Plant Physiol. (1993) 102: 1179–1184

Selected Components of the Shade-Avoidance Syndrome Are Displayed in a Normal Manner in Mutants of *Arabidopsis thaliana* and *Brassica rapa* Deficient in Phytochrome B

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Several growth parameters associated with the phytochrome-mediated shade avoidance syndrome have been measured in seedlings and mature plants of a wild-type and a *hy3* mutant of *Arabidopsis thaliana* deficient in phytochrome B. Growth parameters were compared in plants grown in either white light (high red:far-red [R:FR] ratio) or white light plus added far-red (FR) light (low R:FR ratio). Wild-type *Arabidopsis* exhibited increased hypocotyl and petiole extension under a low, compared with a high, R:FR ratio. The *hy3* mutant did not respond to low R:FR ratio by increase in hypocotyl or petiole length. Extension growth of wild-type plants was stimulated by brief end-of-day FR pulses, but similar treatment had no effect on extension growth of *hy3* mutant plants. However, some responses to low R:FR ratio seen in the wild-type plants were also evident in the *hy3* mutants. The number of days to bolting, the developmental stage at bolting, the leaf area, and the specific stem weight (weight per unit of length) all decreased in the wild-type and *hy3* seedlings in response to low R:FR ratio. Low R:FR ratio caused a larger decrease in leaf area and specific stem weight in the mutant seedlings than in wild-type seedlings. The effects of low R:FR ratio on leaf area and specific stem weight were opposite to those of the *hy3* lesion, which resulted in increased leaf area and specific stem weight in comparison with the wild type. Both leaf area and specific stem weight responses to low R:FR ratio also were unchanged in the *ein* mutant of *Brassica rapa*, known to be deficient in phytochrome B. These responses represent components of the shade-avoidance syndrome, and, consequently, the results indicate that phytochrome B cannot be solely responsible for the perception of R:FR ratio and the induction of shade-avoidance responses. The hypothesis is proposed that different phytochromes may be responsible for the regulation of extension growth and the regulation of lateral or radial expansion.

Phytochromes are a family of photoreceptors having multiple functions (Smith and Whitelam, 1990) and are encoded by a small multigene family that, in *Arabidopsis thaliana*, comprise five distinct phytochrome genes (Sharrock and Quail, 1989). Phytochrome molecules are grouped into two types on physiological and biochemical grounds: type I phytochrome predominates in etiolated tissue and is rapidly degraded in the presence of light, whereas type II phytochromes are expressed at lower levels in both etiolated and deetiolated tissue and are comparatively light stable (see Smith and Whitelam, 1990, for review). Type I phytochrome is now generally accepted to be represented by phytochrome A, which is coded for by the *phyA* gene and accumulates to relatively high levels in etiolated seedlings (Smith and Whitelam, 1990). The consensus is that the type II phytochromes are coded for by the other *phy* genes, which are constitutively expressed and not subject to light regulation, as is the expression of the *phyA* gene. Evidence is accumulating that the individual phytochromes mediate different physiological functions, although overlap of function should not be ruled out (Smith and Whitelam, 1990). Physiological analyses of mutant and transgenic plants have indicated that a major function of phytochrome A is to mediate the FR high irradiance response in etiolated seedlings (McCormac et al., 1991, 1992a, 1992b; Whitelam et al., 1992). Phytochrome B is involved in responses of light-grown plants to R:FR ratio, which include the shade-avoidance syndrome. This paper addresses this subject and provides evidence from studies on mutants deficient in phytochrome B that at least one other member of the phytochrome family must be involved in R:FR ratio perception and in the induction of distinct components of shade avoidance.

Several photomorphogenic mutations have been identified (Kendrick and Nagatani, 1991); several of these affect some aspect of the phytochrome-mediated responses and, although they are pleiotropic, have provided important clues to the functions of phytochrome species. Thus far, four mutants deficient in type II phytochrome have been described; these are the *hy3* mutant of *Arabidopsis* (Koornneef et al., 1980), the *lh* mutant of cucumber (Adamse et al., 1987), the *ein* mutant of *Brassica rapa* (Devlin et al., 1992), and the ma_3^R mutant of *Sorghum bicolor* (Childs et al., 1991). All four mutants have elongated internodes and, where present, hypocotyls, and all have the appearance of shade-avoiding species grown under vegetation shade. Of these mutants, *hy3*, *lh*, and *ein* contain phytochrome A but are deficient in immunochemically detectable phytochrome B (Somers et al., 1991; Devlin et al., 1992; Lopes-Juez et al., 1992). Light-grown plants of *lh*, *hy3*, and *ein* lack an EODFR response and exhibit strongly reduced responses to R:FR ratio compared with wild type (Lopez-Juez et al., 1990; Ballaré et al., 1991; Nagatani et al., 1991; Whitelam and Smith, 1991;

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Abbreviations: EODFR, end of day far-red; FR, far-red light; R, red light; R:FR ratio, the photon fluence rate ratio of red to far-red light in 10-nm bandwidths centered on 660 nm and 730 nm.

Devlin et al., 1992; Smith et al., 1992). The *hy3* mutant of *Arabidopsis* has recently been shown to have a lesion within the *phyB* gene, causing the complete absence of phytochrome B (Reed et al., 1993). The *hy3* mutant does not deetiolate normally, because it has elongated hypocotyls in white light; furthermore, it displays disruption of photomorphogenesis after deetiolation, showing severely reduced responses to low R:FR ratio, although these responses are not entirely absent (Whitelam and Smith, 1991). The *Brassica ein* mutant, like the *Arabidopsis hy3*, has aberrant deetiolation and markedly reduced responses to R:FR ratio (Devlin et al., 1992). The fact that mutants deficient in phytochrome B have reduced responses to R:FR ratio may indicate that they are leaky mutations. However, the existence of nonleaky *phyB* mutants that exhibit shade-avoidance responses, however reduced, argues for a scenario in which another member of the phytochrome family operates together with phytochrome B for full display of the shade-avoidance syndrome. The Bo64 allele of *hy3* has recently been shown by Reed et al. (1993) to have an introduced stop codon in the *phyB* gene.

This study examines the effect of R:FR ratio on a number of growth responses in the normal genotype and the *hy3* (Bo64) mutant of *Arabidopsis*, together with supporting data from the *Brassica ein* mutant. Observations show the unmodified retention of certain responses to R:FR ratio and allow the assignment of particular components of the shade-avoidance syndrome to members of the phytochrome family other than phytochrome B.

MATERIALS AND METHODS

Plant Material and Growth Conditions

Arabidopsis thaliana L. ecotype Landsberg *erecta* and the *hy3* mutant (Bo64) were used in this study. For measurements of hypocotyl length, seeds were sown in 10 × 1 × 1.5 cm high plexiglass troughs filled with 1% (w/v) agar containing mineral salts, as described by Whitelam et al. (1992). Seeds were chilled for 4 d at 4°C in the dark, then germinated under continuous white fluorescent light (photon fluence rate, 400–700 nm, 100 μmol m^{-2} s^{-1}) for 2 d before the onset of light treatments. The high and low R:FR ratio sources were as described below. For EODFR treatments, seedlings were grown in cycles of 10-h light/14-h dark for 4 d before measurement of hypocotyl lengths. Where appropriate, a 15-min pulse of EODFR (photon fluence rate, 700–800 nm, 15 μmol m^{-2} s^{-1}) was provided by the output of water-cooled 100-W incandescent lamps filtered through black plexiglass (type FRF 700, Westlake Plastics, Lemmi Mills, PA).

For experiments with mature plants, seeds were sown onto a 3:1 mixture of peat compost and horticultural silver sand, held at 4°C in the dark for 1 week, germinated under continuous white fluorescent light (photon fluence rate, 400–700 nm, 100 μmol m^{-2} s^{-1}) for 1 week, and then transplanted into pots containing the same sand/compost mixture and transferred to the appropriate light treatment. The R:FR ratio treatment cabinets were the same as those described by Keiller and Smith (1989). Photoperiods of 10 h of light and 14 h of dark were used. The high R:FR cabinet (cool white fluorescent light) provided a fluence rate (400–700 nm) of 228 mmol m^{-2} s^{-1} and a R:FR ratio of 7.37. The low R:FR cabinet (cool white fluorescent light supplemented with FR) provided the same photon fluence rate (400–700 nm), but a R:FR ratio of 0.24 was provided by the addition of FR from incandescent lamps filtered through black plexiglass and cooled by passage through 1 cm of flowing water. All light measurements were made using an LI 1800/12 spectroradiometer (Li-Cor, Lincoln, NE).

Growth Measurements

Hypocotyl lengths were measured from calibrated projected photographic transparencies. Petiole lengths and plant heights were measured with a ruler and, where appropriate, measuring calipers. Values shown are means ± SE of at least 10 plants. Leaf areas were determined using the third pair of leaves with a leaf area meter (Li-Cor LI-3000). The specific stem weight was determined as the weight per unit of length of the cauline stem, averaging across the entire stem.

RESULTS AND DISCUSSION

The stimulation of the increase in hypocotyl length by low R:FR ratio is well documented. Figure 1 shows the effect of continuous illumination with light of high and low R:FR ratio on hypocotyl length in *Arabidopsis hy3* and its isogenic wild type. Clearly, there is no promotion of hypocotyl extension by low R:FR ratio in *hy3*, although a substantial increase is observed in the wild type (Fig. 1). Similarly, no effect is seen after EODFR treatment in the mutant, whereas the wild-type strain shows a clear increase in hypocotyl length after EODFR (Fig. 2). Thus, at the hypocotyl stage, the absence of phyto-

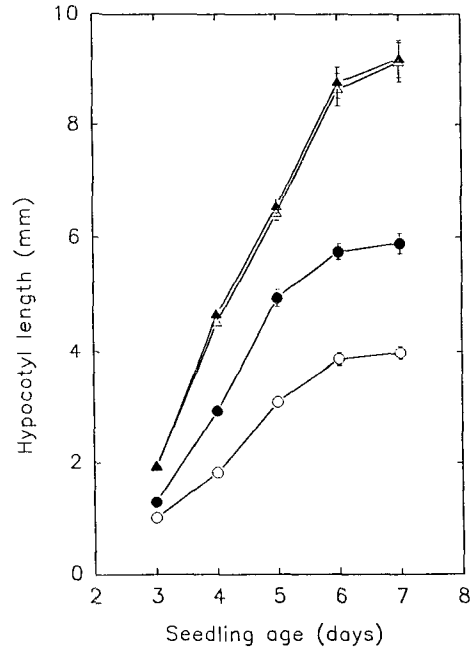


Figure 1. Hypocotyl elongation growth of wild-type (circles) and *hy3* (triangles) *Arabidopsis* seedlings in response to high (open symbols) or low (filled symbols) R:FR ratio. Seedlings were grown for 2 d under continuous white light prior to treatment.

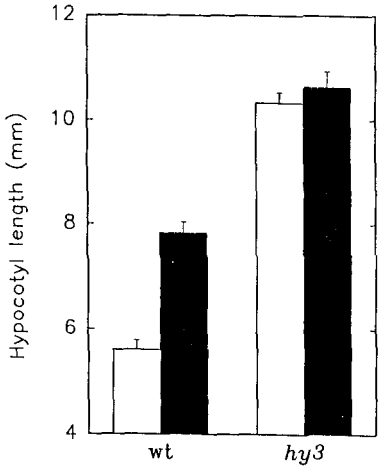


Figure 2. Hypocotyl length of wild-type (wt) and *hy3 Arabidopsis* seedlings grown in a 10-h light, 14-h dark cycle for 4 d without (open block) and with (filled block) 15-min EODFR treatment.

chrome B completely eliminates the extension growth responses to low R:FR ratio and to EODFR.

Similarly, no effect of low R:FR ratio could be seen in petiole extension of *hy3* plants grown for up to 20 d in the light cabinets, whereas the wild types responded to the extent that petiole length at d 19 was approximately 50% greater in a low than in a high R:FR ratio (Fig. 3). Measurements of plant height (Fig. 4A) show an increase in extension growth under low R:FR ratio in both wild-type and mutant plants. Examination of Figure 4B, however, indicates that the in-

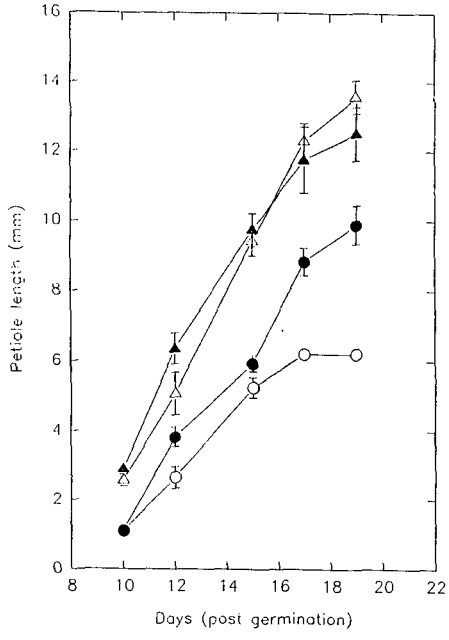
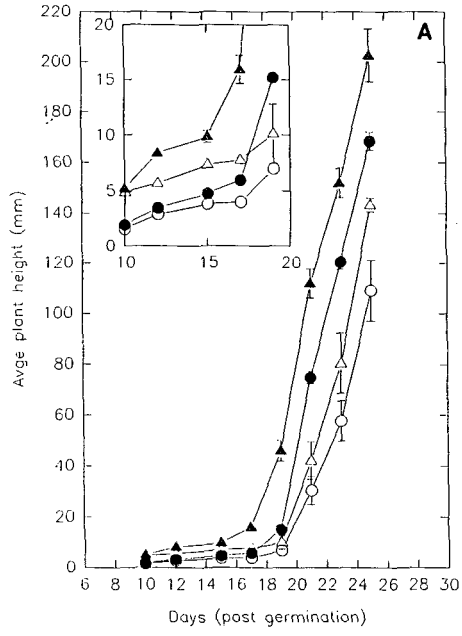


Figure 3. Increase in petiole length of wild-type (circles) and *hy3* (triangles) *Arabidopsis* plants in response to high (open symbols) and low (filled symbols) R:FR ratio. Seedlings were grown for 7 d in continuous white light prior to treatment.



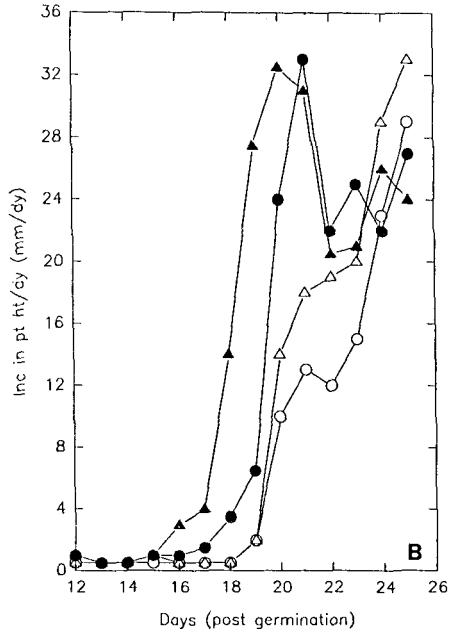


Figure 4. A, Increase in plant height of wild-type (circles) and *hy3* (triangles) *Arabidopsis* plants in response to high (open symbols) and low (filled symbols) R:FR ratio. Seedlings were grown for 7 d in continuous white light prior to treatment. Inset shows expanded portion for d 10 to 20. B, Rate of increase in plant height of wild-type (circles) and *hy3* (triangles) *Arabidopsis* plants in response to high (open symbols) and low (filled symbols) R:FR ratio. Seedlings were grown for 7 d in continuous white light prior to treatment.

crease in height caused by low R:FR is actually due to an acceleration of the onset of cauline stem growth (i.e. bolting) and that actual growth rates do not markedly differ between the two strains or the two treatment conditions. For the wild-type and *hy3* plants grown under high R:FR ratio, cauline stem extension appears to proceed in two phases, beginning at about d 18, reaching a short plateau in extension rate between d 21 and 23, and then increasing to a maximum recorded rate at d 25 (Fig. 4B). Under low R:FR ratio, the extension rate climbed smoothly to a peak reached, in both wild type and *hy3*, about 5 d after the onset of bolting. The wild-type and *hy3* plants achieve similar rates 5 d after bolting under both the high and the low R:FR ratio, although it is uncertain whether the rate is a maximum under conditions of high R:FR ratio. The plant height time courses of Figure 4A may be superimposed simply by moving the curves along the x axis.

These observations suggest that low R:FR ratio does not modulate cauline stem extension in *Arabidopsis*, except through the acceleration of bolting. Growth under low R:FR ratio conditions accelerated the onset of bolting by about 2 d for the wild types and by close to 3 d for the mutant (see Fig. 4A, inset, and Fig. 4B). The *hy3* mutation is known to cause early flowering compared with wild type. Under LD and SD photoperiods and in response to night breaks under an SD photoperiod, the *hy3* mutant shows a decrease in the number of days to, and the developmental stage at, bolting (Goto et al., 1991). Figure 4 shows that the mutation does not, however, remove the effect of low R:FR ratio in decreasing the number of days at which bolting occurs. Similarly, Table I shows that low R:FR ratio causes flowering at an earlier developmental stage in both wild type and *hy3*. When grown under high R:FR ratio, *hy3* has two fewer leaves than wild type at bolting. The effect of low R:FR ratio is to decrease the number of leaves at bolting by two in both *hy3* and wild type; thus, *hy3* displays four leaves at bolting and wild type displays six. Therefore, it may be concluded that although phytochrome B is implicated in flowering by the aberrant flowering times seen in the *hy3* mutant, there is clearly at least one other phytochrome responsible for the acceleration in flowering under low R:FR ratio. These results tie in closely with those of a study of the effects of low R:FR ratio on the acceleration of flowering in *Arabidopsis*, in which the *hy3* mutation, when placed in a late-flowering background, shows no diminution of the acceleration of flowering by low R:FR ratio (G.C. Whitelam, personal communication).

Although developmental effects of low R:FR ratio are most striking in stem extension, correlative effects on leaf development have been reported (Child et al., 1981; Morgan and Smith, 1981). Figure 5 shows that low R:FR ratio treatment

Table I. *Number of leaves at time of bolting of wild-type (wt) and hy3 grown under high and low R:FR ratio*

Plant	R:FR Ratio	Number of Leaves	SE
wt	High	9.5	0.2
wt	Low	7.6	0.2
hy3	High	7.9	0.1
hy3	Low	5.8	0.2

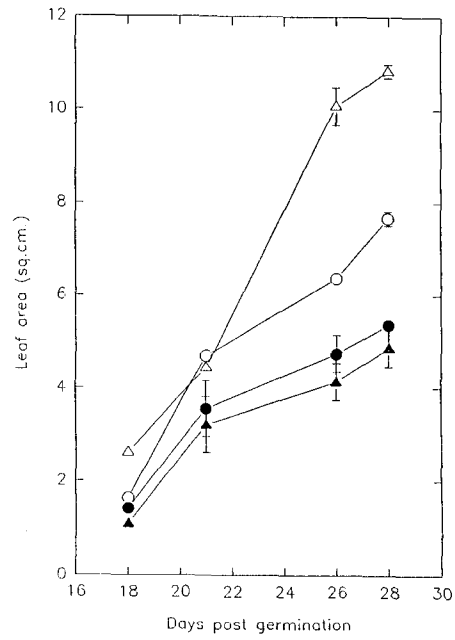


Figure 5. Increase in leaf area of the third pair of leaves of wild-type (circles) and *hy3* (triangles) *Arabidopsis* plants in response to high (open symbols) and low (filled symbols) R:FR ratio. Seedlings were grown for 7 d in continuous white light prior to treatment.

led to a reduction in leaf area in both wild type and *hy3*. At d 28, wild-type plants grown under high R:FR ratio displayed an average leaf area of 7.5 cm^2, and *hy3* plants displayed an average leaf area of 11 cm^2; these values were decreased to 5.25 and 5 cm^2, respectively, under low R:FR ratio. It is interesting that under high R:FR ratio, the *hy3* mutation caused an *increase* in leaf area when compared with the wild type; in other words, the *hy3* lesion causes a developmental effect that is opposite in direction to that caused by low R:FR ratio. Furthermore, the data of Figure 5 indicate that the effect of low R:FR ratio on leaf area is larger in *hy3* than in the wild type, reflecting the greater acceleration of bolting by low R:FR ratio in *hy3* seen in Figure 4. Because, in Figure 5, leaf areas were virtually identical for wild-type and *hy3* plants grown under low R:FR ratio conditions, it may be concluded that the response to low R:FR ratio is unmodified by the *hy3* lesion. It is possible that these values represent the maximum attainable reduction in leaf area.

Identical trends are seen in the study of specific stem weight (i.e. the weight per unit of length of cauline stem). Low R:FR ratio caused a decrease in the specific stem weight in both wild type and *hy3* against a background of higher specific stem weight values in the *hy3* mutant than in wild type when grown in white light of high R:FR ratio (Fig. 6). At d 28, wild-type plants grown under high R:FR ratio displayed an average specific stem weight of 16 mg cm^{-1}, and *hy3* plants displayed an average specific stem weight of 29 mg cm^{-1}. Under a low R:FR ratio, these values were reduced to 8.5 and 8 mg cm^{-1}, respectively. Again, this parameter of growth is affected by low R:FR ratio in the phytochrome B-deficient mutant to an extent as great as, if

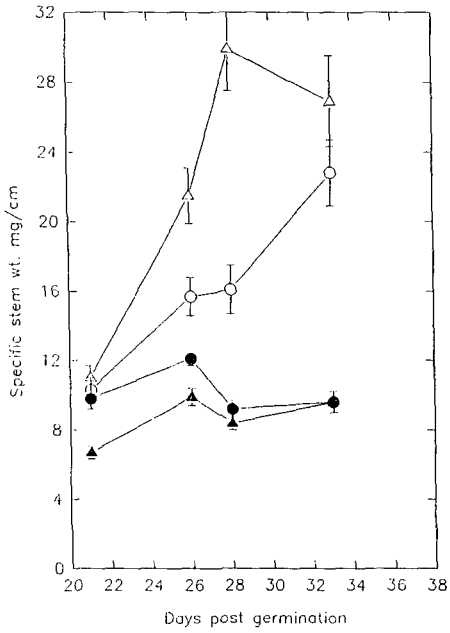


Figure 6. Increase in specific stem weight of wild-type (circles) and *hy3* (triangles) *Arabidopsis* plants in response to high (open symbols) and low (filled symbols) R:FR ratio. Seedlings were grown for 7 d in continuous white light prior to treatment.

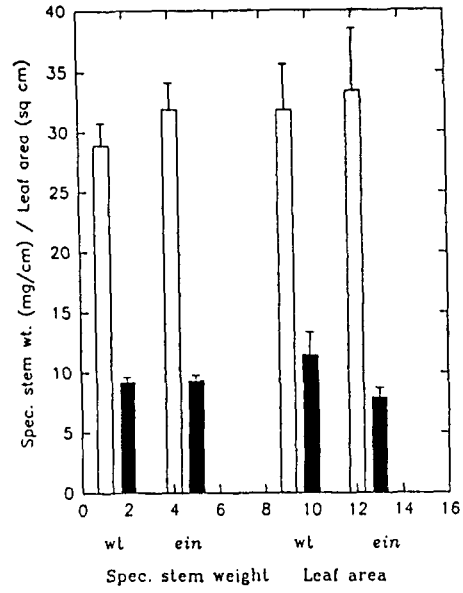


Figure 7. Specific stem weight and leaf area of *B. rapa* wild type (wt) and *ein* after 21 d of treatment under high (open blocks) and low (filled blocks) R:FR ratio. Seedlings were germinated under treatment conditions.

not greater than, in the corresponding wild type. Additionally, as with leaf area, the reduction was to approximately the same value in both wild type and *hy3*, indicating that the response appears unmodified by the *hy3* lesion.

The independence of the effect of low R:FR ratio on leaf area and specific stem weight from phytochrome B was confirmed by examining specific stem weight and leaf area in the *ein* mutant of *B. rapa*, which has been shown to be deficient in immunologically detectable phytochrome B and to lack elongation responses under low R:FR ratio (Devlin et al., 1992). As such, it is an analogous mutant to *hy3*. Figure 7 shows a similar reduction by low R:FR ratio in both specific stem weight and leaf area in both wild type and the *ein* mutant, demonstrating again that these growth responses are unmodified by the absence of phytochrome B.

Together, these results conclusively show that mutants deficient in phytochrome B retain some responses to R:FR ratio. The *hy3* mutant is affected in its time of flowering under high R:FR ratio (Goto et al., 1991). Results concerning days to bolting and number of leaves at bolting, presented here, have shown that the mutant retains the ability to flower early in response to low R:FR ratio. Thus, in addition to a possible effect of phytochrome B on flowering, at least one other phytochrome is also involved in regulating this response. The acceleration of flowering by low R:FR ratio, via phytochrome, may be considered an important facet of shade avoidance in that flowering may represent the final commitment by a plant to escape from shade.

The *hy3* mutant has lost the ability to respond to R:FR ratio by elongation, i.e. of stems and petioles, while retaining the ability to respond by radial expansion, i.e. of leaves and stems. Responses to R:FR ratio are known to be manifested essentially by changes in cell size rather than cell numbers (Child et al., 1981), and Reed et al. (1993) have shown that the *hy3* lesion also predominantly affects cell size rather than cell number. These observations may therefore provide broad functions for at least two of the family of type II phytochromes in *Arabidopsis*. Phytochrome B may be responsible for the regulation of cell elongation growth in response to R:FR ratio, whereas a second phytochrome may be responsible for regulating cell expansion growth in response to R:FR ratio. The parameters measured here that are regulated by a phytochrome other than phytochrome B contribute directly to the shade-avoidance syndrome, in which a plant that is shaded will require resources to be channeled into elongation growth upward at the expense of radial or lateral expansion. On this basis, leaf area in shaded leaves may be sacrificed as part of an overall response in which neighboring vegetation is overtopped, after which the more advantageous leaves developed outside of shade will no longer exhibit the reduction in area. It is established that shade-avoidance responses to low R:FR ratio involve major redistribution of assimilates (Kasperbauer et al., 1984; Keiller and Smith, 1989), and the responses studied here may be manifestations of an underlying mechanism regulating resource partitioning. The concept that different phytochromes may detect identical environmental signals but regulate different components of an overall developmental response is attractive in that it provides for flexibility and precision of response that may not be achievable via a single photoreceptor. It also implies that photomorphogenesis in light-grown plants may be a much more sophisticated phenomenon than hitherto thought.

ACKNOWLEDGMENTS

Graham Benskin and associated staff at the University Botanic Garden are thanked for their careful tending of the *Arabidopsis* plants.

Received March 17, 1993; accepted May 3, 1993.
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