Chapter

2.2

Rice Physiology

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INTRODUCTION

Physiology occurs in physical space through chemical reactions constrained by anatomy and morphology, yet guided by genetics. Physiology has been called the logic of life. Genes encode structural and functional proteins. These proteins are subsequently processed to produce enzymes that direct and govern the biochemical processes involved in the physiology of the plants. The enzymes do the work of the plant in a controlled, coordinated manner so that life can continue and development can proceed.

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The genes and gene order of the rice plant has very much in common with other plants, especially with other grass species (Devos and Gale, 2000). Consequently, literature that describes plant physiological processes in general and in detail are cited. *Some* processes are somewhat different for rice compared with *mast* other plant species, such as selective uptake and deposition of silica, because rice takes up more silica *than* do most crop plant species. We discuss nutritional disorders of rice, which manifest themselves differently in rice compared *with other* plant specks. We discuss the grain-filling process in detail because of its economic importance. Photosynthesis is treated very well in other places (Taiz and Zeiger, 1998), so our treatment of photosynthesis is **limited.**

Initiation of growth from the quiescent stage begins seedling development. During vegetative growth and development, a succession of leaves is formed with each leaf going through initiation, elongation, maturity, and senescence. The leaves are subtended by nodes, internodes, two rows of nodal roots, and in same cases, a tiller bud. After the last leaf on the culm initiates, the apical meristem initiates and begins to differentiate. This differentiation leads to development of the panicle, which successively forms branches, florets, and gametes. Subsequently, the panicle exerts, ovaries are fertilized, embryos and endosperm expand, and endosperm fills and dries down. Even after *drying down*, the seed continues to change and develop internally, which leads to significant changes in milling quality during storage (&maker et al., 1993). The relevant physiology is constrained within this space and time unity of plant development.

ROLE OF COORDINATED FUNCTION IN DEVELOPMENT

Plant development is mathematically regular and follows repeatable leaf and seed arrangement patterns (Jean, 1994). The repeatable arrangement is guided by the microtubules, which guide the production of ceil walls within and between individual cells (Taiz and Zeiger, 1998; Baskin, 2000) and lead to the eventual repeating patterns of leaf arrangement around the orthostichy.

PLANT DEVELOPMENT

Plant development is under tight genetic and physiological control. "The mode in *which one cell* forms *many;* and how these, dependent on the influence of the former, assume their proper figure and arrangement, is exactly the point upon which the whole knowledge of plants turns; and whosoever does not propose this question , , , or does not reply to it, can never connect a clear scientific idea with plants and their life" (Schleiden, 1842, quoted in Taiz and Zeiger, 1998).

Plant development is guided by genetic information that leads to the formation of proteins which function to guide cell wall development (Baskin, 2000). Consequently, the enzymes involved in laying down cell walls are guided to regularity in all normal plant tissues. Once these tissues have begun to senesce, the degradation of the cell components and ceil walls are likewise determined by orderly biochemical activities

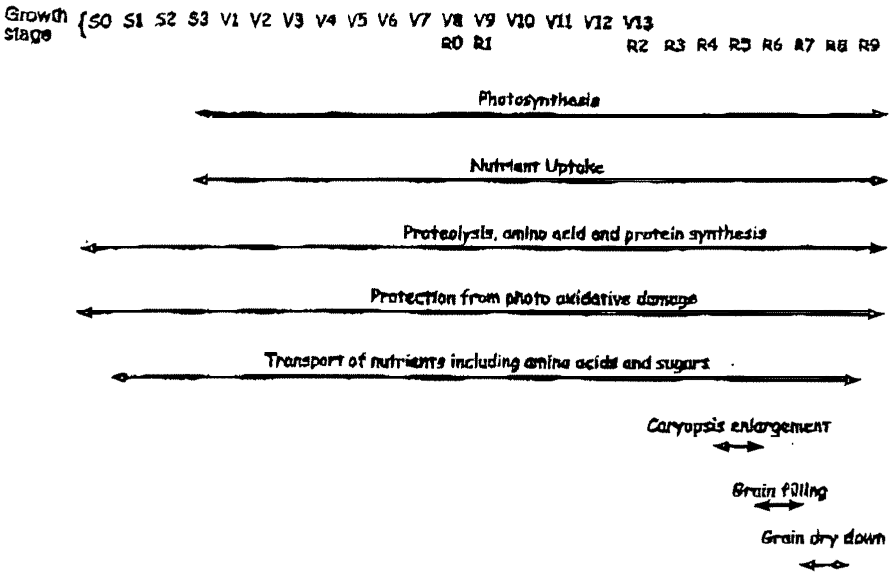


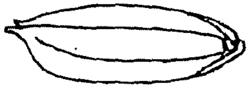
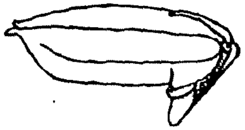
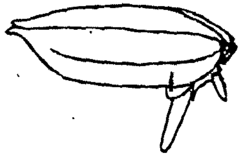
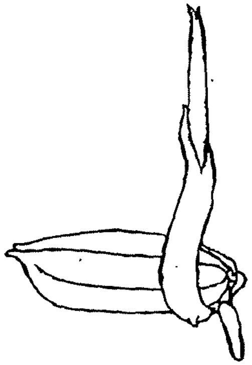
figure 29.1 Physiological processes throughout the stages of rice development.

regulated by the plant's genetics (Taiz and Zeiger, 1998). Several physiological processes are conducted at all stages of a plant's life, whereas others are needed only at certain times (Figure 2.2-I).

GERMINATION AND SEEDLING DEVELOPMENT

Plant growth begins at the quiescent state with the seed's embryo rending gibberellic acid to the aleurone layer where amylase proteins are transcribed- These proteins are transported to the starchy endosperm where the starch is mobilized to provide energy to the developing embryo. The amylase substrates are branched and unbranched starch molecules. The products are maltose and shorter-chained starch molecules.

Rice seeds imbibe water at adequate temperature in the presence of oxygen (Yoshida, 198 I). Counce et al. (2000) described four stages of rice seedling development (Figure 2.2.2). Chaudhary and Ghildyal (1969) and Alocilja and Ritchie (1991) indicate that (1) minimum temperatures for rice germination and development are between 6 and 8°C; (2) the optimum temperature for rice germination and development is 37°C; and (3) the maximum temperature for rice germination is 41°C and for development is 44°C. The majority of temperature studies on rice germination indicate the optimum to be 30 to 32°C (N. Takahashi, 1995c). In dry-seeded rice, the radicle normally appears first, whereas in water-seeded (submerged) rice, the radicle is suppressed and the coleoptile emerges first. This appeared to be related to the low-oxygen environment of water-seeded rice compared to more oxygen for the dry-seeded rice. N. Takahashi (1995a) suggests that emergence of the suppressed radicle is related to water in that formation of the radicle is sensitive to the degree

Growth Stage	S0	S1	S2	S3
Morphological Criteria	Dry, unimbibed seed	Emergence of coleoptile†	Emergence of radicle†	Emergence of prophyll from coleoptile ††
Illustration				

† The sequence of normally occurring seedling developmental events is presented above. There are exceptions to the sequence of events presented. In some cases the rice coleoptile emerges from the seed first and in other cases the radicle emerges first. When either emerges alone then the Growth Stage is S1. When both have emerged, the Growth Stage is S2. If the prophyll emerges from the coleoptile before the radicle emerges from the seed, then the Growth Stage is S3.

Figure 2.2.2. Seedling development. (from Counce et al., 2000.)

of hydration in the root zone. The greater the degree of hydration, the greater the suppression of the radicle (N. Takahashi, 1995a). In rice seeds germinated in aerated water, the coleoptiles emerge before the radicles (Counce et al., 2000). After growth stage S3 in a water-seeded culture, the flood is sometimes removed to allow the rice to *peg down* (to allow the seminal root system to penetrate the soil and anchor the plant).

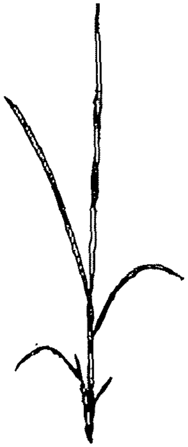
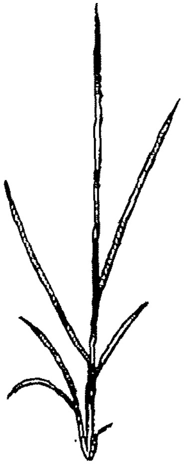
Rice goes into dormancy after harvest in some eases (Cohn and Hughes, 1981; N. Takahashi, 1995b). Domesticated rices frequently lack seed dormancy, whereas their wild *Oryza* relatives typically produce dormant seed. Red rice is a wild (0. *sativa* I,.) relative of domestic rice with a red testa (Juliano and Bechtel, 1985). Red rice and ocher wild *Oryza* species have extensive mechanisms for survival, including seed dormancy (N. Takahashi, 1995b; Vaughan et al.. 1999).

After growth sage S3, the first true (complete) leaf develops. Vegetative development for a rice cultivar with 13 leaves on the main stem are presented in Figure 2.2.3. (Cultivars differ in the total number of leaves produced on the main stem) Events occur in the following order for each node of a rice plant: (1) leaf initiation, (2) leaf elongation, (3) leaf blade maturation, (4) collar formation. (5) leaf sheath elongation. (6) node formation, and (7) internode elongation Internode elongation occurs only for the final five internodes of the rice main stem (Figure 22.4).

PHOTOSYNTHESIS

Photosynthesis is described well elsewhere (e.g., Taiz and Zeiger, 1998) and is critical to the life of rice (and other green plants). Photosynthesis is accomplished by the conversion of light energy into chemical energy to fix carbon from CO_2 into carbohydrates. AU the yield of a plant is a result of photosynthesis. The regulation of photosynthesis ova a plant's life affects the growth and yield of the rice plant (Ishii, 1995a,b). In particular. the integrated photosynthesis of the flag leaf over the grain-filling period is correlated directly with per culm yield (Ishii, 1995a; Yoshida, 1972). Photosynthesis is highly related to the presence and amount of sinks (such as filling rice grains) for carbohydrates (Evans. 1975). Area yield is determined by yield components (number of culms per unit area. number of spikelets per culm, filled spikelet percentage, and grain tight). The yield components are in turn determined by photosynthetic rate. The area yield is also related to the leaf area index (LAI; ratio of leaf area to land area), Usually, the yield-to-LAI relationship is positive (Murata and Matsushima, 1975; Counce, 1992). Tha relationship of LA3 varies greatly with the cultural system, plant type, and the growth stage at which LAI is measured (Murata and Matsushima, 1975). For example, prior to the availability *of* grass herbicides, the rice crop in the dry-seedbed, direct-seeded culture of the southern US. rice-growing area was composed of large, fast-growing rice plants that could compete successfully *with* grass weeds. *in such* a system, nitrogen fertilization was delayed until internode elongation (growth stage R1), to avoid lodging. Consequently, the timing of the midseason nitrogen application in the southern United States was crucial. Elimination of grass weeds by herbicide use allowed development of shorter rice cultivars with more erect leaves, higher LAI, higher harvest indices, and higher yields.

In transplanted culture, where cultivation reduces the impact *of* weeds and the plants grow smaller and more compact, earlier nitrogen fertilization of rice can be

Growth Stage	V1	v2	V3	V4	V5
Morphological Marker	Collar formation on first complete leaf (Leaf 1) on main stem	Collar formation on Leaf 2 on main stem	Collar formation on Leaf 3 on main stem	Collar formation on Leaf 4 on main stem	Collar formation on eaf 5 on main stem
Illustration					

† The number of vegetative growth stages varies with the number of true leaves on the main stem.

‡ V_F denotes flag leaf and it follows that V_{F-n} denotes the n^{th} node before the flag leaf.

Figure 2.2.3. Vegetative development. (From Counce et al., 2000.)

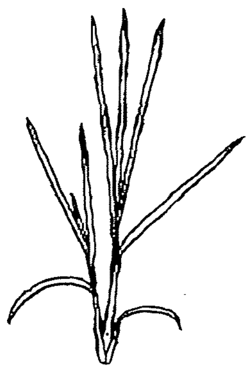
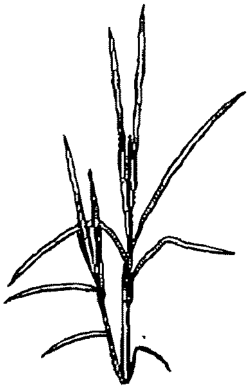
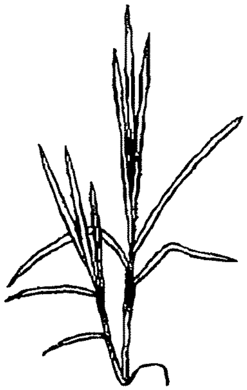
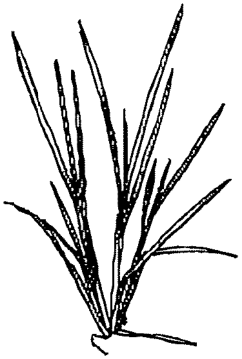
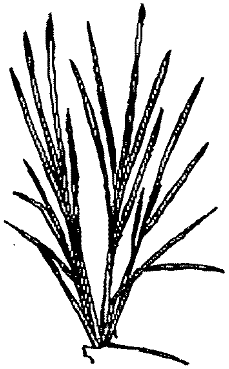
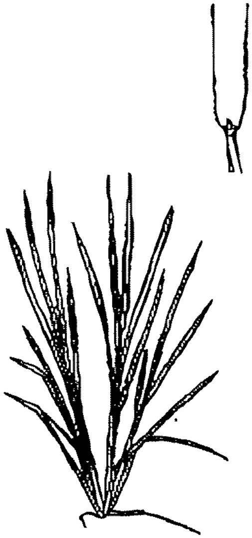
Growth Stage		V7	V8	$V9\ (V_{n-1})^{1}$
Morphological Marker	Collar formation on Leaf 6 on main stem	Collar formation on Leaf 7 on main stem	Collar formation on Leaf 8 on main stem	Collar formation on Leaf 9 on main stem
Illustration				

Figure 2.2.3. *(Continued)*

Growth Stage	V10 (V_{F-3})‡	V11 (V_{F-2})‡	V12 (V_{F-1})‡	V13 (V_F)‡
Morphological Marker	Collar formation on Leaf 10 on main stem	Collar formation on Leaf 11 on main stem	Collar formation on Leaf 12 on main stem	Collar formation on Leaf 13 (flag leaf) on main stem
Illustration				

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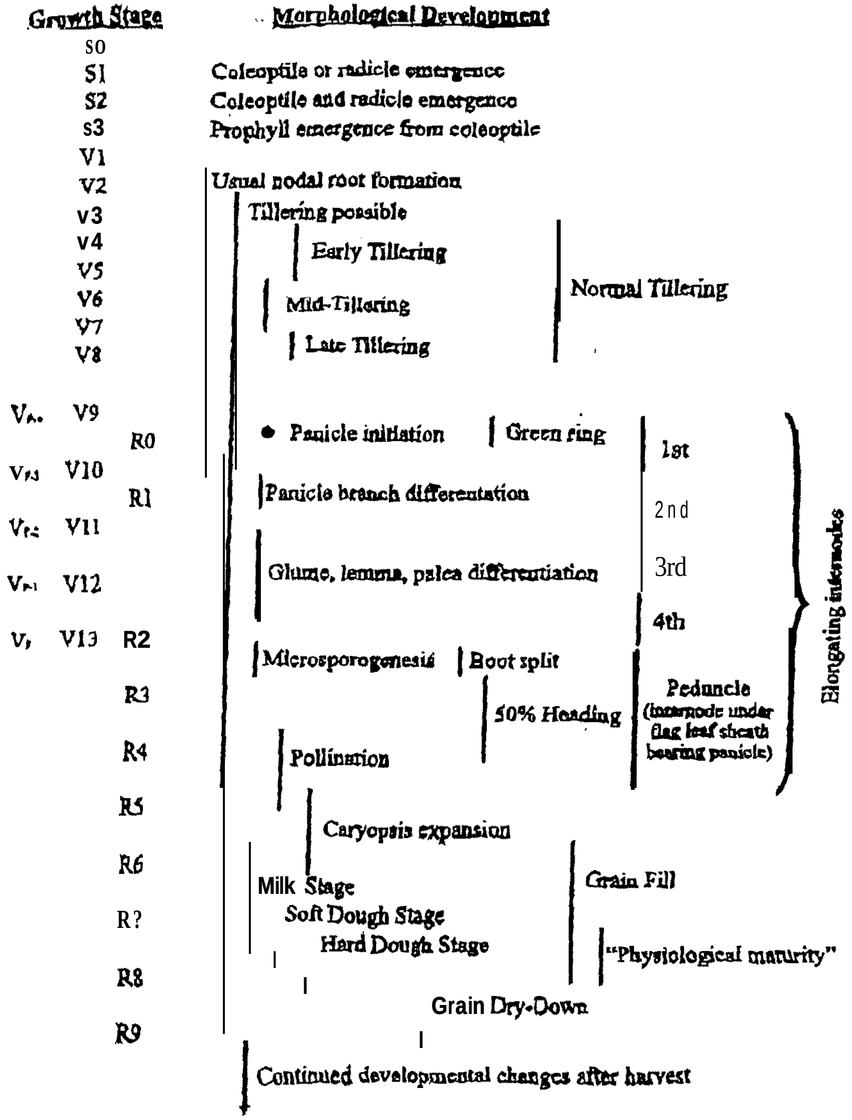


Figure 2.2.4. Rice developmental timeline. (From Counce et al., 2000.)

done and can increase yields substantially. With the development of effective herbicides. rice cultivars with reduced mature height have been selected that can yield well in response to nitrogen, without lodging, which would reduce effective crop yield.

Tillering in rice, as in other grasses, proceeds positively when plant nitrogen contents are at or above 3.5%, and solar irradiance (light) is sufficient to stimulate tiller development (Murata and Matsushima, 1975). Phosphorus levels below 0.25% in the main stem of the plant reduces tillering. Optimum water temperatures for tiller emergence are 16°C at night and 31°C during the day. Water temperatures above or b&w 3 1°C therefore limit tiller emergence. Tillering proceeds as long as light reaches the base of the rice plant, beginning at V3 or V4. and normally ending around V8 far direct, dry-seeded rice. Tillering is enhanced by thin stands (low plant populations per unit area). Isolated plants can easily produce 30 to 40 tillers, which reach growth stage R4 within 3 days of the main stem (Counce et al., 1996). Tillering in rice accounts for large amounts of the rice crop's yield. Some tillers almost always die prior to producing grain. The result of dead, nonproductive tillers may be inconsequential in some cases, but in other cases the yield potential may be decreased, due to tiller death and co reduction in tillers that produce grain. Many of the nutrients of dying tillers are translocated to the rest of the plant (Murata and Matsushima, 1975).

Until internode elongation begins, rice appears to store starch mainly in leaf sheaths. The nodal roots, and even seminal roots, typically live until the grain is mature. Consequently, the roots could potentially store starch. However, it appears that the roots do not store much carbohydrate for growing tie rice crop, although roots do contain starch. Leaf sheaths have the potential for storing either starch or sucrose, and they do store tither or both at various rimes in leaf development, especially as the leaves grow longer and leaf sheaths are not penetrated by the nodal roots on the top five elongating internodes. These top internodes rarely form any nodal roots, except for very short roots, which even more rarely penetrate their covering leaf sheaths. It is well known that leaf sheaths and culms store considerable amounts of carbohydrates, which can potentially increase rice yields (Stansell, 1975; Yoshida, 1981; Dat and Peterson. 1983a,b). Turner and Jund (1993) found that much of the rattoon rice crop yield was attributable to starch stored in leaf sheaths and culms of the first crop. Consequently, there arc several reasons to think that starch stored in the leaf sheaths and culms is a potential source of higher rice yields. Even with large amounts of the rice leaves removed, rice yields can be quite high as a result of stored carbohydrates (Counce, unpublished data; Counce et al., 1994a,b).

AERENCHYMA

Within 24 hours after soil is flooded, the oxygen supply of the soil is depleted by aerobic bacteria seeking oxidants (Ponnamperuma, 1972). Consequently, 2 rice plant is growing in hypoxic (low-oxygen) soil conditions by 1 day after flooding. In carefully excavated rice plants, all roots will be present, including the seminal roots, and all will be functional. The roots require oxygen to stay alive and to function. In most mineral soils that are flooded, the roots will be coated with ferrous Iron. This iron appears to be associated with siderophores. The conversion of ferric iron to ferrous iron requires oxygen. The leaves die within 3 to 6 phyllochrons of their elongation. Consequently the leaves cannot provide the conduit for oxygen. The nodes and internodes, however, persist. These nodes and internodes provide the conduit for oxygen from above the floodwater into the roots. The tissue capable of conducting the oxygen is aerenchyma which is formed by an orderly killing of certain tissues within the plant to produce large intercellular spaces (Dangl et al., 2000). This orderly death of the tissues in organisms is called programmed cell death and occurs in response to a number of stimuli (Dangl et al., 2000). After a period of flooding aerenchyma form and conduct oxygen to the rice roots (Raskin and Kende, 1985; Sharma et al., 1994). Thus, the conduit for oxygen in flooded rice is the continuous line of nodes and internodes containing aerenchyma.

REPRODUCTIVE DEVELOPMENT

Rice reproductive developmental stages have been distinguished by objective morphological developmental criteria by Counce et al. (2000) (Figure 2.2.5). The initiating panicle (growth stage R0) begins with a single cell. Subsequently, panicle branches form at growth stage R1, and at this stage of growth the number of potential grains per panicle are beginning to be determined (Yoshida, 1981). Actual grain number per panicle is readjusted continually until the R5 or even R6 growth stages. After reaching growth stage R6, grains normally fill and complete their development.

GRAIN DEVELOPMENT

The development of the grain proceeds over a relatively long period of the plant's development. At anthesis, the pollen tube germinates and elongates to connect to the ovaries to insert one male gamete into the egg nucleus and one into the polar nuclei (Hoshikawa, 1989). The growth of the pollen grain requires energy provided by the action of acid invertase in the elongating pollen tube. Upon fertilization, the embryo and endosperm must be provided with nutrients, the primary one being sucrose. Sucrose is broken down in rapidly expanding tissue in various parts of the plant through acid invertase located in the vacuole. The caryopsis elongates, because of cell wall expansion, to the maximum space of the lemma and palea (the "hull" for rice). Subsequently, the cells in the endosperm fill primarily with starch. Cells in the aleurone layer are filled primarily with oil and protein. Cells in the subaleurone layer have starch, oil, and protein. Cells in the starchy endosperm contain starch and a small amount (6 to 7%) of protein (Juliano and Bechtel, 1985). The genes of the cereals are, in general, very similar and are in the same order (Bennetzen, 2000; Devos and Gale, 2000; Freeling, 2001). It clearly follows that the cereals share many of the same enzymes, particularly enzymes related to the grain-filling process. We have learned a considerable amount of information about the biochemistry/enzymology of the grain-filling process from cereals, particularly maize and wheat. The process of producing starch from imported sucrose is well documented and applicable to rice.

PATH OF THE CARBON IN THE ENDOSPERM

The primary transport carbohydrate in rice and other vascular plants is sucrose (Avigad and Dey, 1996; Taiz and Zeiger, 1998). Beginning at fertilization of the egg nuclei and polar nuclei, the caryopsis begins to form (growth stage R4) and elongates (growth stage R5) to the length of the lemma and palea (growth stage R6). Sucrose is imported during this time period (growth stage R5), and the primary sucrolytic enzyme powering this cell elongation is acid invertase:

$$\text{sucrose} \rightarrow \text{glucose} + \text{fructose} \qquad (1)$$

After the caryopsis has elongated, the grain-filling process begins, since at the end of cell elongation there is no starch deposition in the cells. There are two cellular compartments where most of the synthesis biochemistry for the grain-filling process takes place: the cytosol and the plastid (Figure 2.2.6).

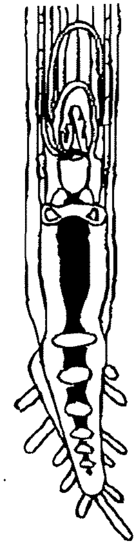
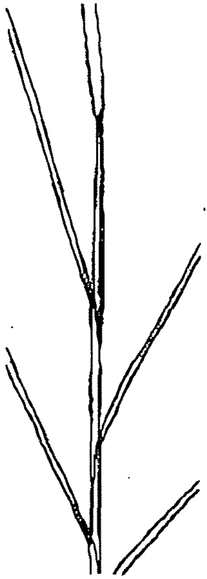
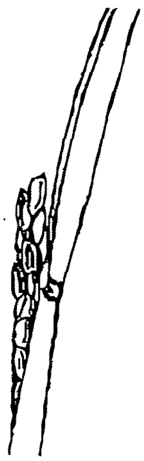
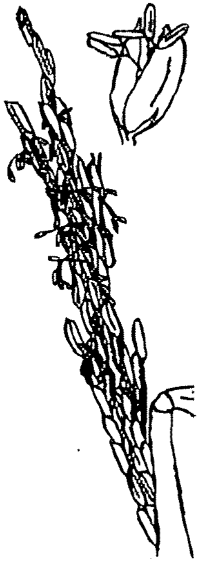
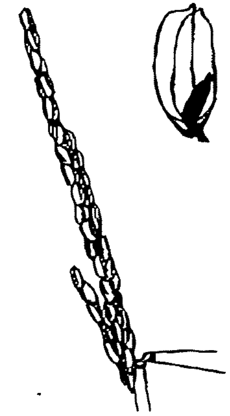
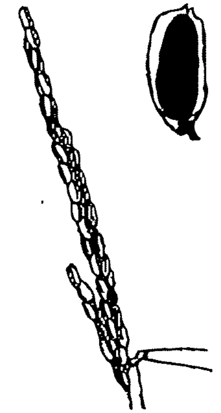
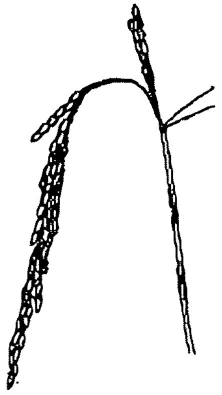
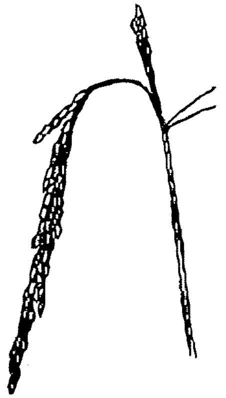
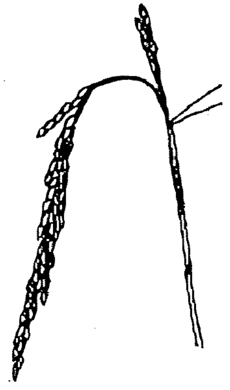
Growth Stage	R0	R1	R2	R3	R4
Morphological Marker	Panicle development has initiated	Panicle branches have formed	Flag leaf collar formation	Panicle exertion from boot, tip of panicle is above collar of flag leaf	One or more florets on the main stem panicle has reached anthesis
Illustration					

Figure 2.2.5. Reproductive growth stages. (From Counce et al., 2000.)

Growth Stage	R5	R6	R7	R8	R9
Morphological Marker	At least one caryopsis on the main stem panicle is elongating to the end of the hull	At least one caryopsis on the main stem panicle has elongated to the end of the hull	At least one grain on the main stem panicle has a yellow hull[†]	At least one grain on the main stem panicle has a brown hull[‡]	All grains which reached R6 have brown hulls
Illustration					

[†] Other authors have chosen to use terms physiological maturity or cessation of dry matter accumulation. We avoid these terms because, for rice such determinations are difficult or impossible to make with any known morphological marker.

[‡] The brown hull indicates the grain has begun to dry.

Figure 2.1.5. *(Continued)*

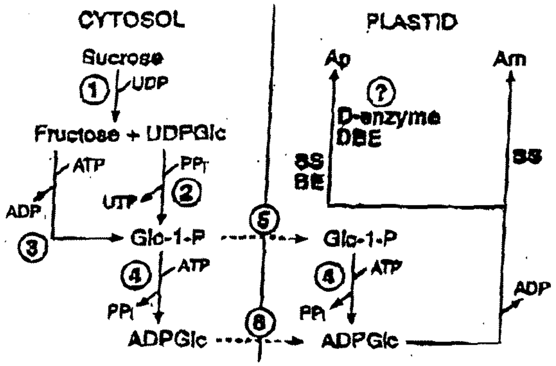


Figure 2.2.6. General pathway of starch biosynthesis. (from Myers et al., 2000.)

In the cytosol the direct route of carbon is from imported sucrose. During grain filling (growth stage R6), sucrose synthase breaks down sucrose, but the action of sucrose synthase is reversible:

$$\text{sucrose} \rightleftharpoons \text{UDP-glucose} + \text{fructose} \qquad (2)$$

During grain filling the primary sucrolytic enzyme *in rice endosperm* is one or more of the isoforms of sucrose synthase (Avigad and Dey, 1996). Two forms of *sucrose synthase have been found in corn endosperm: Sus1 and* Sh1. A lesion in the Sh1 isoform leads to the shrunken 1 mutant of maize. Its sweet flavor comes from the lesion of sucrose synthase, which leads to an inadequate breakdown of sucrose for subsequent production of starch. Huang et al. (1996) have identified three sucrose synthase isogenes for rice. These gents code for different forms of the enzyme, which are active in different tissues and stages of development.

Next, the glucose moiety. UDP-glucose (2), is converted to glucose-1-phosphate by the action of UDP-glucose pyrophosphorylase:

$$\text{UDP-glucose} + \text{PPi} \rightleftharpoons \text{glucose-1-phosphate} + \text{UTP} \qquad (3)$$

(Fructose can also be converted to glucose phosphates and subsequently into starch vie the actions of several enzymes.) Step (3) must be faster than step (2). This is a requirement for grain filling. Without this step preventing buildup of UDP-glucose, breakdown of sucrose by sucrose synthase would be followed immediately by its resynthesis (Avigad and Dey, 1996).

The G-1-P is then either transported into the plastid or converted to G-6-P via the action of phosphoglucose isomerase. At this point, the first step necessary for starch synthesis begins in either the amyloplast or the cytosol with the action of ADP-glucose pyrophosphorylase (AGP):

$$\text{G-I-P} + \text{ATP} \rightarrow \text{ADP-glucose} + \text{PPi} \qquad (4)$$

Just as cytoplasmic production of glucose phosphates is probably limited by sucrose synthase, starch production is probably limited in the plastid by AGP. In maize, and perhaps in rice, AGP *is* located in the cytosol (Shannon et al., 1998). ADP-glucose is thc starting point for starch synthesis. Subsequent starch synthesis reactions take place in the plastid. After initiation of the starch molecule, subsequent single glucosyl units additions to either branched or straight chains are accomplished by starch synthase:

starch chain + ADP-glucose → starch chain + glucosyl unit -t ADP (5)

Branching of starch chains is accomplished by the starch branching enzyme (SBE; *Figure* 2.2.7). During starch synthesis, branching, debranching and resizing of the starch molecule are necessary in what is a continual shaping, assembly, disassembly, and reassembly in the developing endosperm by the actions of starch synthase, starch branching enzyme, D-enzyme, and starch debranching enzyme {Smith et al., 1997; Taylor, 1998; Myers et al., 2000). These activities result in a highly structured granule with starch packed in alternating zones of more branched and less branched amylopectin (Taylor. 1998; Myers et al., 2000). The starch structure in rice and other grains in quite highly repeating, although it is subject to changes due apparently to the environment, particularly the temperature. Rice Starch granules am smaller than starch granules of other cereals. Soluble starch synthase is more sensitive to high temperatures than most other plant enzymes (Keeling et al., 1994). High temperatures during grain filling also lead to chalkiness in *rice* grains (Yoshida and Hara, 1977; Fitzgerald, personal communication). This chalkiness is potentially the result of seduced activity of starch synthase or SBE. The starch synthase enzyme also has a requirement for potassium for optimal activity of the enzyme (Marschner, 1995).

The first element of the process is the production of individual starch molecules. The second component of the process of rice grain filling is the combining of these starch molecules into granules (Smith et al., 1997; Myers et al., 2000). The granules are formations of alternating layers of crystalline and amorphous lamellas (Figure 2.2.8)

For rice in Arkansas, Downey and Wells (1975) found a positive correlation between rough rice yields end the number of hours below 21°C (70° F) during the period between 40 end 110 days after emergence. We found that a 6°C (from 18°C to 24°C) increase in temperatures between midnight and 5 A.M. resulted in a 5 to 7% reduction in head rice yields (P. A Counce, unpublished data).

RESPONSES, SIGNALS, HORMONES, ANO PROTEIN MODIFICATIONS

Although plants cannot think, they do process information. The discovery of several compounds called *hormones was* an early manifestation that plants can process information. Plants are exposed continuously to a number of external signals to which they respond. Some of those responses are internal and lead to the synthesis of hormones. There are at least nine classes of hormones: auxins, abscisic arid, brassinosteroids, cytokinins, ethylene, gibberellins, jasmonic acid, polypeptide hormones, and salicylic acid (Crozier et al., 2000; Ryan and Pearce, 2001). The hormones often have pronounced effects on plant growth and development when applied at relatively high concentrations: application of gibberellins causes internodes to elongate, application of cytokinins may Cause plants to green up, and application of abscisic acid may cause seeds to stop the germination process. Within the plant, however, the amounts of

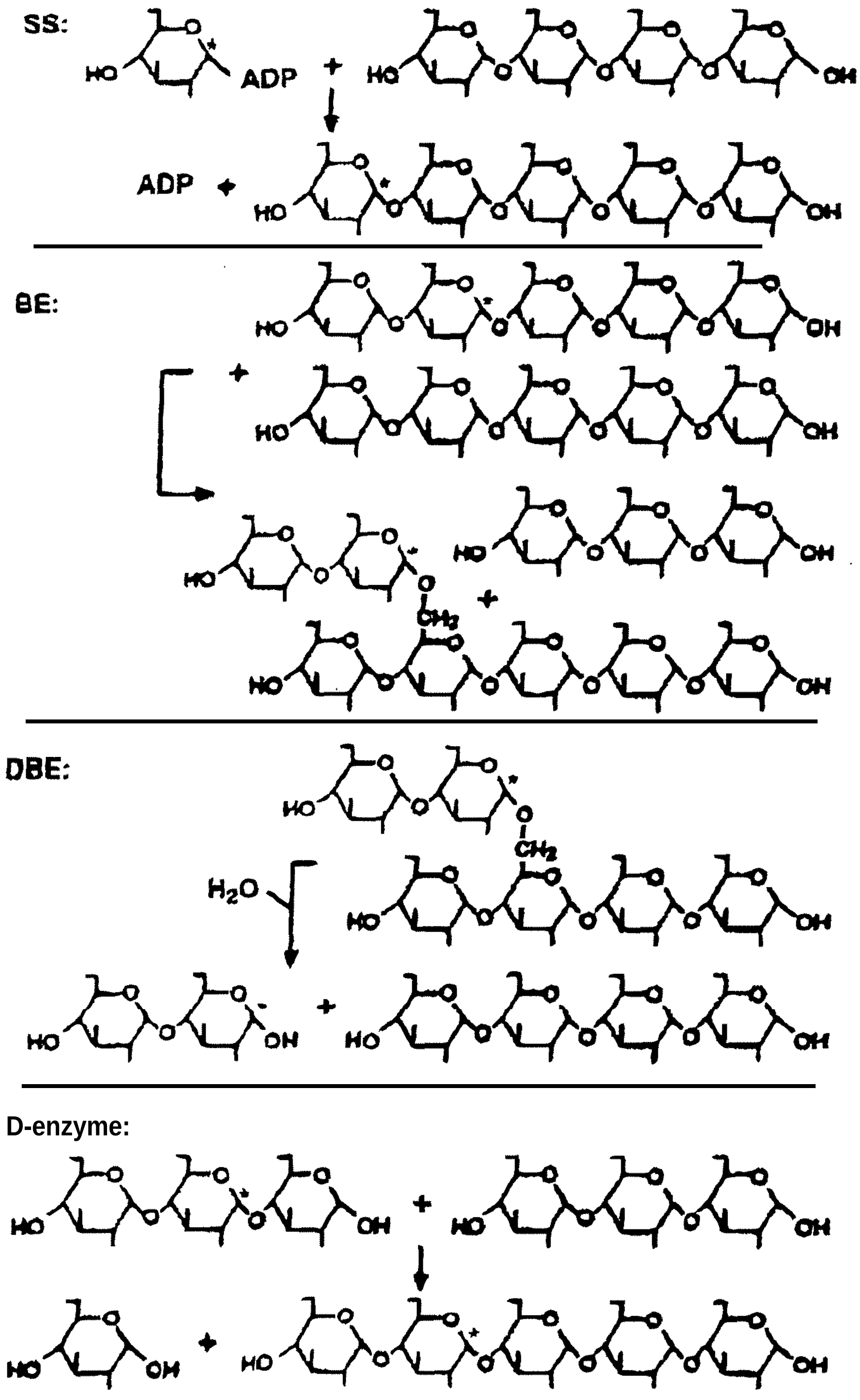


Figure 2.2.7. Diagrammatic representation of notch biosynthesis. (From Myers et al., 2000.)

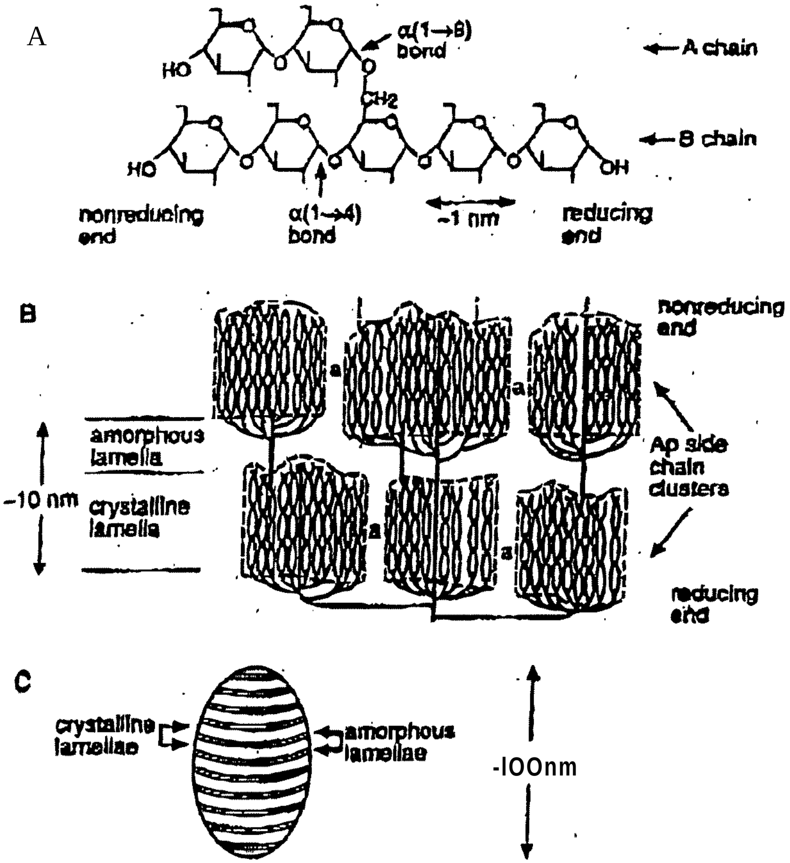


Figure 22.8. Diagrammatic representation of the first three levels of amylopectin structure. (From Myers et al., 2000.)

hormones released are in low concentrations (picomolar concentrations). Both the synthesis and degradation of the hormones is closely regulated. The hormones are part of complex webs of plant signaling networks. The plant hormones signal to a plant to take certain actions in response to other signals. Many, probably all, of the hormones lead to and proceed from signals to encode proteins. Root systems of plants are a part of the central processing center for plants. At least five of the nine classes of plant hormones are produced in the roots (Itai and Birnbaum, 1995). Critical understanding of the role of hormones was pioneering work in plant adaptation and survival. Various stimuli elicit signals that alter genetic expression of metabolism in plants. In plants, various stimuli cause genes to send mRNA to the ribosomes, which, in turn, transcribe proteins. The hormones are part of an interrelated crosstalk of plant signals.

Microorganisms also produce some of the hormones, and consequently, the bacteria and fungi are capable of controlling the plant they inhabit. In fact, fungi often produce much larger quantities of the hormones than do higher plants. Gibberellic acid was discovered through efforts to understand “foolish seedling” disease in rice, which was caused by the fungus *Gibberella fujikuroi*. The disease was characterized by, among other things, excessive shoot elongation (Crozier et al., 2000).

MINERAL NUTRITION OF RICE, PLANT ABNORMALITIES, AND ASSOCIATED STRESSES

A host of biochemical and physical processes are necessary for survival and reproduction. The rice plant must squire the mineral nutrients needed far growth and development The plant must develop the structural components, primarily cell walls, to occupy both aboveground and belowground space. Nitrogen nutrition affects both growth and development of rice plants. Nitrogen is taken up rapidly by seedlings and converted into leaf protein. The leaves successively expand, attain a maximum photosynthetic rate near the completion of expansion, and gradually senesce. Much of this early nitrogen apparently remains in the plant, moving from older leaves to younger leaves until after the grain is filled. During its lifetime a leaf must either repair *or* disassemble damaged proteins. AS the leaves become fess viable due to age, shading, and irreversible oxidative **damage, the balance of protein activity is tilted toward degradation, not repair.**

Various constituent amino acids in leaves of rice are transformed by proteinase activities **into primarily** glutamate, glutamine, and serine. These are readily translocated to sink tissue, such as developing leaf tissue.

Consequently, we expect **the** nitrogen **in** early season growth **to** be redistributed to younger leaves throughout the vegetative period. Leaf area **is** usually maximum just before growth stage R0 (Murata and Matsushima, 1975). Initiation of the young panicle (growth stage R0) at around the time of collar formation of leaf 4 below the flag leaf (growth stage Vw) **for most** U.S. rice cultivars and differentiation of the panicle (growth stage R1) at the completed leaf blade elongation (collar formation) for leaf 3 below the flag leaf (V_{F-3}) leads to a large demand for translocated nitrogen. This demand arises from the differentiating panicle's requirements for nitrogen (Yoshida, 1981). Consequently, rice leaves frequently appear to be somewhat deficient in nitrogen during this period. Similarly, nitrogen fertilization during **panicle** differentiation is a standard practice that usually increases grain yield. Yii components responsible ***For*** the yield increase when nitrogen fertilizer is applied at this time are increased panicle branching and an increase in grains per panicle. Another relevant process is also occurring. Rice leaves may fail to become visibly green after this yellowing occurs, even with nitrogen fertilization. Although it is universally accepted that the developing branching panicles are greater sinks for nitrogen than are the leaves, floret numbers per panicle and grain yield are correlated with leaf area (Yoshida, 1981; Counce, 1992). Consequently **midseason** (i.e., near panicle differentiation, growth stage R1) nitrogen fertilization of rice contributes to maintaining optimum leaf area to maximize yield, thereby supplying adequate carbohydrates to the differentiating panicles.

The nutritional phenomena that commonly occur in rice affect the productivity of the crop- Some nutritional *disorders are* related partially to intensive cropping, saline water, depletion or unavailability of various nutrients, and elevated pH. Reports of the nutritional disorders occur in different languages with different standards of comparison, which makes unified understanding difficult. However, several distinctive nutritional conditions **commonly** occur in rice. All of these conditions are somewhat unique to paddy rice and all can affect grain yield substantially. These conditions include straighthead, akagare, zinc deficiency, and selective silica uptake (and silica deficiency).

E. Takahashi (1995) noted the selective uptake of silicic acid by rice. Silica is laid dawn in cell walls and in epidermal cells of rice and other grasses as a crystalline structure. Silica fertilization increases rice photosynthesis, reduces water use, increases leaf erectness, and reduces excessive and therefore harmful uptake of some nutrients (E. Takahashi, 1995). The failure to include silica as an essential plant nutrient is probably a combination of a flawed definition of essentiality and difficulty in excluding silica from nutrient solutions (Epstein, 1999).

Straighthead is a general condition caused by various factors. When a rice panicle develops normally, the top of the panicle is bent over at maturity and the top of the panicle is yellow or brown. In straighthead conditions, the panicle is erect (or partially erect) and the panicle is often green long after the normal time for grain development from R4 to R9. Two types of straighthead have been found: *Hideri aodachi* and arsenic induced straighthead. *H. aodachi is drought* injury straighthead caused by draining at certain stages of growth.

Straighthead can be either dramatic or barely noticeable. In US. rice-growing areas, straighthead can be induced by arsenical pesticides in fairly high levels in the soil or by relatively low concentration in the plants at the time of male gamete producdon, during growth stags R3. At this stage of growth, application of arsenical materials kills the male gametes. Female gamete production is also reduced but to a lesser degree. In distinction to drought-injury straighthead, arsenic-related straighthead can be prevented by draining and drying rice soils before grow& stage R0.

Akagare disease is caused by iron toxicity in flooded rice due to the plants' inability to exclude iron from inside the plant. Consequently, ferrous iron accumulates in the plant. In most mineral soils, the roots of flooded rice are red. This is because the normal rice plant chelates iron on the root surface which is coated with a layer of oxygen. The red color is due to the iron layer that coats flooded rice roots. The akagare condition also occur6 in acidic soils in Japan.

Akagare (type I) (Tadano, 1995) and similar symptoms (Slaton et al., 19%) on saline or alkaline soils in Arkansas have similarities in symptoms, although there are differences in the conditions leading to these symptoms. The similarities arc leaf bronzing, high ferrous iron content in tissue, and low phosphorus content. The conditions leading to the symptom arc, however, quite different: acid, bumic soils in Japan, and alkaline and saline soils in Arkansas. Akagare is also caused by iodine toxicity and zinc deficiency.

Akagare has many causes in common with a similar problem. Acid sulfate soil. tic deficiency, iodine toxicity, and saline soil conditions lead to rice plants that cannot exclude harmful ions and take up needed nutrients selectively. Rice roots are incapable of functioning effectively to carry out critical iron exclusion and nutrient uptake activities. Depending on the particular situation. different ions are deleterious and deficient. The key similarity is that the integrity of the root system is compromised and the roots cannot function properly. In this situation. mass Row of ions into the roots occurs followed by severe plant osmotic stress, leading to different metabolic conditions in the shoots, predominated by bronzing. The exception appears to be zinc-deficient akagare, in which the midrib become chlorotic but the leaves do not bronze (Tanaka, 1995).

Zinc is a cofactor in several enzymes that perform key oxidation–reduction reactions. Among these enzymes are alcohol dehydrogenase and copper–zinc superoxide dismutase. After flooding of rice and prior to aerenchyma formation, the roots srt in low-oxygen conditions in which ethanol accumulates due to anaerobic respiration. Without detoxification, ethanol accumulation becomes toxic. Kramer and Boyer (1995) note, however, that ethanol probably does not kill flooded plants. Alcohol dehydrogenase must either increase in activity, or more of the enzymes must be transcribed (coded from DNA) in order for the plant to function optimally. Also, soon after flooding, the water and air temperature are low, due to cold water from wells and often, low air temperatures. In this situation, photosynthetic rates are reduced and the radiation normally utilized in photosynthesis is, in fact, directed to reducing oxygen (O_2) (Fridovich, 1991) to superoxides (O_2^-) (Hamilton, 1991). Superoxide radicals (0;) degrade membranes and lead rapidly to degeneration of chloroplast membranes and other membranes unless they are detoxified (Elstner, 1991). Radical oxygen is enzymatically converted to hydrogen peroxide (H_2O_2) by superoxide dismutase. Hydrogen peroxide is also toxic to plants and must be detoxified by ascorbate peroxidase and subsequent action by glutathione reductase in the chloroplast (Figure 2.2.9). As the temperature of water in the rice field and the air increase, the problem of radical oxygen-related stress decreases.

The first line of defense in plants against radiative stress is probably the carotenoids, which are located by the chorophyll molecules. The carotenoids can either absorb light energy or detoxify radical oxygen. Oxidation and reduction of xanthophyll cycle carotenoids is presented in Figure 2.2.10. Probably, radical oxygen-related stress is present at all times during the rice plant's development in all cultural and geographic situations. The shortage of zinc during critical early stages of development may lead to chlorosis of leaf tissue. Zinc-deficient plants sometimes float in the water, indicating that the zinc deficiency leads to root deterioration. The severity of the condition depends on temperature (lower temperatures being worse, especial& below 16°C), the zinc-supplying capacity of the soil, the zinc-extracting capacity of the plant, and the metabolic makeup of the plant. Also, larger plants have larger nodal roots,

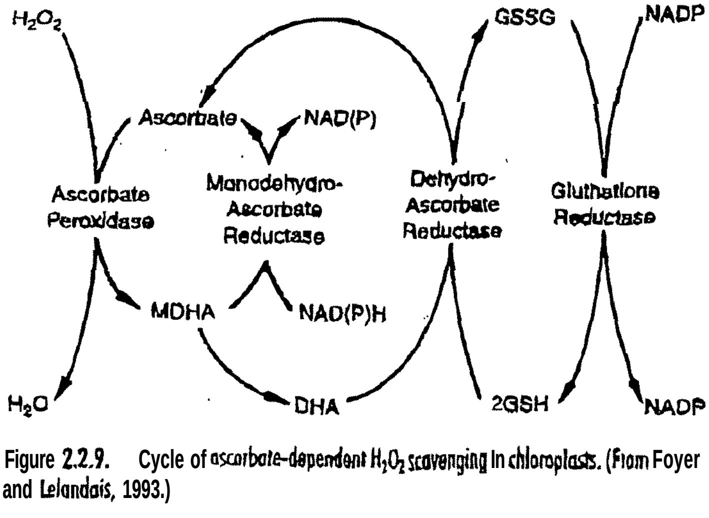


Figure 2.2.9. Cycle of ascorbate-dependent H_2O_2 scavenging in chloroplasts. (From Foyer and Lelandais, 1993.)

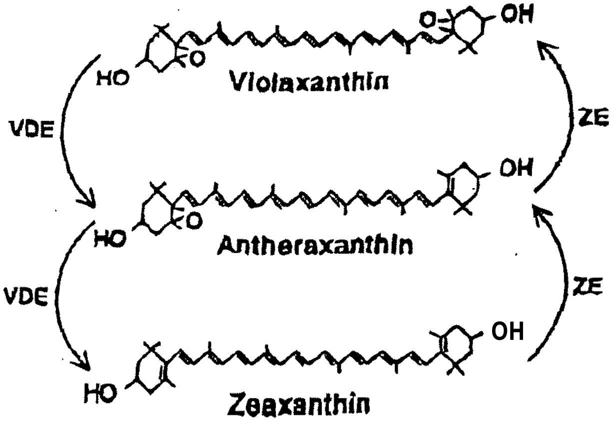


Figure 2.210. Rations of the xanthophyll cycle. (From Adams and Demming-Adams, 1993.)

which extract nutrients and withstand stressful external conditions in the root zone better than do smaller roots.

CONCLUSION

Scientists worldwide have specialized to produce a large body of information on rice plant Physiology. Understanding physiology can lead to more productive rice cultivars having higher quality and greater resistance to various biotic and abiotic stresses.

The rice genome is currently being sequenced. The availability of the DNA sequence coupled with powerful research techniques in proteonomics and genomics should lead to even greater understanding of rice plant biology in the future.

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