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The Effect of Light and Phytochrome on 1-Aminocyclopropane-1-Carboxylic Acid Metabolism in Etiolated Wheat Seedling Leaves[1]

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ABSTRACT

While light-grown wheat leaves produced ethylene at a low rate of <0.1 nanomoles per gram per hour and contained 1-aminocyclopropane-1-carboxylic acid (ACC) at low levels of <2.5 nanomoles per gram, etiolated wheat leaves produced ethylene at a rate of 2 nanomoles per gram per hour and accumulated concentrations of ACC at levels of 40 nanomoles per gram. Upon illumination of 8-day-old etiolated wheat seedlings with white light, the ethylene production rate increased initially, due to the activation of ethylene-forming activity, but subsequently declined to a low level (0.1 nanomoles per gram per hour) at the end of the 6-hour illumination. This light-induced decline in ethylene production rate resulted from a decline (more than 35 nanomoles per gram) in ACC level, which was accompanied by a corresponding increase in 1-(malonylamino)cyclopropane-1-carboxylic acid content. These data indicate that illumination promoted ACC malonylation, resulting in reduced ACC level and consequently reduced ethylene production. However, light did not cause any significant increase in the extractable ACC-malonyltransferase activity. The effect of continuous white light on promotion of ACC malonylation was also observed in intermittent white light or red light. A far-red light treatment following red light partially reversed the red light effect, indicating that phytochrome participates in the promotion of ACC malonylation.

A number of reports have shown that light regulated ethylene production which in turn modified plant growth (4, 5, 9, 18, 19). Depending on the tissues and conditions employed, light promoted (16, 18) and inhibited (2–10, 20) ethylene production. Since the plant tissues used in these earlier studies normally contained low level of endogenous ACC,[3] the effects of light on the changes in ACC levels in relation to ethylene production were not examined. Many investigators have examined the effect of light on ethylene production in tissues which have been supplied with exogenous ACC and in these experiments, the examination of light effect was limited to changes in EFE activity.

In this investigation, we have observed that etiolated wheat leaves have both high ACC levels and rates of ethylene production. Illumination resulted in an accelerated conversion of ACC into MACC resulting in reduced ACC levels, and consequently in reduced rates of ethylene production. This communication describes the characteristics of this light-promoted ACC malonylation and presents evidence showing that the light receptor is phytochrome.

MATERIALS AND METHODS

Plant Materials. Wheat (*Triticum aestivum* var 'Anza'), rice (*Oryza sativa* L.), barley (*Hordeum vulgare*), pepper (*Capsicum annuum* var 'Ace'), mungbean (*Vigna radiata*), and pea (*Pisum sativa*) seeds were soaked in aerated water overnight at room temperature. The seeds were then grown in vermiculite at 25°C under light or dark as required. All the experimental procedures preceding the treatments were performed under dark or green safety lights.

Illumination Conditions. As shown in Tables and Figures, five or ten 3 cm etiolated wheat leaf segments cut from the tip were placed in 14.4 ml test tubes, containing 100 μl water or treatment solution, and the tubes were then placed under fluorescent light (53 $\mu E\ m^{-2}\ s^{-1}$), red light or far-red light. The red and far-red light sources were from a projector equipped with a 650 nm and 730 nm filter, respectively. For the red light treatment, tubes were exposed to red light with intensity of 12 $\mu E\ m^{-2}\ s^{-1}$ for 5 min; for far-red treatment, tubes were exposed to far-red light with intensity of 0.85 $\mu E\ m^{-2}\ s^{-1}$ for 10 min. Tubes were returned to darkness for the subsequent measurements.

Determination of Ethylene Production. Leaf segments in tube were flushed with air and sealed with a rubber serum cap after each sampling. At indicated time intervals, 1 ml gas samples were drawn from the tubes and injected into a gas chromatograph equipped with an alumina column and a FID detector at 90°C.

Determination of ACC and MACC. Samples were extracted twice with 5 ml of 80% ethanol at 55°C for 10 min. The ethanol extract was evaporated under vacuum at the same temperature. The residue was dissolved in 2 ml water and the pigment was removed by the addition of 0.5 ml chloroform. ACC content in 0.2 ml aliquots of the aqueous solutions was determined according to the method of Lizada and Yang (14). The quantitation of MACC in the extract was carried out first by passing 0.2 ml extract through a Dowex 50 (H^+-form) resin column with 0.5 ml bed volume to removed ACC. The effluent solution containing MACC was hydrolyzed in 2 N HCl for 3 h as described previously (13). Following neuralization with NaOH, the resulting hydrolysate was assayed for ACC content, which was taken as the amount of MACC in the extract.

Preparation and Assay of ACC-Malonyltransferase. Leaf segments (0.5 g) were frozen with liquid N_2 and then homogenized

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[3] Abbreviations: ACC, 1-aminocyclopropane-1-carboxylic acid; AVG, aminoethoxyvinylglycine; EFE, ethylene-forming enzyme which catalyzes the *in vivo* oxidation of ACC to ethylene; MACC, 1-(malonylamino)cyclopropane-1-carboxylic acid; Met, methionine; SAM, *S*-adenosylmethionine.

with 1 ml buffer consisting of 0.1 M K-phosphate (pH 7.2), 0.1 M KCl, and 0.4 mM DTT. The homogenate was centrifuged at 12,000*g* for 30 min, and the supernatant was fractionated by precipitation with ammonium sulfate. The fraction precipitated between 30 and 60% saturation was dissolved in a small volume of dialysis solution and dialyzed against 0.01 M K-phosphate (pH 7.2) containing 0.01 M KCl and 0.2 mM DTT. The dialyzed preparation was employed as the ACC-malonyltransferase source. All operations were carried out at 0 to 4°C. The protein content in the enzyme preparation was determined by the method of Bradford (1). The malonyltransferase activity was assayed as reported by Liu *et al.* (13). The reaction mixture contained 1 mM malonyl-CoA, 0.25 mM [2,3-^{14}C]ACC (70 nCi), 0.1 M K-phosphate (pH 8.0), and 10 μl enzyme solution in the total volume of 50 μl. After incubation at 35°C for 1 h, the reaction mixture was passed through a column of Dowex 50-X2 (H^+ form) to stop the reaction and to separate MACC from ACC. The enzyme activity was calculated from the radioactivity in the effluent which contains MACC; radioactivity was assayed by a Beckman liquid scintillation counter.

Metabolism of Radioactive ACC by Excised Wheat Leaves. Three-cm segments were fed through cut ends with 150 μl of K-phosphate (pH 5.8) containing radioactive ACC (2 μCi and 25 nmol, or 4 μCi and 50 nmol) for 1 h. After washing twice with ice water, segments were put into a 5 ml vial and exposed to different light sources. Vials were returned to darkness after each light treatment and sealed with rubber serum caps for ethylene accumulation. Ethylene was determined by withdrawing 1 ml gas sample for GC analysis. The remaining gas in each vial was then transferred to an evacuated 20 ml scintillation vial containing 0.1 ml 0.25 M mercury perchlorate. The radioactive ethylene which was absorbed into mercury perchlorate solution was determined by scintillation counting. The leaf segments were then extracted twice with 5 ml of 80% ethanol, which was then concentrated as described above. An aliquot of the resulting extract was spotted on Whatman 3M paper and developed in the solvent system of butanol:acetic acid:water (4:1:1, by volume) overnight. Radioactivity in the chromatograms was located with a Packard Radio-Scanner and the radioactivity in ACC and MACC was determined by scintillation counting of the corresponding zones cut from the chromatograms.

RESULTS

Ethylene Production and ACC Content in Light Grown and Etiolated Wheat Leaves during Seedling Development. The changes in rates of ethylene production in etiolated and light-grown wheat leaves are shown in Figure 1A. Ethylene production rates were low initially in both tissues. While the green leaves grown under light contained <2.5 nmol/g ACC, and produces low rate of ethylene throughout the growth period, the ACC content and ethylene production rate of the etiolated wheat leaves began to increase on d 4, and reached 54.6 nmol/g in ACC and 45 nl/g-h in ethylene production rate on d 9. The increase in ethylene production rate by the etiolated leaves was paralleled by a similar increase in ACC content (Fig. 1). The accumulation of ACC in etiolated wheat seedling was not due to the inhibition of ACC to ethylene conversion (EFE), since both green and etiolated wheat leaves produced comparable amounts of ethylene when they were supplied with 10 mM ACC solution (data not shown). Moreover, when 0.1 mM AVG, an inhibitor of ACC synthase activity, was applied to 4-d-old etiolated seedlings and the ACC content was monitored daily for the following 4 d, the accumulation of ACC in the seedling was inhibited by about 80%. In addition, the MACC contents in 8-d-old light grown and etiolated seedling leaves were determined as 10 and 120 nmol/g, respectively. These observations indicate that the ACC accumulation in etiolated wheat leaves resulted from an increase in ACC synthesis but not from the decrease in ACC malonylation during the etiolation period.

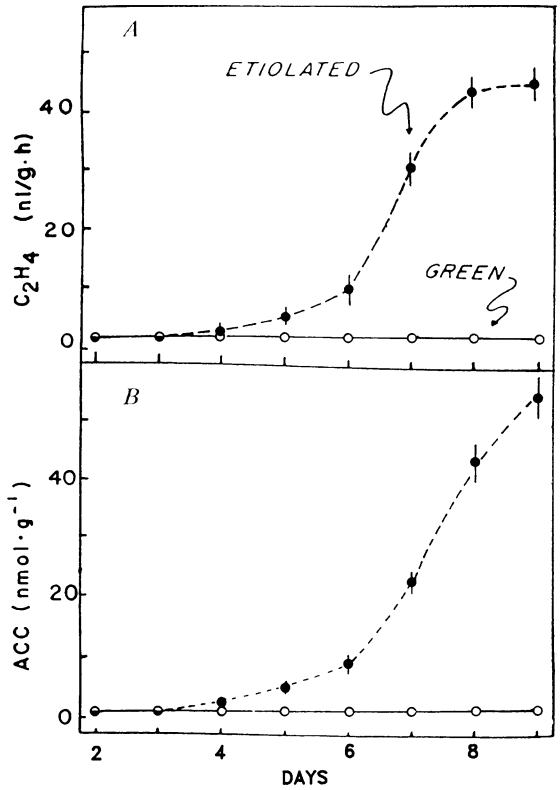

FIG. 1. Time course of ethylene production and ACC accumulation in leaf tissues of dark-grown (etiolated) or light-grown (green) wheat seedlings. Leaf samples, detached daily from the dark- or light-grown seedlings, were measured for their ethylene production rate and ACC contents. For ethylene production determinations the samples were kept under dark for 1 h.

Table I. *ACC Content in Various Parts of 8-d-old Etiolated Wheat Seedling*

Segments weighing 0.5 g were used to measure the ACC content according to the method of Lizada and Yang (14).

Plant Part	ACC Content	Total Seedling Weight
	nmol/g	%
Leaves	46.0 ± 2.2	43
Coleoptiles	2.3 ± 0.4	10
Roots	1.0 ± 0.1	47

The accumulation of ACC in different parts of the 8-d-old etiolated wheat seedlings were examined (Table I). Over 90% of ACC was accumulated in the leaves, which also contained the highest ACC content on a per gram basis. We have also examined the capability of various seedlings of monocots and dicots to accumulate ACC during their etiolated growth. Among the species we examined (Table II), monocots appeared to have greater capability to accumulate ACC during etiolation than dicots.

Effect of Continuous Light on ACC Metabolism in Excised Wheat Leaves. Upon transferring the intact 8-d-old etiolated wheat seedlings from dark to light, their ACC content rapidly decreased from 42 to 2.7 nmol/g in 24 h; in contrast, the ACC content increased to 62 nmol/g under the dark (data not shown). Changes in ethylene production rate, ACC content and MACC content in excised 8-d-old etiolated wheat leaves during illumination were therefore examined (Fig. 2). Upon illumination of excised 8-d-old etiolated wheat leaves, the ACC content de-

Table II. *Comparison of ACC Content in Leaf Tissues of Various Mono- and Dicotyledonous Etiolated and Light Grown Seedlings*

Leaves of 8- to 10-d-old seedlings were used.

Species	ACC Content	
	Etiolated	Light grown
	nmol/g	
Wheat (monocot)	33.5 ± 2.1	1.75 ± 0.25
Rice (monocot)	40.8 ± 4.4	3.60 ± 0.87
Barley (monocot)	32.9 ± 2.0	0.84 ± 0.17
Mungbean (dicot)	0.90 ± 0.01	0.10 ± 0.00
Pea (dicot)	1.56 ± 0.07	0.78 ± 0.20

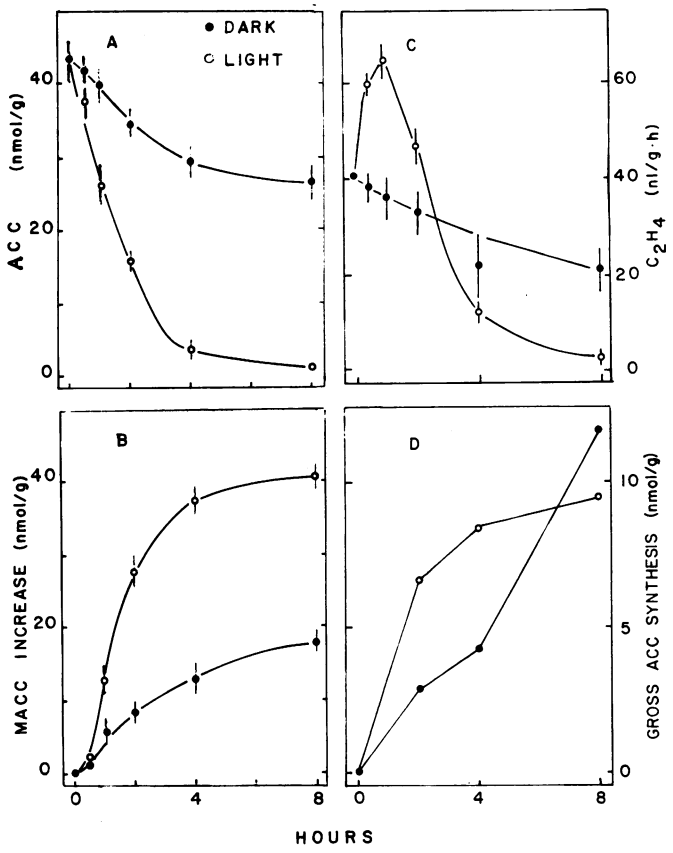

FIG. 2. Effect of light on (A) changes in ACC content, (B) changes in MACC content, (C) changes in ethylene production rate, and (D) gross ACC-synthesis during the incubation period. Lots of 10 leaf segments excised from 8-d-old etiolated wheat seedlings were incubated in 14.4 ml tubes for various periods up to 9 h either in the light or dark, as indicated. Periodically, ethylene production rates, ACC contents and MACC contents were determined. Gross ACC-synthesis during the incubation periods was estimated as the sum of (C_2H_4 production) − (decrease in ACC content) + (increase in MACC content).

creased from 45 nmol/g to 6.6 nmol/g in 4 h. During the same period, the ACC content of the excised etiolated wheat leaves kept in the dark decreased only 16 nmol/g (Fig. 2A). In order to account for the loss of ACC, the ethylene production and the change in MACC content during this period were measured (Fig. 2, B and C). Upon illumination, the ethylene production rate initially increased and attained to 65 nl/g-h in 2 h, but then declined rapidly to 2.2 nl/g-h in 8 h. In contrast, ethylene production rate by etiolated leaves during the same period declined only slightly (less than 50%). Concomitantly, light increased the accumulation of MACC. After illumination for 4 h, MACC content increased 38 nmol/g, as compared to a net

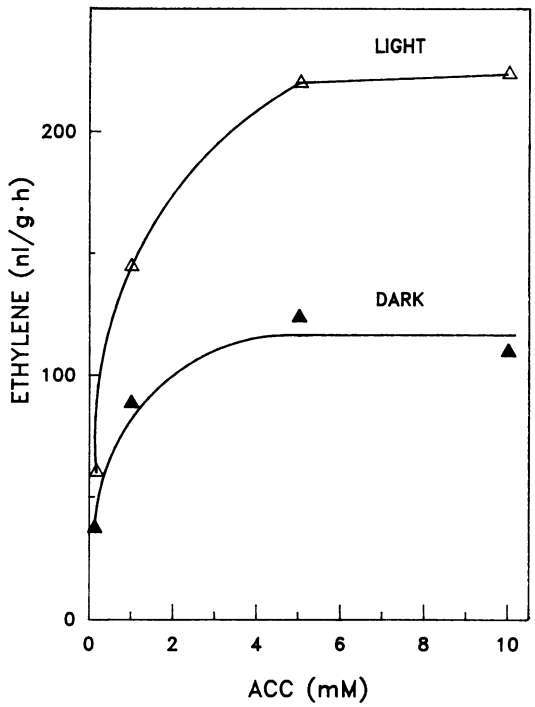

FIG. 3. Effect of light on the conversion of ACC to ethylene by excised etiolated wheat leaf segments. Ten 3-cm long leaf segments were preincubated in various concentrations of ACC for 3 h. The samples were then transferred into water and ethylene produced during the subsequent 1 h under either light (△) or dark (▲) was determined.

increase of 11 nmol/g for the dark control (Fig. 2B). Since light exerted an immediate stimulatory effect on ethylene production (Fig. 2C) without an increase in ACC content (Fig. 2A), light must have acted by increasing EFE activity. In Figure 3, the 8-d-old etiolated leaf segments were preincubated with various concentrations of ACC for 3 h in the dark and their ethylene production rates were then assayed under dark or light. The result showed that EFE which is defined as the ethylene production rate under saturated ACC concentration, was always higher in light than in dark treatments. These data confirm the notion that light has a stimulatory effect on EFE activity. The rapid decline in ethylene production after 3 h of light treatment (Fig. 2C) is expected, since ACC level declined markedly during this period (Fig. 2A). Thus, the decline in ethylene production under light is not due to the decline in EFE, but due to the decline in ACC level.

Since light treatment resulted in rapid decline in ACC level which was accompanied by a corresponding increase in MACC, light-promoted ACC malonylation is predicted. However, it should be noted that the basal level of MACC in the etiolated seedlings was so high (120 nmol/g) that their net increases in MACC content during light/dark treatments could not be accurately estimated. To overcome this problem, we preloaded the excised etiolated leaf segment with radioactive ACC and then monitored the changes in radioactive MACC and ACC content during incubation under light or dark. The ratio of radioactive MACC/ACC in the sample at the end of preloading but before the incubation was 0.2. When the segments was incubated under dark for 2 and 4 h, the ratio increased to 1.5 and 5.3, respectively; by contrast, the ratio increased to 4.4 and 20.8 in 2 and 4 h, respectively, under light. The total radioactive ethylene produced in both treatments were about the same during the 4 h incubation, and it accounted for less than one-fourth of the radioactive ACC lost during the incubation (data not shown). These data clearly show that light promoted the tissue's capability to malo-

nylate ACC.

Comparison of the Effect of White Light, Red Light, and Far-Red Light on ACC Metabolism. As shown in Table III, 6-h continuous white light treatment reduced ACC content. A similar effect was also observed with intermittent white light (5 min illumination at the beginning of each hour) or with red light illumination. A single 5 min illumination with red light followed by 6-h dark incubation was effective to reduce their ACC levels. These observations suggest that the enhanced metabolism of ACC may be mediated by phytochrome. This notion was further supported by the result of Table IV, in which far-red following red light treatment is shown to reverse the red light effect on ACC metabolism. The segments treated with red light followed by far-red light contained higher ACC level and produced ethylene at higher rates than those segments that was illuminated with red light.

The promotion of ACC malonylation by red light and its reversion by far-red light was further investigated by feeding the excised wheat leaves with radioactive ACC. The ratio of radioactive MACC/ACC at the end of preloading period but before 4-h incubation period was 0.05. This ratio increased to 3.4, 9.9, or 4.6 during the incubation period under the dark, illuminated with intermittent red light, or illuminated with red followed by far-red light, respectively. These data collectively indicate that phytochrome is involved in the regulation of ACC metabolism by promoting ACC malonylation, resulting in reduced ACC content and consequently reduced ethylene production.

Table III. *Effect of Various Light Treatments on ACC Metabolism*

Five excised leaf segments (3 cm), cut from the 8-d-old etiolated wheat seedlings, were placed in a 14.4 ml test tube containing 0.1 ml of water. For the intermittent white light treatment, tube was illuminated six times for 5 min at the beginning of each hour; for the red light treatment, tube was illuminated six times for 5 min each before dark incubation or 5 min at the beginning of each hour.

Treatment	ACC Content	
	0 h	6 h
	nmol/g	
Before treatment	39.6	
Dark		30.4
Continuous white light		1.7
Intermittent white light, 6×		1.8
Intermittent red light, 6×		2.6
Red light, 1×		6.2

Table IV. *Effect of Red Light and Far-Red Light on the ACC Malonylation*

Conditions were same as Table III, except that red light was illuminated two times 5 min each at the beginning of first and second hour, and the far-red light (10 min) was applied immediately after each red light illumination. Ethylene produced during the period of 5 to 6 h incubation was determined. After ethylene determinations at the end of 6 h incubation, the segments were extracted and assayed for ACC and MACC content; MACC contents were the average of three experiments.

Treatment	Ethylene 5–6 h	0 h		6 h	
		ACC	MACC	ACC	MACC
	nmol/g	*nmol/g*			
Before treatment		45.4	120		
Dark	0.6			23.4	144
Red	0.2			5.5	175
Red/far-red	0.5			17.9	156

DISCUSSION

Ethylene is biosynthesized from methionine via SAM and ACC. In addition to serving as a precursor of ethylene, ACC can be metabolized to a biologically inactive end-product, MACC as shown below (for review, see Ref. 21)

$$\text{Met} \rightarrow \text{SAM} \rightarrow \text{ACC} \rightarrow C_2H_4.$$
$$\downarrow$$
$$\text{MACC}$$

Since ethylene biosynthesis is regulated at a point after the SAM formation, ethylene biosynthesis can be potentially regulated at one of the following steps: (a) ACC synthesis, (b) ACC-to-ethylene conversion (EFE), and (c) ACC malonylation. In this investigation we have shown that light exerts dual roles in the regulation of ethylene biosynthesis in the etiolated wheat leaves, in which a high level of ACC has accumulated: light promotes ACC to ethylene conversion and ACC malonylation. Consequently, when etiolated wheat leaves were exposed to light, ethylene production initially increased because EFE activity was promoted by light; subsequently the ethylene production rate declined rapidly due to the rapid decline in ACC level (Fig. 2; Table III). Our data indicate that the underlying mechanism which account for the rapid decline in ACC content is light-promoted ACC malonylation. This conclusion was based on the following observations: (a) the net decrease in ACC content corresponded well to the net increase in MACC content; (b) there was no or little difference in ethylene production during 0 to 4 or 0 to 6 h between light and dark incubation, indicating that the rapid decline in ACC content under light could not be attributed to the increased amount of ACC converted to ethylene; and (c) similarly, the rapid decline in ACC content under light could not be due to the decrease in ACC synthesis, because there was no significant difference in gross ACC-synthesis during the incubation between the light and dark treatments (Fig. 2D). Gross ACC-synthesis was estimated as the sum of (ethylene produced during the incubation period) + (difference in ACC content after and before incubation) + (difference in MACC content after and before incubation period). Since the extractable ACC-malonyltransferase activity from light-treated tissue was not significantly higher than that of the dark control (Table V), light must have exerted its promotive effect by an unknown mechanism other than an increase in the level of ACC-malonyltransferase. By employing the conventional red light or red light followed by far-red irradiation, we demonstrated the promotion of ACC malonylation by light was mediated through phytochrome system. However, the mechanism by which phytochrome modulates the ACC malonylation is not understood. Although we have observed that light promoted ACC-to-ethylene conversion, the nature of this light promotion was not further characterized.

Depending on the tissues and conditions employed, light can promote or inhibit ethylene production. Many investigators have

Table V. *Effect of Light on Extractable ACC-Malonyltransferase Activity*

Lots of 0.5 g of leaf segments (3 cm) were cut from 8-d-old etiolated wheat seedlings and illuminated with continuous white light for various periods as indicated. ACC-malonyltransferase was extracted and measured as described in "Materials and Methods."

Duration of Illumination	ACC-Malonyltransferase Activity
h	*nmol/mg protein·h*
0	0.69
2	0.99
4	0.71
7	0.49

observed that light markedly inhibited ACC-dependent ethylene production by excised, green leaf segments in enclosed flasks. Later work (10, 15) has established that a low level of CO_2 is required for the conversion of ACC to ethylene, and that the observed inhibitory effect of light with excised green leaf tissue in the enclosed vessels is due to the depletion of endogenous CO_2 level by photosynthetic fixation. In these systems, when sufficient CO_2 is provided, light becomes a promoting rather than an inhibitory factor. In the present etiolated wheat leaf tissue, we found CO_2 had no effect on ethylene production in the light or the dark. This is expected because etiolated leaf tissue has no or little photosynthetic activity.

Another type of modulation of ethylene production known to be mediated by light is via phytochrome for phototropic curvature or elongation growth of plumule (2, 5) and shoots (9) of pea seedlings, hook portions of beans (17, 19), cucumber cotyledon (4), and the excised coleoptile of rice (8). Since these reports appeared before the discovery of ACC and MACC, studies on ethylene production in relation to ACC and MACC metabolism were not conducted. Although most reports related that white or red light inhibited ethylene production (5, 8, 17, 19), one report observed that red light promoted ethylene production in the shoot of pea seedling (16). It should be noted that ethylene production depends not only upon EFE activity but also upon ACC level. Our present study demonstrates that light exerts dual roles on ethylene production: light may stimulate ethylene production by promoting EFE, when ACC level is not a limiting factor; light may inhibit ethylene production by decreasing ACC level via promotion of ACC malonylation. It has been well established that red light specifically inhibits ethylene formation in the hook regions of pea and bean seedlings and this results in the opening of the hook (2, 5, 9). Possible involvement of phytochrome in inhibiting ethylene formation in these etiolated hook region by promoting ACC malonylation is currently under investigation.

Although the malonylation of ACC occurs widely in plant tissues (21), the present study indicates that this constitutive capability can be further modulated by light via the phytochrome system. Aside from light, ethylene is another factor which has been shown to promote ACC malonylation in various plant tissues (11, 12).

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