities than droopy leaves. The intensity of light received by the leaf surface is determined by the angle between beams of direct radiation and the normal to the leaf surface. If the angle is θ° , the light intensity at the leaf surface (I) is related to the intensity of incident light (I_0) as:

$$I = I_0 \cos \theta. \quad (5.11)$$

When the sun is high, flat leaves receive a higher light intensity per unit of leaf surface but for a smaller leaf area because θ is close to zero. Erect leaves, however, receive a lower light intensity per unit of leaf surface but for a larger leaf area because θ is close to 90° . A rice canopy in which leaves are very erect near the top and become more horizontal toward the ground reduces the foliar absorption coefficient of the upper leaves, leaving more light for the lower leaves. A mathematical crop photosynthesis model indicates that a combination of erect upper leaves and droopy lower leaves in a plant canopy gives the maximum crop photosynthesis (Duncan 1971).

The LAI values necessary to intercept 95% of the incident light in rice canopies suggest that a LAI of 4–8 is needed for good rice photosynthesis.

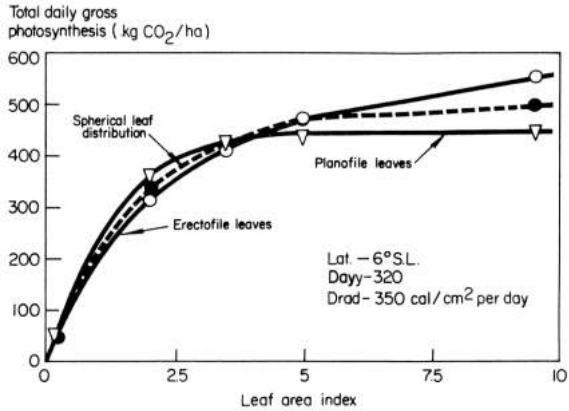
When light intensity reaches the light compensation point, there is no net gain by photosynthesis. Assuming that the light compensation point is 400 lx for a leaf temperature of 25°C and a CO_2 concentration of 300 ppm, and incident sunlight is 20 klx, at what cumulative leaf area per unit ground area (F) is the light compensation point reached? By equation 5.8:

$$F = \frac{\ln (400 \text{ lx}/20,000 \text{ lx})}{(-0.4)} = 9.8 \text{ for erect leaves} \quad (5.12)$$

$$F = \frac{\ln (400 \text{ lx}/20,000 \text{ lx})}{(-0.8)} = 4.9 \text{ for droopy leaves} \quad (5.13)$$

Thus, when the incident sunlight is moderate (about one-fifth of the full sunlight), the upper 10 layers of leaves in the erect-leaved rice canopy are above the light

5.2. The influence of leaf angle distribution of a canopy on total daily gross photosynthesis at high light intensity (van Keulen 1976).



compensation point. Only the upper 5 layers in the droopy canopy receive sunlight higher than the light compensation point.

To get a quantitative estimate of crop photosynthesis, as influenced by LAI and leaf angle, a more complicated mathematical manipulation is needed. In crop photosynthesis models, leaf orientation is usually simplified to extreme arrangements within a canopy. In a planophile (extremely droopy) canopy, all the leaves are oriented at 0° with respect to the horizontal plane. In an erectophile (extremely erect) canopy, all the leaves are oriented at 90°. With these leaf orientations, one crop photosynthesis model (van Keulen 1976) indicates for low latitudes that:

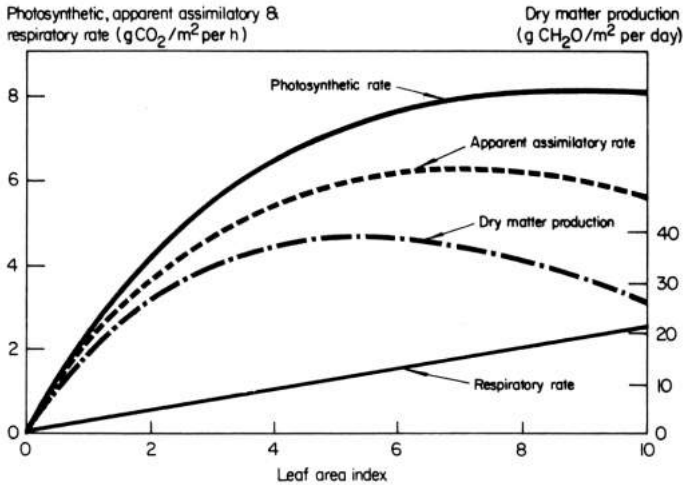
- an extremely planophile distribution gives the highest total photosynthesis at low LAI and,
- at high LAI and high solar radiation, extremely erectophile leaves lead to a 20% increase in gross photosynthesis (Fig. 5.2).

5.1.4. Critical vs optimum leaf area index

Whether there is an optimum LAI for net dry matter production has been a widely debated subject (Yoshida 1972).

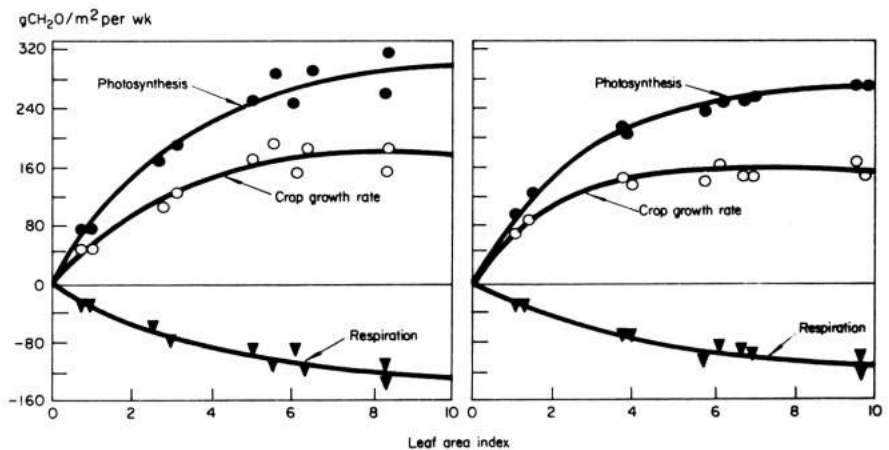
The gross photosynthesis of a canopy increases curvilinearly with increasing LAI because, as LAI increases, lower leaves are more shaded, so the mean photosynthetic rate of all leaves decreases. Net photosynthetic production, usually considered as the difference between gross photosynthesis and respiration, is determined by the nature of respiration. In early models for canopy production, respiration was assumed to increase linearly with increasing LAI and, therefore, the existence of optimum LAI was expected (Fig. 5.3). The concept of optimum LAI was so easy to understand and looked so reasonable that it was accepted by many rice scientists.

Reexamination of the relationship between LAI, respiration, and crop growth rate (Fig. 5.4) indicates that:



5.3. The relationship between LAI, photosynthetic and apparent assimilation rates, and dry matter production (diagrammatic) (Tanaka et al 1966).

- Respiration does not increase linearly with LAI; it increases curvilinearly.
- As a result, there is no optimum LAI for CGR. The CGR reaches maximum at a LAT of about 6 for IR8 and about 4 for Peta, beyond which it remains the same despite further increases in LAI. The LAI at which crop growth rate reaches maximum may be called the critical LAI.
- The maximum CGR of erect-leaved IR8 was greater by $20 \text{ g/m}^2 \text{ per week}$ than that of droopy-leaved Peta.



5.4. Photosynthesis, crop growth rate ($\times 0.9$), and respiration of IR8 (left) and Peta (right) during 4 weeks before flowering (Cock and Yoshida 1973).

At high LAI, the crop tends to bend or lodge, which decreases the CGR. This factor could have jeopardized data interpretation in previous studies. Agronomically, there is an optimum growth size for maximum yield. However, this optimum size is related to the lodging resistance of a variety but it is not related to the balance between photosynthesis and respiration. Crop respiration is closely related to gross photosynthesis; it is approximately 40% of gross photosynthesis over a wide range of values for LAI and leaf area ratio until 2 weeks after flowering (Fig. 5.5).

5.2. RESPIRATION

5.2.1. Growth and respiration

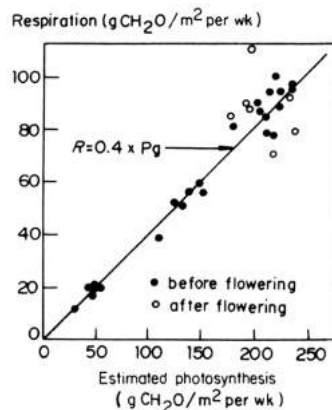
Respiration is a process common to all living organisms during which high energy compounds are formed from carbohydrates. The skeletons of many important new compounds are formed as intermediates. During this process, oxygen is consumed and carbon dioxide is evolved. Growth is closely linked to respiration. Growth, i.e., the production of new organic material or the synthesis of new compounds, is achieved by use of intermediates and the energy stored in high-energy compounds. There is no growth without respiration. For example, major constituents of plant cells such as proteins, lipids, and cellulose are synthesized through respiration.

5.2.2. Growth efficiency

When new organs (GR) are formed during growth, they are synthesized from intermediates and energy is supplied by respiration (R) (Tanaka and Yamaguchi 1968, Yamaguchi 1978). The ($GR + R$) represents the total amount of substrate consumed to produce new organs (GR). The growth efficiency is then defined as:

$$\text{Growth efficiency (GE)} = \frac{\text{amount of growth achieved}}{\text{total amount of substrate consumed}} = \frac{GR}{GR + R} \quad (5.14)$$

5.5. Respiration and photosynthesis of 6 varieties (IR8, Jaya, Sigadis, T141, Chianung 242, IR747B2-6-3) from 2 weeks after flowering (Cock and Yoshida 1973).



The growth efficiency indicates how much of the substrate is converted into the constituents of new tissues. It follows that $(1 - GE)$ is consumed for respiration to produce the energy required for the biosynthesis of new tissues.

When germination occurs in darkness, seedling growth depends entirely on the seed reserve. The growth efficiency can be calculated for such growth:

$$GE = \frac{W_2 - W_1}{S_1 - S_2} - \frac{GR}{S_1 - S_2} - \frac{GR}{\Delta S} \quad (5.15)$$

where W_1 and W_2 and S_1 and S_2 are the dry weights of seedlings and seeds at time t_1 and t_2 , respectively.

The growth rate is strongly affected by temperature but growth efficiency remains about 56–58% for all 3 temperatures (Table 5.3). In other words, about 60% of the substrate is used for seedling constituents and about 40% is consumed by respiration. Similar experiments have been conducted for different plant species and are well documented (Penning de Vries 1972). The relative yields of germinating seeds for 9 species range from 0.48 g/g for *Vigna sesquipedalis* to 0.96 g/g for groundnut. The growth efficiency or relative yield varies with the chemical composition of seeds and of newly formed tissues because the energy content is different among constituents such as carbohydrates, proteins, and lipids. The concept of growth efficiency is applied to growing plants until maturity, and to the growth of individual organs such as leaves or panicles (Yamaguchi 1978). Some important findings from these studies may be summarized:

- When active vegetative growth is taking place, growth efficiency is high, centering around 60–65%.
- Growth efficiency drops sharply after the milky stage of ripening.
- The growth efficiency of panicles is high (65–75%).

Respiration may be conveniently divided into respiration necessary for growth and that for maintenance (this will be discussed in more detail in the succeeding section). Thus, equation 5.14 can be rewritten as:

$$GE = \frac{GR}{GR + R} = \frac{GR}{GR + R_g + R_m} \quad (5.16)$$

Table 5.3. Effect of temperature on the growth efficiency of Peta seedlings germinated in the dark.^a

Temperature (°C)	Wt of seedlings ^b (mg/plant)	Growth efficiency (%)
21	4.5	56
26	8.3	58
32	10.6	57

^aTanaka and Yamaguchi (1968). ^bAt the end of 10-day growth.

Table 5.4. Growth and maintenance respiration of a rice crop during later period of ripening.^a

Days after trans-planting	Dry wt increase (g/plant per day)	Respiration ^b (g CH ₂ O/plant per day)			Rg/R (%)	Growth efficiency (%)
		R	Rg	Rm		
96–103	1.74	1.09	0.74	0.35	68	63
104–110	1.42	1.03	0.61	0.42	59	58
111–117	0.64	0.95	0.27	0.68	29	40
118–124	0.13	0.77	0.05	0.72	7	14

^a Yamaguchi (1978). ^b R (total dark respiration) = R_g (growth respiration) + R_m (maintenance respiration).

where R_g and R_m represent respiration for growth and maintenance, respectively. When the growth efficiency linked with R_g is 70% and this efficiency remains unchanged until maturity, it is possible to estimate R_g and R_m at different stages of panicle growth (Table 5.4). When active grain filling slows down toward maturity, R_g decreases and R_m increases. As a consequence, the proportion of R_g to total respiration and growth efficiency decreases.

5.2.3. Growth and maintenance respiration — physiological approach

The closer relationship of dark respiration of whole plants to photosynthesis than to dry weight led McCree (1970) to propose a two-part model:

$$R = k_1 P_g + cW, \quad (5.17)$$

where R = 24 hours total dark respiration
for the whole plant,

W = plant dry weight,

P_g = gross photosynthesis rate,

k_1 = growth respiration coefficient, and

c = maintenance respiration coefficient.

Conceptually, the $k_1 P_g$ term corresponds to respiratory activity associated with growth and storage and the cW term to the cost of the maintenance.

For white clover (*Trifolium repens* L), the following equation was obtained:

$$R = 0.25 P + 0.015 W, \quad (5.18)$$

where R = 24 hours total of dark respiration,

P = 12 hours total of gross photosynthesis, and

W = CO₂ equivalent of the dry weight.

Growth respiration appears to be the same for different species and is not affected by temperature (McCree 1974). On the other hand, maintenance respiration varies with plant species and is a temperature-dependent process (Q_{10} is about 2.2).

When a plant is placed in darkness for 48 hours, it uses up its substrate and eventually stops growing. At this point, the respiration is due to maintenance.

The equation 5.18 also indicates that when photosynthates are used to produce new tissues for growth, the maximum conversion efficiency would be 75%. This 75% efficiency is very close to the 70% growth efficiency when only growth respiration is considered.

When a plant is young and growing actively, growth respiration is the major component of total respiration. With a mature plant, however, maintenance becomes a substantial fraction of total respiration. It has not been determined yet if all of the maintenance respiration is really needed or if it includes a wasteful consumption of photosynthetic products. Growth respiration is certainly useful respiration and cannot be reduced unless the efficiency of biochemical conversion is increased.

5.2.4. Growth and maintenance respiration — biochemical approach

Growth is a process during which a substrate is converted into new chemical compounds that constitute new tissues. The substrate must be converted into carbon-skeletons appropriate for the biosynthesis of new compounds; it must be consumed to provide energy (ATP) and hydrogen (NADH₂) for biosynthesis. These considerations led Penning de Vries and his associates (1974) to define production value as:

$$\text{Production value} = \frac{\text{wt of the end-product}}{\text{wt of substrate required for C- skeletons and energy production}} \text{ (g/g).} \quad (5.19)$$

Production value indicates the weight (g) of new organs (growth) that can be obtained from 1 g of substrate. Note that this definition is identical with growth efficiency discussed earlier (see equation 5.14). If the substrate's chemical composition and the end product are known, and if the biochemical reactions involved in synthesizing end product constituents are known, it is possible to calculate the production value for a given system (Penning de Vries et al 1974). One useful set of data on production values is shown in Table 5.5. It must be noted that these results are independent of temperature and plant species, and are determined only by the composition of the substrate and end product.

The data indicate:

- 1.00 g glucose produces 0.83 g carbohydrates but only 0.33 g lipids.
- The production value for nitrogenous compounds varies with nitrogen source; 1.00 g glucose produces 0.62 g nitrogenous compounds when nitrogen is supplied from ammonia but the same amount of glucose produces only 0.40 g nitrogenous compounds when the nitrogen source is nitrate.

The chemical composition of the plant varies with plant part (leaf or seed) and with species. When the chemical composition of a given plant part is known, it is

Table 5.5. Values characterizing the conversion of glucose into the main chemical fractions of plant dry matter in darkness. Each fraction consists of a natural mixture of different molecules.^a

Chemical fraction	Yield (g product/ g glucose)	Oxygen consumed (g/g glucose)	Carbon dioxide produced (g/g glucose)	Source of nitrogen
Nitrogenous compounds (consisting of amino acids, proteins and nucleic acids)	0.616	0.137	0.256	+ NH ₃
	0.404	0.174	0.673	+ NO ₃ ⁻
Carbohydrates	0.826	0.082	0.102	
Lipids	0.330	0.116	0.530	
Lignin	0.465	0.116	0.292	
Organic acids	1.104	0.298	-0.050	

^aPenning de Vries (1975b).

also possible to calculate how many grams of substrates are required for biosynthesis of 1.00 g dry matter (Table 5.6). For the biosynthesis of 1.00 g leaf dry matter, 1.36 g mixed organic substrate is required:

$$(1.055 \text{ g sucrose} + 0.305 \text{ g amino acids}) = 1.36 \text{ g substrate}$$

The conversion efficiency in the above example leads to:

$$\frac{\text{Leaf dry matter}}{\text{Total substrate}} = \frac{1.00 \text{ g}}{1.36 \text{ g}} = 0.74 \text{ g/g.} \quad (5.20)$$

This value agrees with 0.75 (= 1 - 0.25) in equation 5.18.

To produce 1.00 g rice seeds, 1.20 g mixed organic substrate is required, and 2.16 g substrate is necessary to produce 1.00 g peanut seeds.

Table 5.6. Requirements for the biosynthesis of 1.00 g dry matter of tissues with different chemical compositions.^a

Nature of biomass	Composition ^b	Sucrose (g)	Amino acids (g)	CO ₂ produced (g)	O ₂ consumed (g)
Leaves	25; 66.5; 2.5; 4; 2	1.055	0.305	0.333	0.150
Non-woody stem	12.5; 74; 2.5; 8; 2	1.153	0.153	0.278	0.135
Woody stem	5; 45; 5; 40; 5	1.515	0.061	0.426	0.176
Bean seeds	35; 55; 5; 2; 3	1.011	0.427	0.420	0.170
Rice seeds	5; 90; 2; 1; 2	1.135	0.061	0.186	0.110
Peanut seeds	20; 21; 50; 6; 3	1.915	0.245	1.017	0.266
Bacteria	60; 25; 5; 2; 8	0.804	0.732	0.573	0.208

^aPenning de Vries (1975b). ^bRefers to percentages of nitrogenous compounds, carbohydrates, lipids, lignin, and minerals, respectively.

Our knowledge of maintenance respiration is much less certain than our knowledge of growth respiration. The most potential maintenance processes in plants are (Penning de Vries 1975a):

- Protein turnover.
- Active transport processes to maintain certain ion concentrations in the cells.

Proteins in living organisms undergo constant renewal by a process referred to as protein turnover. The average turnover rate of leaf proteins may be about 100 mg protein/g protein per day at normal temperatures in leaves assimilating at moderate light intensities. In other words, about 10% of leaf protein are resynthesized everyday. This process consumes 28–53 mg glucose/g protein per day, which corresponds to 7–13 mg glucose/g dry weight per day in leaves. Such a consumption implies that the complete removal of protein turnover would reduce maintenance costs by about 10 mg glucose/g dry weight per day or by about 10 kg glucose/day for every 1 t dry weight. The cost of maintaining the ion concentration in leaves is estimated at about 6–10 mg glucose/g dry weight per day. In addition, more energy is used to break down and resynthesize the lipids that constitute cell membranes. The cost of membrane maintenance is estimated at 1.7 mg glucose/g dry matter per day. Adding these figures gives a maintenance respiration cost of 15–25 mg glucose/g dry matter per day.

This estimated maintenance respiration cost agrees with reported values (compare with equation 5.18), but is lower than other measured values for plants grown under high light intensities. For example, values as high as 50–150 mg glucose/g dry weight per day have been reported for the leaves of *Hordeum* sp. and *Triticum* sp. (Penning de Vries 1975a). There is also a clear difference in the costs of maintenance respiration between species: the maintenance respiration of sorghum is about one-third that of white clover (McCree 1974). The existence of *uncoupled* or *idling* respiration in plants has been suggested to explain unexpected high rates (Beevers 1970) and low yields (Tanaka 1972b). It is also possible that part of the protein turnover represents a process of little use.

5.2.5. Bioenergetics of crop yields

Crop yields can be compared agronomically in several ways: yield per crop, yield per day, and yield per year.

From a physiologist's point of view, a more meaningful comparison of crop yields can be made in terms of the amount of glucose or energy from which a harvested organ is produced. To simplify the pathway of yield formation, consider that glucose is the product of photosynthesis, different compounds such as lipids, proteins, and carbohydrates are synthesized from glucose, and harvested organs of different crops are composed of different proportions of these three.

When glucose is converted into proteins, lipids, and carbohydrates, the conversion efficiency can be defined as:

$$\text{Conversion efficiency} = \frac{\text{grams of a compound produced}}{1 \text{ gram of glucose}} \quad (5.21)$$

Table 5.7. Relative yielding ability of various crops with different chemical compositions.^a

Crop	Chemical content (%)				Yielding ability	
	Protein	Lipid	Carbo- hydrate	Ash	g/100 g glucose	Relative value
Rice	8.8	2.7	87.0	1.5	73	100
Maize	9.5	5.3	83.7	1.5	70	96
Wheat	12.1	2.3	83.7	1.9	71	97
Barley	11.6	2.2	83.4	2.8	71	98
Soybeans	39.0	19.9	35.4	5.7	45	62
Field bean	24.1	2.6	69.0	4.3	62	86
Potato	9.2	0.5	86.3	3.9	75	103
Sesame	21.2	54.7	18.4	5.7	37	51

^a Yamaguchi (1978).

The measured conversion efficiency on dry weight basis is 0.38 for proteins, 0.31 for lipids, and 0.84 for carbohydrates (Yamaguchi 1978). The definition of conversion efficiency is identical with that of the production value discussed in the preceding section (Table 5.5). The conversion efficiency and the theoretically calculated production value agree quite well for lipids and carbohydrates, but not for proteins. This discrepancy may be attributed to the complex nature of protein synthesis.

The yields of different crops on the same basis, i.e., glucose, can be calculated using the conversion efficiency for different compounds when the chemical composition of the harvested organs is known (Table 5.7). Thus, 1 t rice yield is comparable to 0.62 t soybean and 0.51 t sesame. In general, the grain crops and potatoes have similar productivity because grains and tubers have similar chemical composition. The relative yields of soybean and sesame are much lower because the seed of these crops contain higher percentages of lipids and proteins, which require larger amounts of energy for biosynthesis.

A similar calculation can be made using the production values shown in Table 5.5. When nitrate is the nitrogen source, 1 g photosynthate produces yields of 0.75 g for barley and rice; 0.64–0.67 for peas, beans, and lentils; 0.50 g for soybeans; and 0.42–0.43 g for rape and sesame (Sinclair and De Wit 1975). Thus, relative yields of different crops estimated by two different methods appear to be in good agreement.

6

RICE PLANT CHARACTERS IN RELATION TO YIELDING ABILITY

6.1. LOW YIELDS UNDER EXPERIMENTAL CONDITIONS IN THE TROPICS UNTIL MID-1960s

Yields from experimental rice fields in the tropics have increased dramatically with the advent of the new high yielding varieties. However, the farmers' yields still remain low.

When nitrogen is applied at rates exceeding 40 kg/ha, many traditional indica varieties tiller profusely and grow excessively tall, lodge early, and yield less (Chandler 1963). Data from 10 years' work at Chinsurah station in West Bengal, India, shows that rice responded to nitrogen up to 33.6 kg/ha (30 lb/acre). Beyond that rate, yield decreased. When farmyard manure was added, yield decreases from ammonium sulfate were even greater, no doubt simply because of the extra amount of nitrogen contained in the manure. Lack of nitrogen responsiveness thus hampers attempts to increase rice yield through increased application of nitrogen (Table 6.1).

Two reasons for such performance of indica rices in the tropics were considered:

- The genetical association of undesirable plant characters with indica rices.
- The warm climate in the tropics.

Traditional tropical varieties are late maturing, photoperiod sensitive, and high tillering. They have tall, weak, thick culms; long drooping, thin, pale-green leaves; and relatively large lax panicles. These varieties are grown under subopti-

Table 6.1. Response of a traditional tall variety to graded doses of nitrogen, with and without farmyard manure (FYM).^a

	Rough rice yield (t/ha) at nitrogen doses ^b of				
	0	33.6 kg/ha	67.2 kg/ha	100.8 kg/ha	134.40 kg/ha
No manure	2.08	2.59	2.49	2.49	2.22
Farmyard manure at 8.89 t/ha	2.44	2.72	2.47	2.17	1.92

^a Chandler (1963). ^b Added as ammonium sulfate. Converted from lb/acre.

mal water and weed control at moderately wide spacing.

High yielding japonica rices have short, narrow, erect, dark-green leaves; thin, but short and sturdy culms; and short, dense panicles. They respond to increased application of nitrogen, and produce high yields (Jennings 1964). Such observations may suggest that japonica rices be grown in the tropics. In fact, ponlai nces, japonica rices developed in Taiwan and adapted to subtropical climates, perform well in tropical regions. However, the direct introduction of japonica rices into the tropics was not favored for several reasons. First, most japonica varieties mature very early because of daylength and temperature sensitivity, resulting in stunted growth and low yield. Only ponlai rices are adapted to tropical climates; consequently, the amount of genetic resources is quite limited. Second, people in tropical Asia prefer the cooking quality of indica rices. Third, japonica rices lack the grain dormancy desirable for tropical varieties that mature toward the end of the monsoon season.

With this consideration, it was logical to make hybrids between japonicas and indicas to transfer the good characters of japonica rices to indica rices. In the 1950s, the Food and Agriculture Organization (FAO) organized an indica-japonica hybridization program with its headquarters at the Central Rice Research Institute (CRRI) in Cuttack, India (Parthasarathy 1972). From this program came ADT27 in India and Mahsuri and Malinja in Malaysia. However, the over-all results made little impact on rice improvement programs in South and Southeast Asia.

The warm tropical climate was considered another factor responsible for low yields. Because high temperatures increase respiratory losses, net dry matter production — as a balance between photosynthesis and respiration — was thought to be inevitably lower under higher temperatures. Low rice yields in southwestern Japan were attributed to warm climates. For example, yields were correlated with solar radiation and air temperature by the following formula (Murata 1964):

$$Y = S[1.20 - 0.021 (t - 21.5)^2], \quad (6.1)$$

where Y is grain yield (kg/10a [$a = 0.01$ ha]), and S and t are solar radiation (cal/cm² per day) and daily mean temperature (°C), in August and September. The equation indicates that temperatures higher or lower than 21.5°C will decrease



A traditional tall variety vs an improved short variety.



A traditional tall variety vs an improved short variety.

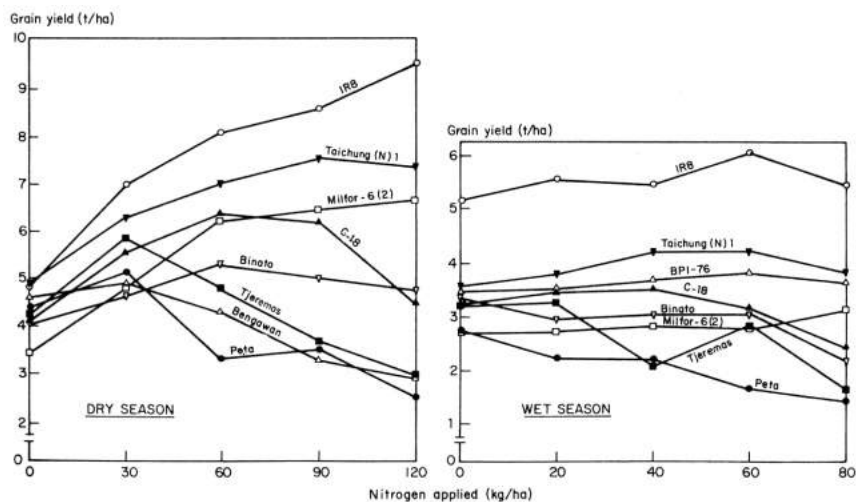
grain yield. But higher solar radiation can compensate for such detrimental temperatures. When 28°C is substituted for t and solar radiation is held constant, a 74% yield reduction, compared with the maximum yield achieved at a daily mean temperature of 21.5°C , is obtained. Equation 6.1 was obtained by statistical analysis. Hence, an extrapolation of variables beyond the range of the collected data should not be allowed. Yet, the equation suggests that high temperature in the tropics could be an important barrier to achieving high yields.

Later work at the International Rice Research Institute (IRRI) demonstrated that high temperature per se in tropical monsoon Asia is not a barrier to increased rice production up to 5–6 t/ha in the wet season and 9–10 t/ha in the dry. It was the variety that hampered attempts to increase rice yields in experimental fields. High temperature may be an important factor when the maximum potential yields in the tropics and temperate region are compared.

6.2. NEW TROPICAL HIGH YIELDING VARIETIES

Emphasis was placed on improving japonica rices in Taiwan when it was under Japanese control and ponlai rices were produced. After World War II the improvement of native indica rices was started (Huang et al 1972).

In 1949, Dee-geo-woo-gen, a semidwarf indica that tillers profusely, was crossed with Tsai-yuan-chung, a tall, disease-resistant variety. Taichung Native 1 (TN1) was selected from this cross and released in 1956. TN1 responds to high levels of nitrogen. The yielding potential of TN1 is similar to that of ponlai rices. It produces 6 t/ha, on the average, with the record yield of 8.1 t/ha. Thus, TN1 is



6.1. Effect of levels of nitrogen on the grain yield of indica rice varieties in dry (left) and wet (right) seasons, IRRI (De Datta et al 1968).

considered the first high yielding indica rice variety. It demonstrated that increasing the yield potential of indica rices can be achieved by improvements within indica rices. Thus, it pointed the way for tropical rice breeding.

In 1962, IRRI began research at Los Baños, Philippines. Its plant breeders crossed Dee-geo-woo-gen and Peta at IRRI. Peta, originating in Indonesia and popularly grown in the Philippines, is a tall, high-tillering variety. From the cross IR8 was selected and released in 1966. IR8 is erect leaved, high tillering, photoperiod insensitive, and about 100 cm tall with stiff culms. It responds well to nitrogen and produces about 6 t/ha in the wet season and 9 t/ha in the dry. Occasionally, the yield exceeds 10 t/ha. Figure 6.1 compares the nitrogen response of IR8 and traditional varieties. IR8 is considered the first high yielding indica rice variety adapted to tropical climates. With good management dwarf rices such as IR8 have enormous potential to boost rice yields in Asia. Their impact was elegantly described as *Dwarf rice — a giant in tropical Asia* (Chandler 1968).

Dee-geo-woo-gen was used as a genetic source of semidwarf stature in both TN1 and IR8. Its usefulness is comparable to that of Norin 10 for Mexican wheat. Both Dee-geo-woo-gen and Norin 10 originated in Asia.

6.3. PLANT-TYPE CONCEPT

6.3.1. Evolution of concept

The term *plant type* refers to a set of morphological characters associated with the yielding ability of rice varieties. The plant-type concept in rice, similar to the wheat ideotype (Donald 1968), emerged gradually from many observations and comparisons between low and high yielding varieties in Japan (Baba 1954, 1961; Tsunoda 1964).

Better varieties of crop species must have been selected for higher yields in the past. In practice, the high yields have been achieved by increased inputs, particularly nitrogen fertilizers. Hence, varieties must have been selected on the basis of their response to nitrogen fertilizers. Tsunoda (1964) compared low and high yielding varieties of rice, sweet potato, and soybean, and summarized their morphological characteristics:

- Low nitrogen responders have long, broad, thin, drooping, pale-green leaves, and tall, weak stems.
- High nitrogen responders have erect, short, narrow, thick, dark-green leaves, and short, sturdy stems.

Tsunoda postulated from physiological knowledge of crop photosynthesis that the thick, dark-green leaves lose less light through reflection. Reduced leaf size and erect habit permit uniform light distribution to all leaves and reduce respiration. Consequently, dry matter and yield increase even under low light conditions. The uniform light penetrations and the short, sturdy culms minimize lodging; thus there is little or no yield loss once panicles are well developed (Tsunoda 1964, Jennings 1964).

The plant-type concept has since attracted considerable attention and more intensive examination in Japan (Murata 1961, Hayashi and Ito 1962, Hayashi 1968, 1969). Experimental data for tropical varieties clearly demonstrate that certain morphological characters are indeed associated with yielding ability (Tanaka et al 1964, 1966a). Work on plant type has been well summarized and the concept appears to have been widely accepted by rice breeders in many countries as a guide for breeding high yielding varieties (Ishizuka 1971, Jennings 1964, Yoshida 1972).

The following morphological characters deserve particular attention:

- Short, stiff culms.
- Erect leaves.
- High tillering.

6.3.2. Short, stiff culms

The increased resistance of improved varieties to lodging appears to be the single character most responsible for high yields. A short, stiff culm makes the rice plant more lodging resistant. Table 6.2 compares the yield performance of Peta, a tall, lodging-susceptible variety, with that of IR8. The mechanical support alone increased the grain yield of Peta by 60% in the wet season and by 88% in the dry. Although height is the most important plant character associated with lodging, a short variety is not always lodging resistant. There are differences in the stiffness of short culms (Chandler 1969).

The importance of lodging resistance has long been recognized, but only in recent years has the semidwarf gene been effectively introduced into tropical rice varieties. In southern Japan, Hoyoku and its sister high yielding varieties are largely characterized by increased lodging resistance (Shigemura 1966).

6.3.3. Erect leaves

Erect leaves allow the deeper penetration and more even distribution of light, which results in increased crop photosynthesis (see Chapter 5).

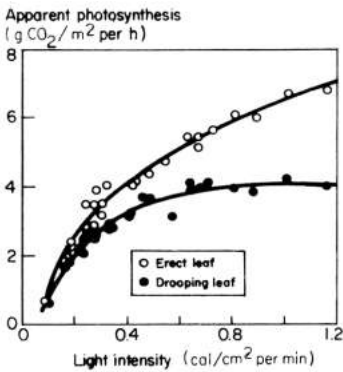
In one model, the crop photosynthesis of an erect-leaved canopy is about 20% higher than that of the droopy-leaved canopy when the LAI is extremely high (van

Table 6.2. An example of the yield performance of IR8 and Peta in the wet and dry seasons. ^a

Variety	Yield (t/ha)		
	Wet season ^b	Dry season ^c	Mean
Peta, not supported	2.83 (100)	3.97 (100)	3.40 (100)
Peta, supported	4.52 (160)	7.46 (188)	5.99 (176)
IR8. not supported	6.10 (216)	9.10 (229)	7.60 (224)

^a Yoshida, et al (1972). ^b 1966, 30– x 30-cm, spacing, 100 kg N/ha.

^c 1968, 20– x 20-cm spacing, 120 kg N/ha.

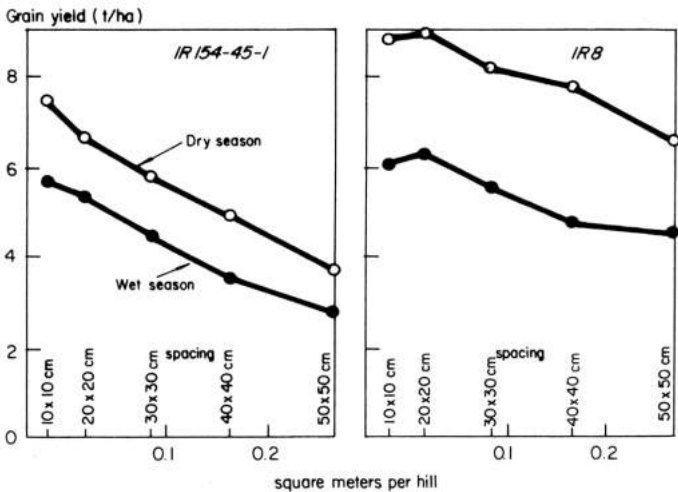


6.2. Difference in light-photosynthesis curves between rice populations with erect and droopy leaves (Tanaka et al 1969).

Keulen 1976). This model assumes that all the leaves are uniformly oriented at angles of 0° or 90° with respect to the horizontal plane.

When we consider leaf angles and the light environment of individual leaves within a canopy, almost intuitively we visualize that a combination of short, erect upper leaves grading to droopy, longer lower leaves is ideal for maximum crop photosynthesis. In fact, theory and experimental evidence shows that this plant architecture leads to the maximization of incident solar radiation (Matsushima et al 1964a, Duncan 1971).

There is only one rice experiment indicating that the droopy-leaved canopy has a lower crop photosynthesis than the erect-leaved canopy at high light intensities (Fig. 6.2); accordingly, the droopy-leaved canopy was lower than the erect-leaved



6.3. Response of high-tillering (IR8) and low-tillering (IR154-45-1) varieties to spacing (adapted from Yoshida and Parao 1972).

Table 6.3. Response of a low-tillering variety (IR154-45-1) and a high-tillering variety (IR8) to different seed rates in direct seeding, IRRI, 1968 wet and dry seasons.^a

Seed rate (kg/ha)	Plants (no./m ²) (dry season)		Panicles (no./m ²)				Yield (t/ha)			
			IR154-45-1		IR8		IR154-45-1		IR8	
	IR154-45-1	IR8	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
50	205	129	585	530	595	555	4.32	7.27	5.20	7.57
100	416	241	610	662	680	645	4.54	7.34	5.33	7.44
200	800	503	740	667	670	644	4.42	6.81	5.04	7.68

^a Yoshida and Parao (1972).

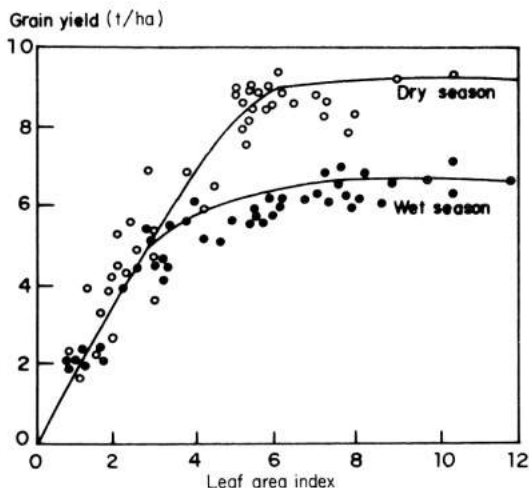
canopy in postflowering dry matter production by 34% and in grain yield by about 33%. In this experiment, Nihonbare, an erect-leaved variety, was field grown up to the beginning of heading, when the field was divided into two plots. In one plot, the leaves were drooped by attaching lead beads about the size of rice grains to the leaf tips. In the other plot, the leaves were kept erect. The LAI of the crop at heading was 7.1. The crop photosynthesis was measured 2 days after the treatment. The results of this experiment support predictions from the crop photosynthesis model. However, it is possible that the droopy-leaved canopy was damaged by attaching lead beads to the leaf tips; hence, the results might have been exaggerated in favor of the erect-leaved canopy.

6.3.4. High tillering capacity

Within a range of spacing from 50 × 50 cm to 10 × 10 cm, tillering capacity affects the grain yield of a variety (Fig. 6.3). The grain yield of IR154-45-1, a low-tillering selection, increased with decreased spacing up to 10 × 10 cm. A high-tillering variety, IR8, reached maximum yield at 20 × 20-cm spacing and levelled at 10 × 10 cm. IR8 is less affected by spacing changes than IR154-45-1. In transplanted rice, conventional spacing ranges from 20 × 20 cm (25 hills/m²)¹ to 30 × 30 cm (11.1 hills/m²). High and early tillering habits are advantageous under such conditions. Under direct seeding, however, tillering capacity rarely affects grain yield within conventional seeding rates (Table 6.3) because total panicle number per square meter depends more on the main culm than on tillers.

Medium tillering capacity was once considered desirable for high yielding rice varieties (Beachell and Jennings 1965). Low yields were believed caused by fast growth and a LAI beyond the optimum, which, in turn, is closely related to high tillering capacity. This conclusion was based on the comparison of unimproved indica and improved japonica varieties. With an improved, lodging-resistant

$$^1 \text{Number of hills/m}^2 = \frac{1 \text{ m}^2}{\text{spacing}} = \frac{100 \times 100 \text{ (cm}^2\text{)}}{20 \times 20 \text{ (cm}^2\text{)}} = 25$$



6.4. Relation between grain yield and leaf area index at flowering in IR8 (wet and dry seasons, 1966–69) (Yoshida et al 1972).

indica variety, there is no optimum LAI for dry matter production, although a critical LAI does exist (see Fig. 5.4, Chapter 5). A LAI as large as 12 at heading is not detrimental to grain yield unless the crop lodges (Fig. 6.4).

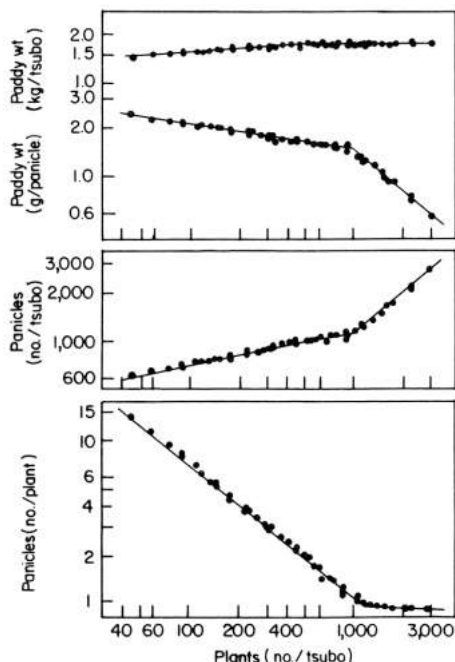
Missing plants due to poor land levelling, insects, diseases, and other stresses may occur in the field. A high-tillering variety is able to compensate for such missing plants.

In the wheat ideotype, a single culm is desirable for high yields (Donald 1968). Similarly, a crop photosynthesis model for corn considers tillering hills the worst arrangement in plant geometry (Duncan 1968). At high plant densities, however, multiculm rice plants either would not produce tillers or would produce only a limited number, thus approaching a single culm plant population. In an experiment, the effect of plant density on yield was tested for 14–909 plants/m² (45–3,000 plants/tsubo) by varying both spacing and plant numbers per hill (Fig. 6.5). Tillering occurred up to a density of 300 plants/m² (1,000 plants/tsubo), beyond which only main shoots grew and produced panicles.

Grain yield increased with increasing plant densities up to 182–242 plants/m² (600–800 plants/tsubo). The number of panicles per unit of land area increased with increasing plant density but the increase was accompanied by a decrease in paddy weight per panicle. In another experiment, all the plants produced panicles at a plant density as high as 1,212 plants/m² (4,000 plants/tsubo) (Yamada 1963). Thus, of the three crops, rice is highly tolerant of high plant densities, wheat is less tolerant, and corn is the least tolerant. In both wheat and corn, grain yield decreases when the plant density exceeds a certain value (Yoshida 1972).

The above discussion leads to the conclusion that exceptional tolerance for high densities makes the rice plant flexible in its response to changes in plant density, and high tillering capacity is desirable for achieving maximum yields in transplanted rice cultivation.

6.5. Number of panicles and paddy weight in relation to planting density (Yamada 1963).



6.4. GROWTH DURATION

The growth duration of a variety is highly location and season specific because of interactions between the variety's photoperiod and temperature sensitivity and weather conditions. Thus, terms such as *early*, *medium*, and *late maturing* are meaningful only under particular locations or seasons.

Traditional tropical varieties in Asia are well adapted to the monsoon season. They are usually planted in June or July, take 160–200 days to mature, and are harvested in November or December. Such long-growth duration varieties are inevitably photoperiod sensitive. In a limited area of tropical Asia, however, irrigation is available and rice can be grown in the dry season, normally from January to May. This is called the *off-season* or dry season crop. Varieties adapted to the dry season are photoperiod insensitive and mature in 90–130 days.

Varieties of too short growth duration may not produce high yields because of limited vegetative growth, and those of too long growth duration may not be high yielding because of excessive vegetative growth, which may cause lodging. About 120 days from seeding to maturity appears to be optimum for maximum yield at high nitrogen levels in the tropics. However, a longer growth duration may produce higher yields when fertility is low (Kawano and Tanaka 1968) presumably because there is more time to extract soil nitrogen.

Table 6.4. Effect of spacing on grain yield and daily production of 3 varieties, IRRI, 1970.^a

Selection	Spacing (cm)	Growth duration (days)	Grain yield (t/ha)	Daily grain production in main field (kg/ha)
<i>Wet season</i>				
IR747B2-6	5 × 5	95	5.62	75
	10 × 10	95	4.70	63
IR22	20 × 20	95	4.15	55
	5 × 5	114	4.92	52
IR8	10 × 10	114	5.01	53
	20 × 20	114	4.57	41
	5 × 5	124	5.32	51
	10 × 10	124	5.31	51
	20 × 20	124	5.14	49
<i>Dry season</i>				
IR747B2-6	10 × 10	98	7.92	102
	20 × 20	98	7.23	93
	10 × 10	110	7.23	80
IR154-18-2-1	20 × 20	110	6.98	78
IR8	20 × 20	132	8.61	77

^aIRRI (1971).

Early maturing varieties allow intensified cropping. At conventional spacing, short growth duration varieties usually give low yields because of insufficient vegetative growth. Close spacing is essential for early maturing varieties to achieve high yields (Table 6.4). In the wet season the grain yield of IR747B2-6 at 5 × 5 cm is as high as that of IR8. In the dry, IR747B2-6 produces about 8 t/ha at 10 × 10 cm, whereas IR8 gives 8.6 t/ha at 20 × 20-cm spacing. At close spacings therefore, the yield potential of IR747B2-6 can be nearly as high as that of IR8. One clear benefit of early maturing varieties is high grain production per day. In both wet and dry seasons, IR747B2-6 is about 30% more efficient than IR8 in daily grain production.

Another advantage of an early maturing variety is high water-use efficiency. As illustrated in Chapter 2, paddy field evapotranspiration is proportional to incident solar radiation and, hence, nearly proportional to the number of days the crop is in the field. Thus, a higher daily production implies a higher water-use efficiency.

How far can growth duration be shortened without sacrificing yield potential? Panicle development is fairly fixed at about 30 days. The duration of ripening depends on temperature; it is about 30 days in the tropics. Thus, about 60 days is necessary for reproductive growth and ripening in the tropics.

How many days are needed for vegetative growth? Although difficult to answer experience suggests that about 30 days is minimum for sufficient vegetative

growth before reproductive growth starts, provided there is no interruption. Thus, the total growth duration of early maturing varieties is about 90 days. Direct-seeding appears essential for a 90-day variety to have sufficient vegetative growth before panicle initiation.

For transplanted rice with a total duration of 90 days, 20 days in the seedbed and 60 days for reproductive growth and ripening leave only 10 days for active vegetative growth, which is not sufficient. About 100 days is the shortest duration for achieving reasonably high yields with transplanted rice. In the comparison above, the number of field days is 10 days shorter for a 100-day variety in transplanted rice than for a 90-day variety in direct-seeded rice (Yoshida 1978). Among the materials now available, IR747B2-6 is one of the best early maturing lines in the tropics; it matures in 95–98 days (Table 6.4). IR36 matures in 105 days. Thus, attempts to shorten growth duration are approaching the limit for the shortest possible growth duration with high yielding potential.

6.5. ASSOCIATION BETWEEN PLANT CHARACTERS

Conceptually, each plant character could be independent; factually, several plant characters are often closely associated.

6.5.1. Foliar absorption coefficient and plant characters

The foliar absorption coefficient (k) is related to light penetration into a plant canopy by equation 5.8:

$$\ln \frac{I}{I_0} = -kF$$

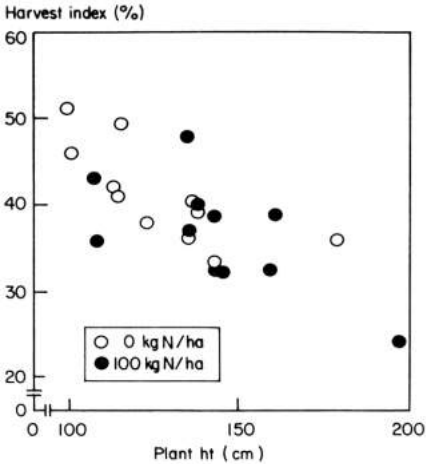
The foliar absorption coefficient is negatively correlated with specific leaf area and the average leaf angle of the upper three leaves when measured from the horizontal plane and weighted for the area of each leaf (Table 6.5).

Culm length is negatively correlated with the average leaf angle of the upper three leaves. As a consequence, the culm length is positively correlated with the

Table 6.5. Correlation between foliar absorption coefficient and some plant characteristics.^a

Plant characteristic	Correlation coefficient
Culm length	+0.549**
Crop ht	+0.130
Number of culms	-0.021
Mean area of single leaf	-0.244
Specific leaf area	-0.544**
Leaf angle	-0.539**
Leaf angle × specific leaf area	-0.717**

^a Hayashi and Ito (1962).



6.6. Relationship between plant height and harvest index (Tanaka et al 1966).

foliar absorption coefficient.

The specific leaf area (cm²/g) is a measure of leaf thickness, and varies with variety, leaf position, growth stage, nutrition, and climatic environment (Murata 1975). Values of specific leaf area for rice varieties range from about 200 to 450 cm²/g. The foliar absorption coefficient is negatively correlated with specific leaf area, which differs from Tsunoda's conclusions (1964).

6.5.2. Plant height vs harvest index vs nitrogen responsiveness

Harvest index is inversely correlated with plant height (Fig. 6.6). Thus, tall varieties usually have low harvest indices (or low grain-straw ratios). The grain-straw ratio of 5 highly nitrogen-responsive varieties ranged from 0.95 to 1.23 and

Table 6.6. Grain-straw ratios for selected varieties.^a

Class	Variety	Grain-straw ratio
Highly nitrogen responsive	IR8	1.15
	Chianung 242	1.14
	Taichung Native 1	1.20
	Tainan 3	1.23
	IR5	0.95
	Mean	1.13
Low or negatively responsive to nitrogen	Hung	0.60
	Peta	0.60
	Nahng Mong S4	0.49
	Puang Nahk 16	0.40
	H-4	0.58
	Sigadis	0.69
	Mean	0.56

^aChandler (1969).

had a mean value of 1.13 (Table 6.6). The grain-straw ratio of 6 low nitrogen-responsive varieties had a mean value of 0.56.

In the above example, the nitrogen responsiveness is largely related to plant height, which in turn is related to lodging resistance and harvest index or grain-straw ratio. A high harvest index is characteristic of the new high yielding varieties, but it may be the result of conscious selection for short, stiff straw rather than for large grain yield with the minimum production of total dry matter (Thorne 1966). A tall variety could have a high harvest index if the panicle is larger (Tanaka 1972a). At the moment, however, it is difficult to find a tall rice variety with a high harvest index.

6.5.3. Growth duration vs harvest index

Harvest index is inversely correlated with growth duration (Fig. 6.7). The correlation, however, appears quite loose.

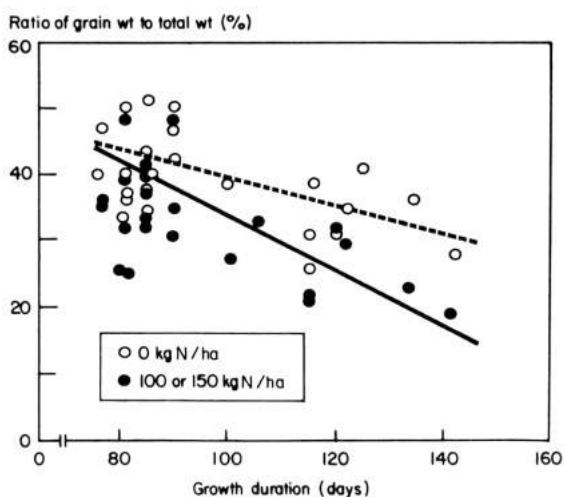
6.5.4. Growth duration vs plant height

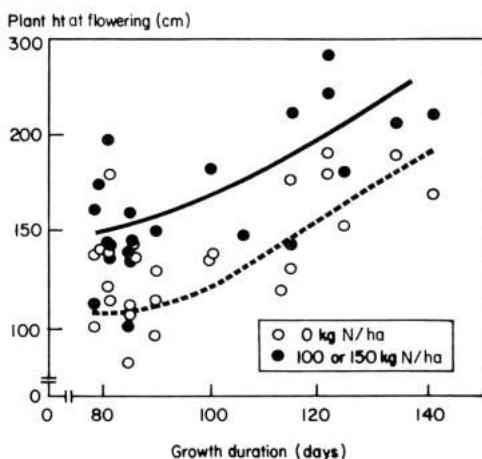
Plant height at flowering is positively correlated with growth duration (Fig. 6.8). Again, this correlation is very loose. For a growth duration of about 80–90 days, plant height is scattered over a wide range from less than 100 cm to about 200 cm. In general, the amount of growth is the product of rate and time:

$$\text{Growth} = \text{rate} \times \text{time} \quad (6.2)$$

If the growth rate is sufficiently high to compensate for a short duration, the rice plant can produce a large amount of growth. This is likely to be true for height growth. For example, Dular, a 100-day variety, is as tall as Mahsuri, a 134-day variety (IRRI 1977).

6.7. Relation between growth duration and harvest index (Tanaka et al 1966)





6.8. Relation between growth duration and plant height (Tanaka et al 1966).

6.6. CHANGES IN MORPHOLOGICAL CHARACTERS OF RICE VARIETIES

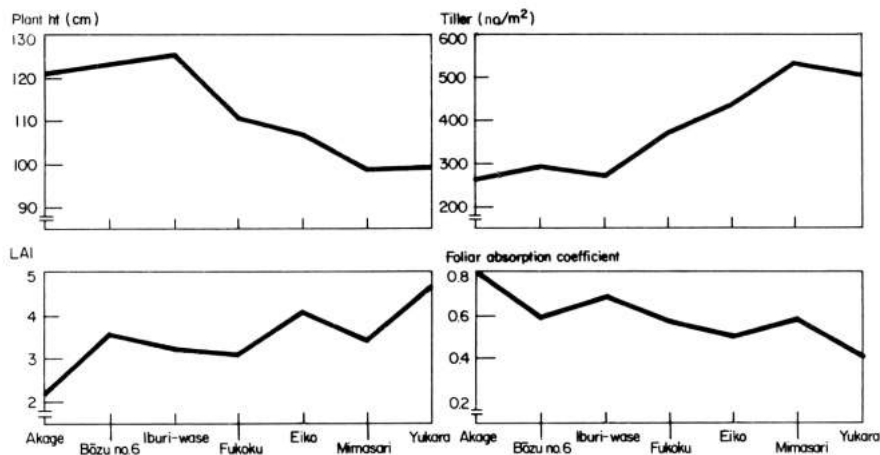
The morphological character that has contributed most to high yields is a short, stiff culm that gives lodging resistance (Shigemura 1966, Chandler 1968).

Changes in the morphological characters of rice varieties that became commercially available between 1905 and 1962 in Hokkaido, Japan, indicate that varieties have been selected for shorter plant height, higher tillering capacity, and more erect leaves (Fig. 6.9). Increasing LAI is associated with higher tillering capacity. Shorter plant height (lodging resistance) and higher tillering capacity (increasing LAI) would have contributed more to increased yield and nitrogen response than a smaller foliar absorption coefficient. The crop photosynthesis model suggests that leaf angle (foliar absorption coefficient) is not too important up to a LAI of 3–4 (Monteith 1965, Duncan 1971, van Keulen 1975). A similar trend is also observed for rice varieties in southern Japan (Ito and Hayashi 1969).

Historically, the selection must have been based on *selection for yield* with liberal use of nitrogen fertilizers and improved cultural practices such as close spacing. However, the outcome of this selection agrees with the present knowledge of the physiological aspects of high yields in transplanted rice.

6.7. MODIFICATIONS OF VARIETAL TRAITS FOR SUBNORMAL CONDITIONS

Under subnormal management conditions, high yielding varieties may or may not be good yielders. The recent recognition of diverse environments in rice-growing regions indicates the need for a better understanding of the benefits and disadvantages of contrasting plant characters (Yoshida 1977b, 1978). With such informa-

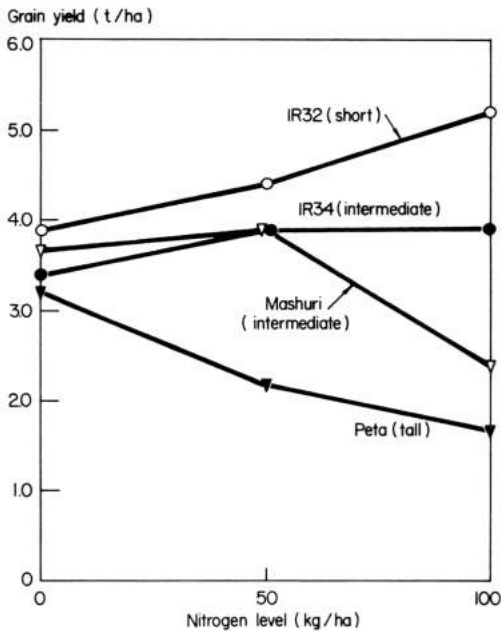


6.9. Changes in plant type of rice varieties in Hokkaido, Japan from 1905 to 1962 (Tanaka et al 1968b).

tion, plant breeders could possibly design and select varieties suitable for particular environments.

The following discussions will reexamine the possible benefits and disadvantages of plant height, leaf habit, and tillering capacity under varying conditions.

6.10. Response of 4 rice varieties to nitrogen application, wet season, IRRI (Yoshida 1978).

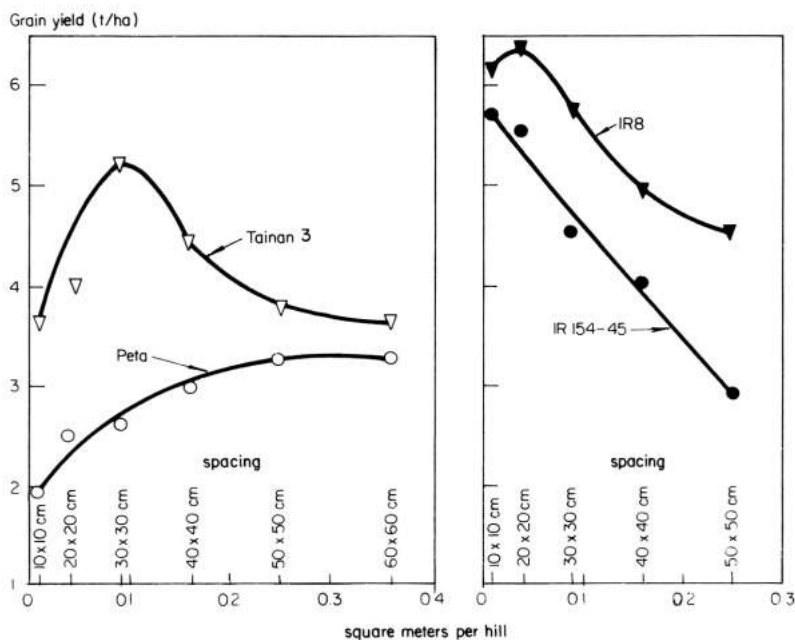


6.7.1. Plant height

In the low-lying rainfed areas of tropical Asia, rice crops are inevitably subjected to variable water depths. It is unlikely that irrigation and drainage facilities will expand greatly within the foreseeable future. Grain yield decreases with increasing water depth (see Table 2.17). Under such conditions, intermediate stature (110–130) is considered desirable over short stature (90–110 cm). Another advantage of a taller plant is perhaps an increase in the ability to compete with weeds. Yield reductions due to weeds decrease with increasing plant height.

A taller plant, however, is more susceptible to lodging and less responsive to nitrogen (Fig. 6.10). Mahsuri, an intermediate variety, produced reasonably good yields at 0 and 50 kg N/ha. IR34, an improved intermediate variety, performed better than Mahsuri at 100 kg N/ha but its grain yield did not increase when nitrogen was increased from 50 to 100 kg N/ha. However, the yield of IR32, a short variety, increased with additional nitrogen application.

Changes in plant height may cause spacing problems. Intermediate and tall varieties tend to lodge at close spacing; short and lodging-resistant varieties give the highest yield at close spacings (Fig. 6.11). In this example, Peta is tall, Tainan 3 has intermediate height, and IR8 and IR154-45 are short. At close spacing and in partial submergence, the culm tends to elongate more, and the crop may lodge.



6.11. Yield of Tainan 3 and Peta at 6 spacings (left), 1962 wet season (Tanaka et al 1964), and yield of IR8 and IR15445 at 5 spacings (right). 1967 wet season (Yoshida and Parao 1972).

Table 6.7. Benefits and disadvantages of contrasting plant characteristics.^a

Plant Part	Characteristics	Benefits and disadvantages
Leaf	Thick	Higher photosynthetic rate per unit leaf area.
	Thin	Associated with development of larger LAI.
	Short and small	Associated with more erect habit.
	Erect	Associated with more erect habit. Even distribution of leaves in a canopy.
	Droopy	Uses solar energy efficiently when LAI is large.
Culm	Short and stiff	Uses solar energy efficiently when LAI is small.
	Tall	Suppresses weeds.
Tiller	Upright (compact)	Prevents lodging.
	High tillering	Suppresses weeds.
Root	Low tillering	Permits greater penetration of incident light into a canopy.
	Shallow and low root/shoot ratio	Adapted to a wide range of spacings; capable of compensating for missing hills; permits faster leaf area development.
	Deep and high root/shoot ratio	Can be used for direct seeding.
Panicle	Low sterility at high nitrogen rates	Uses high proportion of assimilates for shoot.
	High harvest index	Increases resistance to drought.
	Small grain	Uses soil nitrogen and recovers applied nitrogen efficiently.
	Large grain	Permits use of larger amount of nitrogen.
Growth duration	Early maturing	Associated with high yields.
	Late maturing	Related to fast grain filling.
Photoperiod sensitivity	Sensitive	Has potential for high yields (?).
	Insensitive	Increases grain production per day.
Early growth	Fast	Increases water use efficiency.
	Slow	Requires close spacings to achieve high yields.
		Adapted to low fertility (?)
		Adapted to areas of a long monsoon season.
		Can be grown any time of a year; fitted to multiple cropping systems.
		Suppresses weeds.
		Essential for early maturing varieties.
		Prevents excessive growth at later stages under a good management.

^a Adapted from Yoshida (1972, 1977b, 1978) and Yoshida et al (1972).

Thus, an intermediate plant height has some advantages where there is undependable water control but that benefit may not be realized without more lodging resistance.

6.7.2. Leaf angle

Crop photosynthesis models indicate that droopy leaves are slightly better than erect leaves when the LAI is less than 3. And the leaf inclination is not too important when the LAI is less than 4 (Duncan 1971, Monteith 1965, van Keulen 1976). A LAI of 4 at heading is sufficient to produce about 5 t/ha in both the wet and dry seasons (see Fig. 6.4). In other words, the leaf angle per se is not important when grain yield is less than 5 t/ha.

6.7.3. Tillering capacity

High tillering capacity basically relates to the plant's ability to make maximum use of space. High tillering is considered more important under subnormal conditions than under optimal conditions.

6.7.4. Benefits and disadvantages of contrasting plant characteristics

Each plant character has benefits and disadvantages under different conditions. Under a good environment and with good management, IR8 and similar semi-dwarf varieties are ideal. On the other hand, under diverse environments and different management levels, the problem becomes location and management specific. There is no single variety that can meet all the requirements set by the different environment and management levels. Apparently, gains in one aspect are accompanied by losses in another. In such a situation, it is important for plant breeders to recognize the benefits and disadvantages of contrasting plant characteristics (Table 6.7).

7

PHYSIOLOGICAL ANALYSIS OF RICE YIELD

7.1. CONTRIBUTION OF ACCUMULATED CARBOHYDRATE TO THE GRAIN

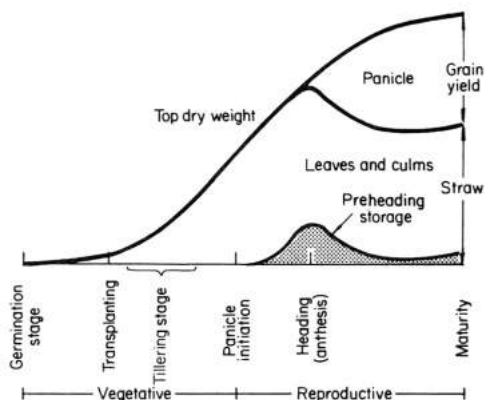
Carbohydrates such as sugars and starch begin to accumulate sharply about 2 weeks before heading and reach a maximum concentration in the plant's vegetative parts, mainly in the leaf sheath and culm, at around heading. The concentration begins to decrease as ripening proceeds and may rise again slightly near maturity (Fig. 7.1). Direct, qualitative evidence that the accumulated carbohydrates are translocated into grains was obtained with a ^{14}C technique (Murayama et al 1961, Oshima 1966).

The accumulated carbohydrate has three possible functions in grain production:

- To supply a portion of the grain carbohydrate.
- To support sustained grain growth under variable weather conditions.
- To stabilize grain yield under unfavorable weather conditions during ripening.

The usual method for calculating the contribution of accumulated carbohydrates to the grain analyzes carbohydrates in the vegetative parts and uses the following formula:

$$\begin{array}{l} \text{Contribution (\%)} \text{ of} \\ \text{accumulated carbohydrate} \\ \text{to grain carbohydrate} \end{array} = \frac{(\text{CHO})_F - (\text{CHO})_M}{(\text{CHO})_G} \times 100, \quad (7.1)$$



7.1. Changes in the amount of temporarily stored carbohydrates (preheading storage) and dry weight of various parts according to growth stages in rice (schematic illustration, Murata and Matsu-shima 1975).

where $(CHO)_F$ = carbohydrate present in the vegetative part at flowering,

$(CHO)_M$ = carbohydrate present in the vegetative part at maturity, and

$(CHO)_G$ = carbohydrate in the grain at maturity.

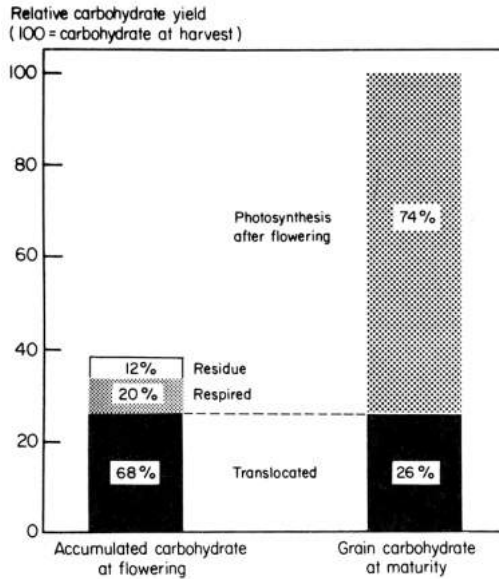
Estimates by the above method range from 0 to 71%, depending on the cultural practices, nitrogen application, and growth duration. Under most conditions the estimate falls between 0 and 40%. However, 71% was obtained when the plant density was extremely high — 146 hills/m² (Wada 1969). The percentage contribution will become high if the grain carbohydrate is small, which may result when grain filling is disturbed by unfavorable weather conditions. The above calculation assumes that all the carbohydrates lost from vegetative parts during grain filling will be translocated to the grains. This assumption is obviously wrong. Some portion of the stored carbohydrate must be used in respiration during grain filling. Hence, the formula tends to overestimate the contribution of accumulated carbohydrates to the grains.

The ¹⁴C technique allows a more accurate estimate. The stored carbohydrates in the vegetative parts can be labelled with ¹⁴C by feeding the rice crop with ¹⁴CO₂ about 10 days before flowering. The contribution of photosynthesis during ripening can be estimated by calculating the difference between the total grain carbohydrate and the carbohydrates attributed to preheading storage.

Figure 7.2 shows that 68% of the accumulated carbohydrate was translocated into the grain, 20% was respired during the ripening period, and 12% remained in the vegetative parts. The amount of the carbohydrate translocated was equal to about 21% of the grain carbohydrate, or the equivalent of about 2 t grain/ha when the yield was 7.8 t/ha. Equation 7.1 gave an estimate of 34% in the same experiment.

When photosynthesis during ripening is restricted by 90% shading, the accumulated carbohydrate supports grain growth at almost a normal rate for about 2 weeks

7.2. The contribution of accumulated carbohydrate in the vegetative parts at heading to grain yield (Cock and Yoshida 1972).



after flowering (Murayama et al 1955). This indicates that when the current supply of assimilate is insufficient for rapid grain growth, the accumulated carbohydrate can be easily translocated into the grain. This translocation may prevent the occurrence of the unfilled spikelets (spikelets that are fertilized but fail to grow at early stages of grain filling) and is important when photosynthesis during ripening is temporarily restricted by cloudy or rainy weather in monsoon Asia.

Grain carbohydrate depends more on accumulated carbohydrate when light intensity after heading is low because photosynthesis during ripening is reduced (Soga and Nozaki 1957).

At low nitrogen levels, large amounts of carbohydrate accumulate in the vegetative parts before heading and contribute substantially to the grain carbohydrate (Murayama et al 1955, Wada 1969, Yoshida and Ahn 1968).

7.2. CURRENT PHOTOSYNTHESIS DURING RIPENING

The contribution of accumulated carbohydrate to grain carbohydrate ranges from 0 to 40% under most conditions. It follows that the photosynthesis during ripening contributes to grain carbohydrate by 60–100% under most conditions.

The photosynthetic contribution by different plant parts to the grain—difficult to assess because of technical problems (Yoshida 1972) — is affected by the potential photosynthetic activity, longevity of the tissue during ripening, and light environment in a crop canopy.

The potential photosynthetic activity of different plant parts can be estimated by measuring dark respiration and photosynthesis when light is not limited (e.g.

Table 7.1. Photosynthetic activity of leaves, sheaths, and panicles at a light intensity of 60 klx at milky stage.^a

		Surface area (cm ²)	Assimilation ^b (mg CO ₂ /h)			Rate (mg CO ₂ /dm ² per h)	
			P_n	R_d	P_g	P_n	R_d
Leaf blade	1 ^c	24	8.3 (30)	0.44 (9)	8.7 (27)	34	1.8
	2	54	10.1 (36)	0.52 (11)	10.6 (33)	19	1.0
	3	51	5.6 (20)	0.46 (11)	6.1 (19)	11	0.9
	4	37	2.2 (8)	0.34 (7)	2.5 (8)	6	0.9
All leaves			26.2 (94)	1.76 (38)	27.9 (87)		
Leaf sheath plus culm			1.2 (4)	0.60 (14)	1.8 (5)	—	—
Panicle			0.6 (2)	2.05 (48)	2.7 (8)	—	—
Total			28.0(100)	4.46(100)	32.4(100)	—	—

^a Yoshida and Cock (1971); variety IR22 grown in the field. ^b P_n = net photosynthesis, R_d = dark respiration, P_g = gross photosynthesis. Figure in parentheses indicate percentage of the total. ^c Counted from the top.

Table 7.1). The potential net photosynthesis of the leaves was 94% of the total. The fourth leaf had a very low net photosynthesis both on a per-leaf basis and on a per-unit-area basis. The top leaf had the highest net photosynthesis per unit area but the second leaf was larger in size and had a greater potential net photosynthesis on a per-leaf basis. In rice, all the leaves from the flag leaf down to the third leaf from the top export assimilates to the panicle. Lower leaves send their assimilates to the roots (Tanaka 1958). The top 3 leaves of plants in an IR8 crop made up 74% of the total leaf area when LAI was 5.5 at heading. Flag leaves were only 19% of the total leaf area, and the second and third leaves made up 55% (Yoshida and Cock 1971).

The net photosynthesis of the leaf sheath and panicle is extremely small. Even in terms of gross photosynthesis (P_g), the panicle (8%) and the leaf sheath (5%) have extremely low photosynthetic capacity. Hence, both can be considered non-photosynthetic tissues (Tsuno et al 1975).

The longevity of the green tissue must be considered when assessing the photosynthetic contribution of different plant parts during ripening. The panicle becomes yellow relatively early in ripening but the leaves remain green much longer. The flag leaf remains green and maintains active photosynthesis until maturity (Takeda and Maruta 1956). At later stages of ripening, however, photosynthesis may not make much of a net contribution to grain production because rapid grain growth occurs earlier and slows down toward maturity.

The light environment of different plant parts in a crop canopy is extremely important for determining the real photosynthetic activity of a given part. Panicles of improved indica varieties tend to bend and become positioned below the flag leaf where they are heavily shaded by the leaf canopy, particularly when the LAI is large. Panicles of these varieties are unable to make a significant contribution to grain filling because of their low potential photosynthetic activity and low light

intensity. In a canopy with flat leaves the whole area of the top leaf is more exposed to sunlight than any lower leaf. But in a canopy with very erect leaves, the tips of lower leaves may receive more sunlight than the basal part of the flag leaf.

7.3. YIELD COMPONENT ANALYSIS

7.3.1. Relative importance of yield components

The grain yield can be divided into several components (see Chapter 1). Equation (1.21) can be rewritten as:

$$Y = N \times W \times F \times 10^{-5}. \quad (7.2)$$

where Y = grain yield (t/ha),
 N = spikelet number/m²,
 W = 1,000-grain weight (g), and
 F = filled spikelets (%).

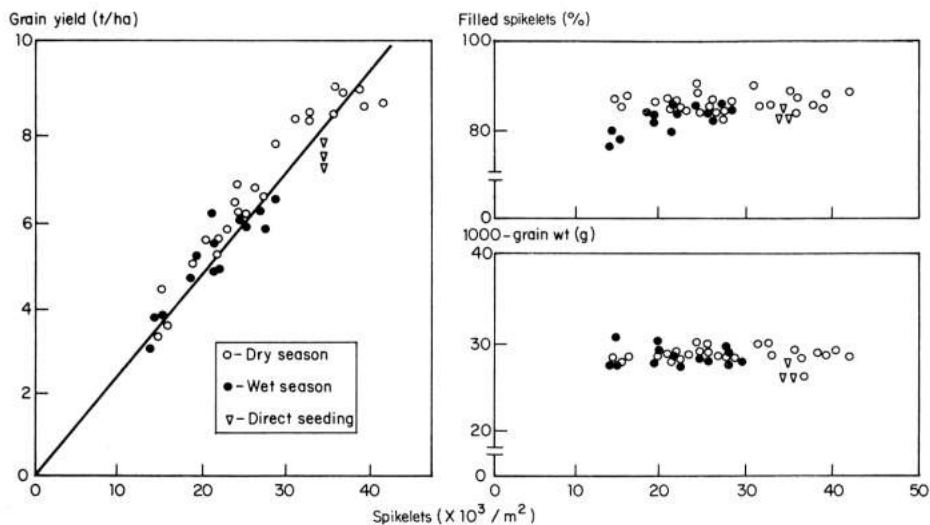
Each of the yield components differs not only in the time when it is determined but in its contribution to the grain yield.

When IR747B2-6, an early-maturing variety, was grown throughout the year at Los Baños, Philippines, the grain yields of 19 crops ranged from 4.6 to 7.1 t/ha. To examine the relative importance of each yield component for grain yield in these crops, the percentage contribution was computed by means of correlation coefficients and multiple regressions based on a log scale (Equation 7.2 was converted to $\log Y = \log N + \log W + \log F + R$). While the combined yield components accounted for 81% of the yield variation, number of spikelets per square meter (N) alone explained 60% of the variation, and filled-spikelet percentages (F) and grain weight (W) together accounted for 21% (Table 7.2). If the contribution of all the yield components were taken as 100, which would have been true had there been no error in measurement, the contribution of number of spikelets per square meter would have been 74% and the combined contribution of filled-spikelet percentage and grain weight would have been 26%. Clearly, spikelet

Table 7.2. Contribution of each yield component to grain yield.^a

Variable ^b	Contribution to total variation in yield (%)
N	60.2
F and W	21.2
N and F	75.7
N and W	78.5
N and F and W	81.4

^aYoshida and Parao (1976). ^b N = spikelet number per square meter; F = filled-spikelet percentage; W = 1,000-grain wt.



7.3. Relationship between total number of spikelets per square meter, grain yield, filled-spikelet percentage, and grain weight of variety IR8 (Yoshida et al 1972).

number per square meter was the most important component limiting yield in this experiment.

A similar conclusion was obtained from IR8 crops grown at Los Baños (Fig. 7.3). The grain yield increased linearly with increasing spikelet number per square meter while filled-spikelet percentage and 1,000-grain weight remained fairly constant regardless of spikelet number. At some locations and in some weather conditions, filled-spikelet percentage may be more limiting to yield than spikelet number per square meter (Yoshida and Parao 1976). The 1,000-grain weight may affect yield to some extent but rarely becomes limiting under most conditions. Therefore, under given conditions it is important to examine the causes of yield variation in components, particularly spikelet number per square meter and filled-spikelet percentage.

7.3.2. Spikelet number per unit land area

Spikelet number per unit land area is affected by:

- Cultural practices — spacing (seeding density) and nitrogen application.
- Growth characteristics — tillering (seedling emergence).
- Climatic conditions — solar radiation and temperature.

Under subnormal cultural practices, the spikelet number per unit land area can be increased by increasing plant density and nitrogen application. Optimum spacing varies with tillering capacity and growth duration of a variety. A higher plant density is required for low-tillering, early-maturing varieties, and low nitrogen levels. The relationships between spikelet number per unit land area and amount of nitrogen absorbed by the crop have been discussed in Chapter 2 (Fig. 2.9).

At an optimum combination of spacing and nitrogen level, the spikelet number per unit land area is strongly influenced by levels of solar radiation and temperature during reproductive growth (see Table 2.10, 2.11, and Fig. 2.13).

7.3.3. Filled-spikelet percentage

Factors such as weather, soil, fertilizer application, and incidence of diseases and insects affect filled-spikelet or sterility percentages. Sterility percentage often refers to the percentage of unfertilized spikelets plus the percentage of partially filled spikelets. Hence, the term *sterility* is not always strictly used. The iodine-potassium iodide method can distinguish unfertilized spikelets from partially filled spikelets (Matsushima and Tanaka 1960).

The sterility percentage determined with the iodine-potassium iodide method is usually low under normal weather conditions. About 9% was the average sterility percentage of 4 crops at Los Baños, Philippines. Crops shaded during ripening had a low percentage of filled spikelets because of increased numbers of partially filled spikelets (see Table 2.11). Except under extremely adverse weather conditions, an unusually low percentage of filled spikelets is attributed to an increased percentage of partially filled spikelets.

A brief account of each factor that affects filled-spikelet percentage follows (Yoshida and Parao 1976):

a. High levels of nitrogen application. Some varieties may have lower filled-spikelet percentages than other varieties at high levels of nitrogen.

b. Lodging or bending. At high levels of nitrogen, lodging or culm bending decreases filled-spikelet percentage. Lodging reduces the cross-sectional area of vascular bundles and disturbs the movement of assimilates and absorbed nutrients via the roots. It also disturbs the leaf display and increases shading.

c. Low solar radiation. The percentage of filled spikelets often decreases as the number of spikelets per square meter increases (Wada 1969). Filled-spikelet percentage is determined by the source activity relative to the sink size (spikelet number), the ability of spikelets to accept carbohydrates, and the translocation of assimilates from leaves to spikelets. When solar radiation is low, the source activity may be insufficient to produce enough carbohydrates to support the growth of all the spikelets. As a result, the numbers of unfilled spikelets may increase. Under a given solar radiation, the sink size relative to the source activity affects filled-spikelet percentage. This is shown by an increased percentage of filled spikelets when the spikelets are partially removed (Matsushima 1970, Wada 1969).

d. Low temperature. Air temperatures below 20°C may cause high percentages of sterility if they persist for more than a few days at booting or heading. This occurs in temperate regions at high latitudes and in the tropics at high altitudes. It may also occur in the tropics during the dry season.

e. High temperature. High temperatures shorten the grain-filling period. Persistent cloudy weather will be more detrimental to grain-filling under high temperatures because of a shorter ripening period. Temperatures higher than 35°C at

anthesis may cause high percentages of sterility.

f. Strong winds. Strong winds can cause sterility at flowering by desiccating the plant, impair grain growth by causing mechanical damage to the grain surface, and cause the crop to lodge. A hot, dry air called *foehn* frequently causes *white head*, particularly when it occurs during panicle exertion (Hitaka and Ozawa 1970). Strong winds from the coast often contain brackish water and cause sterility.

g. Soil salinity. High salinity in the soil causes a high percentage of sterility.

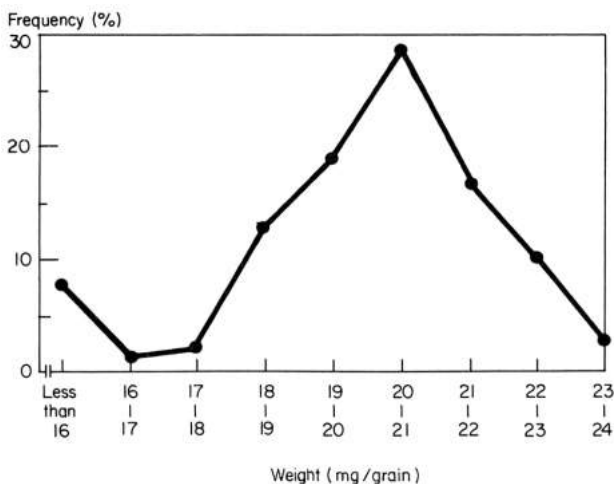
h. Drought. Drought at flowering often causes high percentages of sterility in rainfed lowland and upland rices.

7.3.4. Grain weight

Grain size is rigidly controlled by hull size. When a piece of vinyl film was placed inside the palea and lemma at anthesis, grain filling proceeded normally but the grain weight decreased from 22 mg (untreated) to 18 mg (treated) (Matsushima 1970).

Under most conditions, the 1,000-grain weight of field crops is a very stable varietal character (see Table 2.11, Fig. 2.3, and Soga and Nozaki 1957). The CV of 1,000-grain weight ranged from 2.2 to 4.4%, with a mean value of 3.3% for data collected from 9 varieties for 19 years at Konosu, Japan. The mean CVs of panicle number and yield were 12.4% and 14.1%, respectively (Matsushima 1970).

Heavy shading before heading changed the hull size and decreased 1,000-grain weight from about 26 to 21 g (Matsushima 1970). As will be discussed later, CO₂ enrichment also affects the grain weight to some extent.



7.4. Frequency curve of individual grain weights of Koshiji-wase at 30 days after heading (drawn from data of Nakayama 1969).

The constant 1,000-grain weight of a given variety does not mean that individual grains have the same weight per grain. Individual grain weights vary to some extent but the mean value is constant (Fig. 7.4). The term *ripened grains* has been used in Japan to distinguish between commercially useful grains and chaff. The ripened grains are those that are heavier than salt water with a specific gravity of 1.06 (Matsushima 1970). For indica rices, specific gravity values of 1.10–1.12 are tentatively suggested (Osada 1974).

7.4. COMPARISONS OF GRAIN YIELDS ACHIEVED BY DIFFERENT LEVELS OF TECHNOLOGY

7.4.1. Yield changes associated with technological changes — the Japanese experience

In 900 AD, the average yield of brown rice in Japan was approximately 1 t/ha. In 1868, the year of the Meiji revolution, which was the dawn of modern Japan, it was about 2 t/ha. Thus, it took about 1,000 years to double the average yield (Ishizuka 1969). The introduction of irrigation systems is believed to have contributed to higher yields and to have laid the ground work for further progress in agricultural technology after the Meiji Revolution. The yield increased to about 3 t/ha before chemical fertilizers were introduced around 1930 (Fig. 7.5); compost and other kinds of organic matter were the major sources of added plant nutrients up to that time.

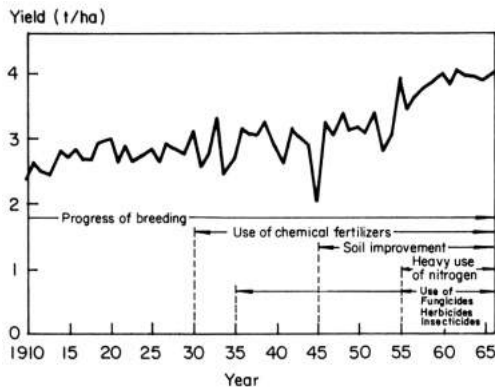
In 1954, the yield increased to 4 t/ha, i.e., the yield doubled in less than 100 years. Heavy applications of nitrogen fertilizers after World War II caused many changes in variety, plant protection, soil improvement, and cultural management. The high national average yield in Japan today has been realized through the integration of technology.

7.4.2. Grain yield comparison among national average, experiment station's record, and the highest yield

From 1949 to 1968, Japan's No. 1 rice yield contest was held to encourage Japanese farmers to produce more rice. In 1960, 13.2 t/ha was recorded in this contest. It was the highest yield ever achieved in Japan (Agricultural Policy Study Commission 1971). National average yields increased from 3.88 t/ha in 1949 to 5.51 t/ha in 1968.

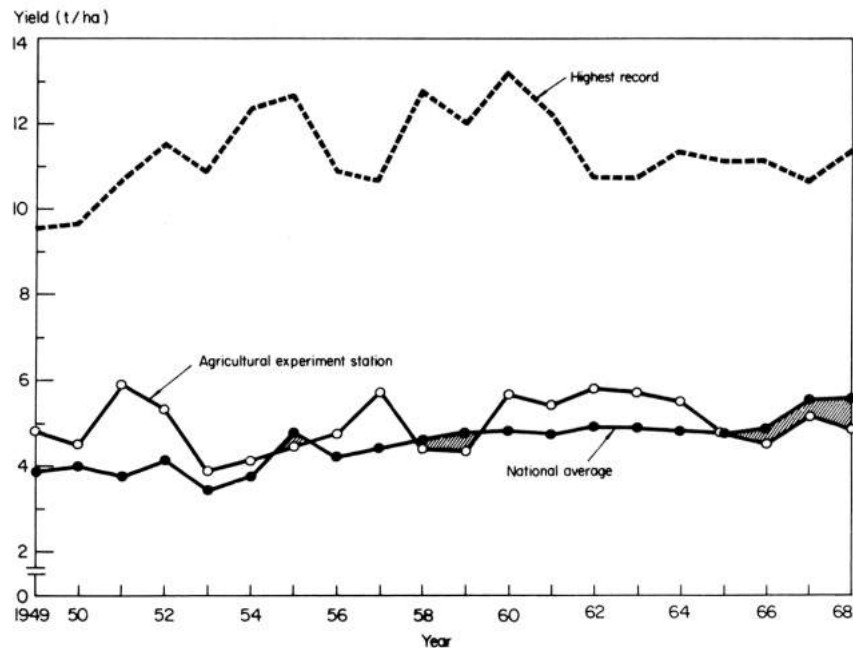
Long-term weather-assessment field trials have been conducted for many years at agricultural experiment stations in Japan. These experiments assess the effects of yearly weather fluctuations on rice yields, using the same cultural practices. A comparison of rice yield from various sources, summarized in Figure 7.6, indicates:

- The national average yield is very similar to the weather-assessment trial yields recorded at agricultural experiment stations.
- The highest yields achieved by farmers are more than two times greater than the national average regardless of weather conditions.

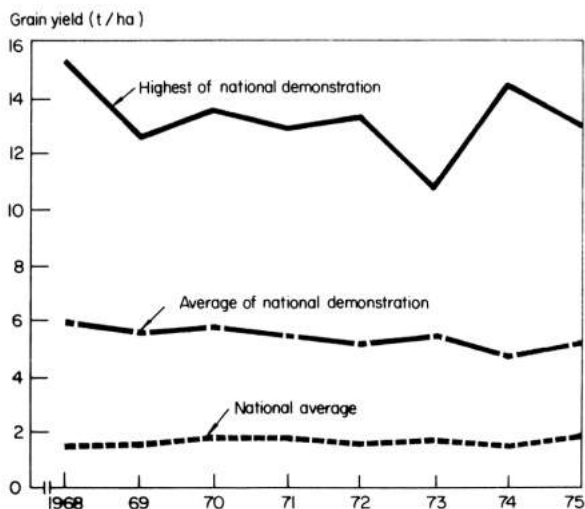


7.5. Rice yields in Japan, 1910–1940 (Ishizuka 1969).

Although each farmer uses different cultural practices, the average farmer's technology can be approximated by the technology adopted in the weather-assessment trials. In these trials, plants were spaced 23.4×23.4 cm (18.2 hills/m²), and nitrogen applications included basal dressing at 60 kg/ha and topdressing at 15 kg/ha. The usual plant protection and weeding practices were followed. Thus, yields of about 5 t/ha were achieved with these practices under



7.6. Comparison of the highest recorded rice yields, weather-assessment trial yields, and the national average yields in Japan from 1949 to 1968.



7.7. Changes in national average rice yields, average yields of national demonstrations, and the highest yields of national demonstrations in India during the period from 1968/69-1975/76 (Annual Report 1976-77, national demonstration trial in India, ICAR).

Japanese weather and soil conditions. Agricultural scientists at the experiment station, however, were able to produce 9.3–10.2 t/ha when they were allowed to use the scientific technology at their disposal (Ishizuka 1969). These yields, almost comparable to yields achieved in the Japan No. 1 yield contest, may imply that the present rice technology has the same capacity to produce high yields as the farmer's long-time and site-specific experience.

A similar record of rice yields can be obtained from India from 1968 to 1975 (Fig. 7.7). Several conclusions can be drawn from the figure:

- The national average yield, slightly less than 2 t/ha, is about one-third the average yield of national demonstration.
- The highest yield recorded is more than two times greater than the average of national demonstration.
- The difference between India and Japan lies in the gap between the national average yield and experiment station yields.

These conclusions indicate that a yield of 5 or 6 t/ha can be achieved with a moderate amount of inputs and by adopting simple technology provided irrigation water is available, and yields of 10–12 t/ha are possible under the present weather conditions if the farmers use more advanced technology.

7.5. ANALYSIS OF HIGH YIELDING CULTIVATION TECHNOLOGY

This section will first summarize the physiological requirements for high rice yields based on crop photosynthesis, mineral nutrition, and yield components. It

will then examine the so-called high yielding cultivation technology.

7.5.1. Physiological requirements for high yields

Present knowledge of crop photosynthesis, mineral nutrition, and yield components indicates several requirements for high rice yields:

- The variety must have a short, stiff culm.
- The most desirable leaf arrangement is that in which the erect upper leaves graduate down to droopy leaves at low canopy levels.
- A LAI of 5–6 is necessary to achieve maximum crop photosynthesis during the reproductive stage.
- During ripening, the LAI will decrease as grain filling proceeds and leaf senescence occurs. While this is a normal event, it is important to maintain as many active, green leaves as possible until the linear phase of grain growth is completed.
- Planting time should be chosen so that the crop is exposed to high solar radiation during the reproductive or ripening stages, whichever is more critical to yield.
- Yield components must meet the requirements for a target yield.
- All the essential nutrients must be supplied to meet the crop's requirements. Nitrogen is the most important. The amount of nitrogen required to produce 1 t rough rice is about 20 kg and it is independent of yield levels. Thus, the amount of nitrogen needed will increase as yield increases. A similar consideration should apply to other nutrients.
- Nitrogen absorption after heading will assume an increased importance when high yields are achieved by increasing the harvest index.

During the ripening, about 70% of the nitrogen absorbed by the straw will be translocated to the grain. Nitrogen content of the grain tends to be maintained at a certain percentage. When a larger number of grains relative to the size of vegetative parts is produced, more nitrogen will be needed to support grain growth, and there will be a sharper drain in leaf nitrogen content. Some grains may suffer from nitrogen shortages.

To produce high yields, it is essential to maintain the level of leaf nitrogen required for high photosynthetic activity. This requirement can be met when nitrogen absorption by a crop is continued after heading, or when the higher nitrogen content of the vegetative parts is attained before heading so that the nitrogen absorbed by heading is sufficient for ripening. The Japanese experience suggests that continuous absorption of nitrogen after heading is important for high yielding crops (Matsushima 1969, Murayama 1967).

7.5.2. Soil culture vs water culture

Water culture has been extensively used in studies of the mineral nutrition of plants. Compared with soil culture as a rooting medium, water culture provides the following features:

- Amounts of all the essential nutrients and the time of their supply can be controlled.

Table 7.3. Yield and yield components of rice crops grown in solution culture and in the field at Konosu, Japan.^a

	Water culture	Soil culture
Grain yield (t/ha)		
Brown rice	10.2	5.8
Rough rice	12.7	7.2
Yield components		
Panicles (no./m ²)	699	379
Spikelets (no./panicle)	75	05
Spikelets (no./m ²)	52.4 × 10 ³	32.2 × 10 ³
Ripened grains (%)	89.5	83.2
1,000 grain wt (g)	26.5	25.7

^a Adapted from Matsushima et al (1963).

- None of the toxic substances produced under reductive conditions are present (e.g. hydrogen sulfide, excess ferrous iron, and organic acids).
- No organic matter (humus) is present.

Thus, water culture provides a convenient means of controlling plant growth through the supply of plant nutrients, and of testing whether soil fertility is essential to high yields (Matsushima et al 1963, Matsushima 1976).

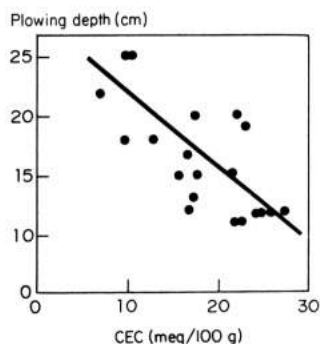
An experiment to compare water culture with soil culture used wooden boxes 10 m² and 20 cm deep, lined with vinyl sheets and filled with gravel. Rice plants of the same variety were grown in water culture in the boxes and in soil culture in the field at similar planting densities. Ample nitrogen, phosphorus, and potassium and about 23 t compost/ha were applied to the field. Both crops were grown under the same weather conditions. The water culture produced 12.7 t/ha and soil culture, 7.2 t/ha (Table 7.3). The grain yield difference, caused by the difference in rooting media, is evidence that soil fertility per se is not indispensable for high yields. It also suggests that the toxic substances produced in the soil hampers high yields under certain conditions. In fact, adequate percolation and drainage are considered essential for high yields because they remove toxic substances from the soil.

7.5.3. Agronomic management

An analysis of Japan's No. 1 prize winners' rice cultivation technology suggests that the component technologies alone may not always give good results (Shiroshita 1963, Togari 1966). However, their combination as a package is important in achieving high yields.

a. Choice of lodging-resistant variety, adequate planting density, and proper plant protection. To achieve high yields, it is essential to use a lodging-resistant variety. Close spacing assures a LAI sufficiently large for maximum crop photosynthesis and the production of a large number of panicles to meet the requirements for yield components of high yielding crops. Diseases, insect pests, and weeds must be carefully controlled.

b. Deep plowing. The depth of the surface soil ranges from 15 to 21 cm among the prize winners' fields, and from 9 to 12 cm among most farmers' fields. A deep



7.8. Relationship between plowing depth and cation exchange capacity (CEC) of high yielding paddy fields that produced more than 7.5 t/ha (Aomine 1955).

surface soil allows rice roots to contact the soil nutrients in a larger volume of soil. Deep plowing improves soil properties by drying the lower soil layers, thereby, promoting the weathering of soil minerals. However, deep plowing may not be effective unless combined with increased applications of fertilizer.

A large soil volume implies a greater supply of soil nutrients and a greater capacity for cation exchange. In paddy soils, applied nitrogen is held by soil clay minerals through cation exchange. In soils whose cation exchange capacity (CEC) is low, more of the applied nitrogen comes into the soil solution. The rice plant can absorb this nitrogen easily and its early growth becomes vigorous. At later growth stages, the rice crop may suffer nitrogen shortages because a considerable portion of the applied nitrogen has already been absorbed and also some nitrogen may have been lost by percolation. An adequately high CEC will hold applied nitrogen and release it to rice at later growth stages.

When plowing depths are plotted against CEC in fields that produce yields higher than 7.5 t/ha, the CEC tends to increase at shallower plowing depths (Fig. 7.8). Thus, if the CEC is sufficiently large, a shallow surface soil can produce a high yield. From Figure 7.8, and on the basis of highly simplified assumptions, such a CEC is estimated at 250 kg equivalent/ha.

c. Heavy application of compost. To produce high yields, the prize winners applied from 8 to 30 t compost/ha. The application of large amounts of compost is usually combined with deep plowing and good internal drainage.

Compost releases nitrogen at slower rates than do chemical fertilizers and thus provides nitrogen at later stages of crop growth. Composts or farmyard manures are good sources of nutrients such as phosphorus, potassium, and silica.

Deep plowing in well-drained fields quickly decreases the organic matter in the surface soil. A liberal application of compost will help maintain the organic matter supply. However, compost is not essential for a high yield (see Section 7.5.2). Moderately high yields can be obtained without compost and on soils low in organic matter.

There is no added benefit in terms of yield between nitrogen added as ammonium sulfate and that provided partially with 10 t compost/ha, if the

Table 7.4. Comparison of rice yields in dry and wet seasons with ammonium sulfate alone and with partial substitution of nitrogen with compost (average from the 10th crop, 1969 dry season, to the 23rd crop, 1975 dry season, IRRI).^a

Season	Nitrogen application (kg/ha)	Paddy yield (t/ha)
Dry	140 ^b	7.43
	Compost (10 t/ha = 24) + 116 ^b	7.23
Wet	60 ^{b,c}	4.74
	Compost (10 t/ha = 24) + 36 ^b	4.80

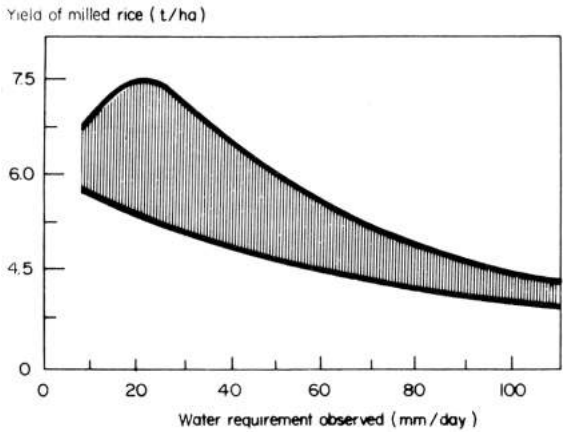
^aTanaka (1978). ^b As ammonium sulfate. ^c 140 kg N/ha only in 1973.

supply of other nutrients is favorable (Table 7.4). When aiming at high yields, however, it is advantageous to build soil fertility. Compost or other kinds of organic matter supply nitrogen to rice plants throughout growth. This continuous nitrogen supply favors high yields by preventing excessive vegetative growth and lodging. Furthermore, it is difficult to simulate such a condition by manipulating fertilizer nitrogen without the help of soil organic matter (Tanaka 1978).

d. Adequate percolation and drainage. High yields can be better achieved on well-drained fields. Although high rates of percolation cause nutrient loss, adequate rates may remove toxic substances from the rooting zone and prevent excessive soil reduction. A percolation rate of 15–25 mm/day is considered adequate in Japan. In Figure 7.9, the lower line indicates that grain yield decreases with increasing percolation rates. The upper line indicates that high yields are obtained at a percolation rate of about 15 mm/day. Percolation rates faster than 15 mm/day decrease yield. Why this is true is not well understood. Most likely percolation removes some toxic substances such as hydrogen sulfide, ferrous iron, and organic acids (Takijima and Konno 1959, Takijima 1960). If the above explanation is correct, it follows that a certain amount of percolation would benefit rice growth only in soils where injurious substances accumulate to levels toxic to rice.

e. Drainage and intermittent irrigation. Drainage and intermittent irrigation, commonly practiced by the prize winners, implies that water is drained until the soil surface is exposed to air, after which irrigation water is reintroduced. The rate of drainage and the interval between the cycles vary with soil characteristics and weather conditions. This practice is believed to remove toxic substances and maintain healthy roots under reductive soil conditions (Agricultural Policy Study Commission 1971, Togari 1966). Table 7.5 shows that drainage and intermittent irrigation treatment increases the root-shoot ratio and improves root growth.

f. Soil dressing. Incorporation of clayey hill soils into paddy fields is also a common practice to improve soil fertility. Hill soils at early stages of weathering supply various bases, silica, and iron that have been depleted by intensive, continuous rice cropping. Soil dressing increases the depth of the surface soil



7.9. Daily field water requirement and rice yield (Isozaki 1967 as cited by Nakagawa 1976). Average evapotranspiration rate of irrigated rice fields in Japan is approximately 5 mm day. Therefore, the daily field water requirement minus 5 mm day would approximately represent the daily percolation rate.

layer; it may increase water-holding capacity and CEC. More nitrogen and phosphorus than usual should be applied when soil dressing is practiced because hill soils are low in these nutrients.

Soil dressing has been practiced by progressive farmers but it is quite laborious. An alternative way to improve soil properties is to apply bentonite clay (10–15 t/ha) or zeolite (5–10 t/ha). Bentonite, largely composed of montmorillonite, has a high CEC and, hence, increases the nitrogen-holding capacity of sandy soils. Bentonite can minimize excessive percolation because of its swelling characteristic. Zeolite is a powdered tuff that has a high CEC (80–160 meq/100 g) and does not swell in water like bentonite (Dei 1978, Shiga 1969).

7.5.4. Examples of high yielding technology

A systematic study at the Central Agricultural Experiment Station, Konosu, Japan, attempted to achieve high yields (Shiroshita et al 1962). The Konosu clay loam soil at the station is representative of alluvial soils derived from the Arakawa River in Kwanto Plain. The clay is mainly composed of allophane with small amounts of kaolinite, vermiculite, and illite. The CEC is about 15 meq/100 g soil.

Table 7.5. Effect of intermittent irrigation and drainage on root growth.^a

Treatment	Maximum root length (cm)	Root dry wt (g)	Root- shoot ratio	Roots (no) at soil depth of						
				0–10 cm	10–20 cm	20–30 cm	30–40 cm	40–50 cm	50–60 cm	60–70 cm
Flooded	48.7	7.48	6.0	416	135	73	39	7	0.5	0
Intermittent irrigation and drainage	77.8	8.79	12.5	463	293	141	74	38	28	11

^aDei (1978).

The water table of the field used in this experiment was 80 cm below the soil surface in winter and 18 cm in summer. The rice grain yield is usually around 4.5 t/ha.

The researchers found that a low number of sunshine-hours during ripening resulted in a low percentage of filled spikelets. To overcome this problem, they shifted the crop season 1 month earlier. Component technologies included drainage, deep plowing, and application of 19–56 t compost/ha (Table 7.6). As a consequence, applied nitrogen exceeded 400 kg/ha. There was not much difference in grain yield between the treatments when the field was poorly drained. When the field received adequate drainage, grain yield increased from 6.6 to 10.0 t/ha.

Another example of high yielding technology is the intensive use of topdressing. Nitrogen topdressing is normally done at panicle initiation or flag-leaf stage in Hokkaido, Japan. Shiga and Miyazaki (1977) studied the nitrogen absorption process of a high yielding crop and simulated that process by topdressing. Nitrogen topdressing was given 5 times between panicle initiation and heading, and the amount of nitrogen applied each time was increased stepwise from 5 kg N/ha at panicle initiation to 10 kg N/ha 5 days later, to 15 kg N/ha after another 5 days after that, to 30 kg N/ha at flag-leaf stage (15 days after panicle initiation), and 30 kg N/ha at heading. By this technique, grain yield was increased from 3.8 t/ha without fertilizer nitrogen to 9.7 t/ha with a simulated topdressing. The simulated topdressing produced high yields of more than 8.8 t/ha over 5 years.

7.6. FACTORS LIMITING THE PRESENT YIELD PLATEAU

Improving grain-filling is one way to increase grain yield. The filled-spikelet percentage is about 85%, even under favorable conditions, which means that grain yield might be increased by 15%. Of the 15% unfilled spikelets, however, around 5–10% are unfertilized, and difficult to eliminate. An increase in photosynthesis (source activity) relative to spikelet number (sink size) would probably increase filled-spikelet percentage by only 5–10% and, hence, yield by a similar degree. Thus, the yield to be achieved by improving grain-filling would be much lower than the estimated potential yield.

It is possible to increase yield by increasing the number of spikelets per unit of land area. In other words, it is important to increase yield capacity when yield capacity is defined as the product of spikelet number and potential weight per grain. To examine this possibility, it must be known whether grain filling, as determined by the amount of solar radiation during ripening, is already limiting to yield. The question implies that the number of spikelets per unit of land area may be increased through improved cultural practices or by genetic manipulation, but a considerable portion of the spikelets produced may remain unfilled because of limited solar radiation.

In Japan, the percentage of ripened grains decreases when the number of spikelets per square meter is increased (Matsushima 1970, Wada 1959). Thus,

Table 7.6. An example of high yielding cultivation technology attempted at the Central Agricultural Experiment Station in Japan.^a

Field drainage	Depth of plowing (cm)	Amt of N applied (kg/ha)			Compost		Total amt of N applied (kg/ha)	Grain (t/ha)	Straw (t/ha)
		Basal	Tillering	Panicle initiation	t/ha	N equiv. (kg/ha)			
Poorly-drained	12	75	18.8	18.8	0	0	112.6	6.00	6.68
	12	75	18.8	18.8	18.75	97.5	210.1	6.74	7.55
	18	75	18.8	18.8	18.75	97.5	210.1	6.29	7.06
	18	75	18.8	18.8	37.50	195.0	307.6	6.67	7.93
	18	75	18.8	18.8	56.25	292.5	405.1	6.47	8.20
	18	112.5	18.8	18.8	56.25	292.5	442.6	6.17	8.20
Well-drained	12	75	18.8	18.8	0	0	112.6	6.06	6.67
	12	75	18.8	18.8	18.75	97.5	210.1	6.92	8.12
	18	75	18.8	18.8	18.75	97.5	210.1	6.18	7.91
	18	75	18.8	18.8	37.50	195.0	307.6	6.92	8.29
	18	75	18.8	18.8	56.25	292.5	405.1	8.58	11.13
	18	112.5	18.8	18.8	56.25	292.5	442.6	10.02	12.05

^aShiroshita et al (1962). Early planting; variety Kin-maze, 1958.

Table 7.7. Effects of carbon dioxide enrichment before and after heading on growth and grain yield of IR8.^a

Treatment	Yield (t/ha)	Sugar and starch ^b in leaf sheath and culm (%)	Crop growth rate (g/m ² per wk)		Grain wt ^c (mg)	Grains (10 ³ /m ²)	Filled spikelets (%)
			Before heading	After heading			
Dry season							
Control	9.0a ^d	22	173a	99a	23.1a	45.7a	74a
CO ₂ before heading ^e	11.6 b	30	224 b	157 b	25.9 b	50.9 b	77a
CO ₂ after heading ^f	10.9 b	22	173a	147 b	25.1 c	44.6a	86 b
Wet season							
Control	5.7a	18	122a	−14a	24.3a	28.8a	78a
CO ₂ before heading ^e	7.7 b	25	179 b	8ab	26.2 b	34.1 b	81ab
CO ₂ after heading ^g	6.9 b	18	122a	38 b	26.1 b	29.5a	85 b

^a Yoshida (1976). ^b As glucose. ^c Dried at 75°C for 3 days. ^d Any 2 means followed by the same letter are not significantly different at the 5% level. ^e For 30 days. ^f For 28 days. ^g For 29 days.

there appears to be an optimum number of spikelets for maximum grain yield under certain conditions and attempts to increase spikelet number per square meter will not result in increased grain yield.

An estimation of potential yield suggests that solar radiation per se is not limiting to the current yield level unless adverse conditions exist. It is highly desirable that the above question be clarified experimentally.

Among climatic factors, the CO₂ concentration in the atmosphere limits rice yield. Yields can be increased by CO₂ enrichment in plastic enclosures (Yoshida 1976). However, it is not practical to increase the CO₂ level around plants growing in a field because the additional CO₂ would diffuse rapidly into the open air and virtually none would be available to the plants. The CO₂ enrichment, however, can be used as a tool for analyzing the factors limiting yield.

Table 7.7 shows that grain yield was increased from 9 to 11.6 t/ha by preflowering enrichment and to 10.9 t/ha by postflowering enrichment in the dry season; it was increased from 5.7 to 7.7 t/ha by preflowering enrichment and to 6.9 t/ha by postflowering enrichment in the wet season.

The preflowering enrichment increased grain yield by increasing the spikelet number per unit of land area and weight per grain. The field-grain percentage remained the same as that for control plants. Because plants subjected to CO₂ enrichment before flowering were exposed to the same environment as control

Table 7.8. Effects of carbon dioxide enrichment before and after flowering on grain yield and yield components of IR8, IRRI, 1972 dry season.^a

Time of CO ₂ enrichment						
In relation to flowering (days)	Developmental stage ^b	Yield ^c (t/ha)	Grains ^c (10 ³ /m ²)	Filled spikelets ^c (%)	Grain wt ^{c,d} (mg)	
Control ^c	—	10.2 c	40.4 c	85.4 b	23.7	d
–33 to –24	I	11.3 b	45.0ab	84.2 b	23.8	d
–24 to –14	II	11.4 b	43.4 bc	86.2 b	24.7	c
–14 to 0	III	10.2 c	38.9 c	85.8 b	25.0	bc
–33 to 0	I–III	13.3a	48.2a	87.6 b	25.7ab	
0 to 30	IV	11.5 b	38.9 c	92.4a	26.0a	

^a Yoshida (1976). ^b I = neck-node differentiation to differentiation of secondary rachis-branch, II = differentiation of spikelets, III = differentiation of pollen mother cell, reduction division stage to flowering, IV = flowering to harvest. ^c Any means followed by the same letter are not significantly different at the 5% level. ^d Panicles have been dried at 75°C for 48 h, threshed, then grains were placed at 50°C for 12 h and weighed. ^e None.

plants after flowering, the results may imply that solar radiation during ripening did not limit grain filling and, hence, the additional spikelets produced by the CO₂ enrichment were well filled in both the dry and wet seasons.

Further CO₂-enrichment experiments in the dry season demonstrated that preflowering enrichment increased grain yield from 10.2 to 13.3 t/ha, i.e., 30% increase over the control, whereas the postflowering enrichment increased grain yield by 10% (Table 7.8). The same experiment also revealed that the effective stages for CO₂ enrichment before flowering is the time from the neck-node differentiation to the spikelet differentiation stages. In the preflowering enrichment, the yield increase is attributed to increased spikelet number, and, to a lesser extent, also to increased grain weight. In the postflowering enrichment, the yield increase resulted from increased filled-spikelet percentage and increased grain weight.

These two experiments suggest that the sink size, largely determined by spikelet number per unit of land area, is not completely limiting. Postflowering enrichment increased the grain yield by increasing filled-spikelet percentage and weight per grain. However, the magnitude of such grain yield increases seem distinctly limited because both filled-spikelet percentage and grain size cannot be increased greatly.

The total spikelet number per unit of land area is greatly increased by the CO₂ enrichment or possibly by increased photosynthesis before flowering. If the total spikelet number can be increased, neither photosynthetic capacity nor light nor CO₂ concentration after flowering is likely to limit grain-filling at Los Baños, Philippines. Thus, to increase yield further, some way of increasing the spikelet number or yield capacity (spikelet number × potential weight per grain) must be found.

One possibility suggested by the CO₂ enrichment is to increase photosynthesis during panicle development before flowering. Increased photosynthesis may be achieved by increasing photosynthetic efficiency or by extending the time for panicle growth. A group of physiologists has been trying to eliminate photorespiration in C-3 plant species either through chemicals or by genetic manipulation; the elimination of photorespiration is believed to increase the net photosynthesis of C-3 species by about 50% (Zelitch 1979).

Relatively small differences exist in the length of the period from the initiation of panicle primordia to heading under normal crop conditions. In general, total growth duration and the length of the period from panicle initiation to heading are positively correlated. Thus, an early maturing rice variety has a relatively short time for panicle growth (Akimoto and Togari 1939). Because longer growth duration is not generally desirable, can the period of panicle growth be extended independently of the whole growth duration? Partitioning of assimilates between developing panicles, leaves, culms, and storage is probably under hormonal control. The distribution of a greater portion of assimilates into developing panicles may produce larger panicles. The flag leaf of most improved rice varieties is relatively small compared with the second or third leaves. Possibly this results from competition with the developing panicle. Attempts to understand and control the mechanism for partitioning assimilates merits much more attention.

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