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The Biophysical Basis of Elongation Growth in Internodes of Deepwater Rice[1]

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ABSTRACT

Partial submergence induces rapid internodal elongation in deepwater rice (*Oryza sativa* L., cv Habiganj Aman II). We measured *in vivo* extensibility, tissue tension, hydraulic conductance and osmotic potential in the region of cell elongation in the uppermost internode. The *in vivo* extensibility of the internode, measured by stretching of living tissue with a custom-made constant stress extensiometer, rose rapidly following submergence of the plant. Both the elastic (E_{el}) and plastic (E_{pl}) extensibility increased when growth of the internode was induced. The submerged internode displayed tissue tension (elastic outward bending of longitudinally split internode sections); in air-grown control internodes, no such bending occurred. The hydraulic conductance, estimated from the kinetics of tissue shrinkage in 0.5 molar mannitol and subsequent swelling in distilled water, was not changed by submergence. The osmotic potential, measured with a dew-point hygrometer using frozen-thawed tissue, was only 18% less negative in the submerged internode than in the air-grown control. This indicates that osmoregulation takes place in rapidly elongating rice internodes. We suggest that the rapid expansion of the newly formed internodal cells of submerged plants is controlled by the yielding properties (E_{pl}) of the cell walls. Experiments with excised stem sections indicate that gibberellin is involved in increasing the E_{pl} of the elongating cell walls.

Deepwater rice belongs to a taxonomically diverse group of semiaquatic plants which are known to respond to partial submergence with a rapid increase in growth (8). This growth response, which occurs in the internodes, enables the rice plants to keep part of their foliage above the rising water level during the flooding season (26). Recent results indicate that the following sequence of events leads to the rapid growth response of the plant: The O_2 concentration within the internode declines; the low O_2 level stimulates the synthesis of ethylene; the concentration of ethylene within the internode rises; ethylene increases the responsiveness of the cells to endogenous GA[3] (11). The GA-mediated growth response is based on enhanced cell division activity in the intercalary meristem and on increased elongation of the newly formed cells (2, 22).

Irreversible cell enlargement is the consequence of two simultaneous, interdependent physical processes: uptake of water, which increases the cell volume, and yielding of the cell wall to accommodate the water influx into the expanding cell (6, 7, 17, 25). The expansion of a single cell can, thus, be limited either by water transport (water conductance) or cell wall yielding (the ability of the wall to become irreversibly extended under stress, *i.e.* plastic extensibility) (4, 6, 7, 16, 17). In growing multicellular organs, an additional mechanical property must be taken into account which has been described by Sachs (23) as tissue tension: the thick outer epidermal wall maintains the thin inner walls in a state of compression and is the expansion-limiting structure of the whole organ (13, 15).

The objective of the present investigation was, first, to determine whether cell wall yielding (measured as *in vivo* extensibility of the tissue) (4, 12, 14, 17) or water transport is the limiting factor in the rapid internodal growth of deepwater rice. We have, furthermore, investigated whether tissue tension is established in the growing organ and the extent to which osmoregulation (maintenance of the osmotic potential of cells) can keep pace with the water uptake of the expanding tissue.

MATERIALS AND METHODS

Chemicals. Gibberellic acid (GA_3) was purchased from Calbiochem (La Jolla, CA); TCY [5-(4-chlorophenyl)-3,4,5,9,10-pentaaza-tetracyclo-5,4,$10^{2,6}$,$O^{8,11}$-dodeca-3,9-diene] was a gift of BASF (Limburgerhof, FRG).

Plant Material. Caryopses of deepwater rice (*Oryza sativa* L., cv Habiganj Aman II, obtained from the Bangladesh Rice Research Institute, Dacca) were germinated and grown in a 13-h photoperiod as described by Métraux and Kende (18). The temperature in the growth chambers was 27°C during an 8-h period centered within the photoperiod and 20°C during the rest of the day and the night. Eight- to 10-week-old plants in which the uppermost internodes had reached a length of 4 to 8 cm were used for all experiments.

Submergence Tests. The position of the nodes in the uppermost and second internodes of selected tillers were marked with ink on the surrounding leaf sheath at the start of the experiment. Some of the labeled plants were partially submerged in 300-L Nalgene tanks (Nalge, Rochester, NY) containing deionized water (18) and some were left in air as controls. The submergence experiments were carried out in the same chambers in which the plants were grown.

Experiments with Stem Sections. Stem sections, 20 cm long, containing the highest two nodes and the uppermost internode, were excised as described by Raskin and Kende (20). The positions of the nodes in the sections were marked with ink on the surrounding leaf sheath at the start of the experiment. For treatments in air, 10 to 15 sections were placed upright into 100-mL beakers containing 40 mL of distilled water or GA_3 (1 μM). The beakers were enclosed in 2.5-L, 60-cm-deep plexiglass cylinders through which moistened air was passed at a flow rate of

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[3] Abbreviations: E_{el}, E_{pl}, E_{tot}, elastic, plastic, and total *in vivo* extensibility; GA, gibberellin; TCY, tetcyclacis.

60 mL min^{-1}. Ethylene (1 μL L^{-1}) was applied as described (20). For submergence tests, 10 sections were fixed with rubber bands to weight-loaded beakers and lowered to the bottom of 4.5-L cylinders filled with distilled water, TCY (1 μM) or TCY (1 μM) + GA_3 (1 μM). TCY-treated sections were isolated from plants that had been watered with a 1 μM TCY-solution for 7 d. The sections were incubated in continuous light (cool-white fluorescent tubes; General Electric, Cleveland, OH; 53 μmol s^{-1} m^{-2}) for 2 d at 27 ± 0.5°C.

Extensibility Measurements. Segments, 18 mm in length, were excised from the uppermost internodes and cut longitudinally into four equal parts (Fig. 1a–c). One of these 2- to 2.5-mm wide segments was fixed between clamps of a custom-made constant-stress extensiometer as described by Kutschera and Briggs (see Fig. 1c in Ref. 14). The distance between the clamps was 8 mm (Fig. 1d). The tissue was submerged in distilled water and subjected to a constant force of 0.098 Newton (N), corresponding to a weight of 10 g, for 6 min. Total (E_{tot}), elastic (E_{el}) and plastic extensibility (E_{pl}) were determined graphically ($E_{tot} = E_{el} + E_{pl}$). The stretching experiments were performed at 27 ± 0.5°C in continuous white light as described above.

Since an extensiometer measures the effect of a one-dimensional force rather than the effect of the three-dimensional force to which a growing cell is exposed when water is taken up, the results of stretching experiments do not permit a direct determination of the yielding coefficient of the cell wall. However, the results provide, in relative units, a measure of cell wall extensibility which controls growth (12).

Determination of the Osmotic Potential. The osmotic potential of the tissue was determined with a Dew Point Microvoltmeter (model U-33T) equipped with a C-51 sample chamber (Wescor Inc., Logan, UT). The dew point hygrometer was calibrated with NaCl solutions of known osmotic potential. The samples consisted of single 18-mm segments excised from the growing region of the uppermost internode (Fig. 1b). The segments were frozen in liquid nitrogen directly upon excision and thawed. The frozen-thawed segments were cut longitudinally into two equal halves and placed in the sample chamber. The osmotic potential of the frozen-thawed tissue was measured at a temperature of 25 ± 0.5°C.

Estimation of the Hydraulic Conductance. The water conductance of the tissue was estimated by measuring the shrinkage (water efflux) and expansion (water influx) of an excised segment (Fig. 1c). In order to increase the water permeability of the waxy cuticle covering the epidermis, the surface of the tissue was abraded with emery cloth (180J; Sancap Abrasives Inc., Alliance, OH). The tissue was fixed between the clamps of the extensiometer as shown in Figure 1d, and the change in length in distilled water (without application of a weight) was recorded. After 1 min, the water was replaced by mannitol (0.5 M) and, after 5 min, the osmoticum was replaced by water. The rate of length change was calculated.

RESULTS

Effect of Submergence on Growth of Uppermost and Second Internode. The growth response upon submergence of the plant takes place in the uppermost and the second internode below it (Fig. 2). After 3 d of submergence, the second internode ceased to grow, while the uppermost internode continued to elongate. Growth of the uppermost internode stopped 4 to 5 d after start of submergence of the plants. At this time, a new internode started to elongate. Hence, submergence leads to the induction of growth of the two upper internodes of the culm, whereby the uppermost one shows the stronger and longer lasting response. In the present investigation, we only analyzed the growth response of the uppermost internode.

Effect of Submergence on Extensibility and Tissue Tension. Based on cell-size analysis, Bleecker *et al.* (2) have described three zones of internodal development: a zone of cell division and elongation at the base of the internode (intercalary meristem); a zone of cell elongation without concomitant cell division and a zone of differentiation where neither cell division nor cell elongation occurs. In the present investigation, we have only analyzed the mechanical properties of the tissue in the zone of cell elongation (Fig. 1d). Submergence of the plants led to an increase in both the E_{el} and E_{pl} *in vivo* extensibility of the growing region (Fig. 3). The time course of elongation growth of the uppermost internode and *in vivo* extensibility of the tissue, measured in the same sections, is shown in Figure 4. Submergence led to a rapid induction of elongation growth; 3 d after

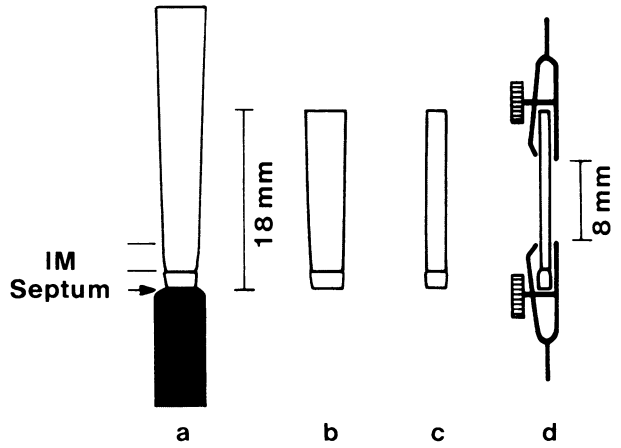

FIG. 1. Scheme illustrating the procedure to obtain internode segments and to measure their *in vivo* extensibility. Segments, 18 mm in length, were cut at the nodal septum of the basal region of the uppermost internode after the leaf sheath had been removed (a). The segments (b) were cut longitudinally into four equal, 2 to 2.5 mm wide quarters (c). One internode segment was fixed between the clamps (distance 8 mm) of a constant stress extensiometer (Fig. 1c in Ref. 14) submerged in distilled water, and stretched by application of a constant force (d). IM = intercalary meristem.

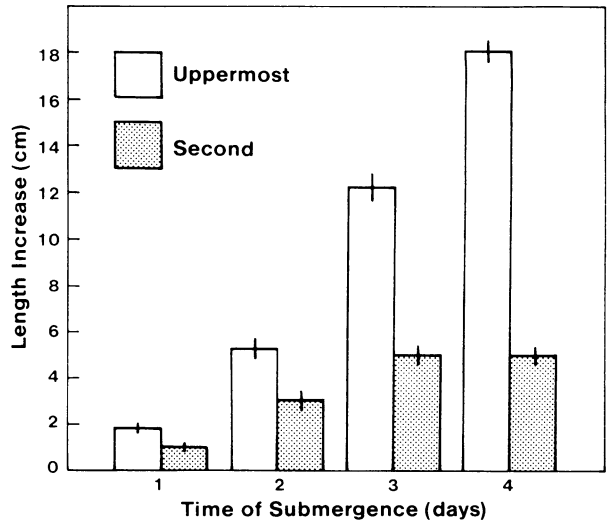

FIG. 2. Effect of partial submergence on growth of the two upper internodes. The nodes of the uppermost and second internodes were marked with ink on the surrounding leaf sheath on day zero. The plants were submerged for 1 to 4 d, and the length increase of the internodes was measured. Mean (±SE) of 10 measurements each.

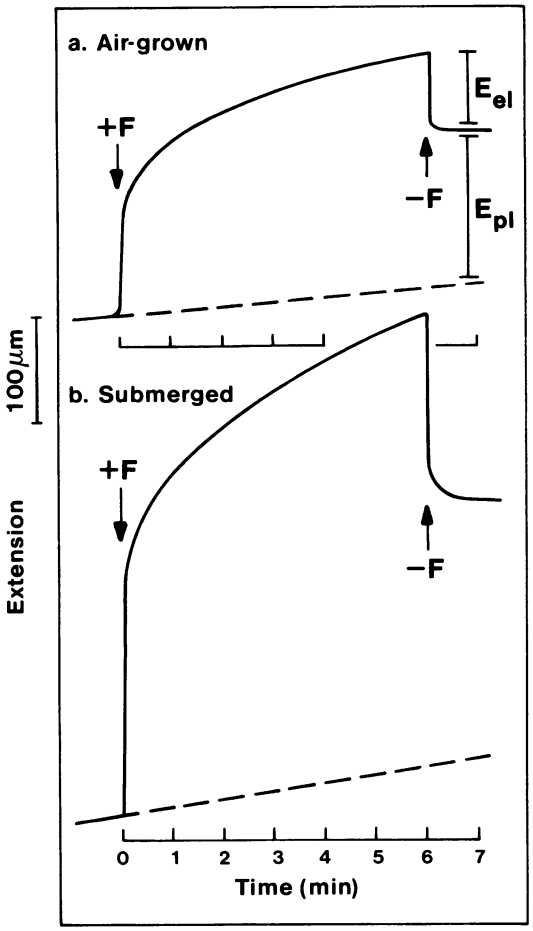

FIG. 3. Chart-recorder tracings (10 mm min^{-1}) showing the length changes of the tissue during *in vivo* extensibility measurements. The plants were either kept in air (a) or were submerged for 3 d (b). Internode segments were excised from the growing region as shown in Figure 1, a to c. The excised segments were fixed between the clamps (Fig. 1d) and submerged in distilled water. After application of a constant force of 0.098 N (10 g, +F) and removal of the force (−F), the elastic (E_{el}) and plastic extensibility (E_{pl}) was determined as indicated. Dashed lines: length change without application of a force.

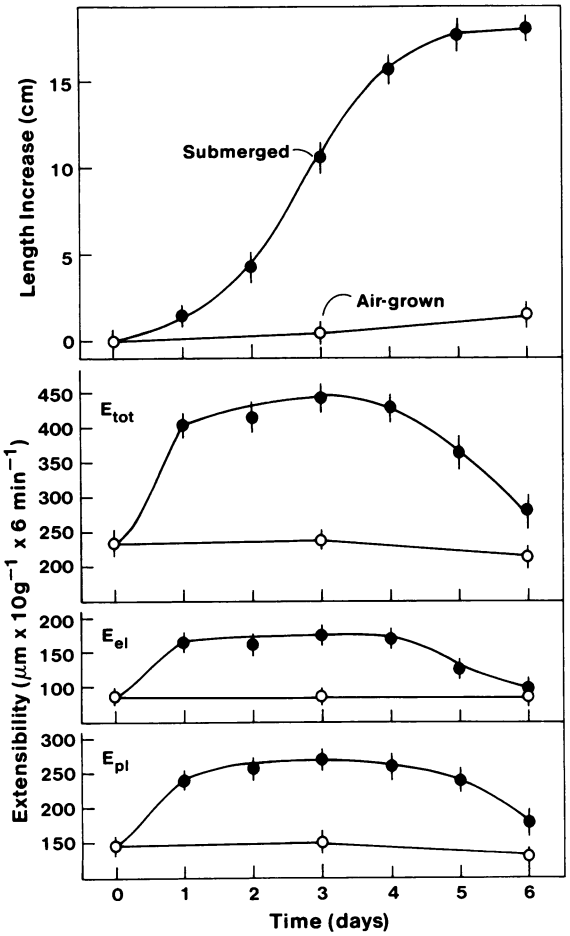

FIG. 4. Time course of the effect of partial submergence on growth of the uppermost internode (top panel) and *in vivo* extensibility of the growing region of the same tissue (lower three panels). The nodes of the internodes were labeled on the surrounding leaf sheath on day zero. After subsequent days, the length increase of the internodes and the extensibility (E_{tot}, E_{el}, E_{pl}) of excised internode segments was measured. Each point represents mean (±SE) of six to nine measurements.

start of submergence, the growth rate reached a maximum of about 2.6 mm h^{-1}, whereas in control (air-grown) plants a rate of about 0.1 mm h^{-1} was measured. Thus, submergence caused a *ca.* 26-fold increase in the growth rate within 3 d after start of the treatment. E_{tot} of the growing region increased rapidly in the submerged plants and reached a maximum (86% increase) 3 d after start of the experiment. Thereafter, E_{tot} decreased as growth of the internode ceased. In the air-grown plants, no increase in E_{tot} was detectable. The rise in both E_{el} and E_{pl} in submerged plants was initially more rapid than the increase in internodal elongation. After 3 d, the decline in E_{el} and E_{pl} was correlated to the decrease in growth of the internode. The increase in E_{el} was, presumably, caused by the development of tissue tension in the growing region of the internodes. During the first 4 d of submergence, excised internode segments displayed a rapid, elastic outward bending upon transfer to water (Fig. 5). In air-grown tissue, no such elastic bending was detectable.

Effect of Submergence on Osmotic Potential. The osmotic potentials of frozen-thawed tissue from the growing region of air-grown plants and plants submerged for 3 d are given in Table 1. In the rapidly growing tissue, the osmotic potential was 18% higher than that in the air-grown control tissue. This indicates that the supply of osmotica into the expanding cells cannot completely keep pace with the water uptake of the growing organ. Nevertheless, the relatively small difference in the osmotic potentials indicates that osmoregulation takes place in the rapidly expanding internodes (7). The osmotic potentials obtained with the hygrometer are, presumably, an overestimation of the osmotic pressure of the cells. Cosgrove and Cleland (5) have shown that considerable amounts of osmotically active solutes can be present in the free space of the cell wall of growing tissues. We have measured the osmotic potential of the whole organ which may include osmotica within the cell walls.

Effect of Submergence on the Hydraulic Conductance. The hydraulic conductance is a complex transport coefficient that includes the specific membrane hydraulic conductivity and the volume and area geometries of the tissue (6). The kinetics of tissue shrinkage (water efflux) and swelling (water influx) were used to evaluate a possible change in this parameter resulting from submergence of the plants. To overcome the low water conductivity of the cuticle, the surface of the segment was abraded before start of the experiment. As shown in Figure 6, no significant difference in the kinetics of tissue shrinkage after addition of mannitol was detectable between air-grown and submerged plants. Likewise, the rapid swelling of the tissue after the osmoticum had been replaced by water was not affected by submergence. In order to quantitate these kinetics, the rates of

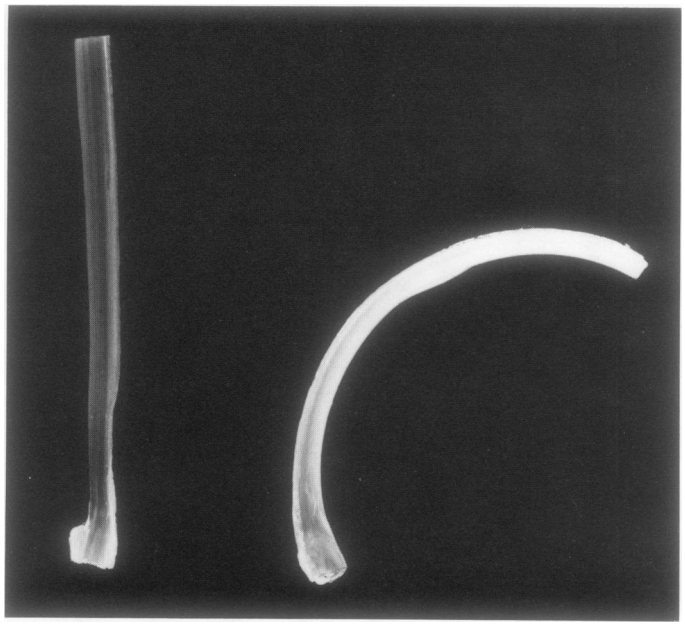

FIG. 5. Demonstration of tissue tension in the growing region of the uppermost internode after submergence of the plant. Longitudinal segments were cut from the internodes of plants (Fig. 1a–c) which were either grown in air (left) or partially submerged for 3 d (right). The internode segments were incubated for 5 min in distilled water before the photograph was taken.

Table I. *Growth of the Uppermost Internode and Osmotic Potential of the Growing Region in Air-Grown and Submerged Plants*

The nodes of the uppermost internodes were marked with ink on the surrounding leaf sheath. After 3 d in air or of submergence, the length increase was measured. The basal growing region (Fig. 1b) was excised and the osmotic potential of the frozen-thawed tissue measured. Mean (±SE) of 16 measurements each.

Treatment	Increase in Internodal Length	Osmotic Potential
	cm	*bar*
Air-grown	1.0 ± 0.2	−18.0 ± 0.6
Submerged	12.3 ± 0.5	−14.8 ± 0.8

length change (V) in the approximately linear range of the curves were calculated graphically as indicated in Figure 6. The results show that submergence does not affect the hydraulic conductance of the tissue.

Effect of Ethylene and GA on Extensibility. Excised stem sections respond to submergence with a rapid increase in growth (20). As shown in Figure 7d, internodes of submerged sections grew by 4.2 cm during 2 d. In intact plants, 2 d of partial submergence led to a length increase of 5.2 cm in the uppermost internode (Fig. 2). Thus, *ca.* 80% of the *in situ* response of the uppermost internode can be observed in excised stem sections submerged for 2 d. The growth response of the sections was accompanied by about a 100% increase in E_{el} and E_{pl} in the growing region of the internode (Fig. 7, a and d). The effect of submergence on growth and increase in extensibility could be simulated by treating nonsubmerged sections with ethylene (1 μL L^{-1}) or GA_3 (1 μM) (Fig. 7, b and c). This result shows that both ethylene and GA affect the mechanical properties of the cell walls. To elucidate the role of GA in the submergence response, TCY, an inhibitor of GA biosynthesis (19), was used. The effect of submergence on growth and increase in extensibility was completely abolished when TCY (1 μM) was included in the medium (Fig. 7e). The submergence response could be completely restored when GA_3 (1 μM) was added to the TCY (1 μM) solution (Fig. 7f).

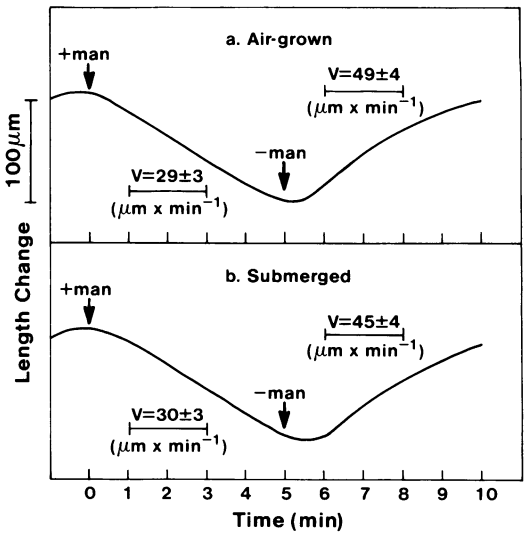

FIG. 6. Effect of submergence on the hydraulic conductance of the growing region. Segments were cut from the uppermost internode of plants which were either kept in air (a) or submerged for 3 d (b) as shown in Fig. 1, a to c. The surface of the tissue was abraded with wet emery cloth. The segment was fixed between the clamps (Fig. 1d) and the shrinkage after addition of mannitol (0.5 mol L^{-1}, + man) was recorded. After 5 min, the mannitol was replaced by distilled water (−man), and the expansion was measured over the next 5 min. The rates of length change (V) in the approximately linear range of the curves were calculated graphically and given as mean (±SE) of nine measurements each.

DISCUSSION

The results presented here demonstrate that the rapid elongation of the newly formed cells of submerged deepwater rice is correlated with an increase in the *in vivo* extensibility of the tissue (Fig. 4). During the first day of submergence, the increase in extensibility was greater than the increase in internodal growth. This may have been due to dilution of cellular solutes during the early response to submergence. Subsequently, this dilution appears to have been compensated by mobilization of osmotica (Table I) (21). Since the water conductance of the tissue is not changed as a result of submergence (Fig. 6) and the osmotic potential of the expanding cells is less negative (Table I), we conclude that growth is limited by the yielding of the cell walls.

The measured increase in E_{el} is probably caused, in part, by the tissue tension of the newly formed internode (Fig. 5). Tissue tension has recently been defined as the difference in the longitudinal wall stress between the outer epidermal wall and the inner cell walls (13, 15). Thus, the elongation response can be accounted for by an increase in the E_{pl} of the growing region. The wall loosening process is presumably localized in the peripheral cell layers of the organ (13, 15).

Using the GA-biosynthesis inhibitor TCY (19), Raskin and Kende (22) provided evidence that GA is causally involved in the stimulation of cell division and cell elongation in submerged deepwater rice internodes. The data reported in Figure 7 confirm and extend this conclusion. The effect of submergence on increase in growth and *in vivo* extensibility of excised stem sections (Fig. 7, a and d) is completely abolished when TCY is included in the medium (Fig. 7e). This inhibition of growth and wall loosening can be restored by adding GA_3 to the solution in which the sections are submerged (Fig. 7f). This result indicates that GA is involved in the loosening process (increase in E_{pl}) of the cell walls.

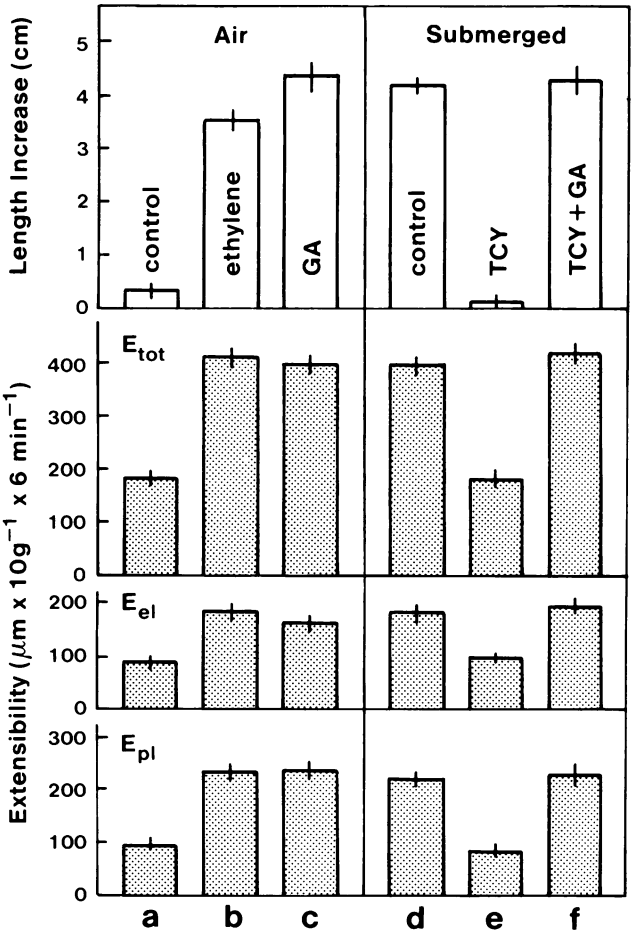

FIG. 7. Effect of submergence, ethylene, GA_3, and TCY on internodal growth (top panel) and *in vivo* extensibility of the growing region (lower three panels) of excised sections. Stem sections were excised from plants which were either pretreated with water (a–d) or TCY (1 μM) (e, f) for 7 d. In the first set of experiments (a–c) the sections were placed in beakers containing 40 ml of either distilled water (a, b) or GA_3 (1 μM) (c) and placed inside 2.5-L cylinders through which air (a, c) or air + ethylene (1 μL L^{-1}) (b) was passed at a flow rate of 60 mL min^{-1}. In the second set of experiments (d–f), the sections were submerged in either distilled water (d) or TCY (1 μM) (e) or TCY (1 μM) + GA_3 (1 μM) (f). After 2 d of treatment, the length increase of the internodes and the extensibility (E_{tot}, E_{el}, E_{pl}) of excised internode segments from the growing region were measured. The data represent means (±SE) of 10 measurements each.

Lockhart (16) was the first to postulate that the mechanism of action of GA is "through an effect on cell wall plasticity." Subsequent extensibility measurements on *Avena* stem sections have shown that GA acts by increasing the yielding properties of the cell walls (1, 9). However, in cucumber hypocotyls Cleland *et al.* (3) were unable to detect a significant effect of GA on cell wall extensibility under conditions where growth was greatly stimulated. They suggested that GA might promote growth in this organ by a decrease in the osmotic potential of the cells. This hypothesis was supported by experimental evidence of Katsumi *et al.* (10). Our results are in agreement with the investigations on *Avena* stem sections, in which a large effect of GA on the plastic extensibility has been reported (1, 9). Thus, GA may stimulate cell elongation in stem sections of monocotyledonous plants such as rice or oat by an increase in wall plasticity.

For continuous organ expansion, the growing cells must maintain a sufficiently high concentration of osmotically active solutes (negative osmotic potential), *i.e.* osmoregulation must take place (7). As pointed out by Cosgrove (7), little is known about the mechanisms controlling cell osmotic potential. Our results (Table I) show that on d 3 the osmotic potential of the rapidly expanding organ is only 18% less negative than that of the slowly growing control. This indicates that osmoregulation takes place in the submerged plant. Raskin and Kende (21) have shown that 3 d of submergence led to the mobilization of 65% of the starch from those regions of the internode which had been formed prior to submergence. The disappearance of starch was accompanied by a 70-fold enhancement of amylolytic activity in the growing internode (21, 24). In addition, submergence caused a 26-fold increase in the translocation of newly synthesized photosynthetic assimilates from the leaves to the growing internode (21). These biochemical and physiological processes may, in part, be responsible for the relatively small rise in the osmotic potential of the rapidly growing cells and are, therefore, important for continued internodal growth.

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LITERATURE CITED

1. ADAMS PA, MJ MONTAGUE, M TEPFER, DL RAYLE, H IKUMA, PB KAUFMAN 1975 Effect of gibberellic acid on the plasticity and elasticity of *Avena* stem segments. Plant Physiol 56: 757–760
2. BLEECKER AB, JL SCHUETTE, H KENDE 1986 Anatomical analysis of growth and developmental patterns in the internode of deepwater rice. Planta 169: 490–497
3. CLELAND R, ML THOMPSON, DL RAYLE, WK PURVES 1968 Difference in effects of gibberellins and auxins on wall extensibility of cucumber hypocotyls. Nature 219: 510–511
4. CLELAND RE 1981 Wall extensibility: hormones and wall extension. *In* W Tanner, TA Loewus, eds, Encyclopedia of Plant Physiology, NS, Vol 13b: Plant Carbohydrates II. Extracellular Carbohydrates. Springer-Verlag, Heidelberg, pp 255–273
5. COSGROVE DJ, RE CLELAND 1983 Solutes in the free space of growing stem tissues. Plant Physiol 72: 326–331
6. COSGROVE DJ 1985 Cell wall yield properties of growing tissue. Evaluation by *in vivo* stress relaxation. Plant Physiol 78: 347–356
7. COSGROVE DJ 1986 Biophysical control of plant cell growth. Annu Rev Plant Physiol 37: 377–405
8. JACKSON MB 1985 Ethylene and responses of plants to soil waterlogging and submergence. Annu Rev Plant Physiol 36: 145–174
9. JONES RL 1983 The role of gibberellins in plant cell elongation. CRC Crit Rev Plant Sci 1: 23–47
10. KATSUMI TM, H KAZAMA, N KAWAMURA 1980 Osmotic potential of the epidermal cells of cucumber hypocotyls as affected by gibberellin and cotyledons. Plant Cell Physiol 21: 933–937
11. KENDE H 1987 Studies on internodal growth using deepwater rice *In* DJ Cosgrove, DP Knievel, eds, Physiology of Cell Expansion during Plant Growth. American Society of Plant Physiologists, Rockville, MD, pp 227–238
12. KUTSCHERA U, P SCHOPFER 1986 *In-vivo* measurement of cell-wall extensibility in maize coleoptiles. Effects of auxin and abscisic acid. Planta 169: 437–442
13. KUTSCHERA U, R BERGFELD, P SCHOPFER 1987 Cooperation of epidermis and inner tissues in auxin-mediated growth of maize coleoptiles. Planta 170: 168–180
14. KUTSCHERA U, WR BRIGGS 1987 Differential effect of auxin on *in vivo* extensibility of cortical cylinder and epidermis in pea internodes. Plant Physiol 84: 1361–1366
15. KUTSCHERA U 1987 Cooperation between outer and inner tissues in auxin-mediated plant organ growth. *In* DJ Cosgrove, DP Knievel, eds, Physiology of Cell Expansion during Plant Growth. American Society of Plant Physiologists, Rockville, MD, pp 215–226
16. LOCKHART JA 1960 Intracellular mechanism of growth inhibition by radiation energy. Plant Physiol 35: 129–135
17. LOCKHART JA 1965 Cell extension *In* J Bonner, JE Varner, eds, Plant Biochemistry, Academic Press, New York, pp 826–849
18. MÉTRAUX J-P, H KENDE 1983 The role of ethylene in the growth response of submerged deep water rice. Plant Physiol 72: 441–446
19. RADEMACHER W, J JUNG, JE GRAEBE, L SCHWENEN 1984 On the mode of action of tetcyclacis and triazole growth retardants. *In* R Menhenett, DK Lawrence, eds, Biochemical Aspects of Synthetic and Naturally Occurring Plant Growth Regulators. British Plant Growth Regulator Group Monograph 11, Wantage, UK, pp 1–11
20. RASKIN I, H KENDE 1984 Regulation of growth in stem sections of deep-water

Rice Planta 160: 66–72
21. RASKIN I, H KENDE 1984 Effect of submergence on translocation, starch content and amylolytic activity in deep-water rice. Planta 162: 556–559
22. RASKIN I, H KENDE 1984 Role of gibberellin in the growth response of submerged deep water rice. Plant Physiol 76: 947–950
23. SACHS J 1865 Handbuch der Experimentalphysiologie der Pflanzen. Engelmann, Leipzig.
24. SMITH MA, JV JACOBSEN, H KENDE 1987 Amylase activity and growth in internodes of deepwater rice. Planta 172: 114–120
25. TAIZ L 1984 Plant cell expansion: regulation of cell wall mechanical properties. Annu Rev Plant Physiol 35: 585–657
26. VERGARA BS, B JACKSON, RS DE DATTA 1976 Deep water rice and its response to deep water stress. *In* Climate and Rice, International Rice Research Institute, Los Baños, Philippines, pp 301–319