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On the Role of Abscisic Acid and Gibberellin in the Regulation of Growth in Rice[1]

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ABSTRACT

Submergence induces rapid elongation of rice coleoptiles (*Oryza sativa* L.) and of deepwater rice internodes. This adaptive feature helps rice to grow out of the water and to survive flooding. Earlier, we found that the growth response of submerged deepwater rice plants is mediated by ethylene and gibberellin (GA). Ethylene promotes growth, at least in part, by increasing the responsiveness of the internodal tissue to GA. In the present work, we examined the possibility that increased responsiveness to GA was based on a reduction in endogenous abscisic acid (ABA) levels. Submergence and treatment with ethylene led, within 3 hours, to a 75% reduction in the level of ABA in the intercalary meristem and the growing zone of deepwater rice internodes. The level of GA_1 increased fourfold during the same time period. An interaction between GA and ABA could also be shown by application of the hormones. ABA inhibited growth of submerged internodes, and GA counteracted this inhibition. Our results indicate that the growth rate of deepwater rice internodes is determined by the ratio of an endogenous growth promoter (GA) and a growth inhibitor (ABA). We also investigated whether ABA is involved in regulating the growth of rice coleoptiles. Rice seedlings were grown on solutions containing fluridone, an inhibitor of carotenoid and, indirectly, of ABA biosynthesis. Treatment with fluridone reduced the level of ABA in coleoptiles and first leaves by more than 75% and promoted coleoptile growth by more than 60%. Little or no enhancement of growth by fluridone was observed in barley, oat, or wheat. The involvement of ABA in determining the growth rate of rice coleoptiles and deepwater rice internodes may be related to the semiaquatic growth habit of this plant.

Rice (*Oryza sativa* L.) has a number of physiological and metabolic adaptations that enhance its chances for survival under conditions of temporary flooding. One of these is the capacity of plants to elongate rapidly when they become submerged. This feature helps rice plants to emerge from the water and to avoid drowning. In seedlings, submergence promotes coleoptile growth (7, 26, 30) and in adult deepwater rice plants, elongation of the internode (12, 27). In both instances, the plants respond to the altered gas composition of their submerged organs, namely to reduced partial pressure of O_2, to increased partial pressure of CO_2, and to the accumulation of ethylene (8, 13, 15–17; for a review, see ref. 5). In rice seedlings, coleoptile growth is promoted independently and to the same extent by low levels of O_2 and high levels of CO_2, and by ethylene (16), and an interaction of the internal gas atmosphere with auxin is indicated (5). In deepwater rice, the chain of events leading from submergence to increased internodal growth is better understood than in rice seedlings. Low partial pressures of O_2 promote ethylene biosynthesis (17) by enhancing the activity of the ethylene-biosynthetic enzyme 1-aminocyclopropane-1-carboxylate synthase (2). Ethylene promotes growth, at least in part, by increasing the responsiveness of the internodal tissue to GA[2] (18).

In the studies described below, we investigated one possible mechanism by which ethylene may modulate the responsiveness of deepwater rice internodes to GA. Zeevaart (31) found that applied ethylene reduced the level of ABA in leaves of *Xanthium strumarium*. Thus, increased responsiveness to GA in deepwater rice may be based on an ethylene-mediated reduction in the level of endogenous ABA, a potent inhibitor of growth in rice. To examine this possibility, we measured the level of ABA in the intercalary meristem and the growing zone of deepwater rice plants that had been induced to grow rapidly by submergence or treatment with ethylene. We also determined the level of GA in the same tissue. These experiments were designed to test our working hypothesis that the rate of internodal growth in deepwater rice is determined by the balance of GA, a growth promoter, and of ABA, a growth inhibitor. We supplemented these studies with experiments with rice seedlings, in which the endogenous level of ABA can be reduced with fluridone, an inhibitor of carotenoid biosynthesis. Results of this work have been reported earlier (4).

MATERIALS AND METHODS

Growth of Plants

Seeds of rice (*Oryza sativa* L., cv M-9 for experiments with seedlings and cv Habiganj Aman II for experiments with deepwater rice), wheat (*Triticum vulgare*, cv Ionia), oat (*Avena sativa*, cv Korwood), and barley (*Hordeum vulgare*, cv Lakeland) were allowed to imbibe in darkness as described by Raskin and Kende (16) and transferred to incubation jars under green light after 2 d. Adult plants were grown as described by Stünzi and Kende (22), except that the day

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[2] Abbreviations: GA, gibberellin; GC, gas chromatography.

temperature was 27°C for 11 h centered within a 13-h photoperiod.

Treatment of Seedlings

Germinated seeds were transferred to 1-L glass jars containing 150 mL of vermiculite wetted with either 80 mL of distilled water, 1 μM ABA, or 30 μM fluridone (1-methyl-3-phenyl-5-[3-(trifluoromethyl)phenyl]-4(4*H*)pyridonone, a gift of Eli Lilly, Indianapolis, IN). Fluridone was dissolved in acetone, which, upon dilution, had a final concentration of 0.5%; in these experiments, the water used for control treatments also contained 0.5% acetone. The jars, which had gas inlet and outlet ports, were sealed, and the seedlings were grown in the dark at 27°C under a continuous flow of humidified air (60 mL/min) from which ethylene had been removed by passage through a column (25 cm long, 7 cm i.d.) packed with Purafil (Purafil, Inc., Atlanta, GA). Four days after imbibition, growth of the seedlings was measured, and the coleoptiles or coleoptiles plus first leaves were harvested and frozen in liquid N_2 for further analysis.

Treatment of Whole Plants

Adult plants were submerged as described by Métraux and Kende (12). For ethylene treatment, they were placed in plastic cylinders through which air or air containing 3 to 5 μL/L ethylene was passed at a rate of 400 mL/min (12). These treatments were performed in the same growth chamber in which the plants had been grown. At various times, the basal 1-cm portion of the youngest internode containing the intercalary meristem and part of the elongation zone above it was harvested and frozen in liquid N_2. Submergence and treatment with ethylene were performed with 8- to 12-week-old plants.

Isolation and Treatment of Stem Sections

Stem sections containing the youngest internode were excised from 9- to 10-week-old plants as described by Raskin and Kende (17). They were either submerged in glass cylinders containing 4 L of water with or without GA and/or ABA or kept in plastic cylinders through which humidified air was passed at a rate of 80 mL/min. The increase in internodal length was measured after 3 d of growth under continuous light.

ABA Extraction and Determination

ABA from the basal 1-cm portion of internodes and from coleoptiles was extracted according to Walker-Simmons (28) and either phase partitioned with ethyl acetate for ELISA or purified by HPLC and measured by GC (32). The ELISA was performed as described by Walker-Simmons (28) with the monoclonal antibody of Mertens *et al.* (11), which was purchased from Idetek (San Bruno, CA). The ABA-4′-conjugate was prepared according to Weiler (29). The results obtained by ELISA were validated by HPLC-GC (results not shown).

GA Extraction and Determination

The basal 1-cm portions of internodes from submerged and air-grown plants were collected over a period of several weeks and frozen. Tissue collected from 40 to 100 plants was lyophilized yielding 1 to 3 g (dry wt) of material. GAs were extracted, purified, and separated according to Talon and Zeevaart (25). In brief, GAs from rice tissue were extracted overnight, first in 100% and then in 80% (v/v) methanol. They were purified by phase partitioning with hexanes and ethyl ether, by adsorption chromatography with charcoal:Celite (1:2), another phase partitioning with ethyl acetate, and chromatography on a QAE-Sephadex A-25 column. They were separated by reverse-phase HPLC. Fractions corresponding to GA_1 and GA_{20} were analyzed by GC-selected ion monitoring as described by Talon and Zeevaart (25). The ions monitored were for $GA_1/[^2H_2]GA_1$-methyl ester trimethylsilyl ether (m/z 508, 506, 450, 448) and for $GA_{20}/[^2H_2]GA_{20}$-methyl ester trimethylsilyl ether (m/z 420, 418, 377, 375). GA concentrations were quantified as in Talon and Zeevaart (25).

Statistical Analysis

The data shown in Figures 5 and 6 were subjected to analysis of variance for a randomized complete block design with three (submergence) or four (treatment with ethylene) replicates (21). One block consisted of one series of ABA determinations from plants that were air grown, submerged, or treated with ethylene for various time periods.

RESULTS

Experiments with Rice Seedlings

In rice seedlings grown on 30 μM fluridone, coleoptile growth was stimulated by more than 60%, and the ABA content was reduced in both the coleoptile and the coleoptile plus the first leaf by 66% and 77%, respectively (Table I). Fluridone inhibited mesocotyl growth as well as root growth. To investigate further the role of ABA in regulating the growth of rice coleoptiles, seedlings were grown on 1 μM

Table I. *ABA Concentrations and Growth in Rice Coleoptiles*

Length (top) and levels of ABA in rice coleoptiles plus primary leaves (middle) and in rice coleoptiles alone (bottom). Seedlings were grown on water (control) or 30 μM fluridone. The values for length represent the means ± SE of 45 seedlings. The values for ABA levels represent the means ± SE of three experiments (each with 50–100 seedlings). The numbers in parentheses indicate percent of control.

	Treatment	
	Control	Fluridone
Length (mm)		
Coleoptile	16.3 ± 0.4	26.7 ± 0.6 (164%)
Mesocotyl	3.2 ± 0.4	2.6 ± 0.2 (81%)
Roots	50.7 ± 3.7	30.4 ± 1.3 (60%)
ABA in coleoptile plus primary leaf (ng/g fresh wt)	9.2 ± 0.9	2.1 ± 0.2 (23%)
ABA in coleoptile (ng/g fresh wt)	7.0 ± 0.7	2.4 ± 1.2 (34%)

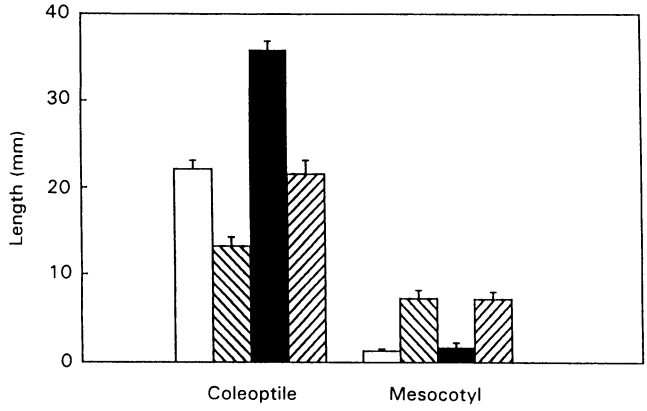

Figure 1. Response of rice seedlings to ABA and fluridone. Treatment was started at imbibition, and measurements were taken after 4 d. □, Water control; ▧, 1 μM ABA; ■, 30 μM fluridone; ▨, 30 μM fluridone and 1 μM ABA. The bars represent the means ± SE of 15 seedlings.

ABA, 30 μM fluridone, or fluridone plus ABA (Fig. 1). ABA treatment reduced growth of rice coleoptiles by 40% when compared with the control, whereas fluridone promoted coleoptile elongation as found before. When ABA and fluridone were added simultaneously, fluridone-induced growth was eliminated. The response of the mesocotyl was the opposite of that of the coleoptile. Its growth was stimulated by ABA as reported earlier by Takahashi (24) and was reduced by fluridone (Fig. 1).

Treatment with fluridone for 4 d promoted the growth of wheat, oat, and barley coleoptiles by 14%, 22%, and 14% above control, respectively (Fig. 2). In the same experiment, rice grown on fluridone for 4 d showed a 67% increase in coleoptile length. When fluridone was added during the last 2 d of incubation, it had no effect on the growth of oat and barley coleoptiles, and the effect on wheat was the same as

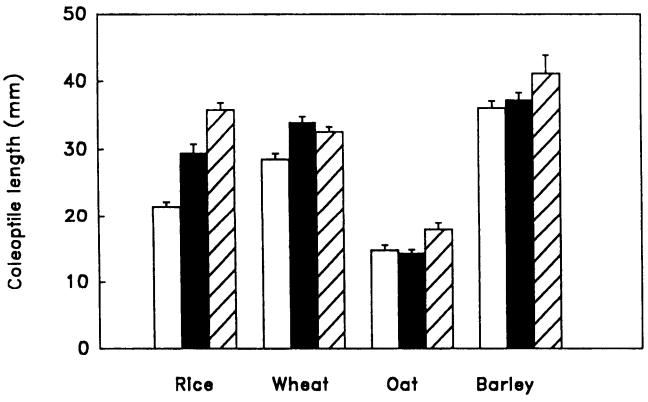

Figure 2. Growth of rice, wheat, oat, and barley coleoptiles in response to treatment with 30 μM fluridone. □, Water control; ■, fluridone present during the last 2 d of growth; ▨, fluridone present during 4 d of growth. The length of the coleoptiles was measured 4 d after the start of imbibition. The bars represent the means ± SE of 20 (control and 2 d of treatment) and 15 (4 d of treatment) coleoptiles.

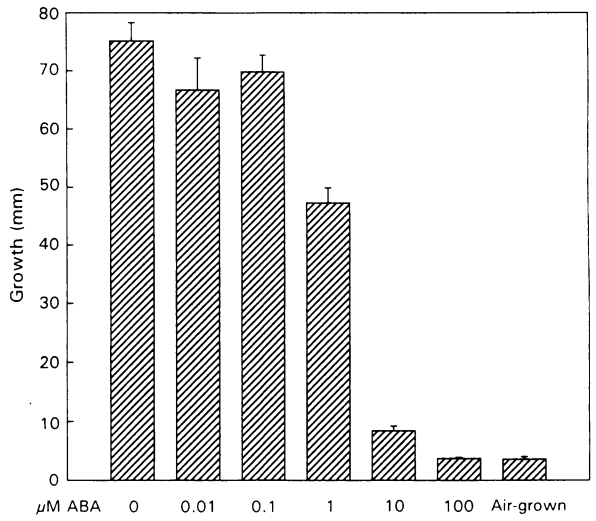

Figure 3. Growth of deepwater rice stem sections submerged for 3 d in water containing one of several concentrations of ABA. The air-grown sections were kept in a glass cylinder with an air flow of 80 mL/min. The values represent the means ± SE of 22 to 30 sections.

that observed after 4 d. Over a 2-d period, fluridone promoted rice coleoptile elongation by 37%.

Experiments with Adult Deepwater Rice Plants

Stem sections isolated from adult deepwater rice plants were either kept in air or submerged in cylinders containing water and one of several concentrations of ABA (Fig. 3). At a concentration of 1 μM, ABA reduced submergence-induced growth by 30%; at 100 μM, it eliminated it completely. This inhibition was reversed by the addition of GA_3 to sections submerged in 3 μM ABA (Fig. 4).

Two sets of experiments were performed to assess the effect of submergence and ethylene treatment on the ABA content of the intercalary meristem and the elongation zone of deepwater rice internodes. In one set, plants were immersed in 300-L plastic tanks filled with water or were kept in air in the same growth chamber. In the second set, deepwater rice plants were placed in plastic cylinders through which ethylene-free air or air containing 3 to 5 μL/L ethylene was passed. Within 1 h of submergence, the ABA level in the intercalary meristem and the cell elongation zone above it decreased by more than 50% (Fig. 5). After 3 h, it was reduced by 75% and it decreased further during the next 21 h. In air-grown control plants, the ABA content remained at its original level. These data were subjected to analysis of variance for a randomized complete block design with three replicates. The differences in ABA levels between different treatments were highly significant (F test; $df = 7,13$; $P < 0.005$) with a highly significant effect of submergence (F test; $df = 1,13$; $P < 0.005$).

In deepwater rice plants treated for 3 h with ethylene, the ABA level in the intercalary meristem and the cell elongation zone was 75% lower than that of the corresponding control plants at the same time (Fig. 6). This difference in the ABA

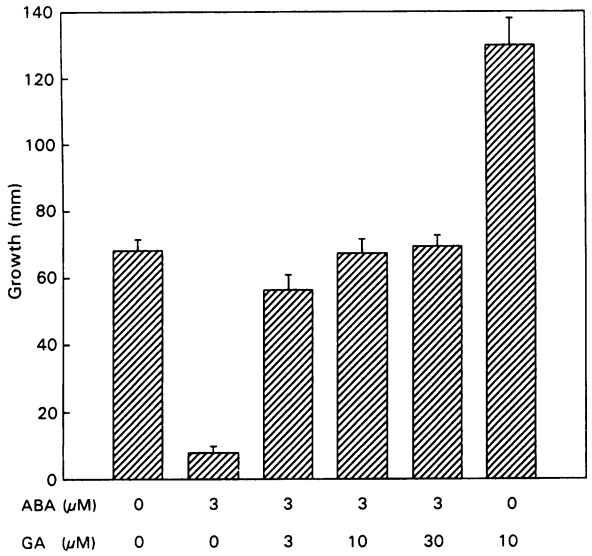

Figure 4. Growth of deepwater rice stem sections submerged for 3 d in water, in 3 μM ABA, in 3 μM ABA plus one of several concentrations of GA_3, or in 10 μM GA_3 alone. The values represent the means ± SE of 22 to 30 sections.

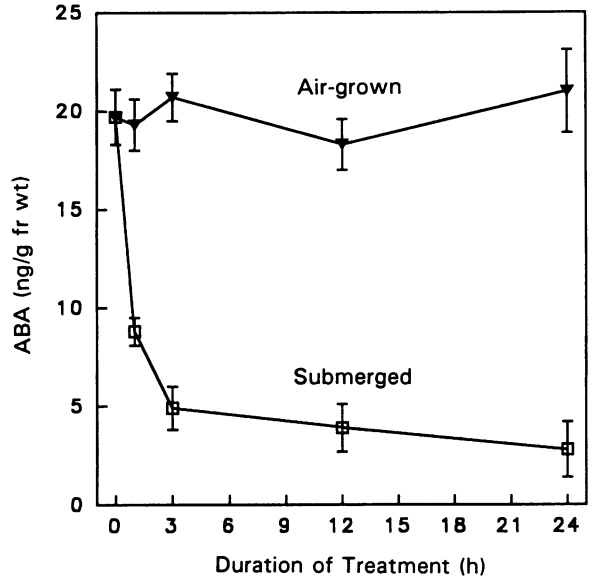

Figure 5. Effect of submergence on the level of ABA in deepwater rice. Plants were submerged in 300-L tanks filled with water (□) or kept in air as a control (▼). One-centimeter portions containing the intercalary meristem and part of the cell elongation zone above it were excised for extraction from the internodes at the times indicated. Each point represents the mean ± SE of three independent experiments. Analysis of variance using a randomized complete block design showed a highly significant effect of submergence ($P < 0.005$; see text).

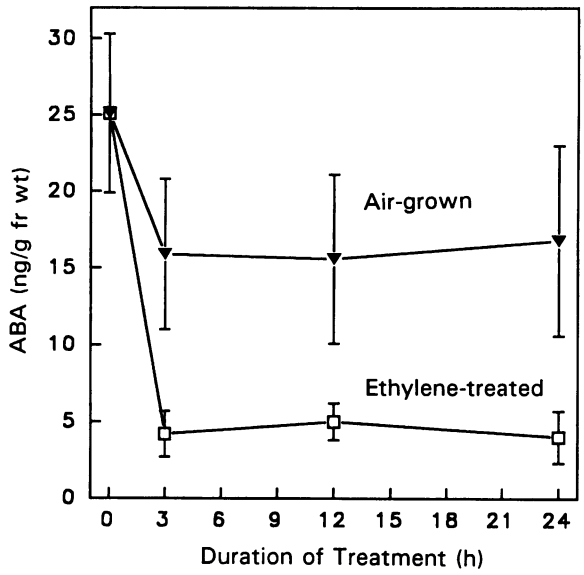

Figure 6. Effect of ethylene on the level of ABA in deepwater rice. Plants were grown in plastic cylinders through which ethylene-free air (▼) or air containing 3 to 5 μL/L ethylene (□) was circulated at a flow rate of 400 mL/min. One-centimeter portions containing the intercalary meristem and part of the cell elongation zone above it were excised for extraction from the internodes at the times indicated. Each point represents the mean ± SE of four independent experiments. Analysis of variance using a randomized complete block design showed a significant effect of ethylene ($P < 0.005$; see text).

concentrations was maintained over the next 21 h. Again, the data were evaluated by analysis of variance for a randomized complete block design with four replicates. There were significant differences in ABA content between different treatments (F test; $df = 5,15$; $P = 0.025$) with a highly significant effect of ethylene (F test; $df = 1,15$; $P < 0.005$).

We determined the amount of the endogenous GA_1 and GA_{20} in the intercalary meristem and internodal elongation zone of deepwater rice plants that had been submerged for 0, 1, 3, and 24 h (Table II). The level of GA_1 increased

Table II. *GA Concentrations in Deepwater Rice*

Levels of GA_1 and GA_{20} in the intercalary meristem and cell elongation zone of internodes of adult deepwater rice plants grown in air or submerged for various time periods. Tissue for this experiment was harvested over a period of several weeks (about 60 plants per time point). A repetition of the GA_1 determinations with a second batch of tissue showed similar increases and similar amounts of GA_1.

Duration of Treatment	GA_1	Relative Level	GA_{20}	Relative Level
h	*ng/g dry weight*		*ng/g dry weight*	
0	15.2	1.0	12.5	1.0
1	18.9	1.2	ND[a]	ND[a]
3	62.3	4.1	19.4	1.6
24	63.0	4.1	40.9	3.3

[a] ND, not determined.

fourfold within 3 h of submergence. The level of GA_{20}, which is the immediate precursor of GA_1, also increased but more slowly than that of GA_1. After 24 h of submergence, it was 3 times higher than the original value. The GA extractions and quantifications were repeated with a second batch of plants and yielded similar results.

DISCUSSION

The results described above support the notion that the growth rate of rice coleoptiles and of deepwater rice internodes is determined not only by a growth-promoting plant hormone but also by a growth inhibitor, ABA. We showed that the level of endogenous ABA in rice seedlings is reduced by treatment with fluridone and that coleoptile growth in fluridone-treated seedlings is enhanced (Table I, Fig. 1). There is strong evidence that ABA is synthesized via an indirect pathway from carotenoids (10, 19). Because fluridone is an inhibitor of carotenoid biosynthesis (1, 3), its effect on ABA levels and growth in rice coleoptiles can be explained in terms of reduced ABA formation. Inhibition of ABA biosynthesis by fluridone has been found previously (3, 20). In maize seedlings, ABA content is increased and shoot elongation is inhibited at low water potential (20). Treatment with fluridone counteracted the effect of low water potential; the increase in ABA level was inhibited and the reduction in shoot growth was suppressed. In contrast to our results with rice seedlings, shoot elongation and endogenous ABA content were little affected by fluridone in maize seedlings at high water potential (20). Similarly, fluridone affected the growth of well-watered wheat, oat, and barley seedlings little if at all (Fig. 2, and ref. 14). We propose that ABA, most likely in concert with auxin, plays a role in regulating coleoptile growth in rice but not in other graminaceous plants, *e.g.* wheat, oat and barley, which are not adapted to grow in water (16).

Elongation of deepwater rice internodes, like that of rice coleoptiles, is stimulated by submergence (12, 17, 27). There are, however, distinct differences in the growth response of seedlings and adult plants. Both are stimulated to grow at low partial pressures of O_2, high partial pressures of CO_2, and in the presence of ethylene (16, 17). In coleoptiles, these gases act independently of each other, each eliciting about one-third of the overall response (16). In adult plants, on the other hand, there is an interaction among O_2, CO_2, and ethylene (17). The hormonal basis for coleoptile and internodal growth appears to be different as well. Elongation of rice coleoptiles is not reduced by inhibitors of GA biosynthesis (S. Hoffmann-Benning and H. Kende, unpublished data) and is thought to require auxin (5). In contrast, internodal growth is completely dependent on the presence of GA (18). Ethylene promotes internodal elongation, at least in part, by increasing the responsiveness of the tissue to low concentrations of GA. In the presence of ethylene, the threshold of the response to GA is lowered and the initial magnitude of the response is increased (18). We hypothesized that ethylene may cause a reduction in endogenous ABA levels, as it does in *Xanthium* leaves (31), and that responsiveness to GA may be a function of ABA content. Our data support this view. The level of ABA decreased in the intercalary meristem and cell elongation zone of submerged and ethylene-treated internodes by 75% (Figs. 5 and 6), and the inhibition of internodal growth by ABA was fully reversed by GA (Fig. 4). The lag phase for the induction of growth by submergence is between 3 and 4 h (22); that for the reduction in ABA content is less than 3 h (Figs. 5 and 6). Therefore, the change in ABA levels precedes the growth response. Fluridone cannot be used to inhibit the biosynthesis of ABA in internodes of green, adult rice plants. Unlike germinating, etiolated seedlings, green tissue contains sufficient amounts of carotenoids that are converted to ABA (9).

The level of GA_1 in the intercalary meristem and cell elongation zone increases fourfold within 3 h of submergence, and that of GA_{20} increases threefold within 24 h (Table II). GA_1 is the active GA in rice, and GA_{20} is its immediate precursor (6). Our results are in agreement with those of Suge (23), who, using a bioassay, found an increase in GA levels upon submergence of deepwater rice plants. It is not known whether submergence or ABA affects GA content directly or whether the level of GA increases as a function of enhanced growth, *e.g.* because of the formation of new cells in the intercalary meristem.

On the basis of the results reported above, we can postulate two new links in the chain of events that leads from submergence to accelerated growth in deepwater rice. The reduced O_2 tension in submerged internodes promotes ethylene synthesis (17) by enhancing the activity of 1-aminocyclopropane-1-carboxylate synthase (2). In addition, ethylene is physically trapped in submerged internodes because of its low rate of diffusion in water. Ethylene enhances the responsiveness of deepwater rice internodes to GA (18), at least in part because of a reduction in endogenous ABA content. While the level of ABA decreases in submerged internodes, that of GA increases. Thus, rapid internodal growth of deepwater rice may result from an altered balance between a growth-promoting (GA) and a growth-inhibiting (ABA) hormone.

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