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GROWTH AND DEVELOPMENT OF THE DEEP WATER RICE PLANT[1]

ABSTRACT

Rice has adapted to a wide range of complex environmental niches – from dry to flooded conditions, from low to high temperature areas, and a variety of soil types. Rices grown in areas where the water depth is more than 30 cm have many specific requirements. Their growth and development are different from those of rices grown in irrigated or upland conditions. These deepwater rices cover more than 10 million ha and millions of farmers depend on them for survival and security.

This review describes the culture and environment of the deep water rices and the attending problems. It emphasizes the growth and development of deep water rices particularly the requirements for their survival under drought or completely submerged conditions, elongation ability, kneeing ability, rooting ability, photoperiod sensitivity, and adaptability to different water regimes and soil types.

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GROWTH AND DEVELOPMENT OF THE DEEP WATER RICE PLANT

Rice grows in a wider range of complex environments than any other crop (142). It grows on dry and flooded soil, in low temperature and high temperature environments, and in many soils.

This review describes growth and development of deep water rice, defined as rice grown where water depth is more than 30 cm for longer than 1 mo. Modern, semidwarf varieties have difficulty surviving such deep flooding. Deep water rice is grown on more than 10 million ha (6), primarily in Bangladesh, Burma, India, Indonesia, Mali, Thailand, and Vietnam (Table 1). In most of those areas, rice is the only crop that can be grown. Yields are generally poor, but millions of farmers, 18 million in Bangladesh alone, depend on deep water rice for survival and security (6).

General Culture

Deep water rice culture varies depending on local hydrology. Where maximum water level is 30-50 cm, rainfed medium deep rice, such as the transplanted photoperiod-sensitive rice of Bangladesh, Burma, Indonesia, Malaysia, and Vietnam, is grown. At 50-100 cm depth, deep water rice is dry-seeded or double transplanted. Where water rises above 100 cm, as in Bangladesh and Thailand, floating rice is dry-seeded.

Although excess water is common to all deep water rices, growth and development vary according to the crop establishment practice, and the onset, depth, speed, and duration of flooding.

Table 1. General information on the deep water rice areas.

Country	Area (x 100,000 ha)	Start of flooding	Rate of flooding increase (cm/day)	Maximum depth (cm) at given date	Sowing/ transplanting	Flowering date	Reference
Mali	1.32-1.56	Jun-Oct	3-10	300 Oct-Nov		Nov-Dec	17, 146
Niger	0.50-0.50	Jun-Oct		300 Aug-Oct			17, 144
Nigeria	0.30	Jun-Oct		300 Aug-Oct	Apr		144, 170
Senegal	0.10	Jun-Oct		300 Aug-Oct			17
Gambia	0.08	Jun-Oct		300 Aug-Oct			17
Sierra Leone	0.12	Jun-Oct		300 Aug-Oct	May	Nov-Dec	17, 171
Guinea, Mauritania, Benin							17
Burma	4.70	Jun	5-30	400	Apr-May	Sep-Nov	89, 188
Vietnam	9.00	Aug	1	300 Nov		Dec-Jan	108, 146, 173
Thailand	5.00-18.00	Sep-Oct	6-8	400 Nov-Dec	Apr	Nov-Dec	117, 136
Sri Lanka				120	Aug	Jan	67
Bangladesh	20.00	May-Jun	5-8	100-1000 Aug-Sep	Mar-Apr	Oct-Nov	1, 6, 11, 13, 46
Indonesia	1.00				Oct-Nov	Feb	105
Malaysia	0.25	Nov					64
Uttar Pradesh	14.00	Jun-Jul		600	Mar-May B-Deeper area Jun-B	Oct-Nov	110, 133
Bihar	12.00-20.00	Jun-Jul		25-400 Dec-Jan	Feb-Apr B Jun-Jul T	Oct-Nov	123, 124 133, 143
West Bengal	13.50			165-300 Dec-	Apr-May	Oct-Dec	99, 102, 110
Orissa	10.00			300			110, 133
Assam	1.0-11.70	May-Jun		600	Apr-May		33, 110, 133
Andhra Pradesh	3.50			150-180			110, 133
Tamil Nadu	1.00			150-180			133
Karnataka	0.50			90-150			133
Kerala	0.30			90-150			133
Maharashtra	0.30						133
Madhya Pradesh	1.25						133
Manipur, Tripura	0.25						133
Gujarat, Rajasthan and Haryana	0.60						133
Total	68.90						133

Rainfed medium deep rice culture (Fig. 1, transplanted)
In rainfed medium deep culture, tall seedlings are transplanted in puddled soil in water as deep as 30 cm. Special implements may be used in transplanting. Water may recede soon after or may submerge the plants. Weeding is minimal and fields are unattended until harvest. Flowering generally occurs as the water recedes.

Deep water rice culture (Fig. 1, dry-seeded)
In deep water culture, the land is plowed after the first heavy rain has soaked the soil. Dry seed is broadcast and the field harrowed lightly to cover the seeds. Germination occurs after a heavy rain. Seedlings grow for 6 wk or longer before flooding but drought or temporary flooding may occur first. Fertilizer usually is not applied and weed control is minimal.

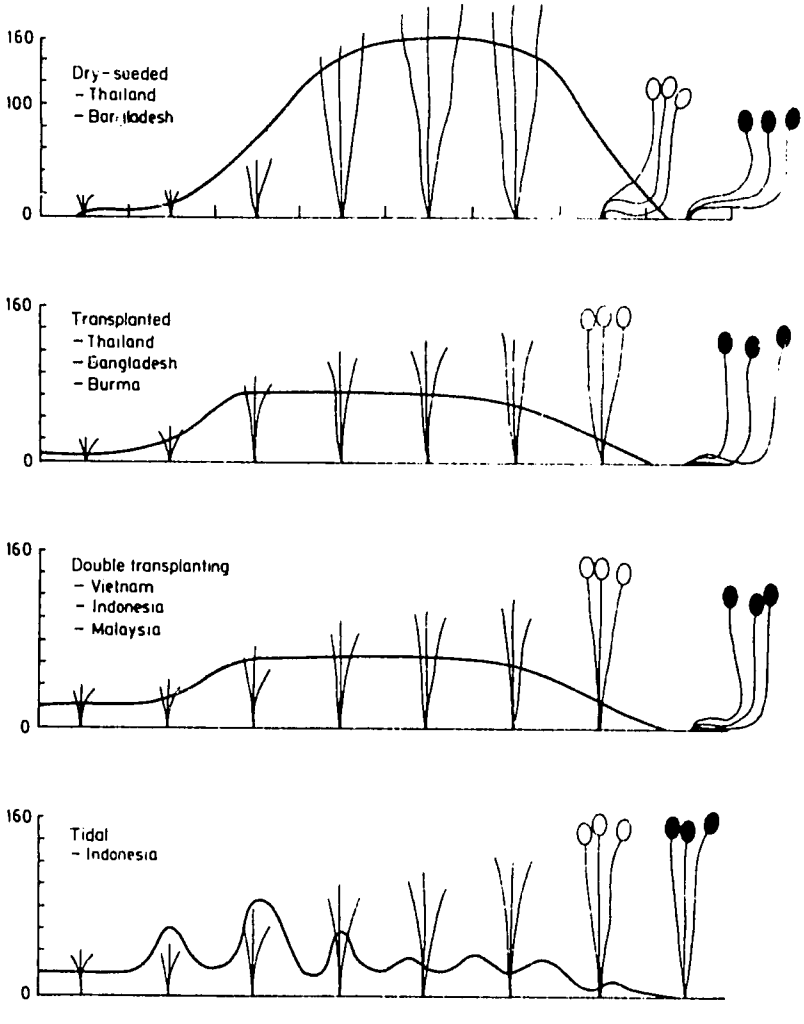
As floodwater rises, plants elongate, produce nodal roots, and may produce nodal tillers. Water level may reach 100 cm near the end of the monsoon season, when photoperiod-sensitive rice varieties flower. As the water recedes, grain ripens. Crop duration may be 300 d, and harvest may be on dry or wet fields.

Where early crop establishment is difficult and flooding is early, tall, old seedlings are transplanted. Sometimes seedlings are replanted once or twice in larger nursery beds to let them grow taller and sturdier before transplanting in the main field.

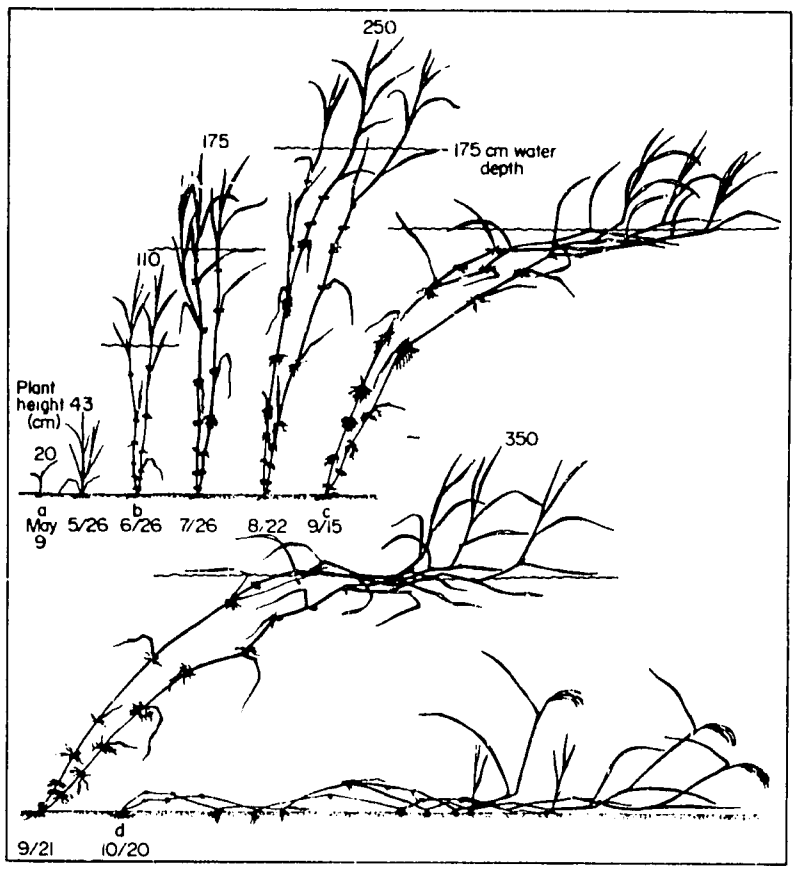
Floating rice culture (Fig 1, dry-seeded)
Cultural practices for floating rice are similar to those for broadcast-seeded deep water rice except that maximum water depth is more than 100 cm (Fig. 2).

Fields are flooded about 6 wk after seeding. Rapid elongation may occur if the water rises above 50 cm. Nodal rooting and, often, nodal tillering occur. When plants grow tall above the water, they lodge, but kneeing ability keeps their tops erect above the water. Alternate lodging and kneeing gives the culms a zigzag shape.

Although the varieties grown in this environment are called floating rice, their roots normally are anchored to the soil. Local hydrologic characteristics and flowering dates determine varietal choice. Once, an estimated 1,500 to 2,000 indigenous varieties were cultivated in various deep water areas of Bengal and Assam (187). Unfortunately, the germplasm collection of floating rice is limited. Before the 1980s, most recommended deep water rice varieties were pure line selections from farmers' varieties.



1. Different flooding patterns in deep water rice areas (151).



2. Growth and development of a deep water rice plant sown on May 9th, (a) seedling stage, (b) initial elongation, nodal tiller emerging, (c) kneeing begins, prepanicle initiation: floating canopy, fully developed nodal roots, water subsiding, (d) milk stage; culms prostrate except the terminal sections; some nodal roots grow down into the soil, late growth flushes of tillers, which are mostly nonproductive, may develop; water almost completely receded (after 12).

Environment

Most deep water rice is grown in the great tropical deltas and basins although some grow as far north as 30°N latitude (135).

Temperature generally does not limit deep water rice growth, but farther north, late flowering under low temperature may cause sterility (35, 99). In Bangladesh, minimum Nov to Feb temperature is 7.2 °C (1), which can cause spikelet sterility in late-maturing rices.

Because most deep water varieties are photoperiod-sensitive, day length determines flowering date (Fig. 3). Average day length during the cropping season varies with planting and harvesting dates and latitude. In India, day length averages 11-13 h (135), and in Bangladesh the late-season crop has 10 h day length in Dec (1). Flowering generally occurs after Sep when the days are shorter.

In India, sunshine averages 4-10 h/d (135). In Bangladesh, skies usually are clear during flowering to ripening period, and evening temperatures are low (1). Both those factors favor high yields.

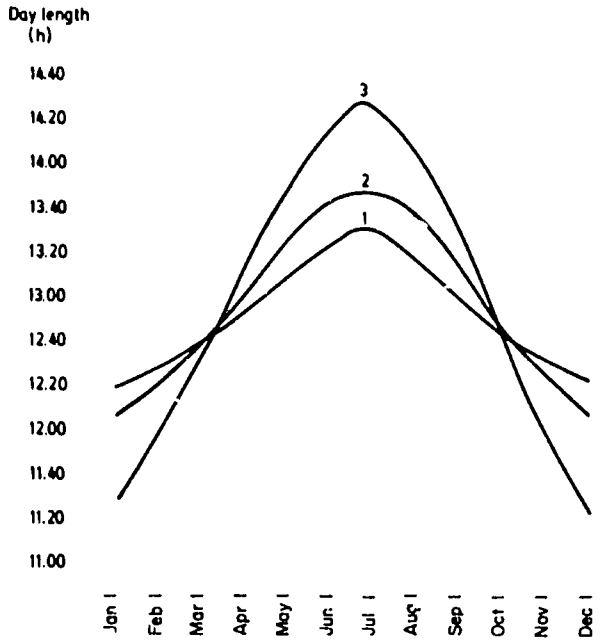
Flooding pattern varies widely in deep water rice environments (Fig. 4). The date of initial flooding, initial and subsequent rate of water increase, fluctuation in water level, maximum and average water depth, and date of recession determine cultural practice and variety.

Initial flooding is from Jun to Aug. Although water rises an average 2-10 cm/d (Table 1), the first flood may be 30-90 cm in 1 d (18, 44). Increasing water depth varies with rainfall intensity and duration. In Bangladesh and India, initial water depth increase may depend on snow melt in the Himalayas rather than on local rainfall. In those areas, total rainfall does not correlate well with maximum water depth (3).

In Bangladesh, temperatures 5 cm below the water surface average 33 °C (31-35 °C) from Jun to mid-Jul, when water is rising; 32 °C (30-35 °C) from mid-Jul to early Oct, when the crop canopy is denser and water depth is 100-300 cm; and 28 °C in late Oct (9). Near harvest, the water is malodorous and filled with decaying organic material.

Soils in deep water areas range from sandy loam to heavy clay, can be saline or peat, and have iron toxicity or phosphorus deficiency. The pH varies from 4.5 to 8.5 in India (135). Acid sulfate soils are common in Thailand (117), Indonesia (138), and Vietnam (173). In parts of India, Indonesia, and Malaysia, deep water rice is grown on peat soils.

Scientific studies on deep water rice began in 1917 in Dhaka and more specific, basic research started in 1934 at the Deepwater Rice Research Station in Habiganj, Bangladesh (187). Most early research concentrated on varietal selection and improvement. Research did not accelerate until the late 1970s, when several workshops were held to encourage scientists to work on this important but neglected rice culture. Most of the literature cited in this review appeared in the workshop proceedings (6, 58, 59, 60).



3. Duration of daylight, including twilight, in 1) Cambodia, 12° N, 2) Thailand, 14° N; and 3) Bangladesh and India, 24° N.

DORMANCY, VIABILITY, GERMINATION, AND SEEDLING GROWTH

Dormancy, viability, and germination

Like most traditional indica varieties, deep water rices have a long dormancy period. Because fields often are wet at harvest, dormancy is necessary to prevent germination. Most deep water rices have 25-56 d dormancy (3, 47); however, the special deep water variety Rayada lacks dormancy (103, 115). Grain should have strong (50 d) dormancy after ripening to protect seed viability before and after harvest (174). Long viability is needed in deep water rices because they are generally harvested from Nov to Jan and are not planted until Apr or May.

Rice seeds germinate in aerobic and anaerobic conditions, but subsequent seedling growth is poor in anaerobic conditions. Deep water rice seedlings probably are more tolerant of anaerobic conditions than other rices (24).

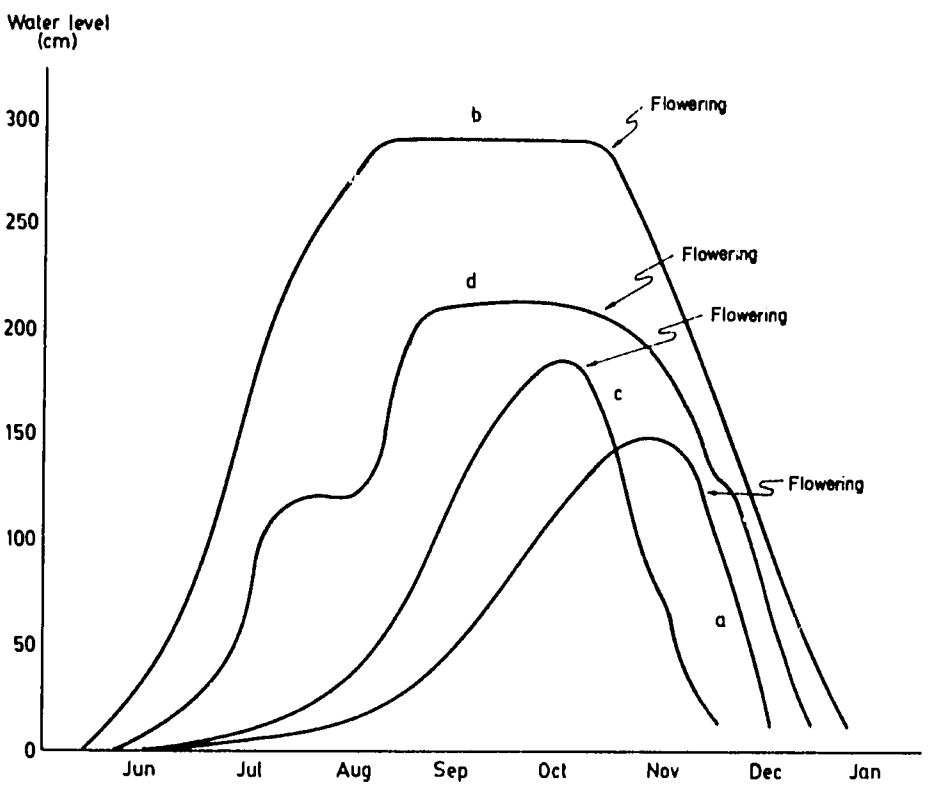
Morphology

Morphology of deep water rice seedlings is not different from that of traditional indica varieties. Deep water rices generally have a short second-leaf blade, emerge rapidly from deep soil, and have a long mesocotyl if they germinate in the dark or were seeded deep (42, 55). However, the long mesocotyl is not a special deep water characteristic (55, 187).

Sowing

Methods of sowing deep water rices differ, depending on rainfall and flooding pattern and soil type. Where the monsoon season starts early and with enough rain to grow plants before heavy rainfall and flooding (Burma, Africa [Mali], Thailand, Bangladesh, and Vietnam) seed commonly is broadcast on dry soil.

Where crop establishment is difficult and flooding sudden (20-40 cm deep within 1 mo), transplanting is common. Transplanting also is practiced in areas prone to



4. Water level patterns. a) water depth during the 1969 rice-growing season at Huntra Experiment Station, Thailand; b) pattern of rise and fall, and deep stagnant flooding in Bangladesh, 1970; c) flood level at Illushi rice swamp gauges, Illushi, Niger floodplain, 1964; d) a possible pattern in deep water rice areas.

early flooding. In some unusual areas or when early floods make resowing necessary, pregerminated seeds are broadcast in puddled soil.

Some studies found early dry seeding better than late wet seeding (33, 45, 125, 173). Others found that on heavy textured soils, sowing pregerminated seeds on puddled soil gave higher yields than dry seeding (187). Crops sown early are well established before flooding and yield better. Very early sowing usually results in low yields because the plants may be subjected to drought. Late sowing causes low yields because the plants are too young and short and many plants die when flooded.

Direct seeding

Various optimum seed rates have been reported (3, 34, 46, 125, 143, 144). Increasing seed rate from 40 to 150 kg/ha did not significantly increase grain yield (34, 43, 61, 125, 144), and different optimum seed rates were obtained for the same variety at the same site (136). This indicates poor improvement in grain yield from seed rate manipulation during broadcasting. Lack of seed-rate effect on grain yield may be because deep water rice produces nodal tillers at low basal tiller density (34), which compensates for low seed rate. Large differences in tiller number of early growth stages in seed rate trials did not necessarily result in significant yield differences (34).

Optimum seed rate depends on variety, seeding depth, soil texture, and moisture. A slightly higher seed rate is used in dry seeding than in wet seeding because uncertain monsoon rains may not provide adequate moisture for seeds to germinate. Because of high mortality of flooding and the crop's high risk factor, using high seed rates usually is a good agronomic practice (34). Growth, nutrient requirements, and improvement in grain yields should be studied at high seed rates.

Little or no yield differences were found between row seeding and broadcast seeding (11, 34, 36, 144). Row seeding may be better because it can be done by machine, but it requires finer tilth and is not practical on heavy soils (11, 36). Row seeding requires lower seed rate and usually results in better germination, uniform stand, and more efficient weeding so that widespread adoption may come.

It is important to understand between-row and intrarow plant interaction in terms of nutrient supply, water supply, and weed management. Applying basal N fertilizer in dry-seeded experimental plots produced more vigorous plants that tillered earlier and more profusely (11, 88). In some experiments, no significant differences were obtained with or without fertilizer in broadcast or row-seeded deep water rice (119). More studies are needed to evaluate growth and nutrient requirements as affected by row spacing and density.

A seeding practice in Bangladesh and in Assam, India, strongly affects the deep water rice growth. Where flooding depth allows, farmers sow a mixture of summer rice (early rice) and deep water rice at different ratios (33, 36, 45, 46). The rice varieties compete. When summer rice is harvested (before deep flooding) deep water rice has more space and light. Mixed cropping either does not affect, or reduces total yields, but the farmer is sure of at least one and sometimes both crops (33, 45, 46). Moreover, summer rice is harvested when the farmer needs it most.

Nursery bed seeding

Seeding transplanted deep water rice varies by country. Pregerminated seeds generally are sown in puddled soil. In Malaysia, pregerminated seeds are sown on a 5- to 7.5-cm-deep mud layer that has been carefully spread on dead leaves and weeds. The nursery usually is on ridges and roadsides (64). The layer of dead leaves makes uprooting for the second nursery bed easier. In Indonesia (106) and Ecuador (68), dry seeds are dibbled in a dry seedbed. Fifty or more seeds are placed in a 7- to 10-cm-diam hole made by pounding a stick into the soil. The compacted soil at the bottom restricts root growth and makes it easy to pull the seedlings with one grasp. Different seeding methods affect the seedling growth, especially nutrient status and root development.

Drought tolerance

Dry seeding is common in the deep water rice areas, as is drought stress. Uncertain rainfall at sowing and seedling growth frequently causes drought damage and poor stand. In Bangladesh, sowing may start in mid-Mar, but the advent and amount of rainfall determine the sowing date. In West Bengal, India, seed is broadcast on dry soil in Apr-May. In Thailand, deep water rice is grown on dry land until the full force of the monsoon sets in anytime from Jun to Aug. Before those months, rice frequently experiences severe drought. Fields often are reseeded if it does not rain for several days after germination. Farmers seed early so plants will be at least 6 wk old before they are flooded. Most deep water rices do not elongate rapidly if they are younger than 6 wk old.

There is natural selection for drought tolerance at the vegetative stage, and the seemingly mutually exclusive traits of drought and deep water tolerance can be combined in a single variety (30). Drought tolerance allows earlier seeding, thus ensuring rapid stand establishment, which reduces the risk that a sudden flood may destroy young seedlings.

Greenhouse and field screening for drought tolerance at the seedling stage have been developed (30, 31), and varietal differences have been found (32, 37, 98, 118, 141). Wild rices in deep water areas have greater drought tolerance than cultivated deep water varieties (98).

There has been no definitive study on drought tolerance of deep water rices at the seedling stage, but efforts should be made to understand drought resistance or avoidance. If plant characters associated with drought resistance at seedling stage are identified, greater advances will be possible in the screening and selection of donor parents and progenies. Fortunately, IRRI findings that traditional deep

water rices generally have drought resistance confirm the possibility of combining drought resistance with elongation ability.

Transplanted seedlings

Most rice-growing areas in tropical Asia are rainfed. Almost 14 million ha of medium deep water rice is included in the rainfed area. Although the crop usually is transplanted before flooding, water level at transplanting often is relatively high, making short-statured seedlings impractical. The time between land preparation and flooding is relatively short and farmers are sometimes unable to plant all their land.

Transplanting has several advantages.

- Transplanting minimizes the need for weed control. Although it requires substantial labor, it reduces the labor needed for weeding, and plant stand is not damaged by weeding (36).
- It ensures uniform tiller stand at a fairly advanced growth stage. Plants can elongate shortly after establishment if there is a sudden water rise.
- Transplanting increases cropping intensity because seedlings can be planted into a maturing winter rice crop (36).

Floods often submerge the crop during early growth stage or just after transplanting. Because floodwaters sometimes come early, seedlings must be tall. Submergence causes severe crop damage and, sometimes, complete crop loss, obliging farmers to replant or replace missing hills. To decrease the chances of crop loss, farmers often transplant old (130 d), tall (50 cm) seedlings.

Seedling age helps determine crop growth and maximize grain yield in medium deep water areas (7). It is important to identify varieties that can be transplanted at different ages and still produce reasonable yields.

Seedling age and height

The need for tall, sturdy seedlings is met by planting old seedlings. Although seedlings grow tall when planted densely or with high N levels, they are weak and easily damaged during transplanting. Planting older seedlings may increase survival if floods occur or water levels are high at transplanting. But their age may adversely affect grain yield by reducing tillering. Higher survival percentage of older seedlings more than compensates for the decreased tillering (7).

The 10-d-old deep water rices generally are shorter than traditional nonfloating varieties. However, the same deep water varieties generally are taller than the nondeep water rices after 40 d (160).

Sometimes, 10-cm difference in seedling height means survival or death. Selection for tall, vigorous seedlings with intermediate plant height at maturity is important.

Older seedlings have stronger culms that are not easily broken by strong water currents. They are taller, therefore, leaves are more likely to remain above the water. Seedling height is due not to dense planting and heavy fertilizer application (which result in long, thin culms) but to naturally longer, thicker culms.

Crop growth is influenced by seedlings/hill and distance between hills. Transplanted deep water rices often are closely spaced or highly seeded because there is little time for basal tiller production before flooding.

Double transplanting

Double transplanting is done in Vietnam (172, 173), Indonesia (106, 138), Malaysia (64), Bihar (110), and Ecuador (68).

In Vietnam, farmers plant seeds in Jun or when rainy season begins. Thirty to 45 d later, seedlings are pulled and transplanted in a bigger seedbed where they grow for another 60 d. Hills of seedlings (20-25 tillers/hill) are uprooted with large knives and transplanted a second time in Sep, when the water is 40-70 cm deep (172).

Farmers prepare the field for transplanting as soon as the water is available. Fields are not plowed or harrowed, but weeds are cut with a large scythe. Wooden daggers are used to make holes in the soil where 90- to 100-d-old seedlings are transplanted. There is little or no management between the second transplanting and harvest. Even without fertilizer, growth is luxurious.

Double and triple transplanting are common in rainfed, tidal swamp, and deep water rice areas in Indonesia (106). At second transplanting, seedlings can be 135 d old. Studies on double transplanting in Indonesia showed no grain yield reduction if the seedlings were less than 50 d old. Using younger or older seedlings reduced grain yields.

In some areas, double or triple transplanting means that soil and surface water are less acidic (147) or less saline by the second and third transplanting because the field has been flooded for 2-4 mo.

Submergence tolerance

Most deep water rice needs submergence tolerance. At seedling stage or transplanting, complete submergence for 1-20 d kills or drastically inhibits rice growth. Crops often are submerged two or three times during the growing season. Most deep water rices have shown poor submergence tolerance (66, 160). Survival percentage after submergence is highly correlated with grain yield (7).

Although survival ability after submergence is a genetic character (96), environmental factors affect submergence tolerance (95, 112, 120). Physiological, anatomical, and morphological differences between tolerant and susceptible varieties have also been studied.

Tolerance is related to submergence duration, water temperature, turbidity, light intensity, water depth, and soil N content. Plants are less submergence tolerant at the early growth stages, and varietal tolerance differs.

Submergence at seedling stage usually kills many small, weak seedlings. At tillering stage it inhibits tiller formation, and submergence at panicle initiation causes degenerated

and sterile spikelets. Submergence near flowering stage prevents complete panicle emergence from the leaf sheaths (113). Submergence at flowering probably is most detrimental because it causes spikelet sterility. Plants cannot recover, and it is too late in the season for farmers to replant.

Environmental factors

The deeper the water (3, 44, 112), the longer the submergence (43, 112, 113), the higher the temperature (78, 79, 81, 112), the more turbid the water (28, 80, 112), and the lower the light intensity (112), the lower the survival percentage. Bacteria in the water during submergence partly causes plant death (81). Plants submerged in sterile water survived better than those submerged in nonsterile water.

High N levels usually increase susceptibility to submergence (112). Although plants with high N are luxuriant, they are succulent and soft, which makes them less resistant to flooding. Irrespective of variety, submergence tolerance decreased as N application increased (28). The factors that influence the survival of submerged plants also determine plant N and carbohydrate levels.

Physiological factors

When rice plants are submerged, their internal O_2 content decreases (175). Aerobic respiration is reduced, anaerobic respiration is promoted, and increased consumption of respiratory substrates with decreased evolution of energy results. Oxygen deficiency inhibits protein hydrolysis. The soluble nitrogenous fraction increases soon after flooding, peaks, and then decreases. These changes suggest that the available substrate of respiration was exhausted under water (177).

Although photosynthesis occurred under water, its rate decreased (164, 177). Photosynthetic capacity is closely related with activity of RuBP carboxylase, which is localized in the chloroplasts. Complete submergence considerably lowered RuBP carboxylase activity (164). Reduced light and oxygen and chlorophyll attenuation may cause reduced photosynthesis during submergence.

Tolerance for complete submergence at the seedling stage does not depend on a single physiological character. Some varieties survive because they elongate so that their leaves are above the water. Others maintain a high carbohydrate level during submergence (40, 175). Other varieties have green, active leaves, stiff culms, and high nitrate reductase activity after submergence. Some varieties maintain high photosynthetic rates and respiration during submergence (95).

Table 2 shows physiological response of submergence-tolerant and susceptible varieties. Submergence tolerance is negatively correlated with the ratio of photosynthesis to respiratory rate, decreased oxygen release rate in water, and decreased nitrate reductase activity.

Submergence tolerance of 60- and 85-d-old plants reportedly increased when the plants were subjected to continuous current of oxygen-free air for 3 d during germination (114).

Submergence tolerance and recovery rate are correlated with K, Si, and NO_3 content of rice plants before submergence (95). High Si in plants is associated with stiff stems and leaves.

Survival during and after submergence is the result of a combination of many characters, including proper morphological and anatomical structure.

Table 2. Physiological differences in rice varieties tolerant of and susceptible to complete submergence (95).

10-d-old seedlings of tolerant and susceptible varieties

SUBMERGENCE (6 d, 30-cm water depth)

Tolerant	*Susceptible*
• Plant height generally taller and in moderately tolerant varieties increased rapidly.	• Shorter plant height.
• Dry weight decreased and related to elongation.	• Dry weight decreased and related to elongation.
• Carbohydrate decreased at lower rate.	• Carbohydrate decreased at faster rate.
• Nitrogen was higher and decreased at lower rate.	• Nitrogen decreased at faster rate.
• High silica in culm, plant stiff protecting the growing point.	• Low silica, culm is soft causing physical damage to growing point.
• Longer roots, inhibited by submergence.	• Shorter roots, inhibited by submergence.
• Oxidizing power of roots did not change.	• Oxidizing power decreased.
• Photosynthesis decreased at lower rate.	• Photosynthesis decreased at higher rate.
• Higher respiratory rate.	• Lower respiratory rate.
• Higher oxygen release rate.	• Low oxygen release rate.
• Higher level of potassium, nitrate, and nitrate reductase activity.	• Lower potassium, nitrate, and nitrate reductase activity.

SURVIVAL (Recovery)

High	*Low*
• Maintained high level of carbohydrate after treatment resulting in faster recovery.	• Low carbohydrate content.
• Fast recovery of lost nitrogen and new chlorophyll synthesized.	• Chlorophyll disintegrated.
• More still and rigid culm to protect growing point.	• Soft and collapsed culm causing physical damage to growing point.
• Maintained high photosynthesis and respiratory rate.	• Low photosynthesis and high respiratory rate.
• High nitrate reductase activity.	• Lower nitrate reductase activity indicating poor recovery.

Morphological factors

Rice is most susceptible to submergence at seedling stage (3, 44, 109, 111, 113), and tolerance increases with age. However, although plants may not die when submerged at booting and flowering, grain yield may be lost completely (77).

Older seedlings generally have high survival rates (7, 110, 113), but their generally poor recovery after submergence delays tillering and may significantly reduce yield. Where double transplanting or long-growth-duration varieties are used, poor recovery of older seedlings may not drastically reduce yield (7).

Within a variety, the amount of accumulated carbohydrates in the plant correlates positively with submergence tolerance (112). Older seedlings have greater submergence tolerance partly because they contain more carbohydrates. Decreasing seedbed soil N level increases seedling carbohydrate content and should therefore increase submergence tolerance. Unpublished data show, however, that decreasing N lowers the recovery and tillering rates of transplanted seedlings, thereby reducing yields.

Although taller seedlings should have an advantage during flooding, initial seedling height is not associated with survival percentage of submerged plants (71, 101, 110). However, after complete submergence and recovery, tolerant varieties were generally taller than susceptible varieties. Within a variety, however, adding N resulted in taller plants which was partly responsible for higher survival and improved crop growth (83).

At seedling stage, there is a high correlation (r = 0.7261**) between overlapping of the first leaf sheath and survival percentage after submergence (72). The role of overlapping leaf sheaths is unclear, but it may be that overlapping stiffens the culm and prevents plant breakage or collapse at the growing point when water recedes (71).

Comparison of some susceptible and tolerant varieties showed that varieties with circular or round culms were more tolerant than varieties with flat culms (72). Culm shape probably determines the degree of leaf sheath overlapping (Fig. 5). There was a high negative correlation (r = -0.7384*) between the length of overlapping and the width: thickness ratio of the culm. Round culms had more overlapping than the flat culms. However, this characteristic alone cannot be used for selecting tolerant varieties because many other factors contribute to submergence tolerance. Leaf pubescence also may influence survival after submergence because mud is more likely to stick to pubescent leaves, thereby reducing photosynthesis.

Anatomical factors

The anatomy of rice plants may be important in determining submergence tolerance. More vascular bundles and thicker sclerenchyma layer may influence culm stiffness and make plants less prone to breakage at the growing point. The number of air spaces or lacunae may also be important – they are O_2 reservoirs, or, if leaf tips are above the water, passageways for O_2 transport from leaf blades to the roots. On the other hand, large lacunae may result in spongy, weak leaf sheaths, which increase lodging as floodwaters recede.

In the varieties studied, the number of vascular bundles on the first and second leaf blades differed; however, differences between tolerant and susceptible varieties were insignificant (70).

At seedling stage, the percentage of lacunae per unit area correlated negatively with submergence tolerance (r = -0.5997*). The lacunae of the susceptible varieties developed earlier. The total number of lacunae in the first and second leaf sheaths also correlated negatively (r = 0.6657*) with submergence tolerance (70, 72).

The number and thickness of the sclerenchyma layers of the first sheath of the rice seedlings tested did not correlate with submergence tolerance. However, two tolerant varieties had one more layer than the other varieties (70, 72). Both tolerant and susceptible varieties have varying thickness.

Submergence promotes the development of sclerenchymatous tissue in the leaf sheath (110). Tolerant varieties usually have sclerenchymatous stems, more starch granules in their ground tissues, and additional vascular bundles in the inner row (92). However, those characteristics are not found in all tolerant varieties indicating that many factors are responsible for submergence tolerance.

Anatomically, the main difference between submergence-tolerant and susceptible varieties is the percentage of area occupied by the lacunae and the number of lacunae. Susceptible varieties have more lacunae (70, 72).

Seedlings per hill

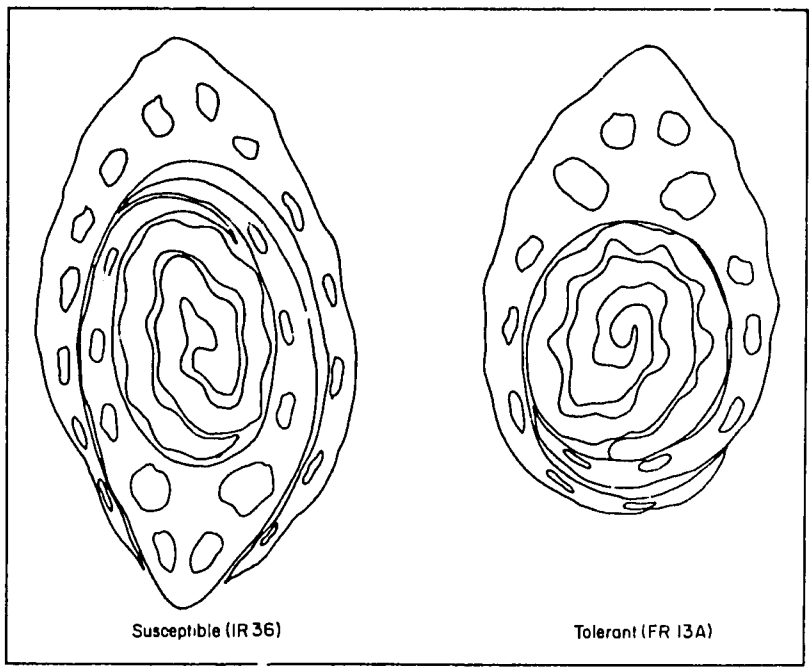
Deep water rice farmers who transplant either use old seedlings or double transplant, and usually transplant more seedlings per hill.

Increasing the number of seedlings per hill ensures a desired plant population. In one experiment, panicles per unit area and grain yield were the same for submerged and nonsubmerged plants at a planting rate of five seedlings per hill instead of one. Grain yield was 40% less when plantings of 1 seedling/hill were submerged (165). The probability of empty hills after submergence is less if more than one seedling per hill are planted, although seedling number may not directly affect grain yield (36, 113, 165).

Planting many seedlings per hill results in primary tillers that are larger and more vigorous than secondary and tertiary tillers. Because tillering is inhibited and small tender tillers are usually killed by submergence, the use of old and several tillers per hill is practical. The development of the rice plant and its nutrient requirements in this practice are different.

Screening for submergence tolerance

Different screening methods for submergence tolerance in



5. Culm comparison of flood-susceptible and tolerant plant type (72).

deep water rice have been developed (33, 37, 127, 140, 154, 155). A collaborative effort to screen for submergence tolerance and to compare the results was agreed upon in a deep water rice workshop (50, 163). Using a common set of varieties, cooperating scientists found the so-classified tolerant varieties the best in the different screening methods used.

Because submergence can occur at any growth stage, screening must consider time of submergence for specific sites and conditions. However, rice plants are most susceptible at seedling stage, when submergence often occurs.

Where water level is greater than 100 cm, seedlings with elongation ability or those that grow rapidly until they emerge from the water are more desirable than non-elongating submergence-tolerant types (26).

Weeds

Weeds compete with rice for both moisture and nutrients. They affect rice growth mostly at seedling stage, when stand density and subsequent tillering activity are determined.

Weed competition is more serious when rice is seeded and grown on dry soil than when grown on wet soil. Deep water rice is seeded primarily on dry soil and fields remain in dryland condition for 6 wk to 3 mo.

Weed problems in deep water rice resemble those in upland rice during stand establishment and early to mid-vegetative stages. But when flooding depth increases, many weeds die and aquatic weeds dominate (29). Among the floating weeds, water hyacinth causes the greatest damage because it can engulf the crop (63).

Deep water rices generally compete well against weeds. Sometimes, weed populations are low and weeding does not greatly improve grain yield, which is why most farmers do not weed deep water rice. Weeding is more common in Bangladesh than in other countries.

If N fertilizer is applied, weed growth increases. Therefore, weeding is necessary to increase grain yields when N is applied (63). When farmers weed their fields, they use tillage, raking, manual or hand pulling, and spot-sprayed herbicides Vigorous weeding before flooding temporarily reduces tillering (Fig. 6), but indigenous varieties recover quickly (14). Broadcasting rice seeds makes weeding difficult, but line sowing tends to promote weed growth (11).

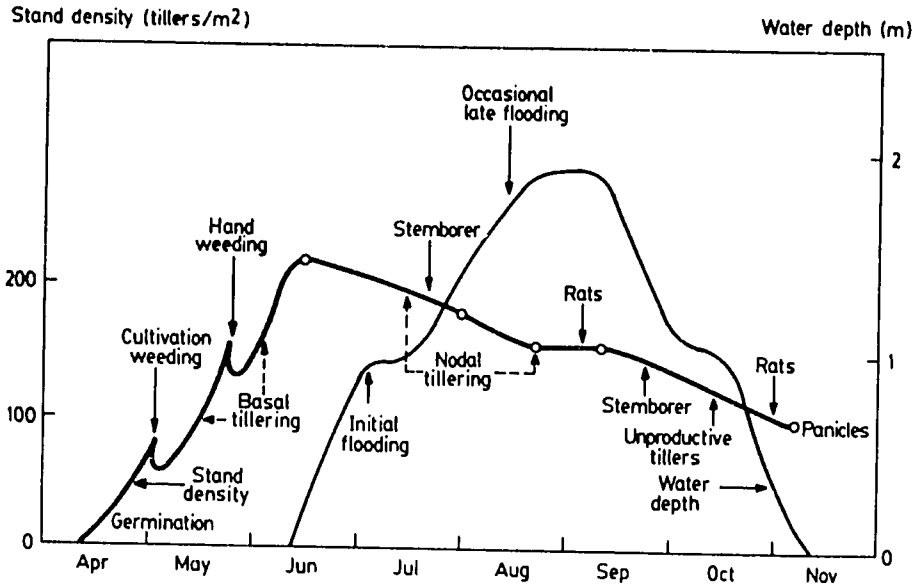
Wild rice species with submergence tolerance and elongation capacity similar to that of the deep water rices can reduce yields in Asia and West Africa (3, 29, 117, 144). Harvesting wild rice panicles, crop rotation, burning stubble, wet seeding, transplanting, and repeated harrowing effectively minimize wild rice infestation.

LEAFING AND TILLERING

Leaf morphology

The leaves of deep water varieties resemble those of most traditional indicas. They usually are pubescent and exhibit morphological features similar to those of other rice varieties (44, 47). Pubescent leaves tend to trap silt in muddy water (142), which may reduce photosynthesis. Silt deposits may also cause leaves to droop. Breeding for glabrous leaf may be desirable.

Rice vegetative growth tends to be excessive in the tropics. With sufficient nutrients, traditional deep water rices grow especially luxuriant. Excessive growth increases shading and often causes low grain yield. Closer spacing to produce more tillers would be difficult with deep water rice because of mutual shading.



6. Seasonal fluctuation of indigenous deep water rice stands in Bangladesh with major factors affecting stand density (14).

Leaf erectness affects sunlight penetration, photosynthesis, and grain yield. Deep water rices generally have open or spreading leaves, partly because leaves are longer (160).

Traditional deep water rices generally do not respond positively to N fertilizer. Applying N increases leaf length and shading. Breeding for erect leaves would improve response to N fertilizer.

Photosynthetic and respiration rates of deep water and traditional rices have not been compared. Leaf photosynthesis under submergence may differ by variety. Research should be designed to identify varieties with efficient leaf photosynthesis even when submerged.

Deep water increases leaf formation rate (97) and the number of leaves produced on the main culm (47, 185). In flooded conditions the number of nodes and leaves almost doubled – 20 to 26 versus 11 to 16 without flooding (47). Although leafing interval is shorter, growing more leaves delays flowering during flooding. Delay is influenced by water depth.

The leaf sheath and the lamina of new leaves elongate considerably in deep water, but elongation capacity declines as leaves become well differentiated or mature.

Flag leaf length is variety dependent and may be longer or shorter in deep water. However, leaf breadth is greater in deep water than in nonflooded fields (47).

At maturity, one to four leaves, depending on the variety, may still be green (47).

Morphology of tillering

Tillers are branches that develop from leaf axils, either from the main culm or from other tillers. The first leaf normally does not produce a tiller. Tillering starts from the second leaf, which is the first leaf with an expanded lamina.

Tillers develop synchronously with leaves on the main culm. Usually, when the fifth leaf on the main culm emerges, the first leaf of the tiller comes out from the axil of the second leaf. A tiller may emerge from the axil of the third leaf on the main culm after the sixth leaf has emerged. 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 general sequence applies not only to tillers from the main culm, but also to all other tillers.

In deep water rices, nonsynchronous tillering occur since tillering is possible at upper nodes after the n+3 leaves emerge. In nondeep water rices the first tiller usually is from the second node, but in direct-seeded deep water rices, tillering starts on the third node (107).

Tillers on the main culm are called primary tillers and those from primary tillers secondary tillers. Tertiary tillers are common in nondeep water rices but they normally die. Deep water rices have quaternary tillers, which seldom grow on nondeep water rices (107).

There was no technical term for tillers that grow from the nodes above the plant base, so deep water researchers agreed to call them *nodal tillers* (58, 159). It is proposed that *upper nodal tillers* would be a better term to use to describe such tillers (Fig. 7).

In deep water rice, tillering commonly occurs from node 3 to node 25, and 31 nodes have been recorded (107). No node can be fixed to distinguish basal tillers from upper nodal tillers (107).

Deep water rices generally have lower tillering capacity than nonfloating varieties (160). However, low tillering ability does not seem to be closely associated with elongation ability. Traditional deep water rices tend to have open tillers (160), which is detrimental when plant density is increased. On the other hand, open tillers may provide better weed control.

Tillering pattern

The tillering pattern of deep water rice is shown in Figure 8. It differs from that of nonfloating rices because of prolonged vegetative growth, high number of nodes, and upper nodal tiller formation at later growth stages.

7. Nodal tillers of a deep water rice variety.

Several factors reduce tiller density of deep water rice. However, indigenous deep water rices have strong ability to regenerate tillers, and preflood stand densities sometimes are poorly related to grain yield. Nevertheless, high plant density before flooding tends to give higher grain yield.

Prior to flooding optimum stand density for direct-seeded rice is 300-320 tillers/m^2 (14). Two to three tillers may form before flooding if the soil is fertile and has sufficient moisture. More older or primary basal tillers survive submergence than young or secondary tillers. Stand density decreases during stem elongation because secondary or tertiary basal tillers may die and because of stem borer damage (Fig. 6). When upper nodal tillering occurs during midflooding, decline in tiller number is offset.

During reproductive stage, stem borer and rat damage reduce the average plant density. Upper nodal tillers may form at heading but they do not contribute to grain yield. At harvest, the optimum plant density is 120-130 panicles/m^2, which yield 3 t/ha (14).

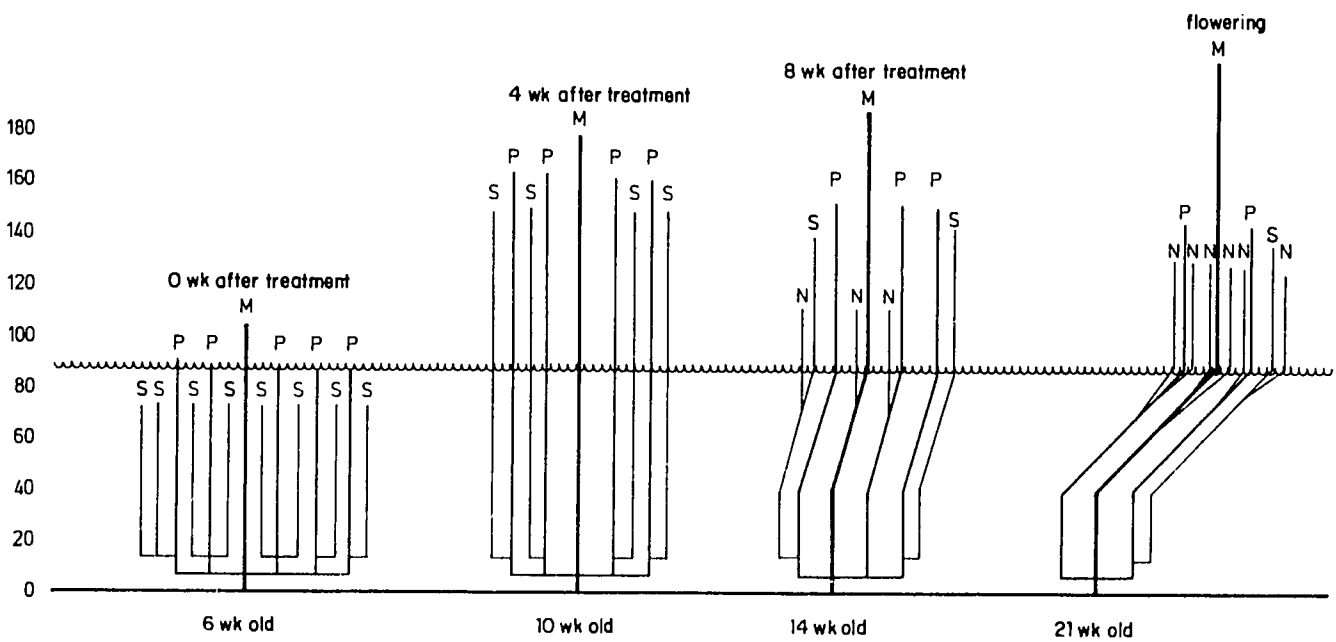
Factors affecting tiller number

In deep water rice areas, water depth, flooding onset and rate of increase, and maximum water depth are the most important yield constraints. Deep water inhibits the production of basal tillers, which reduces panicle number. Improved varieties and agronomic practices can increase panicle number and/or panicle weight.

Variety

Rice varieties differ greatly in tillering ability and survival percentage of tillers, which are affected not only by the environment but also by plant type characteristics such as leaf arrangement and tiller angle. Because traditional deep water rices have open tillers and droopy leaves, heavy mutual shading would limit tiller survival even in shallow water.

Water level up to 40 cm markedly reduces the tiller number of high-tillering varieties, but does not affect



8. Tillering pattern and plant height of Leb Mue Nahng 111 submerged in water at 85-cm depth at various stages. M = main tiller, P = primary tillers, S = secondary tiller, N = nodal tiller.

low-tillering types, which have a high percentage of productive tillers (Fig. 9).

In shallow water, high tillering capacity may be advantageous, but medium tillering may be bettei for deep water. New tillers die when the water level increases, therefore prolonged, prolific tillering is undesirable. Instead of being used to produce new tillers, photosynthates could be accumulated in the culm and used in internode elongation or further translocated to the panicle during grain filling.

On the other hand, high-tillering varieties generally are well adapted to a variety of spacing and planting densities.

Nitrogen application

Tillering ability is closely associated with plant nutrition. In medium deep water, basal N application significantly increased tiller number before flooding and tillers survived in the successive growth stages (39, 73, 74, 85, 86). Although more tillers died at high N application (80 and 120 kg/ha) (Fig. 10), more survived than were produced at low N application levels.

High N application resulted in continuous production of tillers of nonuniform height and growth. Small, short, weak tillers died after flooding, which suggests that photosynthates and nutrients used to grow new tillers were wasted.

Number of seedlings per hill

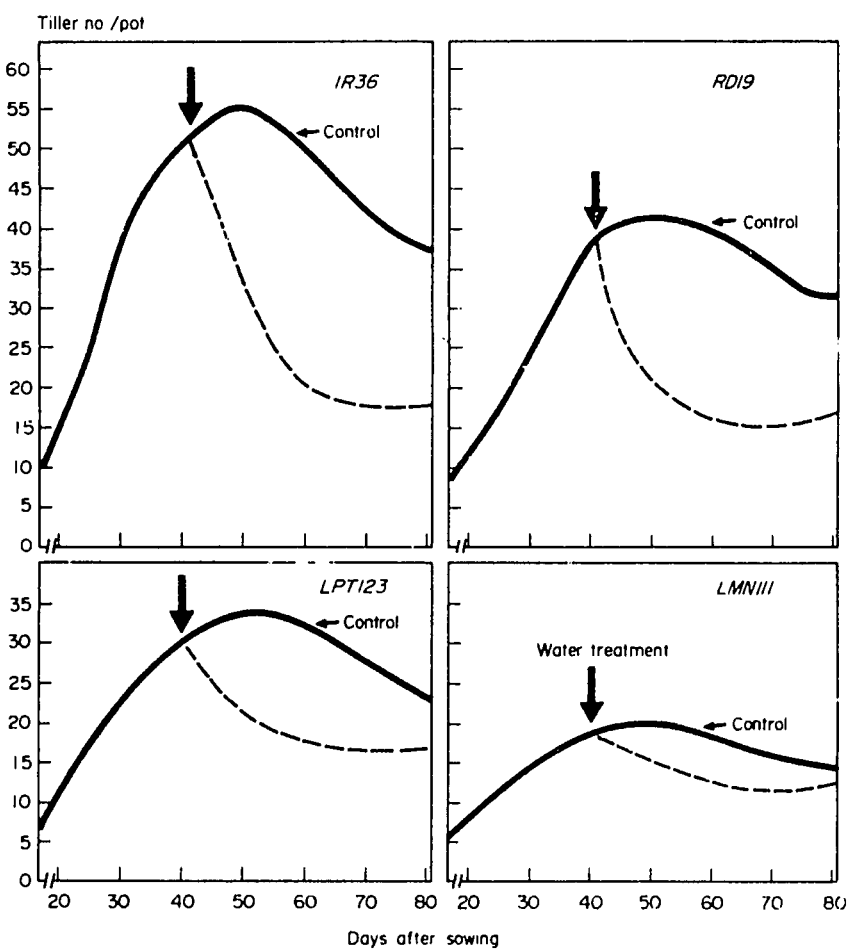
Transplanting more seedlings per hill can increase tiller number per unit area. However, increasing the number of seedlings per hill leads to intense within-hill competition. Seedlings in the center of the hill produce few, if any, tillers, and some tillers and seedlings may die because of competition for nutrients and sunlight.

In deep water rice culture, planting many seedlings per hill produced many panicles (86), and can be used to offset basal N application to increase tiller number and yield. Planting more seedlings per hill is especially effective in deep water areas where fertilizer usually is not applied. Yield increase from planting more seedlings per hill is more pronounced in low or no N application plots than in those with high N application (88).

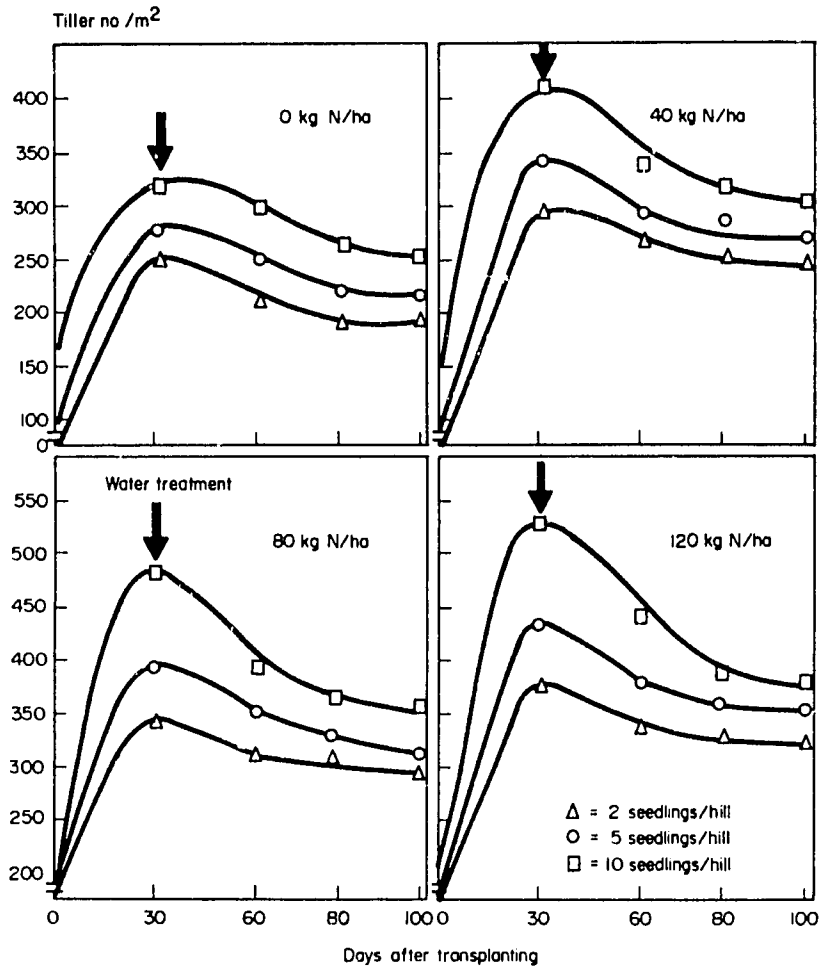
In deep water rice areas where transplanting and double or triple transplanting are practiced, farmers use high seedling rates.

Spacing

Spacing affects yield in transplanted rice. Because tillering activity varies among varieties, the relationship between spacing and variety is important. In general, closer spacing is better for low-tillering than for high-tillering varieties and



9. Secondary reduction of four rice varieties at 40-cm water depth 40 d after sowing, compared to control (86).



10. Tiller number of IR42 grown in medium deep water as affected by number of seedlings per hill at different levels of N fertilizer (86).

for short-growth-duration than for long-growth-duration varieties. Traditional deep water rice varieties have long growth duration. High-tillering varieties generally are well adapted to a wide range of spacing.

In deep water tests in Thailand, 15 x 15 cm spacing was optimal (Fig. 11) and significantly increased tiller number at every growth stage. Flooding 30 d after transplanting reduced tiller number for all treatments and was greatest at closer spacing. At harvest, however, there were more tillers at closer spacing because more had developed before water treatment. Results emphasized the importance of early tiller production and crop establishment in deep water rice areas.

Seed rate

Broadcast seeding on dry soil is common in deep water areas. Tillering at the early stage is determined by soil moisture and weed population. Usually, 90-180 kg seed/ha is planted (86) and farmers often add extra seed where flooding will be deeper.

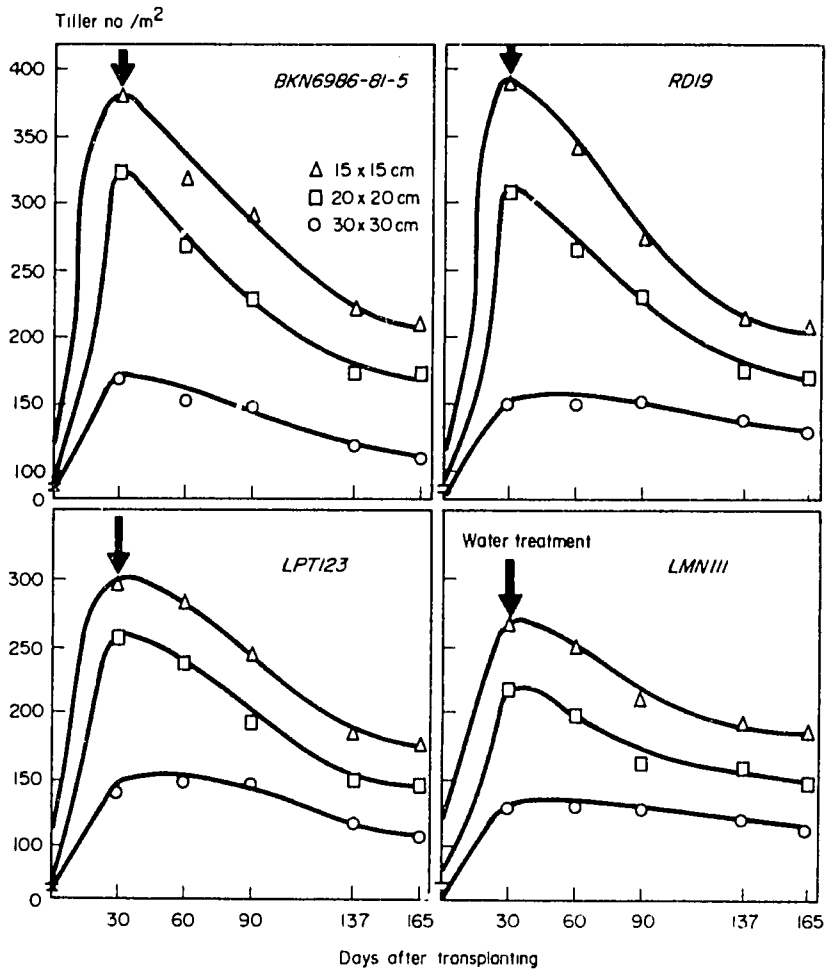
When deep water rice is broadcast on dry soil at a relatively high seed rate (200-600 seeds/m^2), maximum tiller number is observed 10-30 d after seedling emergence (Fig. 12). Drought stress and nutrient deficiency may reduce tiller number 30 d after seedling emergence. More tillers die at higher seed rates regardless of variety planted, and competition for nutrient and moisture is greater. In deep water rice areas, yellowing is apparent at the seedling stage but that slowly disappears as the soil is submerged and floodwaters rise. High seed rate has little impact on final panicle number and grain yield (Fig. 12). Accompanying improvement in cultural practice is probably needed or a more responsive plant type is necessary.

Seeding method

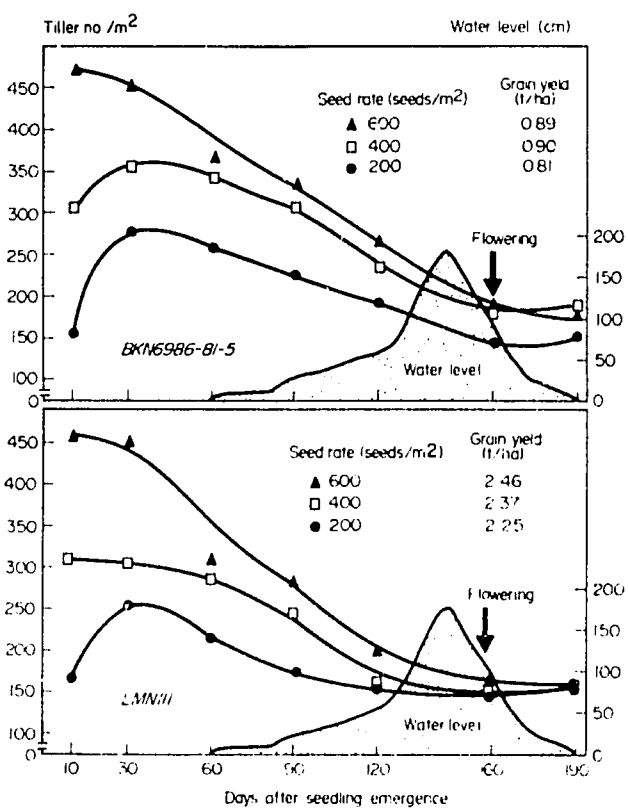
Seeding method not only affects crop stand but also determines subsequent cultural practices. Rice seeds and weeds germinate simultaneously when monsoon rains begin. Weed control is difficult and is generally not practiced.

Ten days after seedling emergence, crop stand was better with row seeding than with broadcasting (Fig. 13), but at harvest tiller number and grain yield did not significantly differ (3, 51, 84, 86, 88). Nevertheless, row seeding makes weeding and fertilizer application easier.

A 35-cm spacing between rows was too wide for 400 seeds/m^2 (Fig. 13). More tillers died at this than at other spacing which indicates that planting more seeds per row creates greater competition for nutrients, causing weak, short tillers. At higher seed rates, similar competition occurs but can probably be overcome by fertilizer applica-



11. Tiller number of four rice varieties grown at 70-cm water depth as affected by spacing (86).



12. Effect of seed rate on tiller number of BKN6986-81-5 and LMN 111 grown under natural deep water conditions (86).

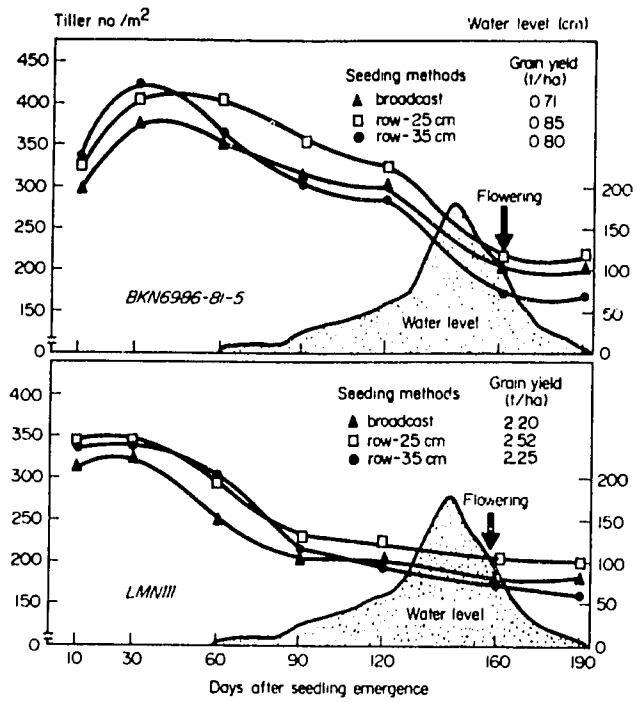
tion. Seeding methods did not significantly affect percentage of productive tillers.

Upper nodal tillers

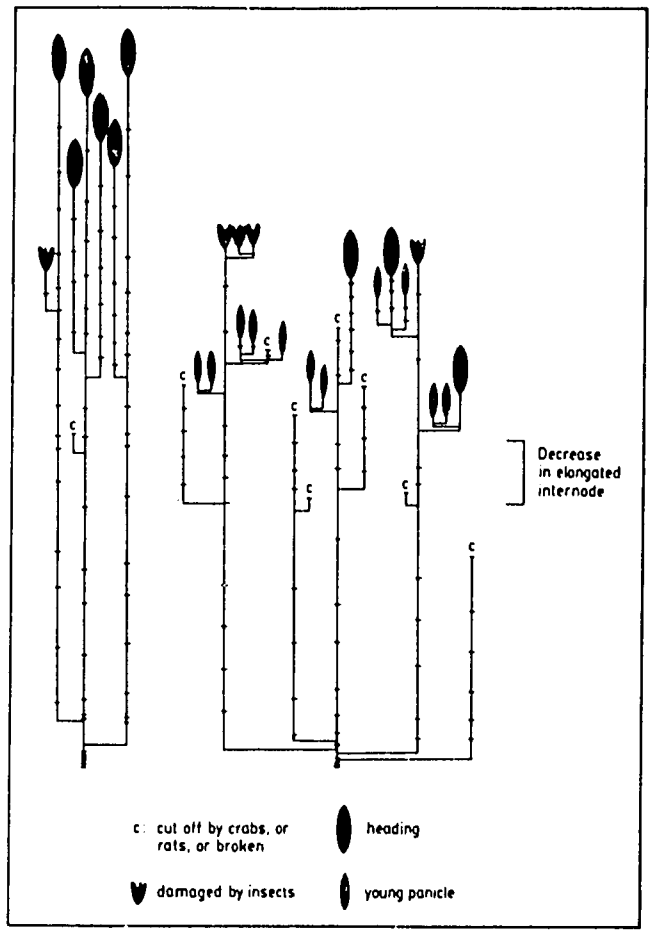
Deep water rices produce upper nodal tillers when subjected to deep water and even when planted in shallow water. In ordinary rice varieties and culture, upper nodal tillers are not produced. Upper nodal tillers grow from submerged nodes (27), and only after the rapid elongation phase stops (3, 21, 26, 27, 33, 44, 128). Figure 14 shows that upper nodal tillers form after internode elongation decreases or after the water level stabilizes.

A method for screening deep water rices for their ability to produce upper nodal tillers has been developed (129). Deep water rice varieties differ in upper nodal tillering ability although their internode elongation ability may be similar. The number of upper nodal tillers produced by a plant varies from 0 to 27.6 (128, 129, 143).

Upper nodal tillers occur from the 3rd to the 25th node (107). They develop on nodes 10-25 cm below the water surface (128), do not form below 45 cm, and are not node



13. Effect of seeding method on tiller number of BKN6986-81-5 and LMN 111 grown under natural deep water conditions (86).



14. Tillering pattern of Khama (107).

specific. Those new tillers also may produce secondary nodal tillers (44). When water recedes and plants lodge, nodal tillers can form near the base of plants. Most upper nodal tillers develop from primary and secondary basal tillers and a few from the main tiller (Fig. 14).

The number of basal tillers produced does not correlate with the number of upper nodal tillers (129). In some cases, primary or secondary basal tillers produced more than one upper nodal tiller.

Nodal tiller development depends not only on water regime but also on plant nutrient status and availability of nutrients in the floodwater. In low-N soils, rices did not produce nodal tillers (74). N availability in the floodwater increased upper nodal tiller production.

Because of upper nodal tiller production, basal tillers of some deep water rices are shorter when grown in deep water than in shallow water (143). The growth and elongation of the main and primary tillers may slow down when the deep water level stabilizes, and growth then diverts to nodal tiller production. In shallow water, basal tillers continue increasing in height, no nodal tillers develop, and plants tend to be taller than those grown at 70- to 100-cm water depth.

Upper nodal tillering and flooding patterns

Upper nodal tillers develop only after rapid elongation stops or when the water level stabilizes for 4 or more wk (128). The importance of the upper nodal tillers to yield depends on the flooding pattern. Elongation, tillering, and panicle development compete. Because elongation and flowering are stronger physiological processes, nodal tiller production usually occurs only after elongation and before flowering.

Figure 4 shows several flooding regimes in the deep water rice areas. Flooding varies by water depth, rate and date of water increase, flood duration, occurrence of peak depth, and duration of *steady depth*. Flooding regimes also varies by year. These factors, plus the timing of panicle initiation, affect the development of upper nodal tillers.

At Huntra, Thailand (or in areas with similar water regimes), water may increase continuously from Jul to Nov, then decrease without stabilizing for 3 to 4 wk. Plants elongate, but none or very few upper nodal tillers form because water depth does not stabilize before flowering. In some years, however, it stabilizes before flowering so potential upper nodal tillering ability cannot be completely ignored.

In some deep water areas of Bangladesh, the water rises in Jun and peaks in early Aug, after which it stabilizes for at least 10 wk. Flowering occurs and the water level recedes (Fig. 4, curve b). In those areas, the plant has sufficient time to elongate and form nodal tillers before flowering, and nodal tillering may contribute appreciably to grain yield.

In Niger, the water level increases steadily and peaks almost simultaneously with flowering (Fig. 4, curve c). Nodal tillers probably will not develop. In that region, early tillering capacity is important, but nodal tillering ability is of little use and may be detrimental.

The flush production of upper nodal tillers after flowering, which should be prevented, occurs in some varieties, and especially with high nutrient levels. Flush tillering may increase if varieties with high nodal tillering ability are used.

Another flooding regime is represented by curve d, Figure 4. The secondary but relatively early stabilizing of the water level between Jul and Aug can produce early nodal tillers. A second set of nodal tillers may be formed just before flowering in Oct. Both sets of nodal tillers could contribute significantly to yields.

Although upper nodal tillers usually form only when the plant is partly submerged, increasing water depth does not produce more nodal tillers. Maximum nodal tillers were produced in medium deep water (27) because there was more time to produce nodal tillers before flowering. In deeper water, the plant had to elongate for a longer period and so had less time to produce nodal tillers.

Several scientists have recommended that nodal tillering ability be incorporated into deep water rices. Where water is more than 100 cm deep and flooding is early, nodal tillers can improve grain yield if water level stabilizes for 3-4 wk before flowering. The analysis of some data on water regime patterns, however, indicates that nodal tillering ability is not needed in some areas.

Importance of nodal tillers

Contribution to grain yield

The contribution of upper nodal tillers to grain was seldom evaluated before 1978 (128). Nodal tillers formed immediately before or after flowering do not contribute to yield, but those initiated during early growth may significantly increase yield.

Recent studies showed that upper nodal tillers contribute 0-88% to grain yield (27, 39, 104, 128, 143), depending on variety and environmental factors such as flooding pattern.

Panicles from upper nodal tillers sometimes are immature at harvest, and therefore do not contribute to grain yield. They usually are smaller than those produced from basal tillers (11, 39, 128).

In parts of West Bengal, India, water level is stable for a long time, and nodal tillers may have time to grow and flower synchronously with basal tillers. Where rice is transplanted in more than 20 cm of water, basal tillering usually does not occur and upper nodal tillering improves yield. Breeding for rapid nodal tiller formation would increase plant density and grain yield in those areas.

Unfortunately, the importance of branching cannot be properly assessed because hydrological data for deep water rice areas are insufficient. Studies of plant samples, however, can help determine the need for upper nodal tillering ability.

Compensating ability

When drought, flash floods, and/or insects drastically reduce tiller number, nodal tiller formation can improve yield (11, 14, 27, 39, 143).

Studies have shown that deep water rices produced more nodal tillers when basal tillers were reduced by artificial pruning or when N was not added to the soil (39). In addition, deep water rices also compensated for artificially reduced basal tillering by producing more spikelets per panicle (39). This compensating ability emphasizes the importance of panicle weight, which probably is more useful in deep water than other rices because the growing season is long and carbohydrate accumulation is possible.

Nodal tillering ability in deep water rice is an adaptive trait that can compensate for tillers killed by drought, submergence, or stem borer attack. Nodal tillering ability partly explains why deep water grain yield can be similar at different plant densities.

The question still to be answered, however, is "What causal agent or agents determine if a node will produce a tiller (107)?"

ELONGATION

Morphological and anatomical changes

The most important morphological feature of deep water rices is the capacity to elongate after deep flooding. By elongating, plants may grow 300-750 cm long (25, 46). The number of elongated internodes may vary from 9 to 30. However, the number of elongated internodes does not indicate actual elongation capacity (20, 47).

Generally, the longest culm and the highest node number appear not on the main culm but on other tillers (107). Many tillers are higher than the main culm, unlike other rices. Deep water rice may produce 7-13 extra nodes when flooded (47).

Submergence increases the internode thickness, the size and number of air spaces, the size of cells around the air spaces, and the diameter of vascular bundles (22, 26, 47, 103, 122). The larger air spaces and surrounding cells account for most of the increased size of vascular bundles. In the deep water rice, air spaces were found even in internodes above the water level (22, 122). The elongation of the internodes and other vegetative plant parts is due to increased cell length according to one report (103) and to increased cell number according to another (139).

Total plant elongation may be 20-25 cm in 24 h during the initial flooding (18, 33) and 9.3 cm/d after initial elongation (185). An internode may elongate 50 cm (44). When floodwaters recede quickly after elongation, the rice

culms may break instead of bending over, causing heavy yield losses (173).

Physiology of internode elongation

Although internode elongation is an important characteristic of deep water rice, its mechanism has received little attention from researchers.

In young rice seedlings, gibberellic acid (GA) caused the first and second internodes, leaf sheaths, and blades to lengthen (42). Adding abscisic acid (ABA) produced longer internodes but shorter leaf sheaths and blades than the control. Presumably, the combination of GA and ABA was responsible for internode elongation. Ethrel appeared to inhibit elongation but its action could not be clearly defined.

Researchers postulated that deep water rices have, or produce after certain stresses, relatively large amounts of GA, ABA, ethylene, and other phytohormones. As a consequence they produce long internodes and short leaf sheaths and blades (41, 42, 181).

Studies of changes in total N, protein N, and amide plus ammonia N content showed that deep water rice plants maintain a normal N metabolism in both shallow and deep water conditions (180).

The content and concentration of nonreducing sugar and crude starch decreased after submergence, but decreased less in deep water rice than in ordinary rice. The large increase in total internode length of the deep water rice after submergence may be related to the increase in reducing sugar (179, 186).

Deep water rices have higher sugar and starch content and higher amylase and invertase activity than the ordinary rices in deep water, suggesting a latent ability for vigorous elongation (186).

Nutrient content studies showed that K and P of deep water plant increased as water level increased but Ca, Mg, Mn, and Si contents were much less than those of plants grown in shallow water (180, 183, 184). Ordinary rices subjected to deep water had decreased K and P but Ca, Mg, Mn, and Si were not greatly reduced (178).

Factors affecting internode elongation

The main distinguishing characteristic of floating rices is ability to elongate rapidly in rising water. Plant elongation can involve the leaf sheath, leaf blade, and the internode. In deep water rices, however, internode elongation is most important because leaf elongation is limited. Leaf sheath and leaf blade elongation causes the plants to emerge faster from the water, which helps the plant to survive. However, if water continues to rise beyond the ability of leaves to elongate, the plant will die unless internodes elongate to expose the leaves above the water surface.

Different factors affect internode elongation, but information is limited. Little is known about how the environment affects elongation or the internal mechanism involved. Usually elongation is more rapid in clear water (80), in short days (52, 53), in bright conditions (44), and in warm (30/27 °C) day/night temperatures than in cool (25/18 °C) temperature (52, 53).

Variety

Varietal differences in elongation ability have been reported by many researchers and plant breeders. Screening methods for elongation ability have been developed (66, 93, 94, 100, 132, 157, 166) and a uniform scoring system has been used by most researchers (157).

The visual scoring system rates total plant elongation. A plant can score good even without internode elongation. Scoring at deep water (100 cm) might not properly determine total internode elongation because height might be mostly leaf sheath and blade (157). Care should be taken in extrapolating the results for deep and very deep water (>100 cm).

Plant age

Most deep water rices must be at least 6 wk old before their internodes can elongate rapidly (3, 20, 33, 42, 47, 92, 110, 125, 134, 158, 160, 187). Therefore, farmers plant deep water rice as early as possible although plants may suffer or die from drought stress.

Several varieties that can elongate at 2 to 4 wk have been identified (94, 158). At 2 wk, some varieties had internode elongation ability but their culms were generally thin and likely to break in strong water currents or winds. Although ability to elongate at 2 wk may not help deep water culture, elongation ability after 4 wk may be a useful survival character.

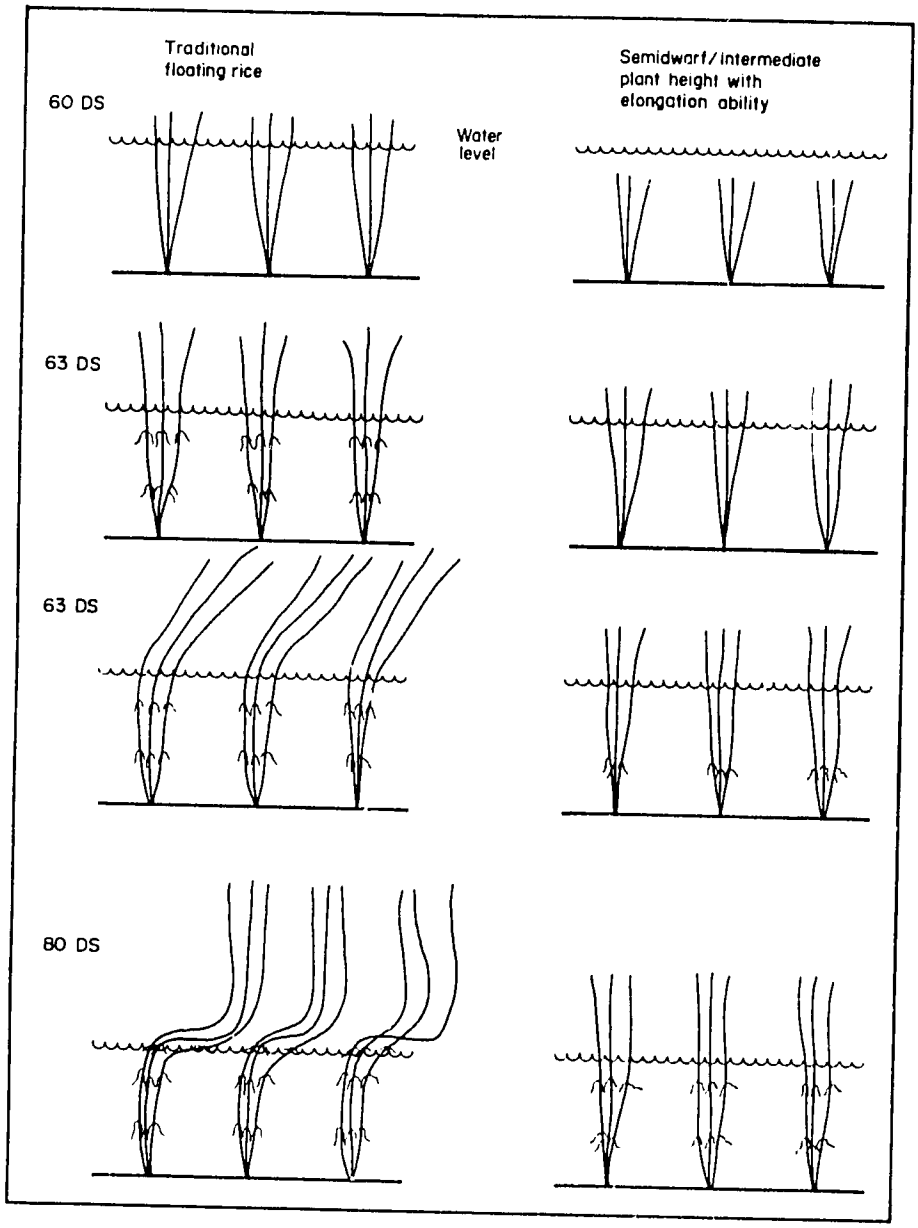
Elongation ability increases with age (20). Whether it is the result of more available carbohydrates or growth regulators or other factors is unknown. The need for 6 wk before elongation or the inability of the first 4-5 internodes to elongate may be the result of early embryonic internode differentiation, and may cause the loss of elongation capacity (47). Among deep water rices, the earliest elongated internodes were in Bangladesh varieties followed by Indian, Thai, Cambodian, Vietnamese, and Burmese (54).

Plant height

Taller plants survive early flooding better (49, 160), but seedling height is not correlated with elongation ability (130).

New varieties for the medium deep water areas have intermediate plant height and intermediate elongation ability. Adding N increases their plant height, which increases tiller survival at first flooding (73).

Although tall plants have a better chance for survival, they may lodge in shallow or no water and continue to elongate (Fig. 15) even if the leaves are already above the water. At flowering, the improved intermediate-height plants have less than 5 elongated internodes above the water level, while tall, traditional deep water rices have 5-8.



15. Internode elongation, rooting, and above-water growth of traditional and improved deep water rice varieties (151). DS = days after sowing.

Added height makes plants top-heavy and causes them to lodge or lean (101, 128). Limited growth after the water level has stabilized or receded is most important in flood-prone and medium deep water areas.

The possibility of developing an intermediate-height plant that will elongate and perform well at 200-300 cm water has been considered (65).

Nutrition

Stem elongation is affected by nutrient availability (69, 85, 86). Applying basal N significantly increased plant height at every growth stage, which was partly responsible for greater tiller survival of the plants after flooding (85, 86).

Because the accumulated carbohydrates in the plant are among the main sources of energy for rapid internode elongation, the total amount accumulated may limit elongation. Deep water rices differ in total carbohydrate content. Within a variety, the greater the carbohydrate content the greater the elongation, but the carbohydrate content does not correlate with total internode length or plant height when different varieties are compared (158).

Rate of increase and depth of water

Very slowly increasing water depth causes most varieties to elongate and survive (3, 93). Deep water rices, however, elongate rapidly when water depth suddenly increases. It can have an initial increase of 25 cm in 24 h (18). Some varieties elongate faster than others, which is useful when water level rises abruptly (20).

Internode elongation is determined by water level and flooding rate (27, 47). When the top leaves are above the water, internode elongation slows down (Fig. 14, Table 3).

Table 3. Length of internodes of the main culms of Leb Mue Nahng 111 and Kalar Harsall at harvest, after the plants were subjected to 85-cm water depth. IRRI, 1978 (128).

Internode number from top	Leb Mue Nahng 111			Kalar Harsall		
	Internode length (cm)		Cumulative length (cm)	Internode length (cm)		Cumulative length (cm)
1	20		146	19		135
2	14		126	15		116
3	10		112	11		101
4	8		102	8		90
5	7		94	7		82
6	6	Full	87	6	Full	75
7	6	water	81	6	water	69
8	8	level	75		level	
				8		63
9	10		67	9		55
10	15		57	13		46
11	17		42	18	Zero	33
12	16	Zero	25		water	
13	7	water		14	level	15
	7	level	9			
				1		1
14	2		2			

The traditional rices, however, have a tendency to have elongated internodes above the water (101, 128).

The rate of increasing water level can be determined by examining internode length. A decrease in internode length indicates decreased or stabilized water level (128).

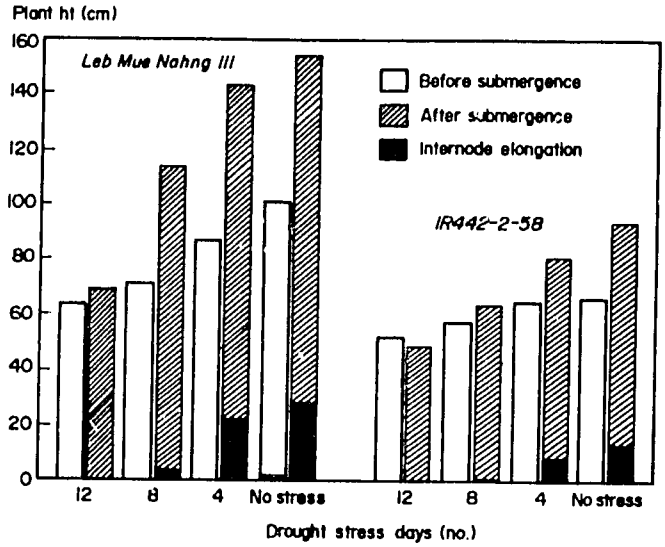
Drought

Deep water rice is generally broadcast on dry soil in the early monsoon season so that the plants will have sufficient time to grow before the rapid rise in water level. Because of irregular early monsoon rainfall, young plants often suffer and sometimes die from drought.

Drought stress reduces potential elongation ability (Fig. 16). Varieties subjected to 12 d of drought stress did not elongate and a 4-d stress reduced elongation ability. Reduced elongation ability greatly affects deep water rice survival and yield. It is important to prevent drought stress in deep water rice culture, either by cultural methods or by varietal improvement.

Varietal contribution to the effect of drought and elongation ability was difficult to ascertain because the intensity of moisture stress differs with a variety's capacity to tolerate drought. When the same amount of water was withheld, the reduction in total dry weight of Leb Mue Nahng 111 was more than that of IR442; however, Leb Mue Nahng's corresponding reduction in elongation ability was less than that of IR442 (156).

Varietal differences in elongation ability after moisture stress should be considered when selecting varieties for deep water areas where seeds are broadcast early in the monsoon and are often subjected to drought.



16. Effect of presubmergence drought stress on the plant height of Leb Mue Nahng 111 and IR442-2-58.

Plant type and elongation ability

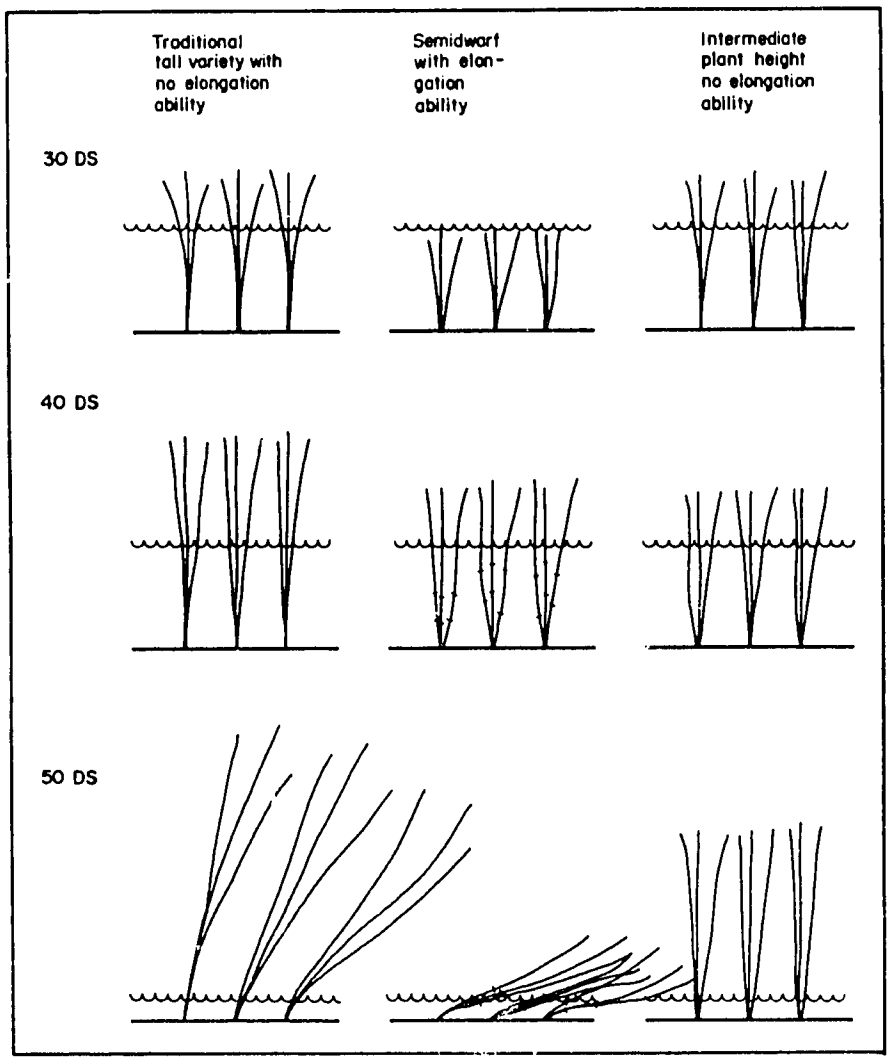
The question of plant type in terms of elongation ability is still being argued (151). The plant type that is needed, however, is gradually becoming clearer as rice scientists better understand local field problems. Deep water rice workshops cosponsored by IRRI have constantly focused on this subject (6, 58, 59) and many scientists agree that the need for elongation ability depends on local flooding pattern.

General characteristics such as positive N response, submergence tolerance, kneeing ability, stem borer resistance, and erect tillers are important. Specific requirements such as upper nodal tillering ability, photoperiod sensitivity, and drought, low temperature, and problem soils tolerance may be necessary for specific sites.

Part of the difficulty in developing an ideal deep water plant type is the diversity in flooding patterns. The desirability of elongation ability is a good example of varying needs in plant type. During the first international seminar on deep water rice in 1974 (6), most rice workers considered elongation ability an essential trait.

Where water depth exceeds 150 cm, it is generally agreed that internode elongation is necessary. However, where water is less than 100 cm deep, internode elongation may be unnecessary. Sometimes limited elongation is necessary, but it also may be detrimental. Plants should not elongate with sudden flooding because elongation produces weak culms that lodge when short-duration floodwaters recede. However, this is not the water pattern we are concerned about in this review.

A variety with intermediate plant height and no or limited elongation ability may be ideal when flooding does not exceed 100 cm and recedes fairly quickly (Fig. 17). The International Rice Deep Water Observational Nursery (IRDWON) is identifying such areas.



17. Effect of elongation ability and plant height on lodging of plants subjected to short periods of submergence. DS = days after sowing.

The possibility of developing a semidwarf or intermediate-height plant that will perform well at 150-300 cm water depths is being studied. Research in Thailand has not identified such a semidwarf variety. Perhaps the question to ask is not whether it is possible to develop a semidwarf but whether it is necessary to develop a semidwarf that can elongate up to 300 cm.

Where the water is generally deep and elongation is most likely to occur, lodging is inevitable and the semidwarf characters are not advantageous. Kneeing ability overcomes the lodging problem. However, the traditional deep water varieties tend to elongate more than a meter above the water level, which causes sequential lodging-kneeing-elongation-lodging (Fig. 17). If the semidwarf character is associated with shorter above-water plant height, then the semidwarf or intermediate-height characteristics are potentially beneficial even in 200-300 cm of water. In medium deep water conditions, the new Thai variety RD19 supports this hypothesis (84). It has a better above-water plant type -not too tall- and has more erect tillers and leaves than traditional varieties.

Where flooding is erratic, a tall, above-the-water plant type is most desirable, especially at panicle initiation stage, when rice is susceptible to submergence. Tallness helps deep water rices to tolerate sudden flooding and temporary fluctuations of water depth of about 50 cm (49). Varietal responses to different water depths vary, and there is a close relationship between varieties farmers plant and local maximum water depth (19). Small differences in water depths may make a big difference in the survival of a variety.

Research should compare above-water height in lines with similar growth duration. Isogenic lines with varying above-water height need to be developed and tested at various water depths to determine the advantages and disadvantages of shorter plant parts above the water level.

Submergence

Deep water rice may be submerged several times during its growth. In the first prolonged flooding of the field, water rises rapidly and plants are normally submerged for several days. Submergence tolerance is not correlated with elongation ability (130), although rapid elongation until the plants are above the water increases survival percentage.

When submerged, the base of the leaves and the adjoining stem rot first, followed by leaves, internodes, nodes,

and buds, in that order (92). Submergence at booting and heading stages can drastically reduce yield (78, 79). Flood tolerance at later growth stages also involves the capacity to withstand uprooting (3).

Submergence near harvest can result in seed germination and rotting of panicles, especially in warm water (78).

Elongation after panicle initiation

Internode elongation ability during early growth differs from elongation after panicle initiation. Only four internodes elongate after panicle initiation, regardless of the number of internodes. The length of internodes that elongate after panicle initiation is genotypically determined. They are almost unaffected by deep water (97).

After flowering, rice plant cannot elongate. Submergence, particularly of the panicle, drastically reduces yield.

ROOTS AND NUTRIENT UPTAKE

Root morphology

When rice seed germinates, the radicle usually comes out before the coleoptile, and the development of both organs depends on environmental conditions. On dry land, the radicle generally develops faster than the shoot, as it does with broadcast-seeded deep water rices. The shoot develops faster on a wet seedbed or when seed is broadcast in water. In deep water rice, the mesocotyl may grow 3-4 cm when the seeds germinate during submergence (47) or when seeded deep on dry land.

The radicle develops and functions for more than 20 d or until about the seventh-leaf stage, and may elongate 15 cm. During that time adventitious roots develop from the lower nodes and take over the function of the radicle. Each node develops 5-31 roots.

The diameter of the adventitious roots is 0.5-1.0 mm. They develop branches and subbranches and the diameter becomes successively smaller.

An important distinguishing characteristic of rice roots is the presence of large air spaces in the mature roots, that provide efficient air passage from root to shoot. The difference between air space development in deep water rices and normal wetland rices has not been examined carefully.

Young roots are usually whitish and turn from yellow to pale brown to dark brown as they mature. Water currents may uproot or break the culms near the base. Uprooting at early growth stage may not affect yield, but late uprooting lowers grain yields (2, 187).

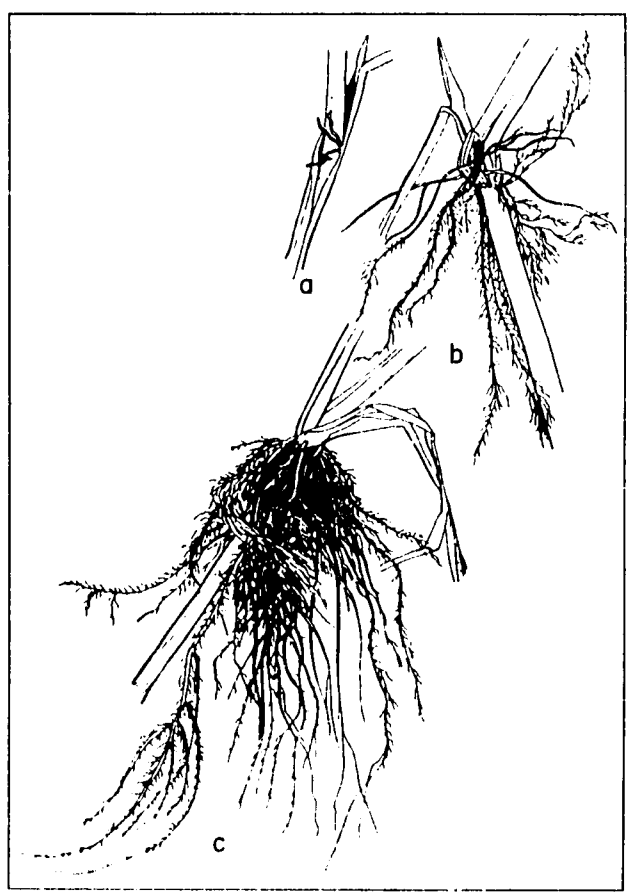
Root physiology of deep water rices differs with variety. Some varieties grow poorly in stagnant water but perform better in moving floodwater (91). When comparing plant nutrient uptake and content, the aerobic status of the water must be considered.

Nodal roots

At later growth, all deep water rice roots are nodal, because the primary root or radicle dies a few weeks after germination. The roots of elongated plants that grow on upper nodes are called upper nodal roots (58, 159). After elongation and when water level has stabilized, upper nodal roots develop (Fig. 18). Each node under water may develop a cluster of 10-20 roots measuring 10-15 cm long (3, 44, 183). A second flush of roots that are longer and unbranched may develop later at a lower level (3, 44). As water recedes, they settle on the mud.

Different varieties have different nodal rooting ability (8, 47, 76, 183). Traditional varieties tend to produce more nodal roots than improved rices. Higher nodal tillering ability does not necessarily correspond with higher nodal rooting. Some varieties had poor upper nodal tillering but high nodal rooting ability or vice versa. High N induced nodal rooting and increased nodal root production (74, 76).

Submerged stems of deep water rices produce clusters of nodal roots that grow freely in the floodwater. It has been assumed that nodal roots absorb nutrients from the floodwater, and deep water rice plants that are uprooted by strong currents and high winds live, obviously nourished by the nodal roots. Upper nodal root structure is like that



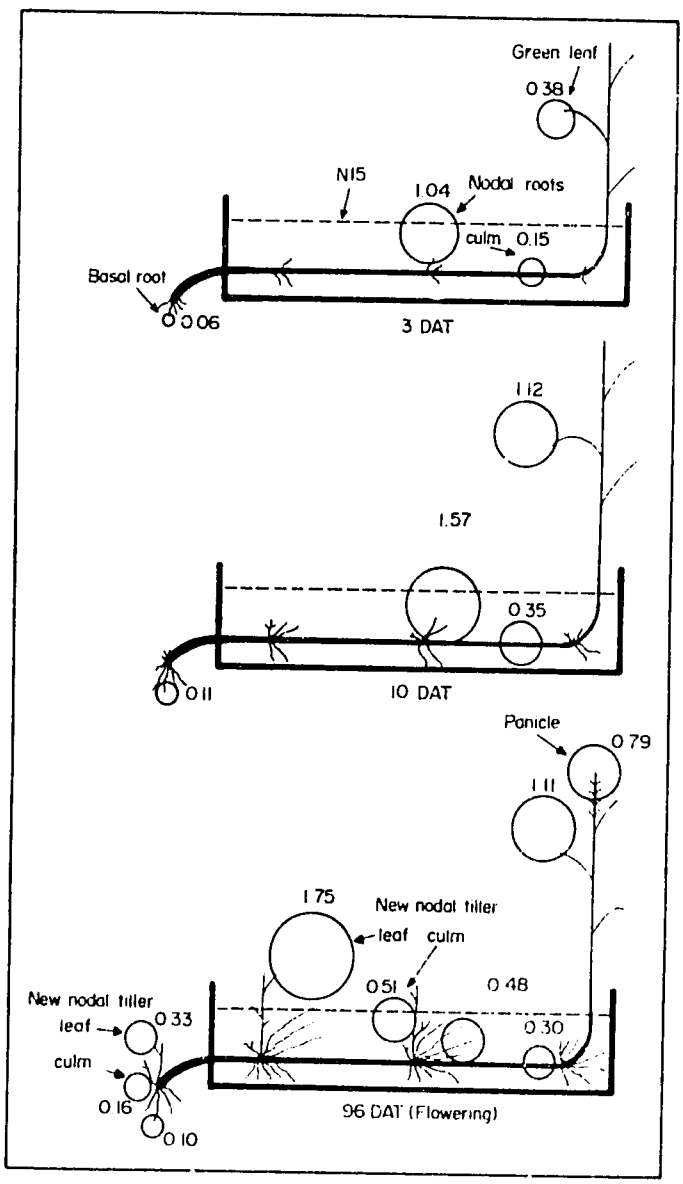
18. Nodal roots: a) nodal roots developing just below the water surface; b) well-developed nodal roots at a knee; c) fully developed nodal root system below the water; a nodal tiller has developed from this node (12).

of basal roots. Removing the nodal roots does not decrease absorption of Mn, Mg, P, Ca, K, and Fe, but does reduce absorption of Si (183).

The function of the nodal roots in N absorption was documented in ^{15}N experiments (76). Nodal roots absorbed a high proportion of ^{15}N from water, as compared with total N uptake. Absorption of ^{15}N was considerably less when most of the nodal roots were removed. N absorbed by nodal roots was distributed to the different plant parts. When N was applied before flowering, that absorbed through the nodal roots was the major component of grain N (Fig. 19).

Nutrient uptake

Studies in Bangladesh showed that silt deposited by the floodwaters has sufficient nutrient for early seedling growth (Table 4). The lower the topography, the higher the amount of silt and nutrients deposited. After nodal root formation, rice plants obtain nutrients directly from the floodwaters. Large amounts of nutrients are removed because plant biomass is large. Where floodwaters have high nutrient content, applying fertilizer may not improve growth or yield. Higher elevation areas farther from the river receive less silt and may require fertilization.



19. Schematic diagram showing comparative tagged N activity (percent) in different plant parts, 3, 10, and 96 (flowering) d after ^{15}N-labeled fertilizer was topdressed in the nodal root regions of Kalar Harsall in the greenhouse. Numbers above the circle indicate percent tagged N. DAT = days after treatment.

Nitrogen response

Experiments on grain yield response of deep water rice to N application had inconsistent results (3, 11, 16, 23, 51, 62, 121, 137, 168, 169, 170, 187). Many different factors affect N response.

Plant population

N application can partially compensate for low plant density caused by poor germination.

Weeds

Applying fertilizer without good weed management can reduce yields.

Soil moisture and characteristics

Low yield response to applied fertilizer may be the result of annual nutrient-rich silt deposits, which are estimated to provide 63 kg N/ha (46). However, low soil moisture during seedling stage inhibits soil and fertilizer nutrient uptake.

Hydrology

The water level, flooding rate, and time of flooding determine tiller survival, and their subsequent response to N. For improved deep water rices, fertilizer response was greatest at 150 cm water depth, and probably contributed to plant survival (87).

Nutrient content of floodwater

Later growth stages and yield are influenced by floodwater nutrient content and N uptake by nodal roots at later growth stages may constitute the greater part of the N in the grain (73).

Table 4. Plant nutrients available from silt. Data from M. A. Islam and H. Rahman (125).

Land class	Average peak water level	Silt deposits (kg/ha)	Plant nutrients (kg/ha) from silt deposits			
			N	P_2O_5	K_2O	CaO
Highland	122	857	9	3	13	6
Medium land	244	1743	20	5	26	11
Lowland	305	2832	32	8	41	19
Very lowland	306	4406	49	12	75	28

Nitrogen-responsive varieties

A recent survey in Bangladesh showed that 19% of the farmers are already using N fertilizer for deep water rice (19), which indicates the importance of developing fertilizer-responsive varieties.

Plant type may determine deep water rice response to fertilizer application, especially N. A 1979 experiment evaluated whether the new deep water rice would respond to N fertilizer better than traditional varieties (65). Recent evaluation of some improved deep water rices confirm that better plant type increases fertilizer response (11, 29, 83, 88, 136). However, very few fertilizer and variety trials have been in farmer fields, which would speed development of appropriate fertilizer-responsive varieties.

Different N fertilizer such as sulfur-coated urea, prilled urea, and urea supergranules have been tried, but results were inconsistent (11, 36, 62, 136). In deep water rices, getting a yield response that can stand statistical analysis is difficult. Fertilizer-induced yield increases usually are not statistically significant and thus are difficult to demonstrate in farmer fields.

In experiments that responded positively to basal N application, seed rate was high to give high initial plant density. More basal tillers formed per unit area, which produced taller plants before flooding. More tillers lived at maximum water level and had greater above-water leaf area index, which produced more dry matter, more panicles per unit area, and higher grain yield (86).

Topdressing

Topdressing N fertilizer in deep water is impractical but experimentally effective. Foliar spray is more practical but difficult if applied from a boat (62, 113).

Preliminary studies showed positive response to topdressing (Prayote Charoendham, pers. comm.) in field tanks where water is confined at later growth stages. Laboratory evidence indicates that topdressing increases yield by increasing upper nodal tiller production and panicle weight (Table 5). In many areas, bunds to hold the water at later growth stages, particularly at panicle initiation, would be worthwhile, and might increase the practicality of N topdressing.

Table 5. Effect of topdressing 40 ppm N, 2 wk after water level has reached 130 cm, on Kalar Harsall grown with low basal N application (75).

Character	0 N	40 ppm N (topdressed)
Plant height (cm)	280	325
Basal tillers	14	13
Nodal tillers	0	9
Total tillers	14	22
Nodal root weight (g)	3.5	11.5
Panicle weight (g)	9.6	16.8
Total dry weight (g)	76.9	146.3
Panicle no.	12	18

Plant type and nitrogen response

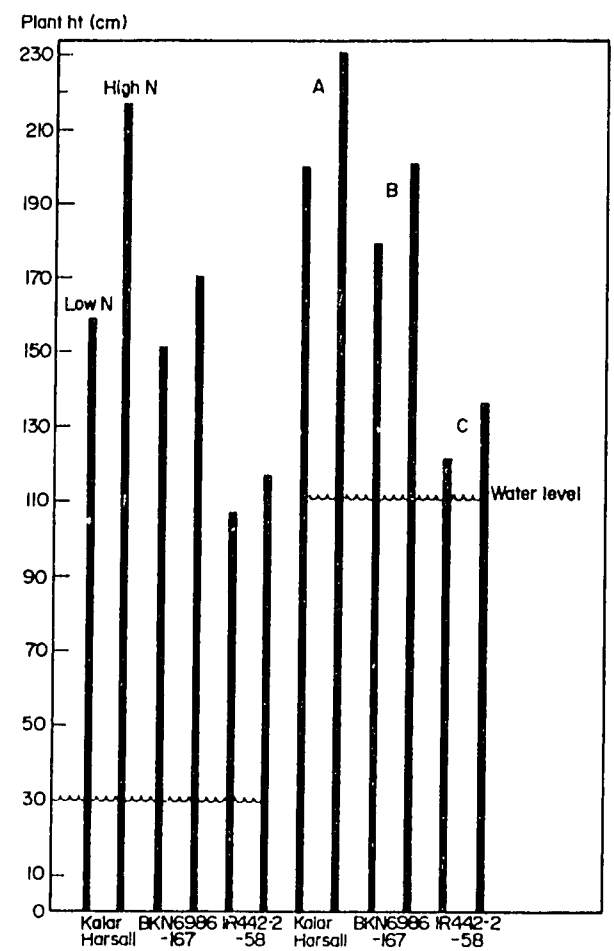
There are distinct varietal differences in the ability of deep water rices to absorb and use low and high basal N levels in medium and deep water (11, 62, 74, 121, 136, 143).

Traditional lowland varieties are tall and they lodge. Traditional deep water rices also are tall, regardless of water depth. Adding fertilizer increases lodging and dry matter production without increasing harvest index.

Plant height or length above the water can be used to classify deep water rice varieties' response to N application (74, 75).

Type A response to high N is characteristic of traditional deep water rices. Plants grew more than 100 cm above the water (Fig. 20). Type B response is exhibited by improved deep water rices. At flowering, their above-water height was optimum, about 80 cm. In type C response, typical of modern varieties with poor elongation ability, most plant parts were beneath the water.

Not all varieties have similar ability to absorb N in terms of production of basal and upper nodal tillers and nodal roots and elongation ability (74). Generally, varieties with high N uptake produce many basal tillers.



20. Variation in plant height at flowering at low and high N levels in medium deep (30 cm) and deep (110 cm) water. A = traditional tall (Kalar Harsall), B = improved (BKN6986-167), and C = modern intermediate tall (IR442-2-58) (75).

Basal tiller number in deep water rice culture may be increased by applying more N and selecting for varieties with high tillering and high N absorption and efficiency.

Phosphorus response

Although deep water rice soils are usually enriched by silt deposits (17, 46, 69, 121), farmers sometimes use soil amendments. In Prajinburi, Thailand, the acid sulfate soil is N and P deficient. Without P, plants cannot live in deep water, even with high N application (69). Applying P and nitrogen makes it possible to use unproductive land and increase rice yields on marginal land.

P content is low in the lateritic soils of West Bengal (135). Some Bangladesh soils responded to applied P, and responded more favorably to combined P and K (121).

Problem soils

Several soil deficiencies and toxicities occur in deep water areas. Salinity is a problem in parts of Bangladesh , India, Burma (116), Thailand, Vietnam (174), Indonesia (5, 105), 147), and Ecuador (68). Acidity or low pH and iron toxicities are common in large areas of Vietnam, Burma, India, and Thailand (116, 147). Peat soils affect deep water rice in Kalimantan, Indonesia (106).

Algae as nutrient source

Algae can provide significant nutrition to deep water rice. They contain 6-11% N and 0.8-4.2% P on a dry weight basis (90), which become available to deep water rice when the cells decompose.

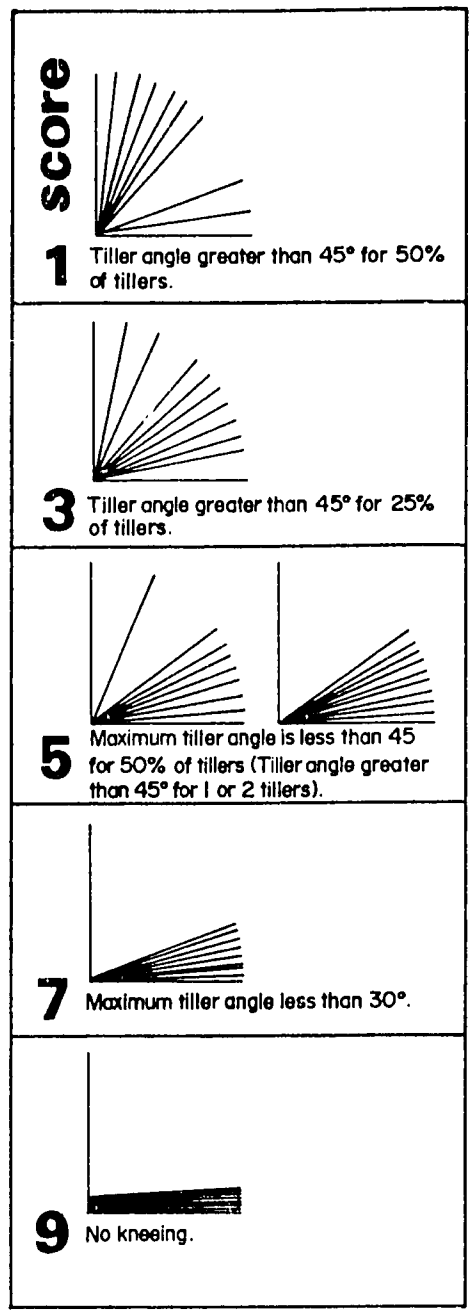
Nodal roots, leaf sheaths, and culms of deep water rices are colonized by epiphytic N-fixing blue-green algae. When deep water rice was exposed to $^{15}N_2$ gas and subsequently analyzed, researchers found that N was fixed. At maturity, about 40% of the fixed N was found in plant parts not directly exposed to $^{15}N_2$ (167).

Algae are important in deep water culture because they grow well where there are many plants available for epiphytism, a large volume of water for planktonic growth, long submersion, and limited mechanical disturbance of the field (90). Fortunately, deep water rices have long growth duration, which makes nutrients released by algal decomposition available to rice at later growth.

KNEEING

Deep water rice plants, especially traditional varieties, usually lodge after the internodes have elongated above the water level. Lodging causes plants to lie on the water at a 45° angle (Fig. 21). Deep water rices can knee - change direction of growth of the upper plant parts from horizontal to vertical.

When culms lie on the water surface and the upper leaves remain vertical above the water, the plants appear to float. Hence, deep water rices are commonly called floating rices.



21. Kneeing ability in deep water rice (162).

When the floodwaters recede, kneeing ability keeps the first three leaves above the water, which prevents leaf decay and provides better leaf arrangement (161, 162). Kneeing keeps panicles above the reach of fish.

A test and scoring system for kneeing ability has been devised (Fig. 21), and varietal differences have been observed (126). Regardless of water pattern, kneeing ability should be considered in deep water rices varietal development programs.

FLOWERING

Panicle morphology

Deep water rice panicles are similar to those of other rices

but are usually large. Deep water rices are considered panicle-weight type.

The panicle axis extends from the panicle base to the apex (Fig. 22). It has 8-10 nodes, from which the primary branches develop. Spikelets are formed from the nodes of the primary and secondary branches. The number of spikelets at maturity indicates the growing conditions at differentiation stage, when plants are most susceptible to the environment. Cloudy weather, rain, low temperature, or submergence during panicle development can increase spikelet degeneration.

Panicle initiation is about 35 d before heading. The panicle primordium can be seen with the unaided eye at the early differentiation stage (0.5 to 0.9 mm long). At 1.0 mm, the panicle has entered the spikelet differentiation stage. Meiosis occurs when the panicle is about 15 mm long, when the distance between the auricle of the flag leaf and the penultimate leaf is around −3 cm. Meiosis usually is complete when the auricle distance is +10 cm. During meiosis the rice plant is very sensitive to the environment, and submergence causes degenerated spikelets and high sterility.

Flowering, heading, and anthesis

Panicle exsertion – heading – is rapidly completed within 24 h. Anthesis – flowering – follows immediately. Because of this quick sequence, the terms flowering, heading, and anthesis often are interchanged – especially in discussions of growth duration, i.e., sowing to heading or flowering.

22. Panicles: a) advanced panicle emergence showing kneeing and terminal leaves; b) mature panicle (weight 2.8 g) (12).

As in other rices, anthesis in deep water rice usually starts in the top spikelets. It may take 7 d for all spikelets to open. In the field, heading date differs not only within a hill but also among plants. Modern photoperiod-insensitive varieties take about 14 d to complete heading. Most deep water rices complete heading within 10 d because panicle initiation occurs about the same time for all plants. This also is why deep water and other traditional photoperiod-sensitive varieties head more uniformly than modern photoperiod-insensitive varieties.

Most rice varieties have anthesis between 0800 and 1300 h. Anthesis is delayed by cool, cloudy weather. Submergence at anthesis can cause complete spikelet sterility. In some deep water areas, drought can occur at anthesis, when rice is most susceptible to stress. Temperature less than 21 °C also can cause sterility, and is a problem in northern Bangladesh.

Photoperiod response

Flowering is affected by day length. Most deep water rices are planted at the beginning of the monsoon season, when days are long (Fig. 3), and begin flowering in Oct to Dec when days are short.

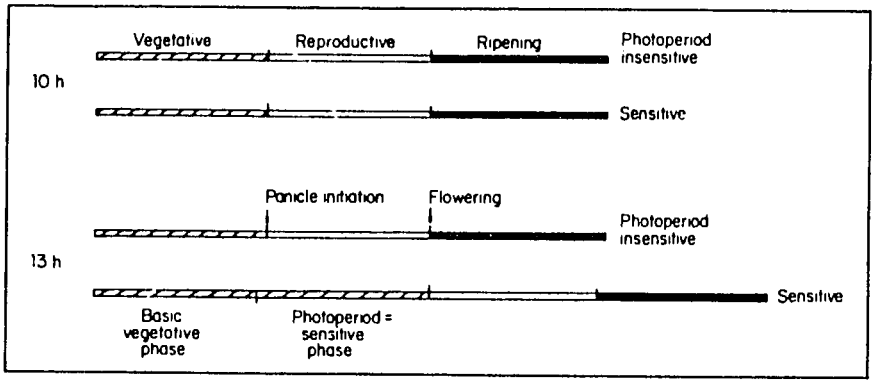
Deep water rice is grown from the equator to 38°N latitude. Day length changes with latitude. In Banjarmasin, Indonesia, which is near the equator (3° 20'S), flowering is affected by day length although there is only 23 min difference between the longest and shortest days (138).

Differences in day length pattern and the required flowering date needed in deep water rices result in a wide range of response to photoperiod.

Rice plant is generally a short-day plant; however, most modern varieties are photoperiod insensitive. Most traditional deep water rices are photoperiod sensitive (4, 17, 48, 89, 123, 131). Following is a review of the flowering response of rice to photoperiod (148, 149).

Rice plant growth usually is divided into three stages (Fig. 23): vegetative phase (germination to panicle initiation, reproductive phase (panicle initiation to flowering), and ripening phase (flowering to harvest). In deep water rice areas, the reproductive phase is about 35 d and ripening takes 30-35 d. Time necessary for both phases is relatively constant, although it may be prolonged by low temperatures. The duration of the vegetative growth phase varies greatly and is largely responsible for the growth duration of a variety.

Vegetative growth phase can be divided into the basic vegetative phase (BVP) and the photoperiod-sensitive phase (PSP). The BVP refers to the juvenile stage when the plant is not affected by photoperiod. Plants respond to the photoperiodic stimulus for flowering only after BVP. Table 6 shows the growth phases of photoperiod-sensitive and insensitive rice varieties planted in different day lengths.



23. Duration of growth phase in photoperiod-sensitive and photoperiod-insensitive varieties planted under 10 and 13 h photoperiod.

Basic vegetative phase

BVP is measured by subtracting 35 d from the growth duration (sowing to flowering) of plants grown at the optimum photoperiod or with the shortest growth duration. This assumes that the period from panicle initiation to flowering is about 35 d. BVP for deep water rices ranged from 5 to 43 d (Table 6).

Variety Habiganj DW 1 had panicle initiation at the age of 9 d in Kalimantan (48). In the greenhouse, its BVP was 6 d (149), one of the shortest recorded.

Photoperiod-sensitive phase

The length of the PSP indicates the rice plant's sensitivity to photoperiod. Generally, varieties with PSP longer than 30 d are considered photoperiod-sensitive and those with PSP less than 30 d are photoperiod-insensitive. Under continually long photoperiods, some varieties have remained vegetative for more than 12 yr (82).

PSP can be determined by subtracting the minimum growth duration from the maximum growth duration of a variety. Because many varieties remain vegetative for a long period if grown in long-day conditions, experiments are usually terminated after 200 d and their PSP is rated as 200+. Most of the deep water rices tested have PSP longer than 30 d (Table 6). Two varieties listed in Table 5 are photoperiod insensitive but are considered deep water rices. They mature early and usually are harvested before the main deep water rice crop.

The response of a rice cultivar to photoperiod may be measured by the length of the PSP, which in turn is determined by the critical and optimum photoperiods of the variety.

Optimum photoperiod

Optimum photoperiod is the day length at which the growth duration of a variety is at a minimum. Optimum photoperiod differs by variety but often is reported to be 9-10 h. Some varieties have longer optimum photoperiods. Most deep water rices tested have optimum photoperiods of about 10 h. A photoperiod longer or shorter than the

Table 6. Growth duration of some deep water rice varieties grown in different photoperiods. International Rice Research Institute, July 1975.

Variety	Country	Growth duration (d) at given photoperiod[a]					PSP (d)	BVP (d)
		10 h	12 h	12½ h	13 h	14 h		
ARC 5955	India	73	78	–	–	88	15	38
Baishbish	Bangladesh	54	120	F	73	–	200+	19
DM 53	Bangladesh	57	68	–	*	*	16	22
Gowai 84	Bangladesh	60	126	F	*	*	200+	25
Kalar Harsall	India	75	142	F	F	*	200+	40
Kekowa Bao	India	59	123	F	*	*	200+	24
Khao Med Lek	Thailand	58	131	F	F	*	200+	23
Laki 192	India	40	94	F	*	*	200+	5
Leb Mue Nahng 111	Thailand	60	126	*	*	*	200+	25
Habiganj DW 1	Bangladesh	41	92	F	F	*	200+	6
Habiganj DW 2	Bangladesh	44	111	F	F	*	200+	9
Habiganj DW 8	Bangladesh	78	135	–	–	*	200+	43
Nang Tay C	Vietnam	58	128	–	–	*	200+	23
Po Ngern	Thailand	61	148	*	*	*	200+	26
Sai Bur	Thailand	59	128	*	*	*	200+	24
Saran Kraham	Cambodia	52	123	*	*	*	200+	17
Tau Binh C	Vietnam	63	129	–	–	*	200+	28

[a] – = no data, F = flowering occurred, * = no flowering after 200 d growth.

optimum delays flowering. Such delay depends on the variety's sensitivity.

Critical photoperiod

Critical photoperiod is the longest photoperiod at which the plant will flower or the photoperiod beyond which the plant will not flower. The critical photoperiod of rice ranges from 12 to 14 h. Table 6 and the report on flowering of deep water rices (48) show that deep water rices have a critical photoperiod ranging from 12 to 14 h. Varieties originating near the equator, such as those from Thailand and Burma, have shorter critical photoperiods than those from higher latitudes such as in India and Bangladesh, where day length is longer during the growing period (Fig. 24). Varieties planted in Bangladesh and India have panicle initiation at longer day lengths than those from Thailand or Cambodia. Critical photoperiod is 13-14 h for Bangladesh varieties and 12-12.5 h for Thai varieties. Because of their longer critical photoperiod, Bangladesh varieties flowered earlier in both Thailand and Bangladesh.

Critical photoperiod values closely agree with field estimates (48). Estimated day lengths at panicle initiation for varieties from Bangladesh were longer than those from Thailand. Critical day lengths occur earlier in Thailand, making Bangladesh varieties flower earlier (Sep) than is needed. Sep flowering in Thailand is undesirable because the water may still be rising and might submerge the panicle. Differing critical photoperiod and flowering date requirements make it difficult to introduce deep water rice varieties from one latitude to another. Breeding for deep water rice for various areas is, therefore, doubly difficult.

The PSP of a variety is probably a measure of the combined effect of its optimum photoperiod and critical photoperiod. The shorter the critical photoperiod, the longer the PSP.

Photoinductive cycles

The minimum number of photoinductive cycles needed to initiate the panicle primordium varies by variety and photoperiod, and increases with photoperiod. In natural conditions, day length changes daily, therefore calculating the necessary number of photoinductive cycles is complicated. This is probably the reason for the seemingly different critical photoperiods obtained within a variety during a survey of deep water rices (48).

Specific flowering date

Next to elongation ability, the most important requirement of deep water rices is correct flowering date.

Most deep water rices are photoperiod sensitive and usually flower when the water level peaks or starts to recede. This adaptation is necessary for survival because plants cannot elongate after flowering.

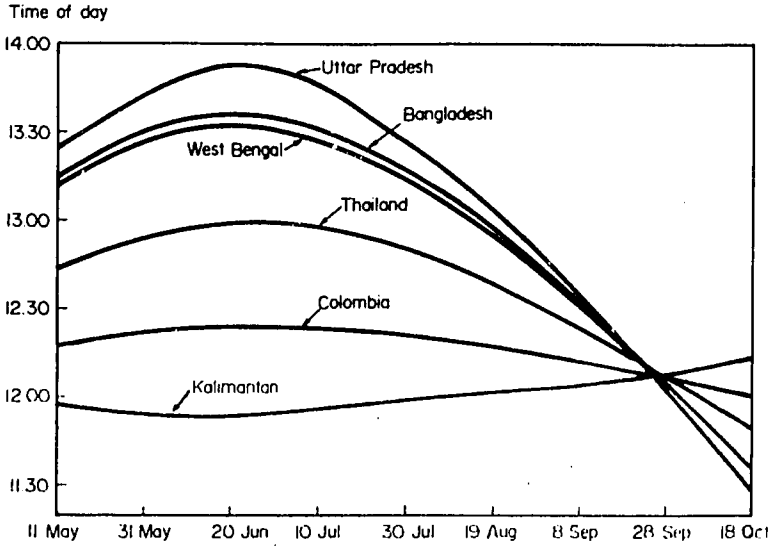
Photoperiodi ·ı is the mechanism that fits the flowering period of deep water rices into local flooding patterns. Because deep water rices need long growth durations (sown in Apr-Jun and harvested Nov-Jan), they must be photoperiod sensitive. There are no known varieties with long growth durations and are not photoperiod sensitive (149).

Deep water rices are planted at different sites and latitudes, and sown and harvested at different dates depending on water availability and floodwater recession. Therefore, a whole range of flowering response is needed even within sites at the same latitude. To avoid submergence or make harvesting easier within the same general area, plants on lower land are sown early but must flower later than the plants on higher land. Optimum flowering date is, therefore, location specific.

Although photoperiod sensitivity is essential where water exceeds 100 cm, the popularity of photoperiod-insensitive IR42, C4-63, and IR442 in medium deep water areas questions strict requirement of photoperiod sensitivity for all deep water areas (151).

Determining possible flowering date

Photoperiod-sensitive deep water rices have different



24. Changes in day length during the growing season in Bangladesh, India, Thailand, Colombia, and Indonesia (48).

critical photoperiods. One should be able to predict the flowering date of a variety if the critical photoperiod, latitude, and day length are known. Based on estimated critical photoperiod or day length at panicle initiation, a variety planted in different latitudes should flower 35 d after the critical day length. However, that is not always true. Many varieties have a wide range of critical photoperiod as shown in the collaborative deep water rice survey of flowering date (48). The above method of computation works if the photoperiod does not change daily and the rate of decrease is accounted for.

Kalar Harsall, an Indian variety, and several other varieties had greatly differing estimated critical photoperiod when planted at different locations (Table 7). The longer critical photoperiod in Colombia could be the result of more photoinductive cycles, which are needed if the day length is near the critical photoperiod but does not approach the optimum photoperiod.

The shorter photoperiod in Thailand for the same calendar date caused Kalar Harsall to reach near optimum photoperiod earlier and to flower earlier in Thailand than in India. Kalar Harsall is from India and flowered at the desired time. However, it flowers too early in Thailand, its critical photoperiod is longer and is reached earlier while the floodwaters are still rising. On the other hand, Leb Mue Nahng 111 is from Thailand and flowers at the right time there. In India, its short critical photoperiod delays flowering because the photoinductive day length for the variety occurs much later.

This aberrant effect of critical photoperiod makes the critical photoperiods in India and in other more northern latitude areas seem shorter because plants flower later.

In devising a testing method for deep water rices, it is probably not necessary to accurately measure flowering date because many factors such as cloudy days, water depth, internode elongation, and temperature affect it. What is needed is a simple method of differentiating, for further field testing, materials with good potential to succeed in or adapt to different deep water conditions.

Because deep water rices must be photoperiod sensitive, field selection should be at specific locations. Even areas at similar latitudes may require different flowering dates, depending on the time of water recession.

Table 7. Day length and date of panicle initiation (PI) of Kalar Harsall and Leb Mue Nahng 111 planted in four locations (48).

Variety	Colombia	Thailand	West Bengal India	Uttar Pradesh India
Kalar Harsall				
Day length at PI	1206	1203	1151	1137
Date of PI	26 Sep	28 Sep	5 Oct	12 Oct
Leb Mue Nahng 111				
Day length at PI	1209	1154	No flowering at end of experiment	1119
Date of PI	15 Sep	9 Oct		24 Oct

Flowering irregularity

When photoperiod-sensitive varieties are planted off-season, irregularities in flowering and morphology may occur (152, 153). Flowering irregularity may be due to insufficient photoinductive cycles, i.e., some tillers receive the right amount of photoinductive cycles needed but later tillers in the same hill do not. Hence, the late tillers do not flower or flower late.

Flowering irregularity between hills of an established deep water rice variety or line has been observed (48). Plantings of the International Rice Deep Water Observational Nursery at different sites also showed that varieties other than those originating in the planting site flowered irregularly.

A variety flowers uniformly in the day length pattern in which it was selected and purified. The same variety will or may flower irregularly if planted where there is a different day length pattern (see day length patterns for Thailand, Bangladesh, and Indonesia during the growing season, Fig. 24). Many varieties and lines that flower uniformly in Thailand flower irregularly in Indonesia and Bangladesh. This emphasizes the need for location-specific testing and selection of lines, especially for flowering date and uniformity.

Because day length controls flowering, the flowering date for a particular variety planted in the same location is similar each year. However, photoperiod-sensitive deep water rices may flower late if water depth is increased, because of competition between elongation process and panicle initiation and development.

Nonflowering in another site

Thai and Cambodian varieties often do not flower when planted in the more northern locations (48). Usually this is because the shorter critical photoperiod of the varieties is not met until late in the season, when temperatures are too low for panicle exsertion. Leb Mue Nahng 111, from Thailand, has one of the shortest critical photoperiods tested (Table 7). It flowered 13 Nov in Thailand and very late in Nov in Uttar Pradesh, but did not flower in West Bengal by late Nov. Even if the panicle was initiated at those late dates, low temperature usually prevented panicle exsertion.

On the other hand, varieties like Habiganj Al and ARC 5955 have long critical photoperiods (12:32 and 12:57 in Thailand) and in Kalimantan and Colombia, where day lengths are below the critical photoperiods, they will take a minimum time to flower. Growth duration of those varieties will vary little when planted any time of the year in Kalimantan, because the day lengths throughout the year are below the critical photoperiod or near the optimum photoperiod.

Progress in breeding photoperiod-sensitive rices for deep water areas has been slow because of the many additional characters needed for adaptation to particular sites. Those characters cannot be easily combined by conventional

crossing. A male-sterile-facilitated composite breeding scheme wherein a number of parents can be combined to develop a base population has been devised (15).

Rapid generation advance of breeding materials, especially photoperiod-sensitive crosses, is now possible. Rapid generation enables the evaluation of two or three generations instead of only one each year (150). This is possible by planting closely and subjecting the plants to high temperature and short days to induce early flowering. Flowering can be as early as 40 d versus 200 d in the field.

RIPENING AND YIELD

Ripening

The duration from flowering to maturity is 30-35 d in the tropics. In deep water rice, harvest time and flooding depths are closely related. Varieties harvested first have the lowest flooding depth or are planted at higher elevations. Sometimes, farmers use boats to harvest early-maturing deep water rices in 60-80 cm of standing water (45, 89).

At maturity, deep water rice plants may have one to four green leaves (47). Deep water rice has many more nonphotosynthetic plant parts than modern and other traditional rices, so harvest index is small. However, reasonable yields are obtained.

Near harvest, grain shattering is a problem (17, 91, 123, 144). The cut upper portion of the plant is usually transported to a dry place for threshing, making shattering a serious problem. Deep water rices tend to shatter more than nonfloating rices (56, 182). Shattering increases from 1 to 3 wk after heading, then remains constant (56).

Yield

Despite severe weather, which completely destroys other rices, deep water yields are consistent over time, although they often are lower than the yields of modern varieties. Yields vary from 0.4 to 4.5 t/ha (Table 8). New varieties must yield better than 4 t/ha before release.

Sampling for yield

At harvest, deep water rice usually lodges and the panicles of a plant may be several meters away from its roots making it difficult to identify single plants. Therefore, yield samples for deep water rice are taken from a quadrat or the panicles within a specified area are harvested. A minimum 16-m^2 harvest area is recommended (35). This method of sampling for yield works in farmer fields, but not in experimental plots where soil and other treatments may be included. In those plots it is important to know the origin of the panicle.

Cultural factors affecting grain yields

Many factors, from land preparation to harvest, affect grain yields. Some factors, such as different flooding patterns, cannot be controlled by farmers and will not be discussed here except to mention that grain yield is generally lower at higher water levels (11, 27). However, cultural factors also affect grain yields. Sometimes a combination of cultural improvements may be necessary to increase grain yield. For example, unless row seeding is accompanied by weed control it may not increase yield.

Table 8. Yield of deep water rice in different countries.

Country	Yield (t/ha)	Reference
Bangladesh	1.2 - 1.8	187
	1.0 - 4.3	19
India	2.0 - 2.5	110
Uttar Pradesh	0.4 - 0.5	135
Bihar	0.5 - 1.0	135
Orissa	0.4 - 0.8	135
West Bengal	1.0 - 1.2	135
Assam	0.8 - 1.0	135
Andhra Pradesh	0.8 - 1.0	135
Tamil Nadu	1.2 - 1.5	135
Kerala	1.2 - 1.5	135
Assam (India)	3.5 - 4.5	33
Thailand	1.3 - 2.1	117
Vietnam	1.0 - 2.0	173
West Africa	1.0 - 2.0	145

Seed rate

Seed rate (200-600 seeds/m^2) does not significantly affect grain yield (84). With improved plant type, panicle number per unit area tended to increase with increased seed rate, but higher seed rate tended to decrease panicle number in the leafy, droopy plants (86). Increased panicle number, however, had little effect on grain yield.

Seeding method

Row seeding tended to produce better grain yields than broadcasting but the differences were not statistically significant (86).

Spacing

In broadcast-seeded rice, increasing plant density by increasing seed rate does not affect grain yield. In transplanted deep water rice, increasing plant density by closer spacing significantly increased rice grain yield (86, 136). Increased grain yield was associated with more panicles per unit area. Close spacing did not affect spikelet number per panicle, percent fertility, or 1,000-grain weight (84). Long growth duration and availability of nutrients from floodwaters probably compensated for the nutrient competition at close spacing at early growth, therefore yielding a constant spikelet number with increase in panicle number.

Those results indicate that within-variety differences in deep water grain yield are determined mainly by panicles per unit area, and suggests that grain yield can be increased if panicle number is increased.

Seedlings per hill

In transplanted deep water rices, farmers plant several plants or tillers per hill, which significantly increases rice

yield, mainly because there are more panicles per unit area. However, yield increase from planting more seedlings per hill was more pronounced without added N or with low N application (86). Those findings reinforce the observation that grain yield can be increased by planting more seedlings per hill in deep water rice areas where fertilizer is normally not applied. A high tiller number before flooding ensures many panicles per unit area at harvest. If floodwaters are nutrient-rich, large panicles may develop and further increase grain yields.

Basal nitrogen application

Applying basal N significantly increased grain yield of improved deep water rices. Grain yield increase was associated with an increased tiller number and plant height, which produced a larger above-water crop canopy and increased plant survival, panicles per unit area, and grain yield (73, 85, 86).

Yield components

Panicle number

Stand density at late elongation stage significantly correlated with grain yield (14). However, at that stage many tillers do not contribute to panicle production (104). Basal tillers generally contribute more to grain yield than upper nodal tillers (27, 128), although upper nodal tillers have been reported to contribute as much as 88% of yield (143). This high proportion may have been because basal tillers were damaged, which resulted in the production of many upper nodal tillers.

Applying more basal N increased panicle number (73). In shallow water, there are 250-300 panicles/m^2, which yield 5-6 t/ha. In deep water, there are less than 250 panicles/m^2.

Panicle weight

As water depth increases, panicle weight and grain yield decline (104).

Fertility

Sterility increases with water depth (27, 143). Gradual reduction in grain yield as water level increases may be caused by submergence of more plant parts and decreased photosynthetic area. Individual tillers in shallow water usually have more than 80% fertility. In deep water, fertility varies from 50 to 85% (143).

Spikelets per panicle

Spikelet number increases with basal N application (73).

SUMMARY

Factors limiting deep water grain yields must be determined and research priorities established to increase grain yields through varietal improvement (151).

Surveys indicate that panicle number per unit land area in deep water rice is low compared with that of high yielding varieties in irrigated conditions. Increasing the seed rate did not increase panicle number per square meter in traditional deep water rices. New varieties seem to respond differently, but more field trials are needed.

If panicle number is the limiting factor, then high tillering ability and basal fertilizer application are necessary. Because deep water inhibits basal tillering, upper nodal tillering may be important in some flooding regimes. Growing low-tillering varieties at high seed rates may be another, and possibly a more effective, alternative in producing high panicle number. Data indicate that for medium deep water, basal fertilizer application increased tiller number and survival. Fertilizer application is necessary if grain yield is to increase, especially for the new high-tillering varieties. Before flooding, marked yellowing of leaves occur. The leaves turn green after flooding.

If panicle size limits yield, then the tiller number of the traditional deep water rices is sufficient and breeding should emphasize large panicles. Basal fertilization may not be necessary because panicle development occurs when sufficient floodwater nutrients are available. The plan to breed for large panicles or high panicle weights corresponds with present farmers' practice of not applying fertilizer. Long growth duration enables plants to accumulate large amounts of carbohydrates, which are used to elongate. If the reserve is not depleted by elongation, it may be available for grain filling. Panicle-weight-type plants with strong culms to hold the panicle should be developed and their yield response should be critically compared with that of the panicle-number type.

The new high-yielding varieties for irrigated areas are panicle-number types with short growth duration. For deep water areas where long growth duration is necessary, the panicle-number type may not be ideal.

Where floodwater nutrients are not sufficient, N application may be necessary at panicle initiation to increase panicle size. In those areas panicle-number type plants and basal fertilizer application may be more advantageous.

The primary tillers yield the heaviest panicles, followed by those from the secondary and tertiary tillers, late tillers, and upper nodal tillers. Although upper nodal tillers contribute to grain yield, their importance needs further evaluation. If a primary tiller produces an upper nodal tiller, it is possible that the total weight of the panicles from the primary tiller and upper nodal tiller is equal to, less, or slightly more than a large panicle from a primary, unbranched tiller. If this is the case, then low tillering or primary tillers should be emphasized. On the other hand, nodal tillers compensate for early damage to the plant and may be an important trait in the adaptability of deep water rices, although not necessarily for high grain yields. This aspect also needs to be studied to enable us to decide the plant type in terms of upper nodal tiller production (151).

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