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In Vivo 1-Aminocyclopropane-1-Carboxylate Synthase Activity in Internodes of Deepwater Rice[1]

ENHANCEMENT BY SUBMERGENCE AND LOW OXYGEN LEVELS

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ABSTRACT

Inasmuch as the activity of 1-aminocyclopropane-1-carboxylate (ACC) synthase cannot be measured in homogenates of deepwater rice internodes (*Oryza sativa* L.), we have employed an *in vivo* assay to determine the activity of this enzyme. This assay is based on the accumulation of ACC in tissue kept under N_2. Submergence of whole plants or stem sections containing the uppermost, developing internode enhances the *in vivo* activity of ACC synthase in the stem. This stimulation of *in vivo* ACC-synthase activity is especially pronounced in the region of the internode containing the intercalary meristem and the elongation zone above it. Enhancement of *in vivo* ACC-synthase activity is evident after 2 hours of submergence and shows a peak after 4 hours. Reduced levels of atmospheric O_2, which promote ethylene synthesis and growth in internodes of deepwater rice, also enhance the *in vivo* activity of ACC synthase. Our results are consistent with the hypothesis that induction of ACC-synthase activity at low partial O_2 pressures is among the first biochemical events leading to internodal growth in deepwater rice.

Deepwater rice is grown mainly in regions of Southeast Asia which are flooded each year during the monsoon season. To keep at least part of the foliage above the rising waters, deepwater rice has the ability to grow very rapidly under conditions of partial submergence. In Bangladesh, internodal growth of up to 25 cm/d has been recorded (21). Under laboratory conditions, we have measured up to 8.5 cm of growth/d for one internode (11). The magnitude of the growth response and the fact that it can be induced rapidly (19) by a natural environmental signal, submergence, make deepwater rice a suitable plant for the study of growth. Accelerated growth of partially submerged plants can serve as reference to which growth elicited by hormonal and environmental factors can be compared. Using such a comparative approach, we found that the growth response of submerged plants can be mimicked by treating nonsubmerged plants or isolated stem sections with ethylene (14, 16), with a gas mixture containing low levels of O_2 (16, 19), or with GA_3 (17). Stem sections respond to growth-inducing conditions similarly as do intact plants (15, 16). They are easier to treat with gas mixtures and growth regulators than are whole plants, and a large number of such sections can be used per treatment. Under all the above conditions, internodal growth is based on acceleration of cell division in the intercalary meristem and on increased elongation of the newly formed cells (2, 15, 17).

The following chain of events appears to lead from submergence to accelerated internodal growth: the level of O_2 inside submerged stems decreases (16); submergence and reduced levels of O_2 induce ethylene synthesis (14, 16); ethylene enhances growth indirectly by increasing the activity of endogenous gibberellin (17). Radiolabeling experiments have shown that ethylene in deepwater rice is formed from methionine via ACC[3] (14). This conclusion is supported by the fact that ethylene synthesis and growth in rice internodes is suppressed by aminoethoxyvinylglycine and aminooxyacetic acid which are inhibitors of ACC synthase (14, 16). Submergence or low O_2 may enhance ethylene synthesis by either increasing the activity of ACC synthase or by stimulating the conversion of ACC to ethylene. The capacity of rice internodes to form ethylene from ACC is not affected by submergence (14). Hence, it seems likely that submergence and low O_2 concentrations enhance the activity of ACC synthase. We report here on the effect of submergence and low O_2 tensions on *in vivo* ACC-synthase activity in rice stems and on the distribution of this enzyme activity in different parts of the stem.

MATERIALS AND METHODS

Plant Material and Growth Conditions. Seeds of deepwater rice, *Oryza sativa* L., cv Habiganj Aman II, were obtained from the Bangladesh Rice Research Institute, Dacca. Conditions of germination, watering, and submergence were as described by Métraux and Kende (14). The growth conditions were slightly modified from those employed earlier (14). Plants were grown in Baccto Growers Mix (Michigan Peat Co., Houston, TX) instead of the complex soil mixture used before; the light period was extended to 16 h, and the temperature was 27°C during the day and 20°C during the night.

Rice stem sections, 20 cm long and containing the uppermost growing internode, were prepared as described by Raskin and Kende (16). To exclude localized effects of wounding on *in vivo* ACC-synthase activity, 'long' sections were used in some experiments. These were 30 to 40 cm in length and included the uppermost developing internode (2–8 cm long) as well as the fully grown internode below it. The long sections were excised 5 to 6 cm below the third highest and 20 cm above the second highest node. Stem sections were submerged or treated with gas mixtures according to Raskin and Kende (16). Ten to 15 sections were placed in upright position in a 100-ml glass beaker which was filled with glass beads to prevent the submerged sections

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[3] Abbreviations: ACC, 1-aminocyclopropane-1-carboxylic acid; MACC, 1-(malonylamino)cyclopropane-1-carboxylic acid.

from floating up. Each beaker containing sections was lowered to the bottom of a 4.5-L glass cylinder which was filled to the rim with distilled H_2O. For treatment with air or gas mixtures, 10 excised stem sections were placed upright in a 100-ml glass beaker containing 30 ml of distilled H_2O. Each beaker containing the sections was placed in a 2.5-L plastic cylinder, 60 cm deep. Air or a gas mixture was circulated through the cylinders at 100 ml min^{-1}. Nitrogen, O_2, and CO_2 were supplied from high-pressure cylinders. Gas mixtures were prepared with gas-pressure regulators and rotameters containing three calibrated flow-meter tubes equipped with high-accuracy valves and a mixing tube (Matheson, Joliet, IL). Compressed laboratory air was used for all flow-through air treatments. Gas mixtures were dispersed to the incubation cylinders through copper tubing. Gas concentrations were determined at the exit port of each incubation cylinder using a Carle model 8700 gas chromatograph equipped with a thermal conductivity detector. The experiments with sections were carried out at 27°C in continuous light (70 μmol m^{-2} s^{-1} photosynthetic photon flux density).

***In Vivo* Assay for ACC Synthase.** For reasons not understood, the activity of ACC synthase in homogenates of vegetative tissues is often either much lower than expected or not measurable at all (10, 23). This is also the case with ACC synthase from deepwater rice internodes (14). Adams and Yang (1) have shown that conversion of ACC to ethylene is blocked in a N_2 atmosphere and that ACC accumulates under these conditions. Therefore, accumulation of ACC under N_2 can serve as a measure for *in vivo* ACC-synthase activity. To estimate the *in vivo* activity of ACC synthase in rice, 10 stem sections were placed upright in a 100-ml beaker containing 30 ml water. Each beaker was lowered into a 2.5-L, 60-cm deep cylinder. Nitrogen, supplied from high-pressure cylinders through copper tubings, was circulated through these incubation chambers at a rate of 1 L min^{-1}. The O_2 content of the gas was checked at the exit port of each incubation cylinder and was found to be between 0.2 and 0.3%. Sections used as controls were treated identically but were incubated in aerated cylinders. The assays were performed under the same light and temperature conditions as described above for the treatment of stem sections. Immediately before incubation in N_2, the level of ACC in the tissue was very low, *e.g.* 0.2 nmol/g fresh weight in the intercalary meristem of submerged internodes. During incubation of these same internodes in N_2, the ACC level in the intercalary meristem rose steadily: it was 1.4 nmol/g fresh weight after 4 h and 4.9 nmol/g fresh weight after 8 h. We choose 6 to 8 h as incubation time in N_2 for the *in vivo* assay of ACC synthase. At the end of this incubation period, the tissue was frozen in liquid N_2.

Determination of ACC and Conjugated ACC. Frozen tissue (0.7–1 g) was ground in liquid N_2 in a mortar with a pestle. The resulting powder was extracted with 3 ml methanol, and the extract was centrifuged at 12,000*g* for 20 min. The supernatant was used for the determination of free and conjugated ACC (presumed to be MACC). The ACC conjugate was hydrolyzed by adding concentrated HCl to the supernatant to a final concentration of 2 N, followed by heating at 110°C for 4 h. The hydrolysate was neutralized with 2 N NaOH, and ACC was analyzed according to Lizada and Yang (13). The amount of conjugated ACC was determined by subtracting the amount of ACC in the nonhydrolyzed sample from that in the hydrolyzed sample. Ethylene was measured by GC (12).

We verified that all ethylene liberated from the extracts was formed from ACC. For this, extracts were chromatographed on cellulose thin layers using 1-butanol-glacial acetic acid-water (60:15:25, v/v) as solvent. An ACC standard was run in a separate lane beside each extract and was visualized with ninhydrin spray. The cellulose was scraped from the plates in zones corresponding to R_F values and was assayed directly for ACC as above. Only the zone corresponding to the R_F of the ACC standard yielded ethylene, and the entire amount of ACC in the original extract was recovered in the ACC zone of the thin-layer chromatogram (results not shown).

RESULTS

Localization of *in Vivo* ACC Synthase Activity in Rice Stems and Effect of Submergence. Twenty stem sections were submerged for 24 h and 20 kept in air as controls. To assay *in vivo* ACC-synthase activity, 10 submerged and 10 air-grown sections were incubated both in N_2 and air for 6 h. Following this, the leaf sheath covering the growing internode was removed, and five segments were excised from the stem as indicated in Figure 1. Zone 1 was a 10-mm segment cut below the node. Zone 2 contained the second highest node and the white region of the internode above it. Zone 3 included the intercalary meristem and some of the elongating internodal tissue (2). Zones 4 and 5 (in some experiments zones 4–6) consisted of 10-mm portions of the internode above the intercalary meristem. The segments corresponding to these zones were frozen immediately in liquid N_2 for ACC analysis. When stem sections were incubated in N_2 during the assay period, ACC accumulated in both air-grown and submerged stem sections, but the level and distribution of ACC was different under these two experimental conditions (Fig. 1). If one adds up the amount of ACC in all five zones, almost twice as much was found in submerged as in air-grown stems. In air-grown tissue, the highest level of ACC was in the node (zone 2). In stems that had been submerged, less ACC accumulated in zone 2 than in the corresponding region of air-grown stems but almost eight times more ACC was found in zone 3, which contained the intercalary meristem, and close to five times more in the elongating region above it (zone 4). Similar results were obtained in all 10 experiments in which the level and distribution of *in vivo* ACC-synthase activity was measured in submerged

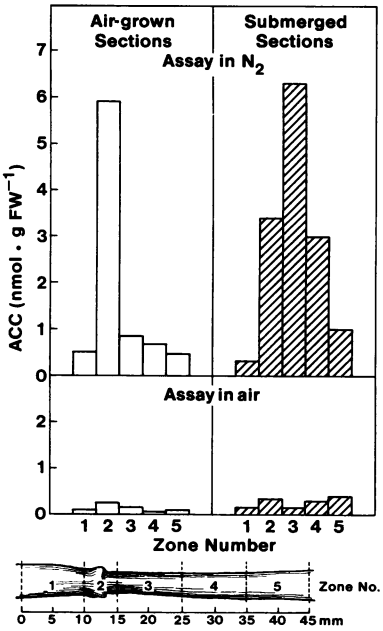

FIG. 1. Effect of submergence on *in vivo* activity and distribution of ACC synthase in stem sections of deepwater rice. Stem sections were either submerged or kept in air for 24 h. To assay ACC-synthase activity, they were subsequently incubated in air or N_2 for 6 h. Segments corresponding to zones 1 through 5 were excised from the stem sections as shown at the bottom of the figure and frozen in liquid N_2 for the analysis of accumulated ACC. The node is contained in zone 2, the intercalary meristem in zone 3.

and air-grown stems.

In stem sections which were incubated in air rather than N_2 during the assay period, the level of ACC in the tissue remained low (Fig. 1). The values obtained were similar to those found in earlier experiments (14).

Free and Conjugated ACC in Rice Stems. The level of ACC in plant tissues is a function of ACC formation and conversion of ACC to ethylene and MACC. To verify that ACC accumulation in a N_2 atmosphere does indeed reflect the activity of ACC synthase, we measured the level of conjugated ACC following incubation in air and N_2 (Table I). The level of conjugated ACC was higher in the node (zone 2) of submerged stems than in the node of air-grown stems. Keeping the tissue under N_2 led only to a small accumulation of conjugated ACC. Again, *in vivo* ACC-synthase activity was highest in zone 3 of submerged internodes and in zone 2 of internodes kept in air.

Examination of ACC Redistribution in Rice Stems. We observed consistently that ACC accumulation under N_2 was highest in zone 2 of air-grown stems; in submerged stems, ACC accumulation was reduced in zone 2 and increased in zone 3. The question arose whether this difference in ACC levels was due to redistribution of ACC from the node to the intercalary meristem and the elongating region. To investigate this, stem sections were separated between zones 2 and 3, and both parts of the original stem section were incubated in air or submerged in water for 24 h. Following this, the tissue was incubated in air or N_2 to assay *in vivo* ACC-synthase activity. After 6 h, the usual segments corresponding to zones 1 to 5 were isolated, and their ACC content was analyzed (Table II). As in the intact stem sections, submergence reduced ACC accumulation in zone 2 and increased ACC accumulation in zone 3. Since the stem sections had been cut between these two zones, redistribution of ACC from zone 2 to zone 3 could not have led to the observed results.

Time Course of the Development of *in Vivo* ACC-Synthase Activity. Partially submerged whole plants were used to determine the time course for the development of *in vivo* ACC-synthase activity in zone 3 containing the intercalary meristem (Fig. 2). Ten long sections (see "Materials and Methods") were excised from three submerged and three air-grown plants at different times after start of the treatment. These sections were incubated for 8 h in air or in N_2, following which zone 3 was excised from uppermost internodes for analysis of ACC accumulation. *In vivo* ACC-synthase activity began to increase within less than 2 h after start of submergence, reached a peak after 4 h, and remained at an elevated level thereafter. *In vivo* ACC-synthase activity in zone 3 of control plants stayed low throughout the experimental period. Similar results were obtained in three other time-course experiments.

Table I. *Effect of Submergence on the Level and Distribution of in Vivo ACC-Synthase Activity in Rice Stems*

Stem sections were submerged or left in air for 24 h. *In vivo* ACC-synthase activity was assayed by incubating stems sections either in air or in N_2 for 6 h and measuring the accumulation of free ACC and conjugated ACC (presumed to be MACC) in different regions of the stem.

Zone Number	Air-Grown Sections				Submerged Sections			
	Assay in air		Assay in N_2		Assay in air		Assay in N_2	
	Free ACC	Conj. ACC	Free ACC	Conj. ACC	Free ACC	Conj. ACC	Free ACC	Conj. ACC
	nmol g^{-1} fresh wt							
1	0.1	3.4	0.2	3.1	0.1	2.2	0.1	2.1
2	0.5	9.5	3.2	10.9	0.5	15.7	1.3	16.4
3	0.04	1.5	1.3	1.4	0.2	1.2	4.3	1.0
4	0.04	0.9	0.4	1.3	0.2	0.7	0.8	0.9
5	0.04	1.0	0.1	1.8	0.1	0.7	0.2	1.3

Table II. *Effect of Separating the Intercalary Meristem and the Node on in Vivo ACC-Synthase Activity in Rice Stems*

Stem sections were separated between zones 2 and 3 and submerged or left in air for 24 h. *In vivo* ACC-synthase activity was assayed by measuring the accumulation of free ACC after incubation in air or N_2 for 6 h. The slightly elevated levels of ACC in zones 2 and 3 assayed for ACC-synthase activity in air are most likely due to wounding when the stems were cut between these two zones.

Zone Number	ACC Accumulation			
	Air-grown sections		Submerged sections	
	In air	In N_2	In air	In N_2
	nmol g^{-1} fresh wt			
1	0.1	0.1	0.1	0.1
2	1.7	2.5	1.4	1.9
3	1.5	1.2	2.3	4.5
4	0.1	0.1	0.6	1.1
5	0.1	0.1	0.3	0.6

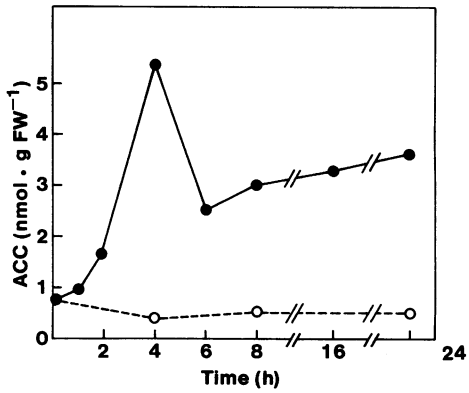

FIG. 2. Time course of the development of *in vivo* ACC-synthase activity in the internodal region containing the intercalary meristem. Long stem sections were submerged (●——●) or kept in air (O- - -O) for the times indicated. To assay ACC-synthase activity, they were subsequently incubated in N_2 for 8 h. Zone 3 containing the intercalary meristem of the uppermost internode was excised, frozen in liquid N_2, and analyzed for accumulated ACC.

Distribution of *in Vivo* ACC-Synthase Activity in the Stems of Submerged Plants. We measured the distribution of *in vivo* ACC-synthase activity along the growing stem of whole plants after 4 and 8 h of submergence (Fig. 3). As in isolated stem sections, submergence enhanced *in vivo* ACC-synthase activity primarily in zone 3; in air-grown control plants, zone 2 contained most of this enzyme activity. *In vivo* ACC-synthase activity was higher in all regions of the stem after 4 h of submergence than after 8 h.

The Effect of Low O_2 Levels on *in Vivo* ACC-Synthase Activity in Rice Stems. It has been shown earlier that the level of O_2 decreases inside submerged stem sections to as low as 2% and that reduced levels of atmospheric O_2 induce growth and ethylene synthesis in nonsubmerged sections (16). Long stem sections were placed for 4 h in cylinders through which gas mixtures containing 5, 10, 13, or 21% O_2 and 0.03% CO_2 in N_2 were circulated. In zones 1 and 2 of the stem, *in vivo* ACC-synthase activity increased markedly when the O_2 concentration was lowered to 13% (Table III). A further decrease in the O_2 level of the atmosphere had little if any effect on *in vivo* ACC-synthase activity in zones 1 and 2. In zone 3, which included the intercalary meristem, *in vivo* ACC-synthase activity rose gradually with

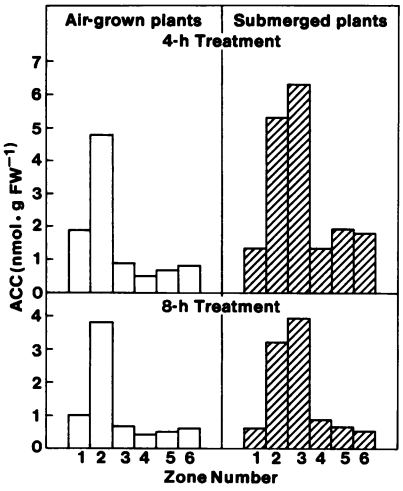

FIG. 3. Effect of submergence on *in vivo* activity and distribution of ACC synthase in stems of whole deepwater rice plants. Whole plants were submerged or kept in air for 4 or 8 h. After this period, long sections were excised, and ACC-synthase activity was assayed by incubation in N_2 for 8 h. In this particular experiment, six segments were excised from the stem as shown in Figure 1 (zone 6 being another 10-mm segment above zone 5), frozen in liquid N_2, and analyzed for accumulated ACC.

Table III. *Effect of Low Partial O_2 Pressures on in Vivo ACC-Synthase Activity in Rice Stems*

Long rice stem sections were incubated in gas mixtures containing 21, 13, 10, or 5% O_2 and 0.03% CO_2 (all by volume) in N_2 for 4 h. *In vivo* ACC-synthase activity was assayed by incubating stem sections in N_2 for 8 h and measuring ACC accumulation in different regions of the stem.

Zone Number	O_2 Concentration (%)			
	21	13	10	5
	nmol g^{-1} fresh wt			
1	0.4	3.5	4.3	4.1
2	1.9	11.6	10.9	11.4
3	0.4	1.3	1.5	4.0
4	0.3	0.4	0.8	1.8
5	0.2	0.4	0.9	1.2

decreasing O_2 concentrations. At 5% O_2, a 10-fold enhancement of *in vivo* ACC-synthase activity was observed.

DISCUSSION

Accumulation of ACC under N_2 appears to be a fair measure for *in vivo* ACC-synthase activity in rice stems. Neither redistribution of ACC within the stem nor conjugation of ACC appear to affect the assay in any significant way. On occasions when some conjugation of ACC has been observed in a N_2 atmosphere, *in vivo* ACC-synthase activities may have been slightly underestimated. We found a consistent pattern with regard to the distribution of *in vivo* ACC-synthase activity in rice stems. In air-grown stems, *in vivo* ACC-synthase activity was highest in the nodal region. Upon submergence, *in vivo* ACC-synthase activity increased up to 8-fold in the intercalary meristem and the elongation zone above it.

From previous work, we know that ethylene formation in submerged stems is a prerequisite for the growth response. When ethylene synthesis is inhibited, submergence does not stimulate internodal growth (14, 16). O_2 deficiency appears to be the signal for enhanced ethylene synthesis in internodal tissue of rice. When a rice plant is submerged, the level of O_2 decreases in the internodal lacunae. The effects of submergence on ethylene synthesis and growth can be reproduced by exposing nonsubmerged stem sections to gas mixtures containing low levels of O_2 (16, 19). Results presented in this paper indicate that hypoxic conditions promote ethylene formation by enhancing the activity of ACC synthase. Other stress conditions, *e.g.* wounding, chilling, and application of toxic chemicals, also stimulate ethylene synthesis in a variety of plants by increasing the activity of ACC synthase (for a review see Ref. 22). Hypoxia does not stimulate ethylene synthesis in all tissues of the rice plant. In the leaf sheath surrounding the internode, *e.g.*, ethylene synthesis is inhibited at reduced partial O_2 pressures (16).

Enhancement of ACC-synthase activity at low O_2 tensions is an adaptive response that may also occur in other cases where the physiological effects of O_2 deficiency are mediated by ethylene (for a review of the effect of low O_2 stress on ethylene synthesis see Ref. 7). A particularly well investigated example is the induction of epinasty in waterlogged tomato plants by elevated levels of ethylene (3, 8). Ethylene is formed in the shoot from ACC which is synthesized in the root as a response to O_2 deficiency (4, 5). The situation may be similar in corn roots where low partial O_2 pressures stimulate the development of aerenchyma via increased ethylene production (9).

We have now identified four growth-related enzymes in rice internodes whose activities are enhanced by submergence. *In vivo* ACC-synthase activity is affected first when plants are submerged. The enhancement of *in vivo* ACC-synthase activity is evident within 2 h and shows a peak within 4 h following submergence. The main increase in activity occurs in the intercalary meristem and in the elongating region just above it. Two enzymes of the polyamine-biosynthetic pathway, arginine decarboxylase (ADC) and *S*-adenosylmethionine decarboxylase (SAMDC), have been examined as markers of cell division in rice internodes (6). Their activity is induced by submergence and by treatment with ethylene or GA_3 within 4 h after start of the treatment, with SAMDC activity showing a sharp peak after 8 h. The increase in the activity of ADC and SAMDC is localized in the intercalary meristem. The internodes of air-grown rice plants contain high levels of reserve starch (18). When the plant is submerged, this starch is broken down, presumably to provide some of the energy and substrate which is needed for the growth response. The activity of α-amylase, which is probably responsible for the hydrolysis of starch in rice internodes, is greatly enhanced by submergence and by treatment with ethylene or GA_3 (18, 20). This amylolytic activity is localized in the nongrowing part of the internode and is induced within 12 h following start of the treatment (18).

We have described internodal growth in deepwater rice at the anatomical level (2, 15) and have established a sequence of physiological events that leads from submergence to the growth response of the plant (14, 16, 17). We are now identifying some of the biochemical processes that are related to this growth response, hoping that we shall be able to understand eventually their regulation at the molecular level.

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