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Effects of Red and Far Red Light on the Initiation of Cold Acclimation in *Cornus stolonifera* Michx.[1]

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ABSTRACT

Red and far red light distinctly influence the initial phytochrome-mediated phase of cold acclimation in red-osier dogwood (*Cornus stolonifera*). Under controlled conditions, short days and end-of-day far red light exposure after long days promote growth cessation, cold acclimation, and subsequent cold hardening of dogwood stems in response to low temperature. Nuclear magnetic resonance absorption spectra of the water in internode stem sections imply that the short day-induced phase of cold acclimation involves a change in tissue hydration, at least in part, due to a substantial reduction in bulk phase water as a result of senescence and loss of water from the pith. Seasonal responses to light and an attempt to induce early acclimation under natural conditions with end-of-day far red light are discussed.

Cold acclimation studies of plants in controlled environments have demonstrated that exposure to low temperatures and noninjurious frosts can stimulate development of maximum freezing resistance in many hardy and semihardy species (14, 17, 32). However, studies of intact plants and plants which have been grafted, girdled, defoliated, or subjected simultaneously to more than one environment (11, 14, 17), indicate that low temperature is not the sole environmental stimulus triggering cold acclimation in nature.

For example, short daylengths can induce 10 to 21 C of freezing resistance in some hardy species. Subsequent acclimation in response to low temperature is also faster in plants which have been preconditioned under short days (32). It is likely that shortening days in autumn, a highly predictable seasonal phenomenon, commonly functions to initiate the cold acclimation process in hardy perennial species.

While manipulation of daylength cannot induce full hardiness in plants, it does apparently influence the time of initiation and the rate of acclimation. This timing can be cruical to winter survival. In nature, injury is common in plants which have the capacity to resist mid-winter minimum temperatures, but which harden too late in the autumn or deharden too early in the spring to avoid damage from unseasonable frosts. The two climatic races of red osier dogwood examined in this study provide an example. Plants of the Dickinson, N.D. clone acclimate early in the autumn under field conditions in Minnesota, but in many years, plants of the Seattle, Wash. clone acclimate too late to avoid injury from autumn frosts. However, both clones can survive −196 C in mid-winter (29).

Previous studies with these climatic races of dogwood have indicated (11, 12) that the photoperiodic induction of acclimation operates via a translocatable hardiness-promoting factor(s) which moves through the phloem from short day-induced leaves to over-wintering tissues. Beyond general descriptive information on hardiness-daylength relationships, little is known about this vital process.

Similarities between the photoperiodic inductions of flowering and cold acclimation have been enumerated by Howell and Weiser (15) who suggest that traditional techniques for studying flowering could be used advantageously to elucidate the control of other vital processes such as cold acclimation in temperate-zone species. This is interesting in view of a recent study by Williams *et al.* (33) which suggested that the photoperiodic induction of cold acclimation in *Cornus stolonifera* and *Weigela* demonstrate typical phytochrome, red/far red reversibility in night interruption experiments. Light quality at the end of a day has also been shown to influence plant development (19, 31) and it is intriguing that FR[4] light at the end of a long day stimulates flowering in *Setaria italica* (L.) Beauv. (Millet) (8), *Sorghum vulgare* Pers. (16) and *Xanthium* (3). It is conceivable that diurnal and seasonal changes in light quality may influence cold acclimation and could account for the anomalous acclimation in apple during the autumn when grown in a warm greenhouse under noninductive long days (14).

Dinus (7) has demonstrated that Douglas fir collected from different latitudes differed in sensitivity to R and FR light. He suggested that this difference was related to different levels of the Pfr form of phytochrome required in stimulating growth. An antagonistic R/FR relationship has been observed also in growth of dormant peach buds (9) where R light promotes and FR light inhibits bud break and leaf expansion.

The physiological status of phytochrome in plants is characteristically determined bv the length of the dark period or by the spectral nature of the final irradiation received (26) or both. At high latitudes, the long periods of twilight rich in blue and FR energy may influence plant development in ways not

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[4] Abbreviations: FR: far red; R: red; NMR: nuclear magnetic resonance; SD: short day; LD: long day.

observed at lower latitudes. According to Robertson (24), the proportion of blue and far red energy increases with decreasing solar elevation until the beginning of civil twilight. The spectral ratio of FR/R light may reach 1.4 during the long twilight period at Ft. Simpson, N.W.T. and 1.5 in Washington, D.C. for 20 to 30 min after sunrise and before sunset (27). In more northern latitudes, the decline in the red portion of the spectrum (relative to FR) during sundown and sunrise may be accentuated due to the longer twilight period and the lower angle of incidence of the sun.

Isolation and identification of the short day-induced translocatable hardiness-promoting factor may ultimately provide a chemical means of initiating acclimation and reducing freezing damage on perennial species. However, it may also be possible to induce acclimation by altering the photo-environment. Paleg and Aspinall (22) have successfully influenced the phytochrome system with lasers to control flowering in *Pharbitis nil* under field conditions over a distance of a quarter of a mile.

This study was designed to further resolve the question of the role of phytochrome in cold acclimation, to evaluate the possible involvement of end-of-day light quality (R and FR) in acclimation, to microscopically characterize changes occurring during acclimation and freezing injury in early phases of hardening, and to determine whether photoinduced acclimation involves changes in the status of tissue water in *Cornus stolonifera*.

MATERIALS AND METHODS

Plant Culture. Two diverse climatic races of red osier dogwood, native to Dickinson, N.D. and to Seattle, Wash., were grown in 14.2-cm pots in a 2:1:1 mixture of soil, sand and peat under 16-hr long days (natural daylength extended with mercury vapor lamps) in a warm greenhouse (20/15 C day/night regime). Plants were pruned to two main stems to provide an adequate number of uniform internodes for hardiness tests. After 8 to 10 weeks, the plants were transferred to controlled environmental chambers for study.

Light Treatments. All light experiments were conducted in controlled environment chambers partitioned into two equal sections. Chamber illumination was provided by 22 Sylvania F96T12 CW-VHO fluorescent lamps and three 25-w incandescent lamps in each section. Total radiant energy (between 400 and 700 nm) was 1.8×10^4 μw/cm^2.

Red and FR radiation used for night interruption and end-of-day light studies was provided by filtered sources situated immediately adjacent to the plants. Red radiation was provided by four 40-w cool-white fluorescent lamps filtered through 10 cm of copper sulfate solution (5 g/l) and a single sheet of red Plexiglas (Rohm and Haas No. 2444) 3 mm thick. The R/FR radiant energy ratio from this source was 15:1 and radiant flux at plant level was 40 μw/cm^2. FR radiation was provided by five 150-w clear incandescent lamps filtered through 10 cm of water and a black Plexiglas filter (Rohm and Haas FRF-700) 3 mm thick. Radiant flux at plant level from this source was 195 μw/cm^2 between 700 and 750 nm. Radiation was measured with an ISCO model SR spectroradiometer. Unless otherwise indicated, exposure times for R and FR light treatments were 30 min.

Hardiness Evaluation. Cold resistance was measured by slowly freezing (5–7 C/hr) triplicate stem sections in Thermos flasks using a technique similar to that previously described by van Huystee *et al.* (32). Uniform internode sections were cut into 4-cm lengths and strips of moistened cheesecloth were wrapped around the cut end of each stem section to facilitate ice nucleation and prevent undue supercooling (21). A thermocouple was inserted into the pith of one section in each flask to monitor sample temperature during the cooling cycle. Internode sections were wrapped in aluminum foil and inserted into a Thermos flask previously equilibrated at 5 C. The end of the damp cheesecloth was draped out of the flask (21). Flasks were then placed in a freezer at −40 C, and the freezing rate of samples was controlled by altering the ambient temperature within the deep-freeze. Internode sections froze uniformly at about −0.5 C, as nucleation via the damp cheesecloth seeded the stem sections.

Flasks were removed from the freezer at successively lower temperatures (2 C intervals for growth chamber studies and 5 C intervals for field studies). The samples were slowly rewarmed by placing the open Thermos overnight in a cooler at 5 C. Thawed samples were then transferred to a humid chamber and incubated for 5 days at 20 C.

Samples were rated for injury by microscopic examination of cortical, phloem, cambium, and xylem parenchyma cells. Discolored, water-soaked, or mascerated cells were considered to be dead or injured. Cambium cells were sometimes severely mascerated by ice crystals. Injured cortical cells became brown or water soaked and xylem cells discolored internally. The extent of damage was estimated on a scale 1 (no damage) to 4 (severely damaged). Internode sections with damaged cambium cells or severely damaged cortical and ray parenchyma cells (greater than 2.5 mean score) were considered to be dead.

This viability rating correlated well with whole plant freezing tests in which intact plants were test frozen (roots protected), thawed slowly at 5 C and observed for regrowth after several months in a greenhouse. Preliminary observations using browning as the only index of injury proved to be less accurate than ratings based on the more detailed microscopic observations described. Generally, cambium cells were less hardy than other tissues during the initial stage of hardening.

NMR Measurements. A Varian A-60D high resolution nuclear magnetic resonance spectrometer was used to determine the spectra of water in the stem sections. Spectra were obtained at 35 to 40 C on the internodes of tender, acclimating and fully hardy stem sections 2 to 6 cm long and 2 to 4 mm in diameter. To assess the influence of specific tissue on the water spectrum, the cortex was removed by stripping from the cambium and the pith removed by drilling a hole through the tissue. Samples were not spun because spinning generates artifacts with nonhomogenous material (4).

RESULTS

Short Day-Phytochrome Relationships. Figure 1 presents the results of a typical acclimating cycle in which plants of the North Dakota clone, grown at short (SD-8 hr) and long (LD-16 hr) photoperiods, were subjected to a 20/15 C day/night temperature regime for 4 weeks, then a 15/5 C regime for 2 weeks. Under SD conditions the first 4 weeks at 20/15 C induced acclimation to −10 C, and the additional 2 weeks at 15/5 C increased cold resistance to −18 C. LD photoperiod treatment precluded acclimation during the 20/15 C temperature treatment, but plants acclimated 2 C (to −8 C) after 2 weeks at 15/5 C. A red light night interruption under short day conditions inhibited hardening during the entire 6-week period. FR light, however, immediately following the R light night interruption, counteracted the R light effect; *e.g.*, FR exposure after R, induced plants to harden normally as if they were under SD conditions.

Plants exposed to SD + R night interruption for the initial 4-week period, then placed under SD for the remaining 2

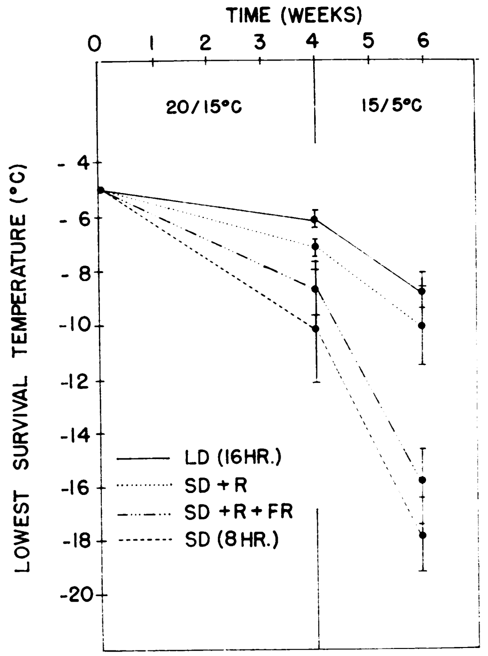


FIG. 1. The influence of day length, red, and red + far red light night-interruption treatments on cold acclimation of the Dickinson, N. D. clone of *Cornus stolonifera*. R and FR irradiation treatments were 30 min in duration. Means and standard deviations shown are based on five replicates at 4 weeks and three replications after 6 weeks.

weeks, increased in hardiness by the same amount as the SD controls, *i.e.*, by an additional 8 C during the 2 week 15/5 C treatment (data omitted). Plants exposed to SD, 20/15 C treatment during the first 4 weeks (survived —9 C), then subjected to SD + R night interruption for the remaining 2 weeks of 15/5 C, acclimated exactly as the short day controls (data omitted). Hence the R-FR light effects were no longer reversible and hardening appeared to be primarily, if not solely, controlled by temperature.

End-of-Day Light Effects. If the threshold level of the Pfr form of phytochrome influences triggering of the SD response, FR light at the end of the day should lower the amount of the Pfr present, and reduce the length of the critical night period.

Terminal bud formation is used as an index that *Cornus stolonifera* has completed the initial phase of cold acclimation and will then acclimate more rapidly in response to low temperature. When FR light was given at the end of a LD (15 hr) treatment, terminal buds formed and plants effectively acclimated to —8 C within 2 weeks (Fig. 2). Red light treatment at the end of the LD promoted a slight increase in hardiness but plants preconditioned by that treatment lacked the potential to acclimate rapidly in response to subsequent low temperature treatments under SD. Both LD and LD + R treatments failed to form terminal buds within the first 2 weeks of treatment. Under SD conditions, 4 weeks were required for terminal bud formation (Fig. 1). Plants treated with LD plus end-of-day FR light at 20/15 C for 2 weeks acclimated to —20 C after an additional 2 weeks of exposure to SD at 15/5 C.

Nuclear Magnetic Resonance Spectroscopy. NMR spectroscopy has been used to characterize the state of water in some woody plant tissues (1). In the present study, NMR spectroscopy proved to be useful for studying maturity of dogwood stem tissue during acclimation. The NMR spectrum of tender dogwood stems displayed a single narrow water absorption band 3 to 20 Hz wide at one-half maximum amplitude (Fig. 3). In contrast, fully hardy (—196 C) dogwood stems displayed an extremely broad NMR water absorption band 200 to 250 Hz wide (Fig. 3). In individual stems, during acclimation band broadening proceeded with time from the proximal older internodes near the ground to distal younger internodes nearer the apex. The change from a narrow to a broad absorption band occurs at a single node (Fig. 4, A and B) and proceeded from the basal to apical internodes as shown in Figure 4 (A, B, C, and D).

The NMR absorption band represents an average composite band for all the tissues in an internode sample. By dissecting

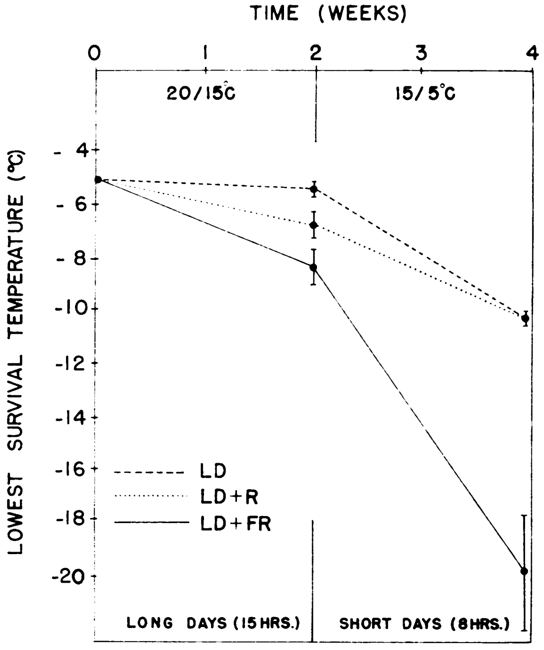


FIG. 2. The influence of red and far red light treatments on stem hardiness of *Cornus stolonifera*. R and FR treatments, 30 min in duration, were given at the end of a long day (15 hr) for 2 weeks at 20/15 C but not during the subsequent 2 weeks under short days (8 hr) at 15/5 C. Points represent the means and standard deviations of three replications. Day length of LD control was 15 hr and 30 min.

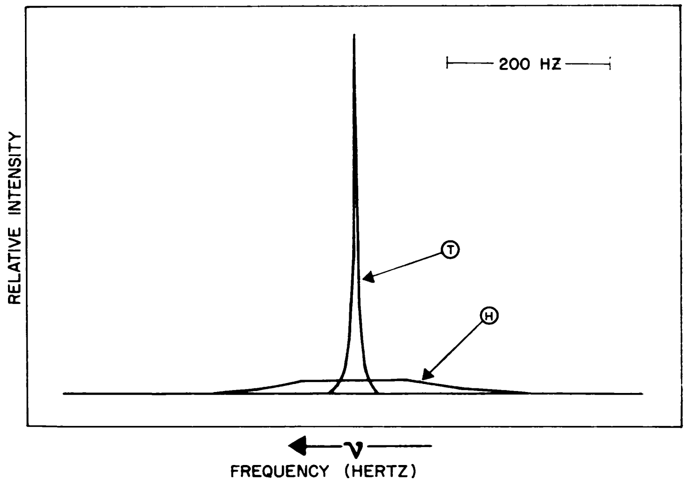


FIG. 3. A schematic diagram of the NMR absorption bands of water in tender and hardy stem-internode sections of *Cornus stolonifera*. T: tender internode section, and survives —5 C; H: hardy internode section and survives —196 C.

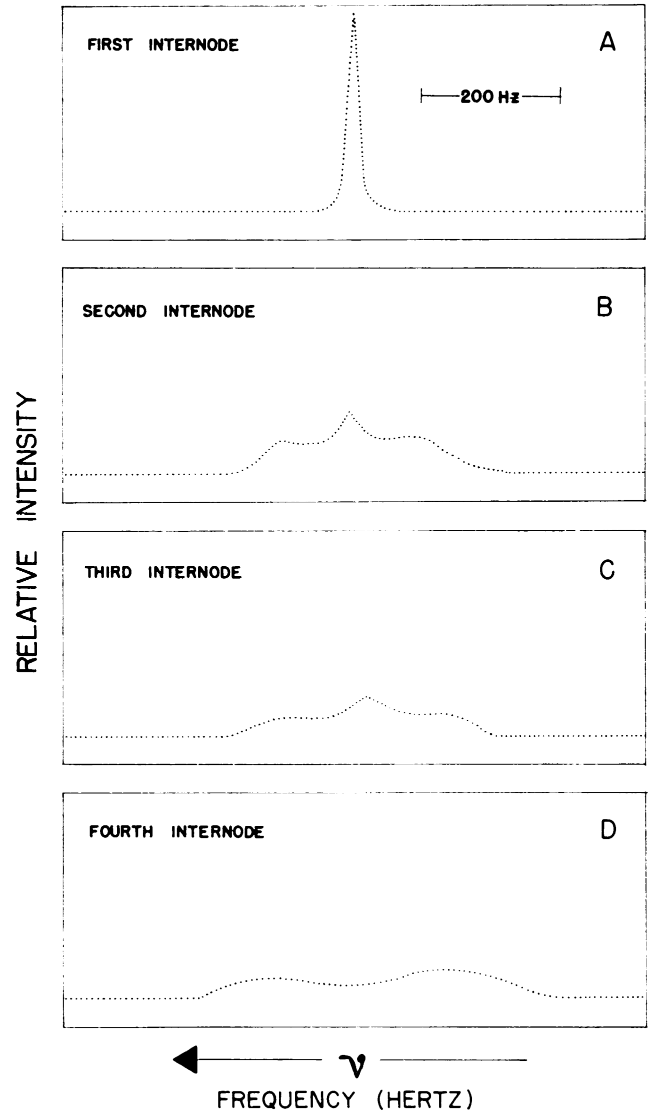


FIG. 4. Typical NMR water absorption bands at successive internodes from the apex (first internode) of a single stem of *Cornus stolonifera* during hardening under short days (8 hr) after 3 to 4 weeks at 20/15 C.

samples one can evaluate the contributions of various tissues to this composite spectrum. For example, although the band width from a tender internode section is characteristically narrow (Fig. 3), the band widths produced by excised cortex (phloem and cortical cells) from tender internodes are characteristically broad (150–200 Hz) (data omitted). The band widths produced by the xylem and pith after cortex was removed did not change appreciably and retained the original narrow configuration characteristic of intact internode sections as shown in Figure 3. However, when pith cells were removed, the xylem cylinder remaining produced a broad (150–200 Hz) band. This suggests that the narrow absorption band characteristic of tender internodes is derived mainly from the large hydrated pith cells.

Studies of NMR spectra of winter twigs dehardened at room temperature provides additional evidence that the pith is the source of the narrow absorption band in tender stems and that pith senescence is the cause of band broadening in the autumn. Winter twigs are characteristically devoid of living pith cells and the absorption band of winter twig internodes remains broad (Fig. 3) even after stems have been dehardened to −5 C of hardiness by dehardening the whole plant for 3 weeks at 21 C on the laboratory bench.

Pith cells in dogwood mature (senesce) from the basal internode towards the apex during cold acclimation in autumn. Under LD regimes the pith remains immature and alive in the terminal internodes of succulent stems. The maturation of the pith cells correlates very well with the timing of initiation of acclimation in *Cornus stolonifera; e.g.,* pith cells, in the second or third internode from the apex, always senescenced before the plant acclimated to −12 C.

Figure 5 is a histogram of the NMR band width of the third and fifth internodes (from apex) of the North Dakota clone of dogwood grown under various photoperiodic conditions (*e.g.,* LD, SD, SD + R, and SD + R + FR) for 2 weeks at 20/15 C. The R and FR night interruption treatments were 15 min in duration. At this third internode, there were no differences in the band width (15–20 Hz) between any of the treatments after 2 weeks (Fig. 5). At the fourth internode (data omitted) band

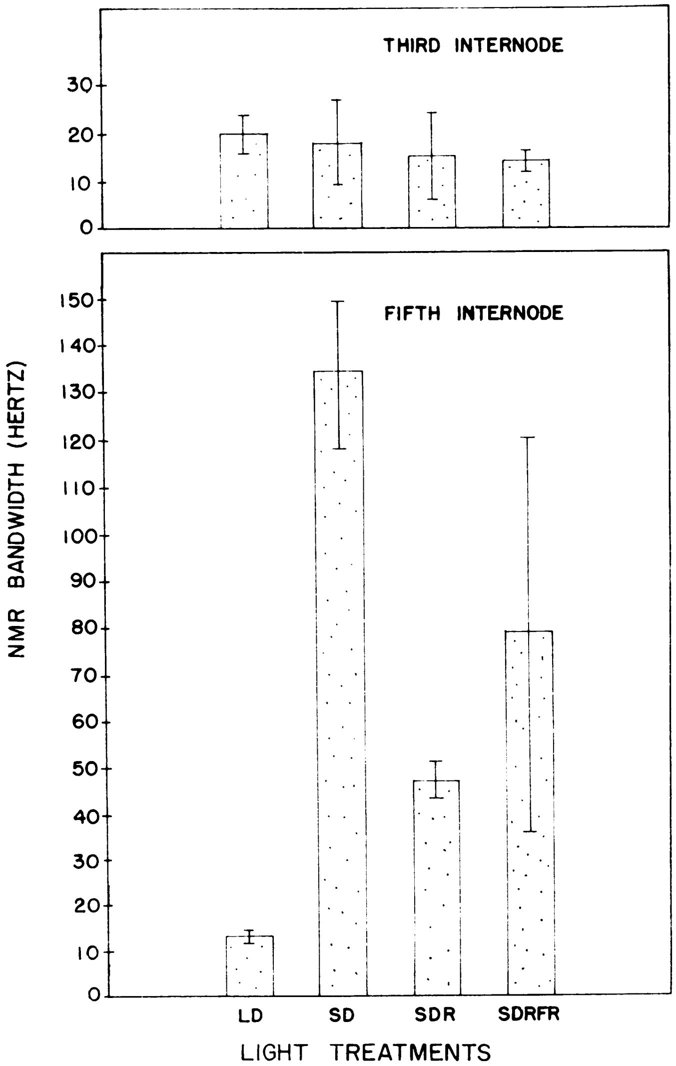
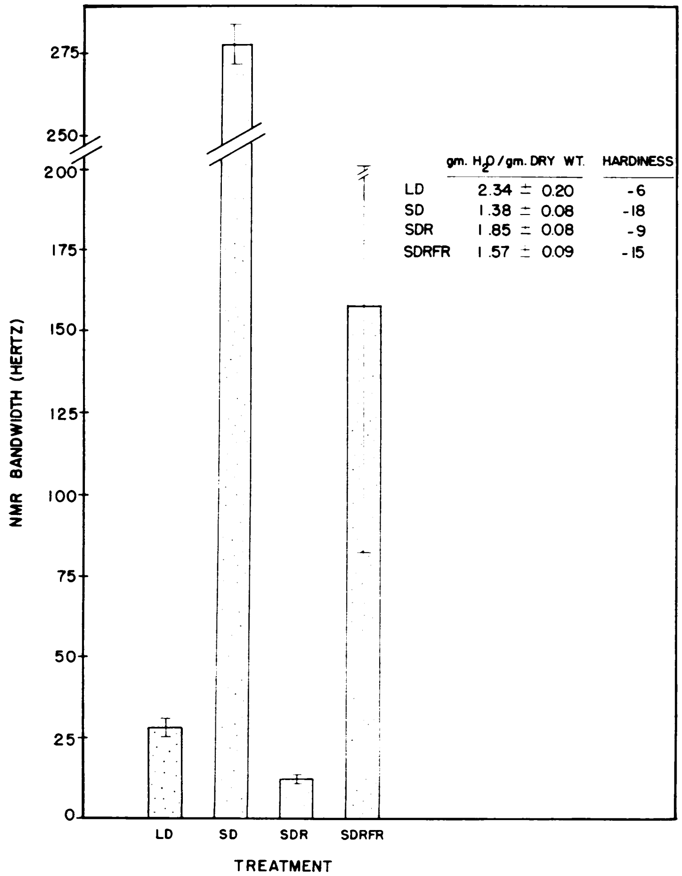


FIG. 5. The NMR absorption band width of water from the internode sections of the Dickinson, N.D. clone of *Cornus stolonifera* after 2 weeks of SD (8 hr), LD (16 hr), SD + red night interruption, and SD + red + far red night interruption at 20/15 C. Duration of red and far red radiation was 15 min each. Data represent means and standard deviations of measurements from the third and fifth internodes from the apex of three stems.

width broadening initiated in all treatments. At the fifth internode (Fig. 5), the band width broadened further, particularly in the SD and SD + R + FR treatments. The band width in the SD + R treatment had also started to broaden at this internode.

While this night interruption study did not demonstrate phytochrome mediation of NMR band width broadening in the North Dakota clone, R-FR reversibility was observed in the case of the Washington clone.

Figure 6 demonstrates R-FR reversibility of NMR band width broadening in plants grown 4 weeks at 20/15 C under the LD, SD, SD + R, and SD + R + FR light treatments. Band width broadening correlated well with the respective hardiness of stems from these treatments. Stems in the SD treatment which survived to −18 C had the widest band width and the lowest water content. Plants in the SD + R + FR treatments contained more water and survived to −15 C. Plants in the SD + R treatment had a narrow NMR band and showed only a slight increase in hardiness to −9 C as did LD plants which survived only −6 C. Growth cessation has been shown to be a prerequisite for the first stage of acclimation in dogwood (32) and initiation of acclimation has been shown to be phytochrome-mediated in this and a previous study (33). These results also indicate that pith maturity is phytochrome-mediated in the Washington clone of dogwood.



	gm. H_2O/gm. DRY WT.	HARDINESS
LD	2.34 ± 0.20	-6
SD	1.38 ± 0.08	-18
SDR	1.85 ± 0.08	-9
SDRFR	1.57 ± 0.09	-15

FIG. 6. The NMR absorption band width of water from internode sections of the Seattle, Washington clone of *Cornus stolonifera* after 4 weeks of SD (8 hr), LD (16 hr), SD + red night interruption, and SD + red + far red night interruption at 20/15 C. Duration of red and far red radiation was 15 min each. Data represent means and standard deviations of measurements of the third internode from the apex of two stems. Water content (on a dry weight basis at 85 C) of the third internode and stem hardiness are also shown.

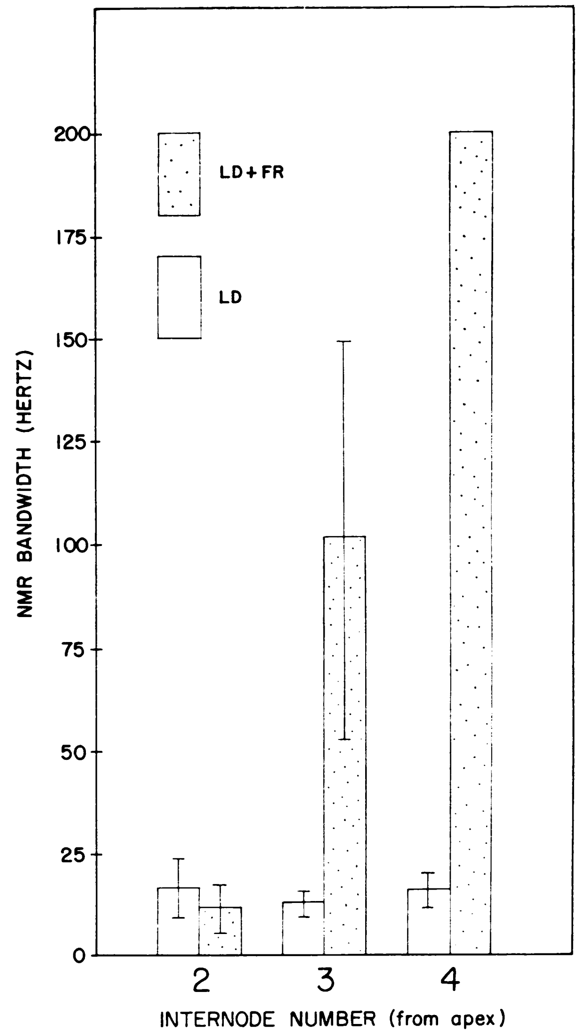


FIG. 7. The influence of 30 min of far red light at the end of a 15-hr day on the NMR water absorption band width of various internodes sections of *Cornus stolonifera* (numbered from the apex) after 2 weeks at 20/15 C. Most data presented represent the means and standard deviations of samples from four plants. Data for internode four of the LD + FR treatment was based on measurements from a single plant.

Figure 7 demonstrates that FR light at the end of a LD also induces NMR band broadening. Under LD conditions, the second, third, and fourth internode all had narrow band widths. FR light at the end of the long day regime effectively induced an increase in the NMR band broadening. These results support the view that maturation of pith cells, growth cessation, and cold acclimation are, or can be, a phytochrome-mediated process.

DISCUSSION

The initiation of cold acclimation in *Cornus stolonifera* was shown to be phytochrome-mediated. This is in agreement with the findings of Williams *et al.* (33). The threshold hypothesis proposed by Borthwick (2), suggesting that the level of Pfr must be below a critical threshold value in order for a process (acclimation) to proceed, agrees with these findings. This is exemplified by the marked promotion of acclimation by end-of-day FR light treatment which reduces the critical night length for the short day-induced process and promoted earlier terminal bud formation.

Duration of the R and FR light exposure also influenced the responses of the two clones. For example, 15 min of R light night interruption were ineffective in preventing acclimation in the North Dakota clone, but effectively inhibited acclimation of the Washington clone. Dinus (7) observed similar responses in Douglas-fir seedlings where short R light night interruption was more effective in eliciting growth responses in plants native to mild climatic regions as compared to those from northern regions. He suggested that the difference was related to different levels of the Pfr form of phytochrome required for the response.

In the present study, R light night interruption treatments at low temperatures (15/5 C) failed to inhibit plants from further hardening after they acclimated to −9 C. This suggests that light effects on acclimation function via triggering basic irreversible changes which induce acclimation, after which time hardening appeared to be primarily, if not solely, controlled by temperature. In woody species, these changes may involve growth cessation and a shift in metabolic priorities from processes favoring vegetative growth to processes which favor cold acclimation.

The initiation of acclimation in dogwood is probably closely associated with growth cessation and terminal bud formation. Terminal bud formation occurred earlier under LD + FR conditions than under the normal SD conditions. This increases the potential for earlier hardening. It would appear that once the phytochrome system (FR exposure) triggered growth cessation, extended photosynthetic duration might accelerate the process to favor more rapid induction to withstand low temperature stress. Far red light has similarly been found to induce earlier dormancy in Douglas fir (7).

Light quality also affects a variety of other physiological processes in plants. For example, when parent plants of the crucifer *Arabidopsis thaliana* L. are grown under white light containing markedly different proportions of red and far red energy, the seeds harvested have different germination responses (27). R and FR irradiation at the end-of-day, can also influence apical dominance (19, 31), levels of auxins, cytokinins and ABA (10, 13, 31), alkaloids, soluble phenols (30), free sugars and organic acids (18). Furthermore, far red light at the end of a long day may stimulate floral initiation in some short day plants (3, 5, 8, 16). Since the ratio of the Pr and Pfr forms of phytochrome in the plant depends primarily upon the intensity of R and FR light to which plants are exposed (25, 26), it is tempting to speculate that the sudden rapid shifts in the R/FR ratio of solar energy at the end of each day (24, 27) may provide part of the timing cue for acclimation. In nature, however, the R/FR ratios at sundown are usually much higher than the ratios employed in many growth chamber studies. This may explain atypical plant developmental patterns which sometimes occur in controlled environmental studies.

In *Cornus stolonifera*, the initial broadening of the NMR band width was correlated with growth cessation, autumn maturation, senescence of pith in stem internodes and survival of the stem to −12 C. Band broadening occurred in response to short days or far red light at the end of a long day. At this juncture, however, broadening of the NMR band width relates mainly to loss of free bulk water primarily from the large hydrated pith cells during the initial stage of cold acclimation. Further work will be needed to establish whether or not there is a causal relationship between band broadening and cold acclimation. In either case, NMR spectral measurements may provide a valuable diagnostic screening tool for selecting genotypes capable of acclimating early in the autumn.

Circadian rhythms also influence some developmental processes in plants and further complicate interpretation of light effects. Cumming and Wagner (6) report that in some plants, endogenous rhythms of flower induction provide a partial basis for time measurement and control of flower induction in daily dark/light cycles. Seasonal endogenous rhythms have been suggested to partially explain acclimation in apple (14), black locust (28) and in pine (20). A frustrating but informative feature of the present study also implicates endogenous rhythms. For example, plants transferred from the greenhouse for growth chamber studies during the months from January to late July effectively hardened to −20 C in 6 weeks under the conditions outlined in this study. However, plants selected during the remaining months required 2 to 6 weeks longer to attain the same degree of hardiness. Similarly, end-of-day light effects were also retarded or completely inhibited during the same period (August–December) in growth chamber studies. In addition, and attempt in late August to induce early acclimation under field conditions with far red light exposure at the end-of-day also failed. The period from August to December is the time of the year when plants are dormant or in physiological rest (23) and although the plants in this study were grown in the greenhouse under long day conditions, it seems likely that natural endogenous rhythms may have influenced the physiological state of the plants and their response to changes in daylength, red and far red light.

At high northern latitudes, short growing seasons, long days, and early autumn frosts influence the agricultural potential of many annual and perennial plants. Hopefully, further studies of the processes influencing the photoperiodic-induced stage of cold acclimation will benefit plant breeders with new selection techniques for developing adapted cultivars, and provide crop management specialists with means by which acclimation can be controlled.

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