Plant Physiol. (1998) 118: 1105–1110

Update on Development

Deepwater Rice: A Model Plant to Study Stem Elongation[1]

Hans Kende*, Esther van der Knaap[2], and Hyung-Taeg Cho

Michigan State University-Department of Energy Plant Research Laboratory, Michigan State University, East Lansing, Michigan 48824–1312

Semiaquatic plants grow mostly in flood plains and along river beds and are adapted to survive partial submergence during periods of flooding (Blom and Voesenek, 1996). Among their adaptive features are the development of internal air channels (aerenchyma) that facilitate aeration of submerged organs and the capacity for rapid elongation when the plants become partially covered by floodwaters. Submergence-induced growth enables semiaquatic plants to keep part of their foliage above the rising waters and to avoid drowning.

Rice (*Oryza sativa* L.) is a semiaquatic plant whose growth, at both the seedling and adult stages, is well investigated. It is cultivated in five ecosystems where the source of water supply and the degree of flooding are the major environmental determinants. The rice types corresponding to these ecosystems are rain-fed low- and upland rice, rice grown under controlled irrigated conditions, deepwater rice, and rice in tidal wetlands. Rice grown in the deepwater ecosystem distinguishes itself from most modern rice varieties by its ability to survive in water depths of more than 50 cm for at least 1 month (Catling, 1992). Among the deepwater rice types, the so-called floating rices exhibit extreme elongation capacity. They can grow at rates of 20 to 25 cm/d when partially submerged and can reach a length of up to 7 m in water depths of up to 4 m (for a detailed description of the deepwater rice ecosystem, see Vergara et al. [1976]; Catling [1992]).

Figure 1A illustrates the growth habit of deepwater rice. Seedlings are allowed to establish themselves before the onset of flooding. The potential for submergence-induced rapid internodal elongation develops with the differentiation of internodes (Métraux and Kende, 1983). As the floodwaters rise, the internodes elongate and adventitious roots are formed at the nodes. When the waters recede, the rice plant sinks to the ground and gravitropic stimulation causes the top of the stem and the panicle to grow upward. Figure 1B illustrates the growth response of one internode during 2 d of submergence.

Deepwater rice is a subsistence crop for about 100 million people in areas of Southeast Asia, where severe flooding occurs during the monsoon season. Whereas yields of modern rice cultivars average 6 tons/ha, the average yield of deepwater rice is only 2 tons/ha (Vergara et al., 1976; Catling, 1992). Efforts to improve yield and grain quality of deepwater rice have been met with limited success. Increases in yield and retention of floating ability have not yet been combined in one single cultivar. Since deepwater rice is the only crop that can be grown in many flood-prone areas of Southeast Asia, developing cultivars with increased yield and growth potential is of major agronomic importance.

The genetic basis for submergence-promoted internodal elongation of deepwater rice has received relatively little attention. It appears that this trait is controlled by a number of minor and perhaps as few as two major genes (Catling, 1992). Suge (1987) proposed that elongation during submergence is based on the capacity of an internode to elongate, as well as the degree of elongation, and identified one gene with incomplete dominance that determined elongation ability. Deepwater rice is of the Indica type and can be crossed with Japonica rice. It can be transformed (Alam et al., 1998), and investigating its unique biological properties such as the signal transduction pathways leading to accelerated internodal growth is greatly aided by the rapidly expanding genetic database of rice.

In addition to its importance as a crop plant, deepwater rice is also excellent for studying basic aspects of plant growth. The growth response is induced by an environmental signal and is mediated by at least three interacting hormones, namely ethylene, ABA, and GA. Internodal elongation is based on increased cell-division activity and enhanced cell elongation in well-delineated zones of the internode. This allows one to study both processes of growth in an integrated manner. Also, the unusually high growth rates magnify growth-related cellular, physiological, biochemical, and molecular processes, thereby facilitating their analysis. In addition to yielding fundamental insights into the growth process, studies of internodal elongation in deepwater rice may ultimately help to identify genes that could confer at least limited elongation capacity onto modern, high-yielding cultivars.

[1] This work was supported by the National Science Foundation and the U.S. Department of Energy. This paper is dedicated to the memory of Paul B. Green (1931–1998).

[2] Present address: Department of Plant Breeding and Biometry, Cornell University, Ithaca, NY 14853–1673.

* Corresponding author; e-mail hkende@pilot.msu.edu; fax 1–517–353–9168.

Abbreviations: CMF, cellulose microfibril; DZ, differentiation zone; EZ, elongation zone; IM, intercalary meristem.

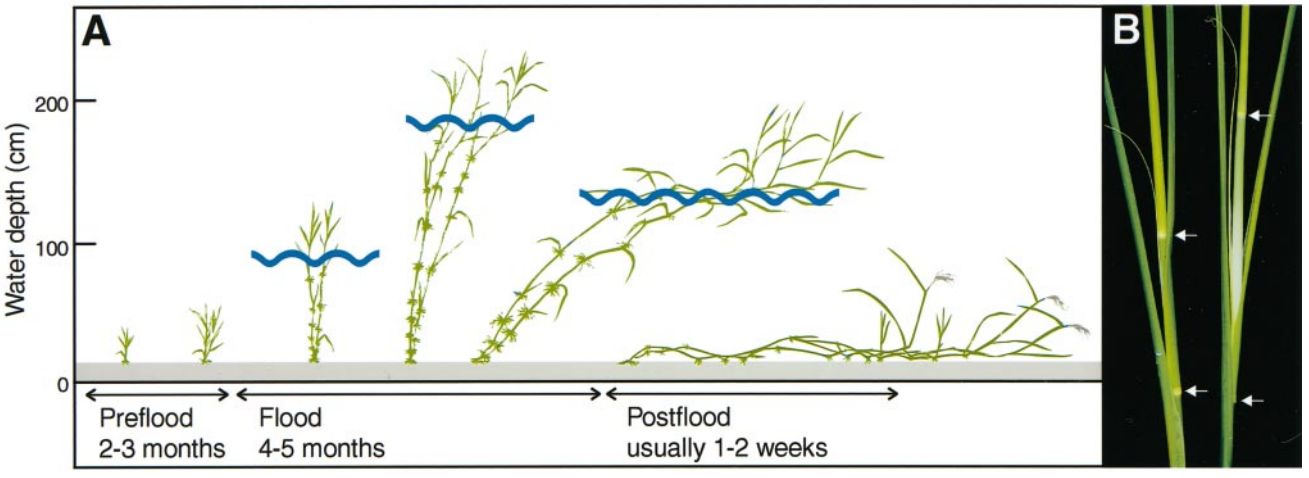

Figure 1. A, The growth cycle of a deepwater rice plant. Young plants are allowed to establish themselves before the annual flood arrives. As the floodwaters rise, rapid internodal growth permits the plants to maintain part of their foliage above the water. Adventitious roots develop at the submerged nodes. After the flood recedes, the upper internodes show gravitropic sensitivity and grow upward (modified with permission from Catling, 1992). B, Youngest internode of an air-grown (left) and a submerged plant (right). The upper and lower arrows indicate the positions of the highest and second highest node, respectively. The whitish tissue of the internode on the right corresponds to about 10 cm of new growth during 2 d of submergence.

INTERNODAL ELONGATION IN DEEPWATER RICE IS REGULATED BY ENVIRONMENTAL AND HORMONAL FACTORS

The original growth experiments with rice were carried out with coleoptiles, which were found to elongate under water or at low partial pressures of O_2 at a faster rate than in air. This feature helps coleoptiles to emerge from shallow waters and to act like a snorkel for the aeration of the growing seedling (for review, see Jackson, 1985). In 1970, Ku et al. discovered that growth of rice coleoptiles is stimulated by ethylene. The growth-promoting activity of ethylene was subsequently found in a number of other semiaquatic plants (Jackson, 1985). The response of semiaquatic plants to ethylene is the opposite of that observed with most terrestrial plants, in which growth is inhibited by ethylene.

Elongation of deepwater rice internodes can be induced in the laboratory by immersing adult plants in water of increasing depths (Fig. 2, A and B; Métraux and Kende, 1983). The ethylene concentration inside submerged internodes increases 50-fold, from approximately 0.02 to 1 μL L^{-1} (Fig. 2C), and ethylene applied to nonsubmerged plants promotes internodal growth (Fig. 2D). The accumulation of ethylene in submerged tissues of rice is the result of two processes. Ethylene is physically trapped because its diffusion coefficient in water is 10,000 times lower than in air (Jackson, 1985). In addition, ethylene synthesis is enhanced in submerged internodes (Raskin and Kende, 1984a). Isolated stem sections containing the highest internode respond to submergence just as intact plants do (Raskin and Kende, 1984a). When such sections are exposed to the same gas atmosphere that prevails in submerged internodes—namely 3% O_2, 6% CO_2, and 1 μL L^{-1} ethylene in N_2—the submergence response is fully mimicked. Therefore, deepwater rice plants respond to submergence by sensing the altered composition of their internal gas atmosphere. Lowered O_2 and increased CO_2 tensions promote ethylene synthesis and also enhance the growth-promoting effect of ethylene (Raskin and Kende, 1984a).

Does ethylene induce elongation of deepwater rice internodes directly or via one of the "classical" plant growth hormones? Work of Musgrave et al. (1972) with the semiaquatic plant *Callitriche platycarpa* showed that submergence-induced elongation was mediated by an interaction of ethylene and GA. Thus, GA was the prime candidate for the hormone that would ultimately promote elongation of deepwater rice internodes. Indeed, when air-grown plants were treated with GA, their growth was greatly enhanced, and submergence- and ethylene-induced growth were inhibited when plants were treated with GA-biosynthesis inhibitors (Raskin and Kende, 1984b; Suge, 1985). The requirement of GA for internodal growth of deepwater rice was also demonstrated genetically by Suge (1987), who examined the growth habit of F_2 plants derived from a cross between a deepwater rice and a rice mutant deficient in GA biosynthesis.

What is the relationship between ethylene and GA? When GA was applied to nonsubmerged plants at increasing concentrations, the threshold of the growth response was shifted to a lower GA concentration in plants treated with ethylene when compared with plants kept in air, and the magnitude of the response was greater (Raskin and Kende, 1984b). This indicates that ethylene increases the responsiveness of the internode to GA. How is this achieved? ABA is a potent antagonist of GA action in rice internodes, and both applied ethylene and submergence reduced endogenous ABA levels in internodes by 75% within 3 h (Hoffmann-Benning and Kende, 1992). At the same time, there was also a 4-fold increase in the endogenous content of GA_1. Submergence- and ethylene-mediated reduction of ABA levels in deepwater rice has also been

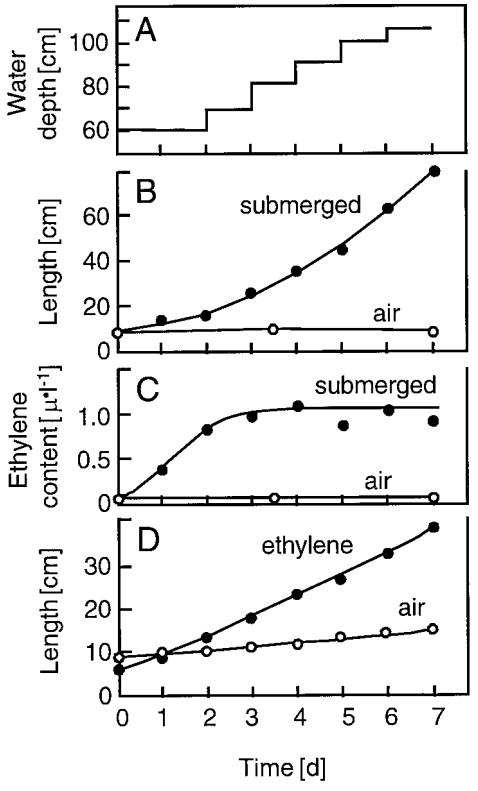

Figure 2. Promotion of growth by submergence and ethylene in deepwater rice. A, Regime of submergence. The plants were partially submerged in a 1-m-high tank so that one-third of their foliage was above the water. They were lowered progressively into the tank to compensate for growth. B, Total internodal length in submerged (●) and air-grown (○) plants. C, Ethylene content in the internodal cavity of submerged (●) and air-grown (○) plants. D, Total internodal length of plants treated with 0.4 μL L^{-1} ethylene (●) and of air-grown plants (○). After Métraux and Kende (1983).

described by Azuma et al. (1995). Thus, rapid internodal growth of deepwater rice may result from an ethylene-mediated increase in the ratio of an endogenous growth promoter (GA) and a growth inhibitor (ABA). The proposed chain of events connecting submergence and GA-stimulated internodal elongation is shown in Figure 3.

INTERNODAL ELONGATION IS BASED ON INCREASED CELL DIVISION ACTIVITY AND ENHANCED CELL ELONGATION

Based on [^{3}H]thymidine incorporation (Métraux and Kende, 1984) and anatomical studies (Bleecker et al., 1986), the rice internode can be divided into three regions (Fig. 4). At the base of the internode is the IM, where cell divisions generate new internodal cells. These cells are displaced into the EZ, where they reach their final length, and growth ceases in the DZ, where secondary wall and xylem formation take place. The transition from one zone to the other is reflected in cell size measurements (Fig. 5). The IM is about 2 mm above the node and is characterized by small, brick-like cells (Fig. 4). Cell sizes increase above the IM in the EZ and stay constant in the DZ (Fig. 5). The rate at which new cells are produced in the IM increases 3-fold in response to submergence, the EZ expands about 3- to 5-fold, and the cells attain a 3- to 5-fold greater final length (Fig. 5). Similar observations have been made in GA- and ethylene-treated internodes (Métraux and Kende, 1984; Raskin and Kende, 1984b; Sauter and Kende, 1992a; Sauter et al., 1993). From these results it is apparent that both the regulation of cell division in the IM and the regulation of cell elongation in the EZ must be studied to gain an understanding of internodal growth in deepwater rice.

GA ACTIVATES THE CELL CYCLE IN THE IM

Progression of cells in the IM through the cell cycle has been followed by measuring [^{3}H]thymidine incorporation, by flow cytometry and by determining the expression of genes whose products regulate the entry of cells into mitosis and the S phase (Sauter and Kende, 1992a; Sauter et al., 1995; Lorbiecke and Sauter, 1998). The activation of the cell cycle by GA and submergence was reflected in increased expression of a gene encoding a $p34^{cdc2}$-like histone H1 kinase (*cdc2Os-2*) and of the corresponding enzymatic activity (Sauter et al., 1995; Lorbiecke and Sauter, 1998). Similarly, the transcript levels of two cyclin genes, *cycOs1* and *cycOs2*, increased in GA-treated and submerged internodes during the G2 phase, indicating that the corresponding cyclins control entry into the M phase (Sauter et al., 1995; Lorbiecke and Sauter, 1998). In a screen for GA-regulated genes using differential display of mRNA, two genes were identified whose products function in the cell cycle. GA promoted the expression of a gene encoding a histone H3, which is a marker for the S phase (Van der Knaap and Kende, 1995), and the expression of *RPA1*, a gene encoding one of the subunits of replication protein A (Van der Knaap et al., 1997). RPA is a heterotrimeric protein that functions in DNA replication, recombination, and repair, and may also be involved in the regulation of transcription.

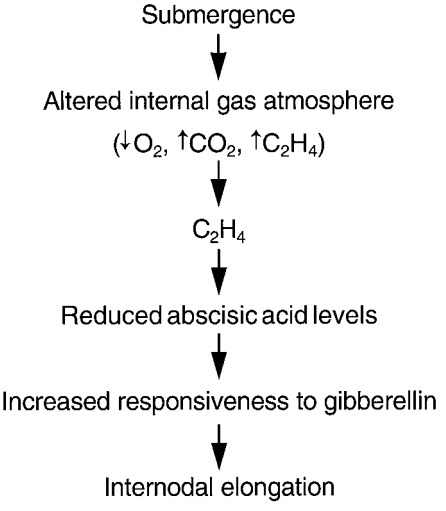

Figure 3. The proposed sequence of events connecting submergence and enhanced internodal elongation.

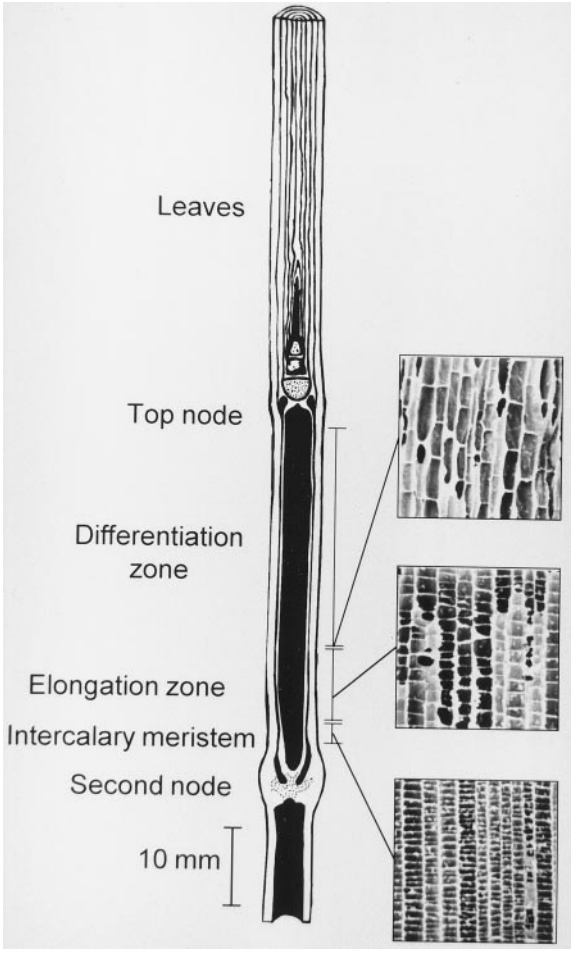

Figure 4. Rice stem containing the uppermost elongating internode. The insets show scanning electron micrographs of cells in the IM, in the EZ, and at the base of the DZ. After Sauter and Kende (1992a).

The availability of molecular markers for the S and M phases of the cell cycle make it possible to examine by in situ hybridization the functional organization of the IM, which has not yet been studied in detail. The IM is a rib meristem that produces internodal cells only, and therefore lacks some of the complexities of shoot apical meristems. It will be necessary to investigate whether GA promotes cell division activity and cell elongation independently of each other or whether entry into the cell cycle is a consequence of GA-induced cell elongation as has been suggested by Sauter and Kende (1992a).

GA ALSO ENHANCES CELL ELONGATION

Cell elongation is driven by uptake of water into the central vacuole. Flow of water into the cell is a function of the osmotic potential of the cell, the wall pressure potential or turgor, and the hydraulic conductivity. Elongation of internodal cells in deepwater rice is not the result of decreased osmotic potential or increased hydraulic conductance. However, the cell walls of rapidly growing internodes exhibit increased plastic and elastic extensibility (Kutschera and Kende, 1988). Therefore, work aimed at understanding the mechanism of cell elongation in deepwater rice has focused on chemical and structural features of the growing cell wall and on the action of wall-loosening proteins, the expansins.

The mixed-linked polysaccharide (1→3),(1→4)-β-D-glucan accumulates transiently in growing cell walls of graminaceous monocotyledons and is thought to play a role in wall expansion (Carpita, 1996). The content of β-D-glucan correlates well with cell elongation in deepwater rice internodes (Sauter and Kende, 1992b). Its level reaches a maximum in the EZ and decreases toward the DZ. In rapidly growing internodes, the EZ and the region of high β-D-glucan content expand in parallel, and lignification of internodal cell walls is delayed. Azuma et al. (1996) determined the cell wall composition of deepwater rice internodes and found that the pattern characteristic of the IM—mainly the relatively low ratio of cellulosic to noncellulosic material—expanded with the EZ in rapidly elongating internodes.

Several lines of evidence indicate that the IM is the primary site of GA action (Sauter and Kende, 1992a; Sauter et al., 1993). Cells that have been displaced from the IM before the start of GA treatment do not respond to the hormone by further elongation. Responsiveness to GA may be determined by the orientation of CMFs. In the epidermal walls of the IM, CMFs are oriented perpendicularly to the direction of growth (Fig. 6). Such transverse orientation of CMFs permits cell elongation. In slowly growing control internodes, the orientation of CMFs in epidermal cells above the IM changed to oblique, a configuration that impedes growth. In rapidly growing GA-treated internodes, the reorientation of CMFs from transverse to oblique was gradual and extended over the entire EZ (Fig. 6). Thus, there was a close correlation between the rate of growth along the internode and the orientation of CMFs. At least in rice internodes, GA does not reorient the direction in which CMFs are deposited and enhances only elongation of cells with CMFs that are still in transverse orientation. Herein may lie one of the basic differences between

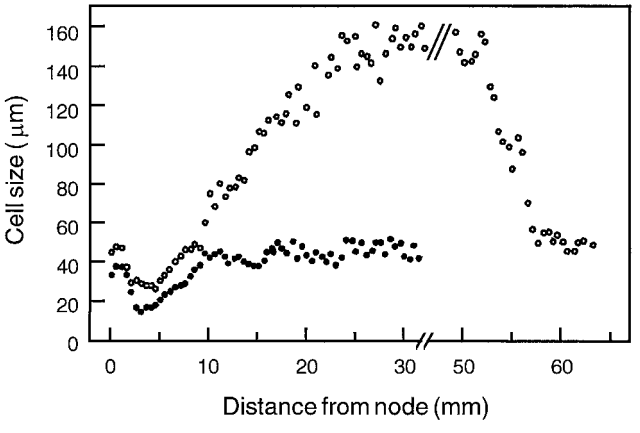

Figure 5. The size of cells in the growing internode of submerged (○) and air-grown (●) plants. The IM corresponds to the region with the smallest cell size 2 to 5 mm above the second highest node. The EZ is between 5 and 10 mm in air-grown plants and 5 and 25 mm in submerged plants. From Bleecker et al. (1986).

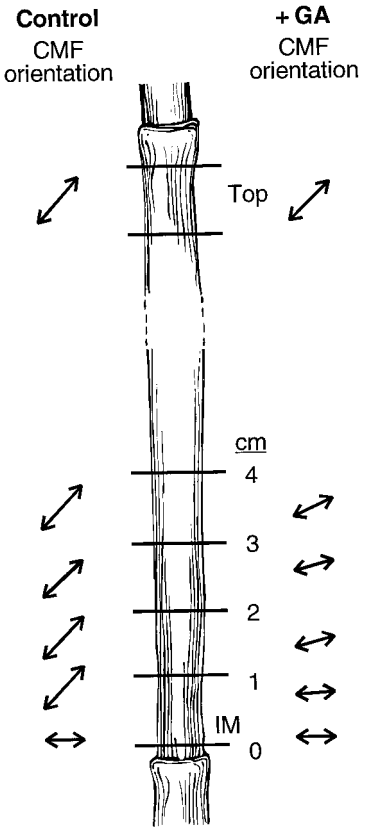

Figure 6. The direction of CMFs in the epidermal cell walls of control internodes and internodes treated with 5 μM GA_3. The lines with double arrows indicate the measured average angle of CMF deposition in the respective regions of the internode. After Sauter et al. (1993).

GA and auxin action. Auxin is known to change the deposition of CMFs from the oblique/longitudinal to the transverse and to promote elongation of cells that have stopped growing (Bergfeld et al., 1988). GA action usually requires the presence of a meristem in which cells still have transversely oriented CMFs.

The observed increase of cell wall extensibility in rapidly growing deepwater rice internodes (Kutschera and Kende, 1988) is consistent with a large body of evidence indicating that plant cell elongation is based on stress relaxation of the cell wall. Stress relaxation is thought to be regulated, at least in part, by wall-loosening factors. A family of cell wall-loosening proteins, the expansins, was recently discovered by Cosgrove and coworkers (for a review, see Cosgrove, 1998). They are thought to mediate cell expansion by disrupting noncovalent bonds between wall polymers, most likely between CMFs and hemicelluloses. Cell walls of deepwater rice internodes underwent long-term extension (creep) when placed under tension in acidic buffers (Cho and Kende, 1997a). This is indicative for the action of expansin. The distribution and activity of rice expansin was correlated with internodal growth (Cho and Kende, 1997b). Acid-induced extension of native cell walls and reconstituted extension of boiled cell walls were confined to the growing region of the internode.

Susceptibility of cell walls to added expansin was increased in submerged internodes, and analysis by immunoblotting showed that cell walls of submerged internodes contained more expansin than did cell walls of air-grown internodes. Two expansins were purified from the cell walls of rice internodes, and their N-terminal amino acids were sequenced (Cho and Kende, 1997a). One sequence was identical to that deduced from the rice expansin cDNA *Os-EXP1*, and the other corresponded to the deduced amino acid sequence of *Os-EXP4* (Cho and Kende, 1997c). In total, four expansin genes have been identified in rice (Shcherban et al., 1995; Cho and Kende, 1997c). In the coleoptile, root, leaf, and internode, there was increased expression of *Os-EXP1*, *Os-EXP3*, and *Os-EXP4* in developmental regions where elongation occurs (Cho and Kende, 1997c). This pattern of gene expression was also correlated with acid-induced in vitro cell wall extensibility. Submergence and treatment with GA induced accumulation of *Os-EXP4* mRNA before the rate of growth started to increase. Taken together, these results indicate that expansins mediate, at least in part, the growth response in deepwater rice.

GA INDUCES THE EXPRESSION OF GROWTH-RELATED GENES

GA is the growth hormone that ultimately promotes elongation of deepwater rice internodes. Because of the magnitude of this response, it is likely that GA regulates, directly or indirectly, the expression of growth-related genes. Such genes were identified principally by a targeted approach, e.g. genes encoding cyclins and expansins, and by differential display of mRNA. Three genes whose function in growth is unknown but that appear to be of particular interest encode a Leu-rich-repeat receptor-like protein kinase (*Os-TMK*), a putative type 1a plasma membrane receptor (*Os-DD3*), and a putative transcription factor or activator (*Os-DD4*) (Van der Knaap, 1998). The expression of all three genes is enhanced by GA and occurs in growing regions of the plant. The kinase domain of Os-TMK autophosphorylates on Ser and Thr residues and phosphorylates the kinase interaction domain of a protein phosphatase. *Os-DD3* contains a functional signal sequence and has a predicted transmembrane region. However, no homologous proteins were found in the databases.

In the internode, expression of *Os-DD4* is restricted to the IM, which is the primary site of GA action. The deduced protein sequence has two conserved regions for which homologies exist in the Arabidopsis and rice databases. One of these regions includes a putative nuclear-localization signal. OS-DD4 also has a Gln-rich motif, an acidic region, and high Pro content. These characteristics are indicative of a function as a transcription factor. The other region, which is also found in yeast and animals, may mediate interactions with proteins. Overexpression of *Os-DD4* in Arabidopsis led to pleiotropic effects. In severe phenotypes flowers developed in the rosette and bolting was delayed. This growth-related defect may signify a dominant negative effect, resulting, for example, from the displacement by Os-DD4 of the corresponding Arabidopsis

protein from a transcription complex. Severe phenotypes also had fasciated stems, reduced apical dominance, curled leaves, and altered flower morphology. Because *Os-DD4* shares homologies with a number of Arabidopsis genes, it is possible that ectopic expression of *Os-DD4* in Arabidopsis interferes with several developmental pathways, thereby yielding the observed pleiotropic phenotypes.

PROSPECTS

The mechanism by which environmental factors and hormones induce growth is largely unknown. The results obtained with deepwater rice illuminate some of the questions that need to be answered. First, there is the sensory pathway that connects influences from the environment with the activity of the hormone(s) regulating growth. Next is the mode of action of the respective hormone(s). Does a growth hormone such as GA activate one key reaction via one signal transduction pathway, or are there several GA response pathways that control different aspects of growth? In intact plants growth consists of the production of new cells in the meristems and of subsequent elongation of these cells. Are these two processes interconnected or are they separately controlled? Does the increase in cell size trigger the entry of meristematic cells into the cell-division cycle? What biochemical reactions control cell wall loosening? Does wall extension cause accelerated synthesis and deposition of new cell wall material? Work with deepwater rice has contributed to identifying pieces of the puzzle, but much more needs to be done to complete the picture. As pointed out at the beginning of this *Update*, deepwater rice is not only a "model system" for studying growth, the remarkable growth response of submerged plants is also the process that needs to be understood in order to introduce elongation capacity into high-yielding rice cultivars. The resulting increased rice production in deepwater areas would elevate the living standards of some of the poorest farming populations of Southeast Asia.

Received June 24, 1998; accepted August 31, 1998.

LITERATURE CITED

Alam MF, Datta K, Abrigo E, Vasquez A, Senadhira D, Datta SK (1998) Production of transgenic deepwater indica rice plants expressing a synthetic *Bacillus thuringiensis cryIA(b)* gene with enhanced resistance to yellow stem borer. Plant Sci **135:** 25–30

Azuma T, Hirano T, Deki Y, Uchida N, Yasuda T, Yamaguchi T (1995) Involvement of the decrease in levels of abscisic acid in the internodal elongation of submerged floating rice. J Plant Physiol **146:** 323–328

Azuma T, Sumida Y, Kaneda Y, Uchida N, Yasuda T (1996) Change in cell wall polysaccharides in the internodes of submerged floating rice. Plant Growth Regul **19:** 183–187

Bergfeld R, Speth V, Schopfer P (1988) Reorientation of microfibrils and microtubules at the outer epidermal wall of maize coleoptiles during auxin-mediated growth. Bot Acta **101:** 57–67

Bleecker AB, Schuette JL, Kende H (1986) Anatomical analysis of growth and developmental patterns in the internode of deepwater rice. Planta **169:** 490–497

Blom CWPM, Voesenek LACJ (1996) Flooding: the survival strategies of plants. Trends Ecol Evol **11:** 290–295

Carpita NC (1996) The structure and biogenesis of the cell walls of grasses. Annu Rev Plant Physiol Plant Mol Biol **47:** 445–476

Catling D (1992) Rice in Deep Water. MacMillan Press, London

Cho H-T, Kende H (1997a) Expansins in deepwater rice internodes. Plant Physiol **113:** 1137–1143

Cho H-T, Kende H (1997b) Expansins and internodal growth of deepwater rice. Plant Physiol **113:** 1145–1151

Cho H-T, Kende H (1997c) Expression of expansin genes is correlated with growth in deepwater rice. Plant Cell **9:** 1661–1671

Cosgrove DJ (1998) Cell wall loosening by expansins. Plant Physiol **118:** 333–339

Hoffmann-Benning S, Kende H (1992) On the role of abscisic acid and gibberellin in the regulation of growth in rice. Plant Physiol **99:** 1156–1161

Jackson MB (1985) Ethylene and responses of plants to soil waterlogging and submergence. Annu Rev Plant Physiol **36:** 145–174

Ku HS, Suge H, Rappaport L, Pratt HK (1970) Stimulation of rice coleoptile growth by ethylene. Planta **90:** 333–339

Kutschera U, Kende H (1988) The biophysical basis of elongation growth in internodes of deepwater rice. Plant Physiol **88:** 361–366

Lorbiecke R, Sauter M (1998) Induction of cell growth and cell division in the intercalary meristem of submerged deepwater rice (*Oryza sativa* L.). Planta **204:** 140–145

Métraux J-P, Kende H (1983) The role of ethylene in the growth response of submerged deep water rice. Plant Physiol **72:** 441–446

Métraux J-P, Kende H (1984) The cellular basis of the elongation response in submerged deep-water rice. Planta **160:** 73–77

Musgrave A, Jackson MB, Ling E (1972) Callitriche stem elongation is controlled by ethylene and gibberellin. Nature New Biol **238:** 93–96

Raskin I, Kende H (1984a) Regulation of growth in stem sections of deep-water rice. Planta **160:** 66–72

Raskin I, Kende H (1984b) Role of gibberellin in the growth response of submerged deep water rice. Plant Physiol **76:** 947–950

Sauter M, Kende H (1992a) Gibberellin-induced growth and regulation of the cell division cycle in deepwater rice. Planta **188:** 362–368

Sauter M, Kende H (1992b) Levels of β-glucan and lignin in elongating internodes of deepwater rice. Plant Cell Physiol **33:** 1089–1097

Sauter M, Mekhedov SL, Kende H (1995) Gibberellin promotes histone H1 kinase activity and the expression of *cdc2* and cyclin genes during the induction of rapid growth in deepwater rice internodes. Plant J **7:** 623–632

Sauter M, Seagull RW, Kende H (1993) Internodal elongation and orientation of cellulose microfibrils and microtubules in deepwater rice. Planta **190:** 354–362

Shcherban TY, Shi J, Durachko DM, Guiltinan MJ, McQueen-Mason SJ, Shieh M, Cosgrove DJ (1995) Molecular cloning and sequence analysis of expansins—a highly conserved, multigene family of proteins that mediate cell wall extension in plants. Proc Natl Acad Sci USA **92:** 9245–9249

Suge H (1985) Ethylene and gibberellin: regulation of internodal elongation and nodal root development in floating rice. Plant Cell Physiol **26:** 607–614

Suge H (1987) Physiological genetics of internodal elongation under submergence in floating rice. Jpn J Genet **62:** 69–80

Van der Knaap E (1998) Identification of gibberellin-induced genes in deepwater rice and the role of these genes in plant growth. PhD thesis. Michigan State University, East Lansing

Van der Knaap E, Jagoueix S, Kende H (1997) Expression of an ortholog of replication protein A1 (RPA1) is induced by gibberellin in deepwater rice. Proc Natl Acad Sci USA **94:** 9979–9983

Van der Knaap E, Kende H (1995) Identification of a gibberellin-induced gene in deepwater rice using differential display of mRNA. Plant Mol Biol **28:** 589–592

Vergara BS, Jackson B, De Datta SK (1976) Deep water rice and its response to deepwater stress. *In* Climate and Rice. International Rice Research Institute, Los Baños, Philippines, pp 301–319