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Effect of Vernalization, Photoperiod, and Light Quality on the Flowering Phenotype of Arabidopsis Plants Containing the *FRIGIDA* Gene[1]

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We have compared the flowering response to vernalization, photoperiod, and far-red (FR) light of the Columbia (Col) and Landsberg *erecta* (L*er*) ecotypes of Arabidopsis into which the flowering-time locus *FRIGIDA* (*FRI*) has been introgressed with that of the wild types Col, L*er*, and San Feliu-2 (Sf-2). In the early-flowering parental ecotypes, Col and L*er*, a large decrease in flowering time in response to vernalization was observed only under short-day conditions. However, Sf-2 and the L*er* and Col genotypes containing *FRI* showed a strong response to vernalization when grown in either long days or short days. Although vernalization reduced the responsiveness to photoperiod, plants vernalized for more than 80 d still showed a slight photoperiod response. The effect of *FRI* on flowering was eliminated by 30 to 40 d of vernalization; subsequently, the response to vernalization in both long days and short days was the same in Col and L*er* with or without *FRI*. FR-light enrichment accelerated flowering in all ecotypes and introgressed lines. However, the FR-light effect was most conspicuous in the *FRI*-containing plants. Saturation of the vernalization effect eliminated the effect of FR light on flowering, although vernalization did not eliminate the increase of petiole length in FR light.

The control of flowering time in Arabidopsis has been studied extensively. Late-flowering mutants that are developmentally delayed in the floral transition have been isolated from several early-flowering ecotypes of Arabidopsis (McKelvie, 1962; Redei, 1962; Vetrilova, 1973; Koornneef et al., 1991). Natural variation of flowering time in many ecotypes of Arabidopsis has also been studied (Van der Veen, 1965; Napp-Zinn, 1969; Karlovska, 1974; Burn et al., 1993; Lee et al., 1993; Clarke and Dean, 1994). Physiological analyses of late-flowering mutants and various ecotypes have shown that flowering is controlled by several environmental factors, such as daylength, temperature, and light quality (Laibach, 1951; Napp-Zinn, 1969; Martinez-Zapater and Somerville, 1990; Koornneef et al., 1991; Bagnall, 1993).

Arabidopsis is a quantitative LDP. Although increased daylength accelerates flowering time of most ecotypes, LDs are not an absolute requirement for flowering. Certain Arabidopsis ecotypes flower under daylengths as short as 4 to 5 h (Laibach, 1951). Cold treatment (vernalization) accelerates flowering in many winter annual ecotypes of Arabidopsis, which otherwise exhibit a strong delay in flowering under LD conditions (Chintraruck and Ketellapper, 1969; Napp-Zinn, 1979; Bagnall, 1993; Burn et al., 1993; Lee et al., 1993; Clarke and Dean, 1994). Although the effect of vernalization is not conspicuous in common early-flowering ecotypes such as Col and L*er* grown under LD conditions, early strains grown under SD conditions flower more rapidly after vernalization (Napp-Zinn, 1985; Koornneef et al., 1991). The flowering of Arabidopsis is also influenced by light quality. FR-light enrichment or FR-light night breaks promote flowering (Brown and Klein, 1971; Martinez-Zapater and Somerville, 1990; Goto et al., 1991; Eskins, 1992; Bagnall, 1993).

A large acceleration of flowering in response to vernalization is also observed in some of the late-flowering mutants such as *fca*, *fve*, *fy*, and *fpa*, whereas other mutants such as *co* and *gi* show no response to vernalization (Martinez-Zapater and Somerville, 1990; Koornneef et al., 1991; Bagnall, 1993). The response to vernalization and the response to FR light are highly correlated; mutants and ecotypes that show a strong response to vernalization are very responsive to FR light, and mutants that show no response to vernalization are not responsive to FR light (Bagnall, 1993). In the *fca* mutant, for example, vernalization eliminated the response to light quality and FR-light enrichment eliminated the vernalization response, indicating that vernalization and FR light can substitute for each other (Bagnall, 1993).

We have reported that a single locus, *FRI*, is responsible for the difference in flowering time between winter annual ecotypes such as Sf-2 and Le-0 and the early-flowering ecotype Col (Lee et al., 1993); however, in the L*er* genetic background, *FRI* causes an extreme delay in flowering only in the presence of another locus, *FLC* (Lee et al., 1994b). (*FRI* was previously referred to as *FLA* as described by Lee et al. [1994b].) Thus, the role of *FRI* and *FLC* is to suppress flowering in contrast to genes that confer a late-flowering

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Abbreviations: Col, Columbia; *FLC*, flowering locus C; FR, far red; *FRI*, *FRIGIDA*; Le-0, Leiden-0; L*er*, Landsberg *erecta*; LN, leaf number; Sf-2, San Feliu-2.

phenotype when mutated; the wild-type role of genes defined by late-flowering mutants is to promote flowering. Similar to the effects on certain late-flowering mutants discussed above, the delay in flowering caused by the presence of *FRI* and *FLC* can be overcome by vernalization (Napp-Zinn, 1979; Lee et al., 1993; Clarke and Dean, 1994).

In this work, the interaction of vernalization, photoperiod, and light quality on the control of flowering time in *FRI*-containing lines was analyzed. For this study, lines were created in which *FRI* was introgressed into the common laboratory strains Col and L*er* to permit a comparison of lines that were essentially isogenic except for the *FRI* locus. Thus, in this study we focused on the effects of *FRI* in the absence of other differences in genetic background that can influence flowering behavior. Furthermore, since extensive genetic and physiological analyses have been performed on flowering time mutants in the Col and L*er* genetic backgrounds, the introgression of *FRI* into these genetic backgrounds allowed a direct comparison of the effect of *FRI* on flowering with that of mutations that have been previously analyzed.

MATERIALS AND METHODS

Plant Lines

The ecotypes and *FRI*-containing lines of *Arabidopsis thaliana* (L.) Heynh. used in this work have been described (Lee et al., 1993, 1994b). Seeds were sown on 0.8% agar containing one-fourth of the recommended level of minerals in Murashige-Skoog medium (Murashige and Skoog, 1962) and incubated at 23°C under SD conditions (8 h of light/16 h of dark) for 7 d prior to transplanting. For vernalization studies, seeds were incubated at 4°C under SD conditions for the times indicated and then cultured at 23°C for an additional 7 d under SD conditions prior to transplanting. The vernalization treatment was performed in SDs, so that the cold treatment was the only environmental signal promoting flowering (i.e. the photoperiod was not inductive for flowering) and because vernalization is most likely to occur under relatively SDs in nature. When incubated at 4°C the seeds germinate slowly: the radicle emerges after 2 weeks and cotyledons have started to expand and accumulate Chl after 4 weeks.

Growth Conditions

Plants were grown at 23 ± 2°C, 60 ± 10% RH, in growth chambers. SD conditions consisted of 8 h of full-intensity light (190 μmol m^{-2} s^{-1}, provided by a mixture of cool-white fluorescent and incandescent bulbs, Fig. 1, top) and 16 h of dark. LD conditions consisted of 8 h of full-intensity light and 8 h of a low-intensity light extension (30 μmol m^{-2} s^{-1}, Fig. 1, top), followed by 8 h of dark. FR-light-enriched conditions consisted of a higher ratio of incandescent to fluorescent bulbs than other conditions (Fig. 1, middle), and cool-white light conditions consisted of only cool-white fluorescent bulbs (Fig. 1, bottom). In comparisons of FR-enriched and cool-white light, plants were grown under 16 h of light and 8 h of dark, and the light intensity was approximately 160 μmol m^{-2} s^{-1}. The red

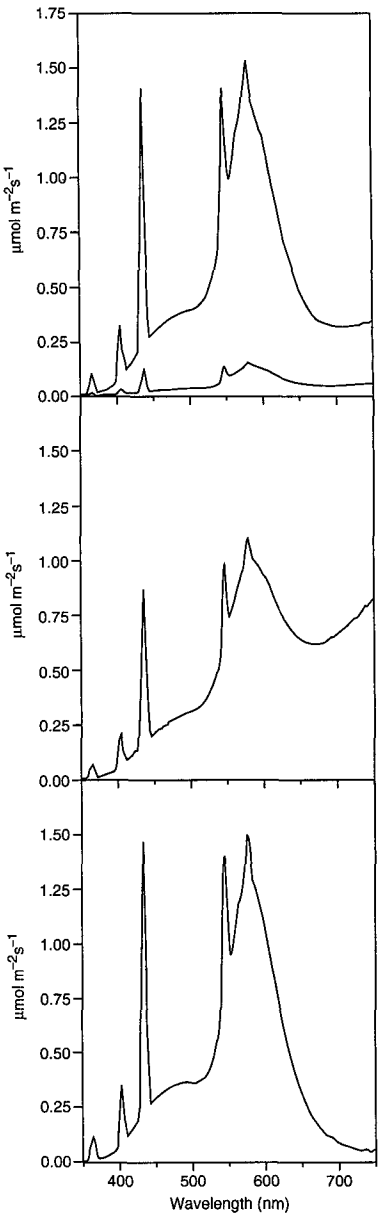

Figure 1. Irradiance spectra for light conditions used. Top, Full-intensity light (top line) and the low-intensity light extension (bottom line) for photoperiod experiments. Middle, FR-enriched light. Bottom, Cool-white light.

(655–665 nm) to FR (725–735 nm) ratios were 0.8 for FR-enriched light and 4.6 for cool-white light. The irradiance spectra for each light condition are shown in Figure 1. The spectra were measured by a Li-Cor 1800 spectroradiometer (Lincoln, NE).

Flowering Phenotype and Petiole Length

The flowering behavior of the plants was measured as the number of primary rosette leaves present when the flowering stalks reached 0.5 cm. This value is referred to as LN. Primary rosette leaves refer to those leaves in the rosette that are derived from the apical meristem; leaves

derived from lateral buds were not scored. The LN values are highly correlated with flowering time (Koornneef et al., 1991). Petiole length was measured for the fifth rosette leaf after full-leaf expansion.

RESULTS

Introduction of *FRI* into the Col and L*er* Genetic Backgrounds

To study the effect of *FRI* on floral induction, the *FRI* locus from the late-flowering, winter annual Arabidopsis ecotype Sf-2 was introgressed into the common laboratory strains, Col and L*er*. The late-flowering trait of Sf-2 is derived from a single locus, *FRI*, in the cross with Col and two loci, *FRI* and *FLC*-Sf-2, in the cross with L*er* (Lee et al., 1993, 1994b). A *FRI*-containing line in the Col genetic background was obtained after the sixth backcross generation. For the introgression of *FRI* into L*er*, a *FRI* monogenic line with *FLC*-L*er* was obtained from the fourth backcross into L*er*, and *FRI* with homozygous *FLC*-Sf-2 was obtained from the seventh backcross into L*er* (Lee et al., 1994b).

Interaction of Vernalization and Photoperiod

In the following experiments, LD photoperiods were provided by an 8-h extension of low-intensity light to minimize differences in photosynthesis under different daylengths (Fig. 1, top), and vernalization was conducted under SDs.

Parental Lines

The LN at flowering of Col, L*er*, and Sf-2 was determined after vernalization periods of up to 100 d and subsequent growth in LDs or SDs (Fig. 2). When grown in LDs, the early-flowering ecotypes Col and L*er* did not show a significant decrease of LN after long periods of cold treatment; however, under SD conditions, vernalization caused a large decrease in LN in these lines (Fig. 2, A and B). The winter annual ecotype Sf-2 flowered much earlier after vernalization when grown in either LDs or SDs (Figs. 2C and 3). Sf-2 plants grown in SDs without vernalization flowered after more than 100 d with more than 100 leaves (Fig. 2C). The flowering stalks of these plants were usually derived from axillary buds and not from the primary meristem, and these experiments were terminated before the final LN of these plants could be determined.

FRI-Containing Lines

Introduction of the *FRI* locus into Col caused an extreme delay in flowering time under both LDs and SDs in plants that were not vernalized (Figs. 2D and 3). In the L*er* genetic background, the late-flowering effects of *FRI* were suppressed by the *FLC*-L*er* allele (Lee et al., 1994b); hence, plants containing *FRI* and *FLC*-L*er* showed only a slight delay in flowering compared to L*er* (Fig. 2E). When *FRI* was introgressed with *FLC*-Sf-2 into L*er*, an extreme delay in flowering that could be overcome by vernalization was observed (Figs. 2F and 3). Col-containing *FRI* and L*er*-containing *FRI* and *FLC*-Sf-2 grown under SDs without vernalization flowered after forming more than 100 rosette leaves, and the flowering stalks of these lines were usually derived from axillary buds similar to Sf-2 grown under these conditions (Fig. 2, D and F). In all *FRI*-containing lines, vernalization resulted in a large reduction in LN in either LDs or SDs (Figs. 2 and 3). The effect of *FRI* on flowering was eliminated by 30 to 40 d of vernalization; thereafter, no difference in LN was observed between *FRI*-containing lines and the early-flowering parental lines, Col and L*er*, grown in either LDs or SDs (Fig. 2, cf. A with D, cf. B with E and F). However, in both *FRI*-containing lines and parental lines grown in SDs, further vernalization reduced LN until the vernalization effect was saturated by 80 d of cold treatment (Fig. 2).

The difference in LN between plants grown under LDs and SDs was progressively decreased by increasing days of vernalization treatment; i.e. vernalization decreased the large delay in flowering caused by noninductive photoperiods (Fig. 2). However, prolonged vernalization did not eliminate the photoperiodic responsiveness of plants, since LN was reduced in LDs compared to SDs after saturation of the vernalization effect under SDs (Figs. 2 and 3).

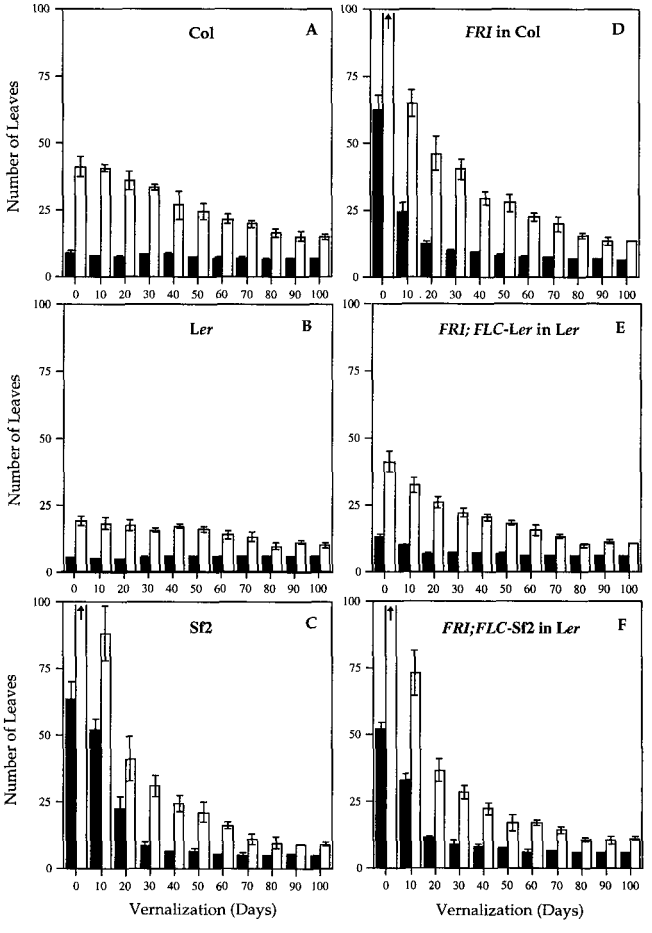

Figure 2. Effect of vernalization on LN of each line grown under LDs (black bars) and SDs (white bars). The values are the average of six plants, and the SDs are represented by error bars. The arrow indicates a value beyond the axis.

Vernalization Eliminates the Responsiveness to Light Quality

The interaction of vernalization and light quality was analyzed at red:FR ratios of 0.8 and 4.6. To minimize an effect of photosynthesis on flowering, a similar light intensity was administered for the two light conditions (Fig. 1, middle and bottom).

The early-flowering ecotypes Col and *Ler* showed only a slight acceleration of flowering in response to FR-enriched light (Fig. 4, A and B). The winter annual Sf-2, *FRI* in Col, and *FRI* with *FLC*-Sf-2 in *Ler* showed a strong response to FR light; the LN of these lines grown under FR-enriched light was reduced more than 50% compared to growth under cool-white light in plants that were not vernalized (Fig. 4). The response of these lines to FR light was greatly reduced by vernalization. After 30 to 40 d of vernalization, these lines showed only a slight response to FR light similar to the early-flowering parental lines. Thus, similar to the effects of *FRI* in different photoperiods that are discussed above, the effect of *FRI* on the response to FR-enriched light was eliminated by 30 to 40 d of vernalization. Prolonged vernalization eliminated the responsiveness to light quality in all of the lines. After 80 d of vernalization, no difference in LN between the two light conditions was observed (Fig. 4). *Ler* containing only *FRI* (i.e. with *FLC*-*Ler*) flowered much earlier in LDs than did *FRI* with *FLC*-Sf-2 and, therefore, showed a smaller reduction in flowering time under FR light (Fig. 4).

Light Quality Effect on Petiole Length

FR-enriched light conditions also had an effect on petiole length (Fig. 5). In all six lines, FR-enriched light increased petiole length compared to cool-white light. Whereas long periods of vernalization eliminated the flowering response to FR-enriched light, vernalization did not eliminate the increase of petiole length by FR-enriched light. Generally, plants with an *Ler* genetic background had a shorter petiole length than plants with a Col or Sf-2 genetic background, but the effects of FR light were consistent in each genetic background.

DISCUSSION

We have shown that the introgression of *FRI* into the early-flowering ecotypes Col and *Ler* causes an extreme delay in flowering time and that this delay in flowering can be overcome by vernalization. Thus, *FRI* (and *FLC*-Sf-2 in *Ler* genetic background) fully accounts for the flowering behavior of the winter annual ecotype, Sf-2. It is likely that *FRI* is a major determinant of the flowering behavior in many winter annual Arabidopsis ecotypes, since the loci conferring lateness in other late-flowering ecotypes occur at a similar chromosomal position (Burn et al., 1993; Lee et al., 1993; Clarke and Dean, 1994).

FRI-containing lines exhibit responsiveness to photoperiod. Although without vernalization these lines flower relatively late in inductive photoperiods, flowering time is further delayed by noninductive, SD photoperiods (Fig. 2). Thus, *FRI* does not appear to change photoperiodic responsiveness but shifts the response to much later flowering times. This phenotype is similar to that observed in plants containing mutants in *FCA*, *FPA*, *FVE*, *FY*, and *LD* (Koornneef et al., 1991; Lee et al., 1994a).

The delay of flowering time caused by *FRI* is eliminated by vernalization. After 30 to 40 d of vernalization, the flowering time of *FRI*-containing lines is the same as their parental lines in both LDs and SDs (Fig. 2). However, approximately 80 d of vernalization are required to saturate the promotion of flowering in SDs, regardless of the

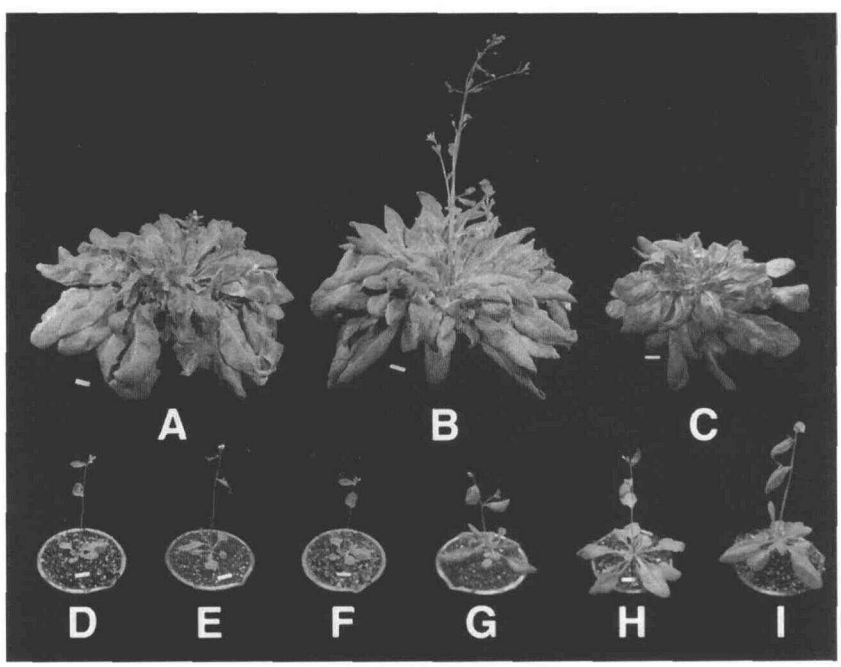

Figure 3. Flowering phenotypes of Sf-2 and *FRI*-introgressed lines. Plants were grown under LDs without vernalization (A–C), under LDs after 100 d of vernalization (D–F), and under SDs after 100 d of vernalization (G–I). A, D, and G, Sf-2; B, E, and H, *FRI* in Col; C, F, and I, *FRI* and *FLC-Sf-2* in *Ler*. Plants are shown when the first flowers had opened. White bar = 1 cm.

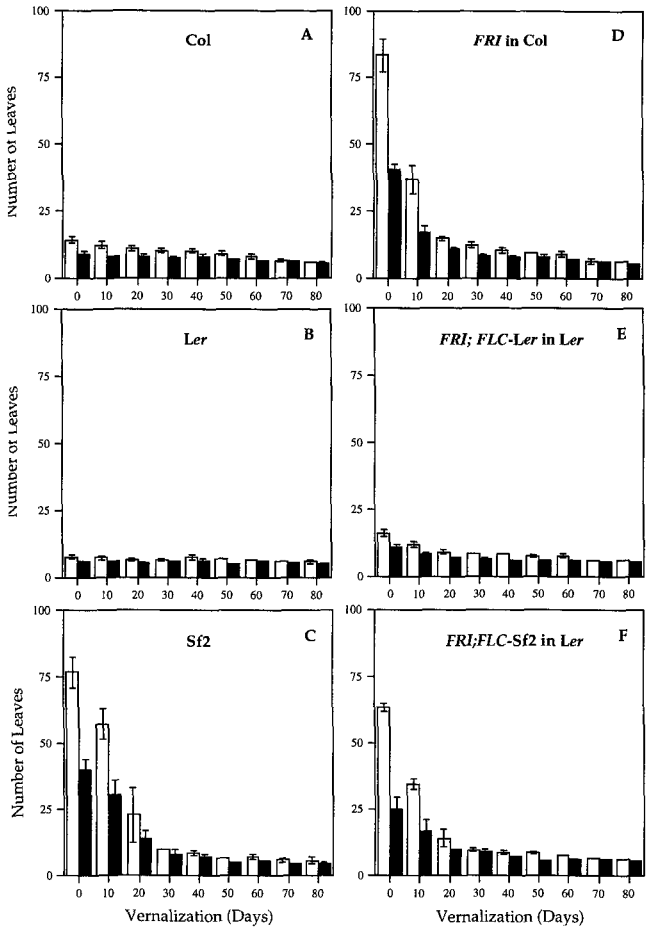

Figure 4. Effect of vernalization on LN of each line grown under cool-white light (white bars) and FR-enriched light (black bars). The values are the average of six plants, and the SDs are represented by error bars.

FRI genotype. Furthermore, saturation of the vernalization effect greatly reduces but does not completely eliminate photoperiodic responsiveness. Thus, the *FRI*-mediated inhibition of flowering is more readily negated by the flower-promoting effects of vernalization than SD-mediated inhibition.

The *FRI* locus also confers a strong responsiveness to light quality. Specifically, the flowering time of *FRI*-containing plants is greatly reduced in FR-enriched light (Fig. 4). This is similar to the response of the late-flowering mutants *fca, fve,* and *fy* and other late-flowering ecotypes (Martinez-Zapater and Somerville, 1990; Bagnall, 1993). As is the case with other *FRI* phenotypes discussed above, to obtain a maximal response to light quality in the L*er* genetic background, *FRI* must be combined with a non-L*er* allele at the *FLC* locus such as *FLC*-Sf-2. The strong responsiveness to light quality caused by *FRI* was eliminated by 30 to 40 d of vernalization. Further vernalization totally eliminated the responsiveness to light quality; plants vernalized for 80 d did not show any significant difference in flowering time in FR-enriched versus cool-white light.

FR-light enrichment also affected petiole length. The petiole length of the plants grown under incandescent light is longer than that of plants grown under fluorescent light. The phytochrome B-deficient mutant, *hy3*, shows increased petiole length as well as early flowering, demonstrating that petiole length and flowering are influenced by phytochrome (Reed et al., 1993). Although vernalization could eliminate the flowering response to FR light, vernalization did not eliminate the FR stimulation of petiole elongation. Therefore, vernalization is not likely to affect the perception of FR light, and the effects of vernalization on flowering are presumably downstream of FR-light perception.

The similarity in the flowering phenotype of *FRI*-containing plants and plants containing induced mutations in genes such as *FCA, FPA, FVE, FY,* and *LD* indicates that these genes act in a common flowering pathway. Since *FRI* is naturally occurring and widespread among late-flowering ecotypes (Burn et al., 1993; Lee et al., 1993; Clarke and Dean, 1994), it is likely that this dominant *FRI* allele evolved to delay flowering by acting as a suppressor of this pathway. The wild-type role of genes such as *FCA, FPA, FVE, FY,* and *LD,* which delay flowering when mutated, is to activate this flowering pathway.

The presence of *FRI* essentially causes Arabidopsis to behave as an "obligate" LDP, since the primary meristem of most *FRI*-containing plants that are not vernalized fails to produce a flowering stalk under SDs. An obligate response to photoperiod is also observed in the GA biosynthetic mutant *ga1–3*, which fails to flower under SD conditions (Wilson et al., 1992). Treatment with GA accelerates flowering of *FRI*-containing ecotypes (Napp-Zinn, 1969) and overcomes the flowering effect of the *ga1–3* mutation (Wilson et al., 1992).

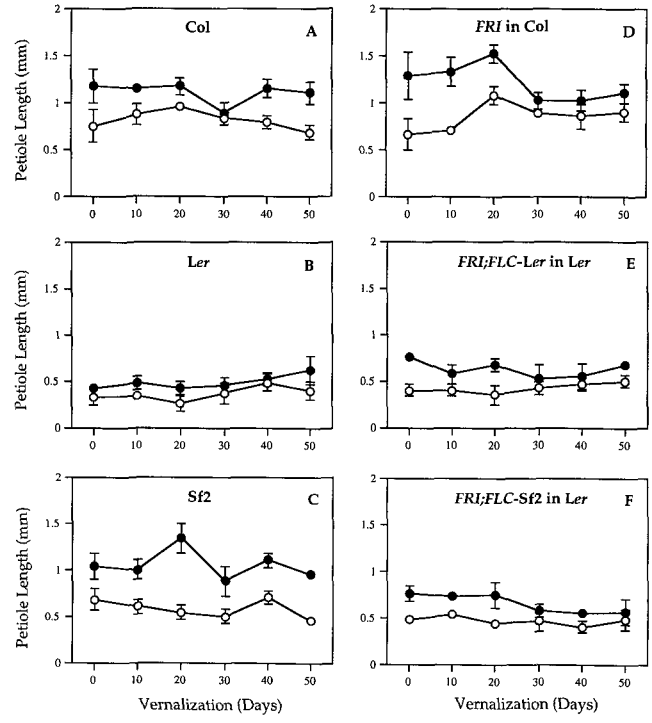

Figure 5. Effect of vernalization on petiole length of each line grown under cool-white light (○) and FR-enriched light (●). The values are the average of six plants, and the SDs are represented by error bars.

However, unlike *FRI*, the block to flowering imposed by *ga1–3* under SDs cannot be overcome by vernalization, and the delay in flowering imposed by *ga1–3* under LDs is minimal (Wilson et al., 1992). Flowering in Arabidopsis appears to be controlled by multiple pathways (Martinez-Zapater and Somerville, 1990; Koornneef et al., 1991). It is possible that *FRI* and *ga1–3* affect separate flowering pathways and that GA metabolism is required for the promotion of flowering by vernalization and flowering in noninductive photoperiods. In this model, the activation of the separate vernalization pathway and the resulting alterations of GA metabolism would bypass the block to flowering imposed by *FRI*. As discussed previously (Napp-Zinn, 1979; Lee et al., 1993), *FRI* therefore creates a requirement for vernalization for rapid flowering to occur.

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LITERATURE CITED

Bagnall DJ (1993) Light quality and vernalization interact in controlling late flowering in *Arabidopsis thaliana* ecotypes and mutants. Ann Bot **71:** 75–83

Brown JAM, Klein WH (1971) Photomorphogenesis in *Arabidopsis thaliana* (L.) Heyhn. Plant Physiol **47:** 393–399

Burn JE, Smyth DR, Peacock WJ, Dennis ES (1993) Genes conferring late flowering in *Arabidopsis thaliana*. Genetica **90:** 147–155

Chintraruck B, Ketellapper HJ (1969) Interaction of vernalization, photoperiod and high temperature in flowering of *Arabidopsis thaliana* (L.) Heynh. Plant Cell Physiol **10:** 271–276

Clarke JH, Dean C (1994) Mapping *FRI*, a locus controlling flowering time and vernalization response in *Arabidopsis thaliana*. Mol Gen Genet **242:** 81–89

Eskins K (1992) Light-quality effects on *Arabidopsis* development. Red, blue and far-red regulation of flowering and morphology. Physiol Plant **86:** 439–444

Goto N, Kumagai T, Koornneef M (1991) Flowering responses to light-breaks in photomorphogenic mutants of *Arabidopsis thaliana*, a long-day plant. Physiol Plant **83:** 209–215

Karlovska V (1974) Genetic control of the speed of development in *Arabidopsis thaliana* (L.) Heynh. Lines obtained from natural populations. Biol Plant **16:** 107–117

Koornneef M, Hanhart CJ, van der Veen JH (1991) A genetic and physiological analysis of late flowering mutants in *Arabidopsis thaliana*. Mol Gen Genet **229:** 57–66

Laibach F (1951) Uber sommer und winterannuelle Rasse von *Arabidopsis thaliana* (L.) Heynh. Ein Beitrag zur Atiologie der Blutenbildung. Beitr Biol Pflanz **28:** 173–210

Lee I, Aukerman MJ, Gore SL, Lohman KN, Michaels SD, Weaver LM, John MC, Feldmann KA, Amasino RM (1994a) Isolation of *LUMINIDEPENDENS*, a gene involved in the control of flowering time in *Arabidopsis thaliana*. Plant Cell **6:** 75–83

Lee I, Bleecker A, Amasino RM (1993) Analysis of naturally occurring late flowering in *Arabidopsis thaliana*. Mol Gen Genet **237:** 171–176

Lee I, Michaels SD, Masshardt AS, Amasino RM (1994b) The late-flowering phenotype of *FRIGIDA* and mutations in *LUMINIDEPENDENS* is suppressed in the Landsberg *erecta* strain of *Arabidopsis*. Plant J **6:** 903–909

Martinez-Zapater JM, Somerville CR (1990) Effect of light quality and vernalization of late-flowering mutants of *Arabidopsis thaliana*. Plant Physiol **92:** 770–776

McKelvie AD (1962) A list of mutant genes in *Arabidopsis thaliana* (L.) Heynh. Radiat Bot **1:** 233–241

Murashige T, Skoog F (1962) A revised medium for rapid growth and bioassay with tobacco tissue cultures. Physiol Plant **15:** 473–497

Napp-Zinn K (1969) *Arabidopsis thaliana* (L.) Heynh. *In* LT Evans, eds, The Induction of Flowering: Some Case Histories. MacMillan, Melbourne, Australia, pp 291–304

Napp-Zinn K (1979) On the genetical basis of vernalization requirement in *Arabidopsis thaliana* (L.) Heynh. *In* P Champagnat, R Jaques, eds, La Physiologie de la Floraison. Coll. Int. Centre National de la Recherche Scientifique, Paris, pp 217–220

Napp-Zinn K (1985) *Arabidopsis thaliana*. *In* AH Halevy, eds, CRC Handbook of flowering, CRC Press Inc, Boca Raton, FL, pp 492–503

Redei GP (1962) Supervital mutants in *Arabidopsis*. Genetics **47:** 443–460

Reed JW, Nagpal P, Poole DS, Furuya M, Chory J (1993) Mutations in the gene for the red/far-red light receptor phytochrome-B alter cell elongation and physiological responses throughout *Arabidopsis* development. Plant Cell **5:** 147–157

Van der Veen JH (1965) Genes for late flowering in *Arabidopsis thaliana*. *In* Arabidopsis Research, report of an international symposium, University of Gottingen, Arabidopsis Information Service, Gottingen, West Germany, pp 62–69

Vetrilova M (1973) Genetic and physiological analysis of induced late mutants of *Arabidopsis thaliana* (L.) Heynh. Biol Plant **15:** 391–397

Wilson RN, Heckman JW, Somerville CR (1992) Gibberellin is required for flowering in *Arabidopsis thaliana* under short days. Plant Physiol **100:** 403–408