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Circadian Ethylene Synthesis in *Sorghum bicolor*: Expression and Control of the System at the Whole Plant Level

S. A. Finlayson,[1]* H. L. Gohil,[2] H. Kato-Noguchi,[3] I.-J. Lee,[4] and P. W. Morgan[1]

[1]*Department of Soil and Crop Sciences, Texas A & M University, College Station, Texas, 77843, USA;* [2]*National Research Centre on Plant Biotechnology, IARI, Pusa Campus, 110 012, New Delhi, India;* [3]*Department of Biochemistry and Food Science, Kagawa University, Miki, 760-0795, Kagawa, Japan;* [4]*Division of Plant Bioscience, Kyungpook National University, 702701, Taegu, South Korea*

Abstract

Ethylene production by sorghum is rhythmic and the amplitude of the rhythm is increased both by dim, far-red enriched light and in mutant plants deficient in phytochrome B. The mechanisms involved in controlling ethylene production were examined in detail by measuring the rate of ethylene production among organs and tissues, examining the organ-specific levels of ACC (1-aminocyclopropane-1-carboxylic acid, the ethylene precursor) and investigating the contribution of the roots to shoot ethylene production. The results demonstrate that the expanding leaves were the major source of ethylene under dim, far-red enriched light and in the phytochrome B mutant. Enhanced ethylene production by the expanding leaf appeared to be the result of targeted delivery of ACC to this tissue. Root ACC levels were much higher than those in the shoot but roots converted much less of this endogenous ACC to ethylene. Applying ACC to the roots had only a marginal effect on their ethylene production, but greatly increased that of the shoots. Decapitated shoots continued to produce ethylene in a rhythmic pattern but the amplitude decreased with time compared to intact plants. The results collectively suggest that some, but not all, of the shoot ethylene rhythm depends on the transport of ACC from the roots to the shoots.

Key words: Ethylene; *Sorghum bicolor*; Phytochrome B; 1-aminocyclopropane-1-carboxylic acid; circadian rhythm; red light; far-red light; Photon flux density; Shoot:root

Introduction

Rhythmic ethylene synthesis was discovered in *Sorghum bicolor* (L) Moench seedlings (Finlayson and others 1998) as a result of an investigation of

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*Corresponding author; e-mail: sfinlayson@tamu.edu

genes that alter the photoperiod requirement for floral initiation (Quinby 1973). Previously, diurnal rhythms in ethylene synthesis with peaks during the light period had been observed in cotton, bean and *Chenopodium rubrum* (Lipe and Morgan 1973; Rikin and others 1984; Morgan and others 1990; Machácková and others 1997). A similar phenomenon in *Stellaria longipes* was shown to be controlled by a circadian rhythm that correlated with the abundance of ACC (1-aminocyclopropane-1-carboxylic acid) oxidase mRNA and ACC oxidase activity (Kathiresan and others 1998).

Interest in the rhythmic production of ethylene in sorghum was increased by two facts: (1) the rhythm is controlled by a circadian clock and (2) the amplitude of ethylene synthesis was over expressed by approximately 10 X in a cultivar homozygous for a null mutant form of the phytochrome B gene (Finlayson and others 1998). The cultivar 58 M contains a mutation in the *phyB* gene that results in a stop codon prior to a dimerization site (Childs and others 1997). Phytochrome B is immunologically undetectable in this cultivar. The phenotype of 58 M is similar to other *phyB* mutants (Childs and others 1997), and it exhibits the shade avoidance syndrome of plants grown in dim, far-red enriched light (Smith 1995). In bright, red/far-red balanced light wild-type plants (homozygously dominant for the *PhyB* gene) show a faint but recognizable rhythm in ethylene synthesis, but in dim, far-red enriched light (simulated shade) these plants exhibit day time peaks of ethylene nearly as high as the mutant (Finlayson and others 1998).

The mechanism by which ethylene synthesis is regulated appears rather complex. Expression of *SbACO2*, one of two ACC oxidase mRNAs cloned from sorghum, was cyclic and commensurate with ethylene biosynthesis rates in *phyB-1* plants (Finlayson and others 1999b). ACC oxidase enzyme activity followed the same pattern. Levels of ACC were elevated in *phyB-1* line but not clearly rhythmic. Simulated shading increased the rhythmic production of ethylene and expression of *SbACO2* in both *phyB-1* mutant and wild-type plants and both cultivars also exhibited peaks of ACC that correlated with times of peak ethylene production. Collectively, the data indicate that at least two mechanisms may be involved in generating the ethylene rhythms in sorghum; one in response to loss of phytochrome B function and another in response to shading.

Comparisons of shoot and root development and the localization of ethylene synthesis in sorghum seedlings have produced some interesting results. *phyB-1* mutant plants exhibit increased shoot/root ratios (Morgan and others 1997), one of the symptoms of the shade avoidance syndrome (Smith 1995). Maize and sorghum roots form aerenchyma or air spaces by expression of programmed cell death (Drew and others 2000). Roots of the *phyB-1* mutant contained about twofold more open or void area than wild-type (He, Drew, Finlayson and Morgan, unpublished data). In response to hypoxia or ethylene, wild-type plants displayed over 20% cell death, but the same treatments did not increase cell death in *phyB-1* plants (Finlayson and others 1999a). The roots of *phyB-1* plants also appear smaller in diameter than wild-type. It is apparent that major differences occur in the development of roots in plants with and without PHYB.

The rhythmic synthesis of ethylene in sorghum seedlings may serve some signaling role in plant development because the rhythmicity is regulated by PHYB, is responsive to light and temperature signals, is controlled by different mechanisms in bright and dim light and correlates with shoot and root phenotypes. Experiments to date have not investigated the role of the root in the generation of the ethylene rhythm. In some systems, ACC from the root is transported to the shoot where it is converted to ethylene (Bradford and others 1980; Finlayson and others 1991). Given the profound differences in root and shoot development between the wild-type and phyB-1 mutant sorghum plants and the possibility that the roots might contribute to rhythmic ethylene production, the present study was undertaken to more fully characterize root/shoot development, the localization of ethylene synthesis, and the role of ACC synthesis and roots in the rhythmicity.

Materials and Methods

Plant Material and Growth Conditions

Wild-type (100 M) and *phyB-1* (58 M) seeds were grown in fritted clay medium as described previously (Finlayson and others 1998, 1999b) with environmental parameters as indicated in the text and legends. Lighting was provided by various mixtures of fluorescent and incandescent lamps and measured by a Licor 1800 spectroradiometer. For determinations of shoot:root, plant parts were excised and dried in foil packets at 70°C after which the mass of each organ was measured. ACC treatments were provided by watering plants grown in 20 mL of fritted clay with 0.6 mL of 1.0 mM or 0.9 mL of 0.5 mM ACC solution at 8:00 AM (dawn). Ethylene production was measured 6 hours after treatment.

Ethylene Measurements

Ethylene was measured using a Photovac 10sPlus GC equipped with a photoionization detector as described previously (Finlayson and others 1998). For studies investigating tissue localization of ethylene production, tissue pieces were dissected at 14:00 (6 h after dawn) and placed in 6.2 mL tubes sealed with rubber serum caps. After a 20 min incubation, a 0.5 mL headspace sample was withdrawn for subsequent injection on the GC. Our unpublished studies show that wound-induced ethylene production takes more than 30 min to develop from these tissues. For studies investigating ethylene production by intact seedlings vs. excised shoots or intact roots, plants were grown for 5 days in 20 mL vessels filled with 20 mL of fritted clay. The seedlings were left intact and the entire vessel/seedling complex was placed in a 65 mL test tube (intact plants) or the shoot was cleanly excised using a sharp razor blade. Excised shoots were quickly placed with their cut ends immersed in dilute nutrient solution in 65 mL test tubes and the remaining intact roots (in their 20 mL vessels) were similarly placed in the larger tubes. Beginning 3 hours after excision, the tubes were capped every 3 hours for 20 min at which time a headspace sample was withdrawn and analyzed for ethylene on the GC.

Analysis of ACC and MACC

ACC and MACC (*N*-malonyl-ACC, an ACC conjugate) were measured using isotope dilution SIM-GC-MS as described previously (Finlayson and others 1999b).

Results

Shoot/Root Ratio

When 58 M was shown to be a phytochrome B mutant (Childs and others 1997), it was apparent that its phenotype was quite similar to the shade avoidance syndrome (Smith 1992; Morgan and others 1997). A key feature of shade grown plants is an increase in the shoot/root ratio (shoot:root). We have carefully characterized that feature in *phyB-1* (58 M) and wild-type (100 M). The increase in shoot:root was apparent in 16-day-old plants grown under 12 h photoperiods but was even more obvious in 18 h photoperiods (Figure 1A). In younger plants (5 days old) dim, far-red enriched light promoted an increase in shoot:root in both cultivars (Figure 1B). The enhanced shoot:root in *phyB-1* was

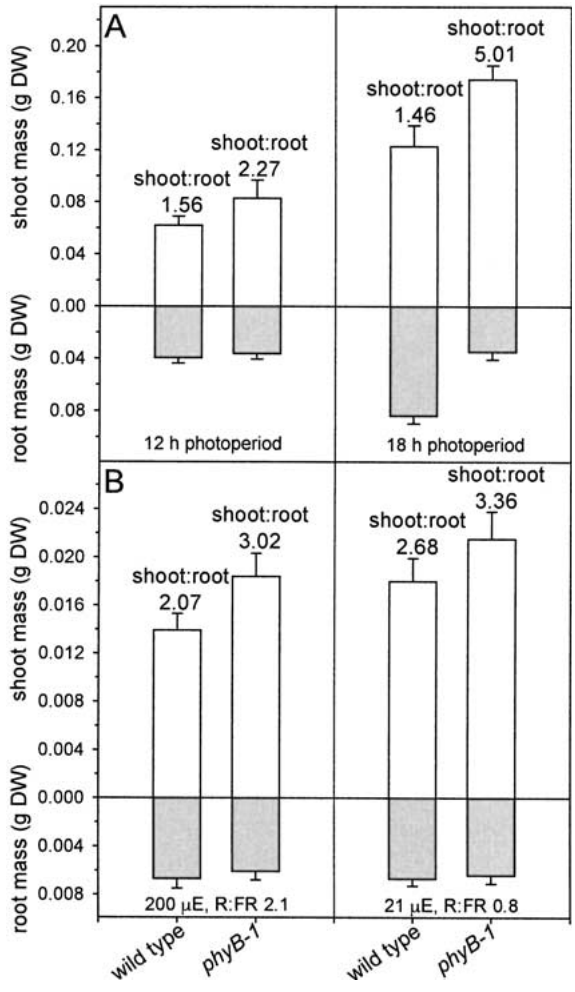

Figure 1. Shoot and root masses and shoot:root of wild-type and *phyB-1* sorghum. (**A**) Plants were grown in growth chambers for 16 days under either 12 or 18 h photoperiods with 31/22°C day and night temperatures. Light was provided at 350 °E PAR with a R:FR of 2.5. Results are means of 5 replicates of 6 plants +/− SE of the mean. (**B**) Plants were grown in a growth chamber for 5 days under 12 h photoperiods with 31/22°C day and night temperatures. Light was provided as indicated. Results are means of 5 replications of 3 plants +/− SE of the mean.

due almost exclusively to greater shoot mass in all cases except that of 12-day-old plants in an 18 h photoperiod. Under this regimen the elevated *phyB-1* shoot:root was a result of both greater shoot mass and reduced root mass compared to the wild-type.

Tissue Localization of Ethylene Synthesis

Finlayson and others (1998) showed that in *phyB-1* sorghum about 87% of the ethylene is produced by the shoot and only 13% by the roots. The amount of ethylene production by roots of the wild-type was

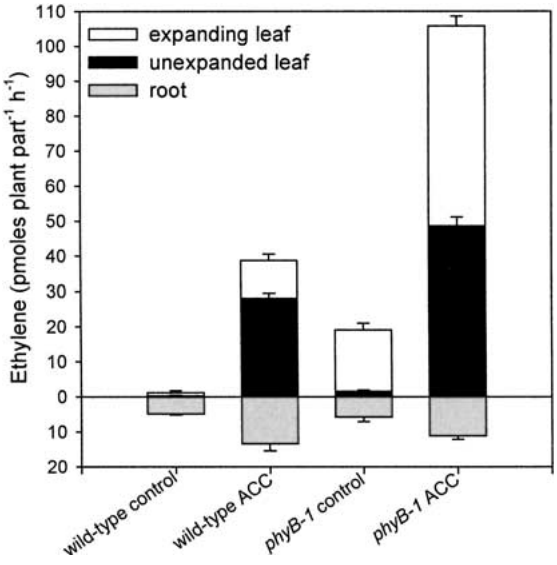

Figure 2. Ethylene production by wild-type and *phyB-1* sorghum seedling parts. Plants were grown for 6 days under 12 h photoperiods with 31/22°C day and night temperatures and 200 °E PAR, R:FR 2.1. Plants were watered with 600 °L of 1 mM ACC (ACC treated) or water (control) at 8:00 and both ACC treated and control plants were dissected and analyzed for ethylene production at 14:00. Results are the means of three plants +/− the SE of the mean.

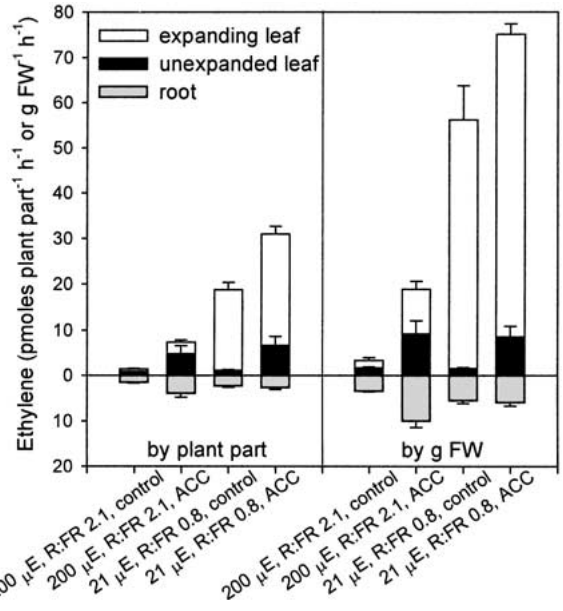

Figure 3. Ethylene production by wild-type sorghum seedling parts. Plants were grown for 5 days under 12 h photoperiods with 31/22°C day and night temperatures and light as indicated. Plants were watered with 900 °L of 0.5 mM ACC (ACC treated) or water (control) at 8:00 and both ACC treated and control plants were dissected and analyzed for ethylene production at 14:00. Results are the means of three plants +/− the SE of the mean.

quite similar to that in *phyB-1* seedlings but in the latter, production by the shoot was much higher. Similar data from a different experiment were published earlier (Morgan and others 1997). To extend this information, plants grown in bright, high R:FR light were dissected and ethylene production rates were determined. As observed earlier, in wild-type plants, more ethylene was made by the root than the shoot (Figure 2) whereas in *phyB-1* plants the opposite was true. To estimate the relationship between substrate (ACC) availability and the ability to convert the substrate to end product, we treated plants with ACC and analyzed ethylene production by various plant parts. In both cultivars, ethylene production by roots increased approximately twofold whereas ethylene production by the unexpanded leaves increased many fold (Figure 2). The increase in ethylene production by the expanding leaf was intermediate between the root and the unexpanded leaves.

The interaction of light intensity and quality (R:FR) with native substrate or applied ACC on localization of ethylene production was examined in young wild-type plants. The dim/low R:FR condition increased ethylene production dramatically and most of the effect was in the expanding leaf blade and little or no effect on production by the unexpanded leaves (Figure 3). Application of ACC generally raised the rate of production by each part, but the proportional largest increase was with the unexpanded leaves.

To examine the dynamics of ethylene production under conditions more nearly intact, we detached shoots and measured ethylene released by the detached shoot standing in dilute nutrient solution versus the intact roots with shoots removed. In bright light with relatively high R/FR, intact *phyB-1* plants produced ethylene (Figure 4) in a rhythmic pattern with daytime peaks as had been documented earlier (Finlayson and others 1998). The amplitude of the peaks for *phyB-1* seedlings was about 3.5 to 5 × higher than for wild-type. The wild-type seedlings exhibited a weaker but discernable rhythm. For detached shoots, rhythmic ethylene synthesis persisted, but the amplitude of the rhythm was lower and decreased with time. Ethylene production by roots was very low, ranging from 0.7 to 4.2 pmoles plant^{-1} h^{-1} with no discernable peaks and no difference between the two cultivars.

The experiment in Figure 4 was repeated under dim, low R/FR light and the average of two experiments is illustrated in Figure 5. Rhythmicity was

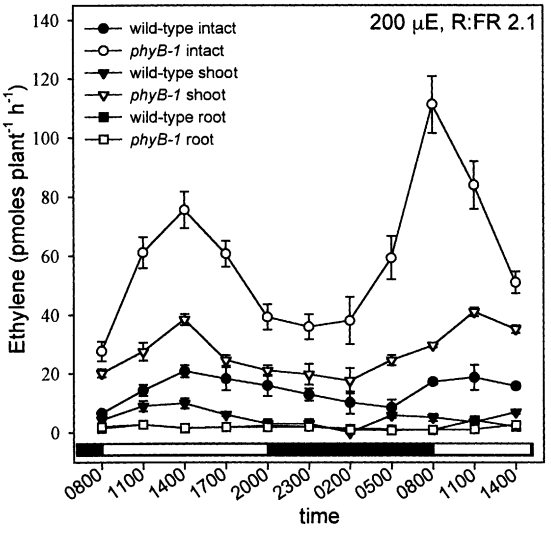

Figure 4. Diurnal ethylene production by wild-type and *phyB-1* intact seedlings and detached roots and shoots. Plants were grown under 12 h photoperiods with 31/22°C day and night temperatures and 200 °E PAR, R:FR 2.1. Measurements began at dawn of day 5. The results are the average of two replicate experiments each with 5 observations per time point, +/− the SE of the mean. White and black bars near the bottom indicate light and dark periods, respectively.

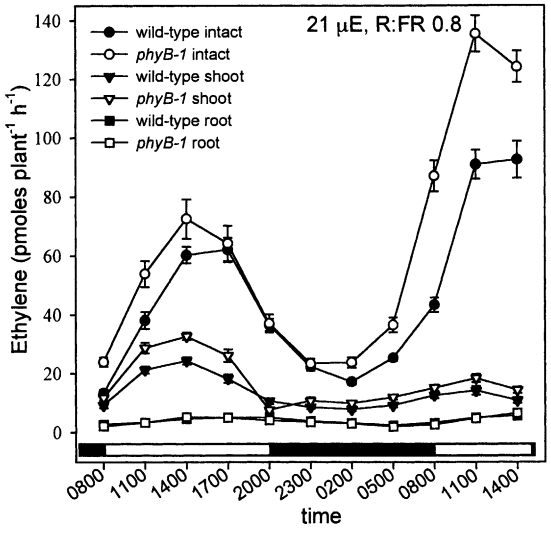

Figure 5. Diurnal ethylene production by wild-type and *phyB-1* intact seedlings and detached roots and shoots. Plants were grown under 12 h photoperiods with 31/22°C day and night temperatures and 21 °E PAR, R:FR 0.8. Measurements began at dawn of day 5. The results are the average of two replicate experiments each with 5 observations per time point, +/− the SE of the mean. White and black bars near the bottom indicate light and dark periods, respectively.

observed in ethylene synthesis by both cultivars. The peak heights of ethylene production by intact plants were approximately 1.2 to 1.5 × higher for *phyB-1* plants compared to the wild-type. Ethylene peak heights in detached shoots were about 1.3 × greater in *phyB-1* compared to wild-type. The amplitude of the rhythm again decreased with time. As for the bright light experiment (Figure 4), the rate of ethylene production by detached roots was much lower than other tissue and varied little between cultivars (Figure 5), although there was some indication of a rhythm between day and night.

Tissue Localization of ACC

Because previous data on ACC levels in sorghum seedlings have not agreed with ethylene synthesis rates, especially for plants grown in normal light (bright, high R/FR), we decided to further examine the ACC levels in bright-light grown plants. Shoot ACC levels were both rhythmic in *phyB-1* and elevated above levels in wild-type (Figure 6). Shoot MACC levels rose during a 39 h period in *phyB-1* but remained level in wild-type. Using the same assay technique we found peaks of ACC levels in the roots of *phyB-1* but not in roots of wild-type (Figure 7). The peak levels in roots were roughly 3 times higher than in shoots. MACC levels showed no pattern or rhythm in roots and the levels were higher in roots than in shoots.

Discussion

The phytochrome B mutation in sorghum cultivar 58 M (*phyB-1*) markedly alters the allocation of dry weight to shoots and roots compared to wild-type plants (cultivar 100 M) (Figure 1A, B). The mutant plants have greater shoot:root ratios regardless of photoperiod length or light intensity/R:FR ratio. Presumably this aspect of the *phyB-1* phenotype is due to a limitation on the transport of assimilates to the roots or preferential use of assimilates to synthesize shoot tissues. Although all the treatments demonstrated the enhanced shoot mass of the *phyB-1* plant, only in older (12 day old) plants grown under 18 h photoperiods did *phyB-1* plants also have reduced root mass compared to the wild-type. Our results contrast with those reported earlier showing that roots of one-week-old *Arabidopsis phyB* mutants are shorter than wild-type, irrespective of the presence or absence of light (Reed and others 1993). Because the systems used for studying the phenomenon were very different it is difficult to come

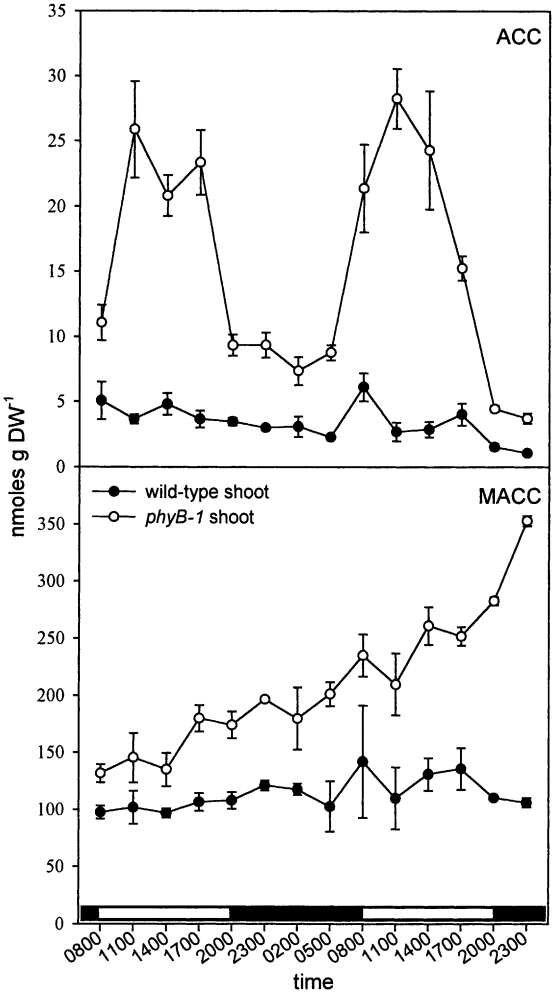

Figure 6. Diurnal levels of ACC and MACC in wild-type and *phyB-1* sorghum seedling shoots. Plants were grown under 12 h photoperiods with 31/22°C day and night temperatures and 200 °E PAR, R:FR 2.1. Measurements began at dawn of day 5. The results are the means of 3 to 4 samples per time point, +/− the SE of the mean. White and black bars near the bottom indicate light and dark periods, respectively.

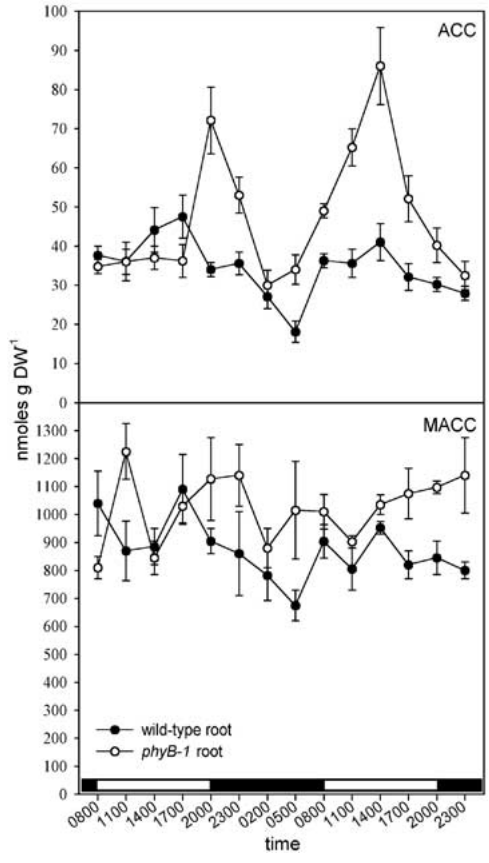

Figure 7. Diurnal levels of ACC and MACC in wild-type and *phyB-1* sorghum seedling roots. Plants were grown under 12 h photoperiods with 31/22°C day and night temperatures and 200 °E PAR, R:FR 2.1. Measurements began at dawn of day 5. The results are the means of 3 to 4 samples per time point, +/− the SE of the mean. White and black bars near the bottom indicate light and dark periods, respectively.

to a reasonable hypothesis for the discrepancy. Whether the alteration in shoot/root development observed in sorghum is related to the increased production of ethylene in the mutant or is more directly connected to the absence of phytochrome B is unknown at this time.

When plants were separated into major components, previous observations on the localization of ethylene production were confirmed and extended (Morgan and others 1997; Finlayson and others 1998). Excess ethylene synthesis in *phyB-1* seedlings in relatively bright, high R/FR occurs mainly in the expanding leaf blades (Figure 2), with little difference between *phyB-1* and wild-type unexpanded leaves and roots. When ACC, the substrate for ethylene, was supplied, the major effects were on the unexpanded leaves (Figure 2). The data indicate that the unexpanded leaves have a potential for ethylene production that is equal to or greater than the expanding blade, but that ethylene production occurs mainly from the expanding blade as a result of greater endogenous availability of ACC in these tissues. Although the ACC applied entered the plant through the roots, roots themselves were less able to convert ACC to ethylene than shoot tissues, possibly as a result of reduced ACC oxidase activity in the roots. Because it seems clear that the majority of ACC taken up by the roots was transported to the shoot, it is possible that the roots might be a natural source of ACC for subsequent generation of ethylene rhythms by the shoot tissues.

Because wild-type plants make little ethylene in bright light, we extended the experiment in Figure 2 to wild-type plants in both dim and bright light. The large increase in ethylene synthesis in dim light was due mostly to the expanding leaf blades (Figure 3). ACC treatment again suggested that availability of this precursor may limit ethylene synthesis in unexpanded leaves, but the expanding leaf and roots are less limited by ACC availability under dim light. Presumably, some of the increase in ethylene production under dim, low R:FR light is due to the elevated endogenous ACC levels we previously measured under these conditions (Finlayson and others 1999b); the present results suggest that this increase in ACC is preferentially available to the expanding leaf blade. Again, it is noteworthy that although the roots were the site of ACC uptake, they apparently transported the majority to the shoot rather than converting it to ethylene themselves. Our findings support a model of carefully controlled delivery of ACC to specific tissues with subsequent highly regulated conversion of this ACC to ethylene.

There is always some concern about the relevance of ethylene production by excised plant parts. In addition, these measurements represent a single time point on a rhythmic time course. To address these issues, we compared ethylene produced by intact plants to that produced by detached shoots and their separate, but intact, root systems over a 30 h time course (Figures. 4 and 5). These data confirmed the earlier studies (Finlayson and others 1998; Morgan and others 1997); in both cultivars, ethylene synthesis was rhythmic and the peak height was increased by dim, FR rich light. Furthermore, rhythmicity persists in the detached shoots in both cultivars, indicating that the existence of rhythmicity does not depend solely on the roots delivering substrate (ACC) in daily pulses. Detachment of the shoot reduced the production of ethylene in both cultivars under both bright and dim light conditions. Possible explanations for the reduction in ethylene production by detached shoots and the reduction being relatively greater on the second day of two-day experiments include the fact that: (a) the shoot receives a significant amount of ACC from the root and detachment removes that source of ethylene substrate and (b) detachment results in a general decrease in growth and vigor which increases with time. The first of these explanations is favored by the peaks of ACC content detected in roots of *phyB-1* seedlings in bright light (Figure 7A). However, the first peak in *phyB-1* roots occurs late in the day and the existence of a peak in wild-type plants is questionable. It is noteworthy that in most cases the conversion of ACC to ethylene by root tissue is low (Figures 2, 3), but ACC levels in roots are relatively high (Figure 7A). It is possible that some of the ACC synthesized in the root could be exported to the shoot where it contributes to rhythmic ACC abundance (Figure 6A) and rhythmic ethylene production.

The abundance of MACC reflected the elevated levels of ACC in roots compared to shoots, as this conjugate was much more abundant in roots. MACC levels are much higher than ACC levels in both cultivars and MACC abundance increased in the *phyB-1* mutant shoots over the duration of the time course, indicating that they normally synthesize more ACC than is necessary for the amount of ethylene produced. It is possible that the conversion of ACC to ethylene may be more important than the synthesis of ACC in controlling the rate of ethylene synthesis in these shoots. Deconjugation of MACC to ACC is generally not thought to occur at appreciable rates (Hoffman and others 1983) and is unlikely to impact ethylene synthesis.

Taken together, it is apparent that the bulk of the ethylene produced in sorghum seedling tissues is made in the expanding leaf blades, especially in *phyB-1* and in wild-type seedlings in dim, FR-enriched light. Because rhythmicity persists in detached shoots and ACC oxidase mRNA and enzyme activity are rhythmic in shoots (Finlayson and others 1999b), it is unlikely that rhythmicity is due exclusively to the pattern of ACC synthesis in and transport from the roots. On the other hand, because ACC levels vary in a strongly rhythmic pattern in both shoots and roots, and there is indirect evidence for limited ACC oxidase activity in roots, it seems likely that part of the ACC converted to ethylene in leaves originates in roots and arrives in the shoots in a rhythmic pattern. Further analysis of the manner in which this tropical grass manages the synthesis of ethylene will be possible when ACC synthase genes, which are circadianly regulated, are identified.

ACKNOWLEDGMENTS

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