THE EFFECT OF DORMANCY INDUCTION, LOW TEMPERATURES AND MOISTURE STRESS ON COLD HARDENING OF CONTAINERIZED BLACK SPRUCE SEEDLINGS

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Abstract.--Cold hardening and acclimatization of coniferous seedlings are discussed and reviewed in relation to plantation success. A reduction in temperature and photoperiod at the end of the production period is the best acclimatization treatment for cold stress. Moisture stress, deprivation of nitrogen and low temperature in the dark did not improve hardening of black spruce (*Picea mariana* [Mill] B.S.P.) material. Preliminary field observations indicate that acclimatized seedlings have a superior survival rate.

Résumé.--Cette communication traite de l'endurcissement au froid comme facteur du succès de la plantation et de l'acclimatation de semis de conifères. La réduction de la température et de la photopériode au terme de la période de production constitue le meilleur traitement d'endurcissement au froid. La contrainte hydrique, la privation d'azote et le froid dans l'obscurité n'ont pas amélioré l'endurcissement de nos semis d'épinette noire (*Picea mariana* [Mill.] B.S.P.). Des observations préliminaires faites sur le terrain indiquent que les semis acclimatés ont un meilleur taux de survie.

INTRODUCTION

The degree of cold hardiness of a crop is an important consideration for the container nurseryman faced with moving a crop out of a greenhouse in spring or late summer for outplanting or overwintering.

Interest in cold hardiness is not new in Canada. Early work by Scarth (1936), Siminovitch and Briggs (1949) and more recently Glerum (1976) has indicated some fundamental changes in the plant during its annual cycle. Winter hardiness is a characteristic of temperate climate perennial species. The cold acclimatization process to obtain hardiness is the result of interactions between the plant genome and the environment. For example, the sensitivity of red spruce (*Picea rubens* Sarg.) to winter desiccation, as compared with black spruce (*P. mariana* [Mill.] B.S.P.), is well recognized (Roche 1969). However, winter hardiness is a very broad term and is defined as the capacity to avoid or tolerate the stresses imposed by winter conditions (low temperature, dry air, frozen ground, frost heaving, sunscald, etc.). The cold hardiness component is of major importance and is defined as the ability to withstand freezing temperatures. In this paper, discussion is restricted to cold hardiness and the acclimatization process, termed cold hardening.

PRACTICAL LIMITATIONS

Ideally, the field forester or nursery manager would like to specify, as part of a quality index, the cold hardiness of his stock. Aside from the obvious technical difficulties, the precision of such an estimate in a production facility with a variety of

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seed sources will be limited by a number of factors.

The genetic variation of eastern boreal conifers is well recognized. The work of Holst and Yeatman (1961), Roche (1969), Morgenstern (1978) and others has indicated a clinal within-species variation and, in some cases, a variation with latitude and an altitudinal interaction as well. A further complication arises from hybridization among spruces (Manley 1972). It is therefore important that seed and seedling movement be confined within defined seed zones (Fowler and MacGillivray 1967). For stand improvement, superior material from remote locations can be introduced following proper testing (Corriveau and Boudoux 1971, Neinstaedt and Teich 1971, Fowler and Mullin 1977, Morgenstern 1978).

Large geographical areas have historically been subdivided into zones or regions according to major climatic and ecological factors (Fowler and MacGillivray 1967, Ouellet and Sherk 1967, Rowe 1972). A critical factor limiting plant distribution is mean minimum temperature of the coldest month of the year. However, within these divisions there are year-to-year variations and no one can accurately forecast meteorological conditions in any given winter. Therefore, depending on location, the probability of frost occurrence and severity is variable. Such uncertainty requires that biological material be prepared for the most severe seasonal condition in the field.

In practice, then, despite excellent work on agricultural crops and some field and nursery measurements with forestry material, both intrinsic factors and current lack of data preclude the use of a precise prescription for hardening off[3] of each boreal species.

AVOIDING THE REQUIREMENT

Avoidance of those months when the risk of frost is high is impractical because of cultural restraints other than cold hardiness, notably drought, cold soils, and effect of planting date on post-outplanting survival and performance. With bare-root stock, emphasis is on spring and fall planting (Bonner 1960, Ackerman and Johnson 1962). However, bare-root stock in Ontario has given unreliable results with fall planting (Anon. 1977). Seedling root regeneration potential and rooting of cuttings show a bi-modal pattern of activity, with maximum rooting generally recorded in the spring (Girouard 1975, Day et al. 1977). Arnott (1972) and Van Eerden (1972) have also indicated a tendency towards a bi-modal curve for survival and growth with container stock on the west coast, while Scarratt (1972) in the east has reported that all summer planting of tubed seedlings was feasible with the Ontario tube. Undoubtedly, the use of container stock extends the possible planting period, but until better performance data are available, the consensus is that the best season for planting is the spring, and that results are variable in the fall.

Aside from the obvious application of cold hardening to overwintered stock, the seasonality of outplanting requires the use of cold-stored material to optimize use of the planting periods. The physiology of the association between survival and particularly regrowth is unclear in relation to a) a certain minimum number of degree-hardening days[4] before lifting in fall (Mullin and Hutchison 1978), or to b) lifting of bare-root stock for cold storage in spring, which is limited by degree-days above 0°C (Mullin 1978). There appears to be a low temperature interaction with the seedling which induces a state of readiness for cold storage and eventual re-growth. Cold storage is essentially a mild freezing condition, and cold acclimatization for this storage process has some similarities with the conditioning of seedlings (containerized or otherwise) to withstand low temperatures (Hocking and Nyland 1971).

INDUCTIVE FACTORS

The literature on cold hardiness indicates that a number of factors influence its induction. Cessation of rapid vegetative growth appears to be a prerequisite (van den Driessche 1970, Weiser 1970, Levitt 1972, Aronsson 1975, Sandvik 1976, Christersson 1978). A minimum light intensity, provided in a short-day regime, is essential (van den Driessche 1970, Timmis and Worrall 1975, Sandvik 1976). Cold temperature, in some cases, can replace the short-day requirement (van den Driessche 1970, Sandvik 1976, Christersson 1978). Light frost can also increase the degree of cold hardening (Weiser 1970, Levitt 1972, Timmis and Worral 1975). Finally, moisture and nutrient regimes have occasionally had some influence on hardening off (Levitt, 1972, Christersson 1973, Tanaka

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[3] Hardening off: the process of adaptation by plants so as to tolerate cold, heat and drought.

[4] Degree-hardening days: the cumulative daily minimum difference between 10°C and the temperature at root level (15 cm depth).

and Timmis 1974, Timmis 1974). Species differ in their response to acclimatization factors. Norway spruce (*Picea abies* [L.] Karst.) is less sensitive than Scots pine (*Pinus sylvestris* L.) to lowering of temperature during hardening off (Aronsson 1975), and with some conifers, the photoperiodic control seems to be a less dominant factor than the amount of light (McGuire and Flint 1962).

It is evident that actively growing seedlings have to be acclimatized properly before outplanting or storage. In an effort to assess the importance of the various inductive factors, the first author has been carrying out preliminary experiments on black spruce. Details of cultural methods are reported elsewhere (D'Aoust 1978, 1980). Black spruce is important to reforestation in eastern Canada, as it accounts for approximately 59% of container stock raised east of the Ontario-Manitoba border (Smyth 1980).

CESSATION OF VEGETATIVE GROWTH

Although true dormancy may not be an absolute necessity, growth cessation appears to be a prerequisite for primary stage cold acclimatization. One way to modify the growth pattern of black spruce seedlings is to reduce the photoperiod so as to slow down the rate of dry matter accumulation. Seedlings under long-day (LD) and short-day (SD) regimes respond differently in height growth (Fig. 1). Cessation of height growth is evident soon after the imposition of a SD treatment, but height growth recovers as soon as daylength is again increased. Cessation of height growth is not the only effect of short days, as the development of axillary buds and branches also ceased under these conditions (Fig. 2).

TEMPERATURE-PHOTOPERIOD INTERACTION

In fall, both temperature and photoperiod decline. Growth chamber simulation of the autumn environment (with the exception of temperatures lower than 4°C which were beyond the capacity of the chamber) in the Quebec region (Table 1) indicates that 2 to 3 weeks are sufficient to stop height growth in black spruce at different ages (Fig. 3).

When the two factors are separated and seedlings are compared with an actively growing (LD) control, it can be seen that a short photoperiod, with little effect from temperature regime, stops height growth. Shortening the daylength also reduces dry weight accumulation of the shoot (Fig. 4A), but the daylength effect is less pronounced on the root system (Fig. 4B).

The effect of temperature/photoperiod on cold hardiness (as opposed to vegetative growth rate) can be seen from the combination of four inductive treatments: LD-warm (control), SD-warm, LD-cool, and SD-cool (Fig. 5).

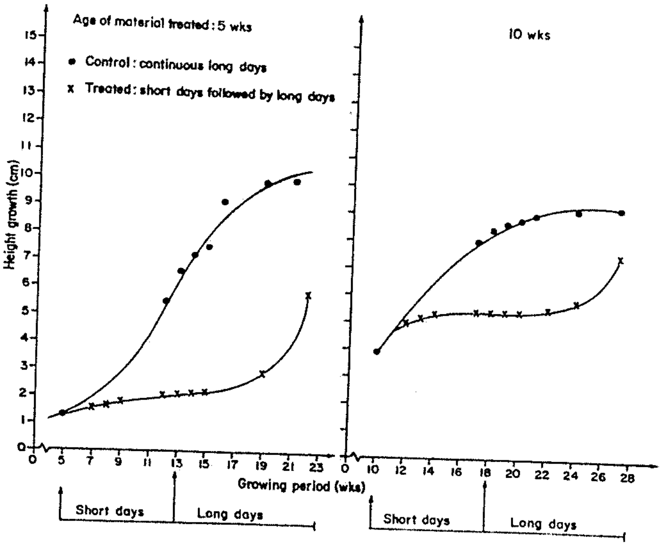

Figure 1. Effect of changing the photoperiod on growth of black spruce seedlings.

Table 1. Meteorological data for 1943 to 1971, at Quebec airport, and the artificial climate prescribed to imitate autumn conditions.

	Natural conditions[a]			Artificial conditions[b]		
	min. (°C)	max. (°C)	photoperiod[c] (h)	min. (°C)	max. (°C)	photoperiod[d] (h)
August	11.9	23.4	13.4	16	21	13.3
September	7.7	18.6	11.8	12	17	11.6
October	2.6	11.8	10.2	8	13	9.8
November	−3.2	3.5	9.0	4	9	8.0

[a] Climatic data from the Atmospheric Environment Service.

[b] Artificial conditions were programmed by using one week for each month to be reproduced.

[c] Minimum monthly hours of sunlight.

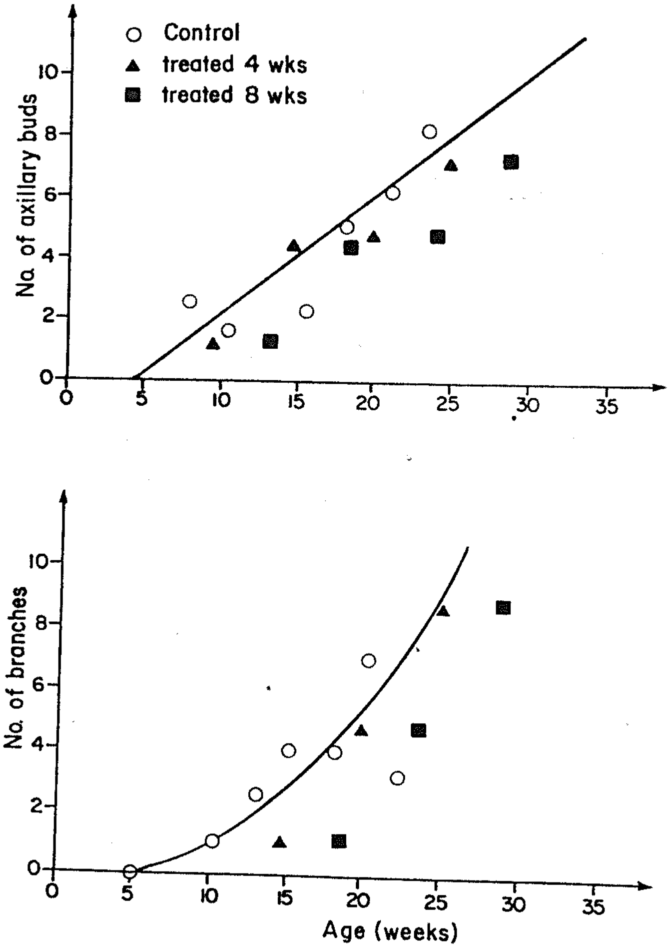

Figure 2. Effect of shortening the photoperiod on morphological development of black spruce seedlings.

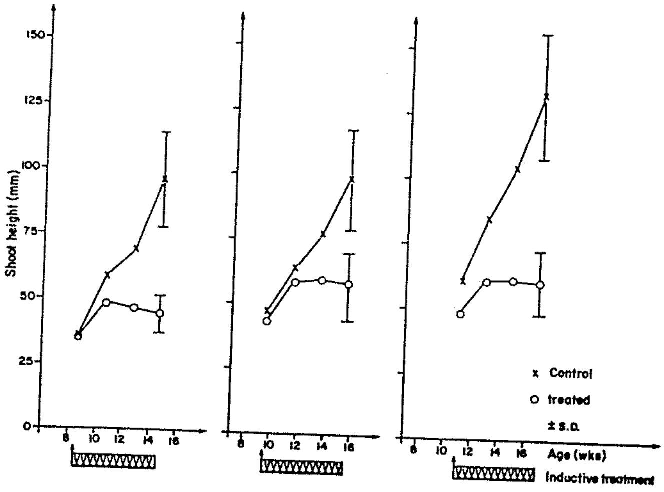

Figure 3. Effect of a gradual decline in temperature and photoperiod on the growth of black spruce seedlings.

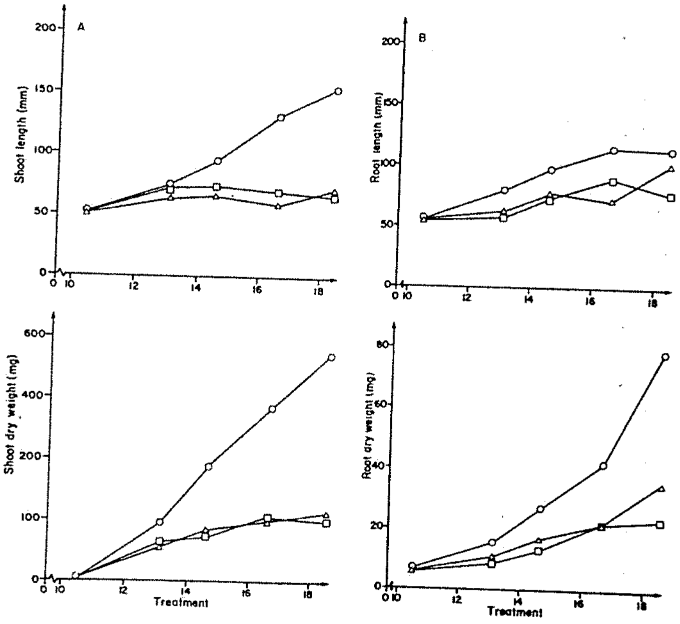

Figure 4. Effect of a gradual decline in temperature and/or photoperiod on the growth of black spruce seedlings. Shoot (A) and root (B) measurements; control (○) with constant long days and day-night temperatures (15 hr 25°/20°), a second treatment with a declining photoperiod (□), and a third with a weekly decline in both photoperiod and temperature (△).

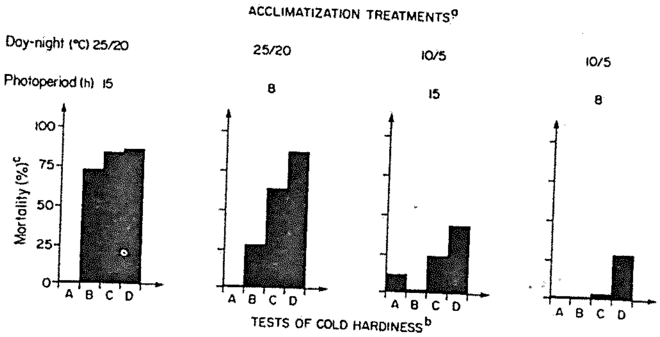

Figure 5. Effects of different cold acclimatization treatments on cold hardiness of 14-wk-old black spruce seedlings.[5]

Each regime results in a different degree of cold hardening after similar induction times, as judged by regrowth and mortality after periods of controlled freezing at -4°C, which, when prolonged, are increasingly lethal.[6]

Low temperatures induce a strong cold hardiness effect. The effect of short days is not as important as that of low temperature, but short days still affect the cold hardening of black spruce seedlings significantly. The seedling root systems exhibited a mortality pattern identical to that of the shoot for the different conditions (data not shown).

DROUGHT AND FERTILIZATION

The effect of drought during cold hardening was assessed by periodically imposing moisture stress until a visible wilting occurred. When the same freezing tests and the four temperature/photoperiod combinations described above were used, moisture stress did not markedly improve the cold hardiness of cold acclimatized seedlings (Fig. 6).

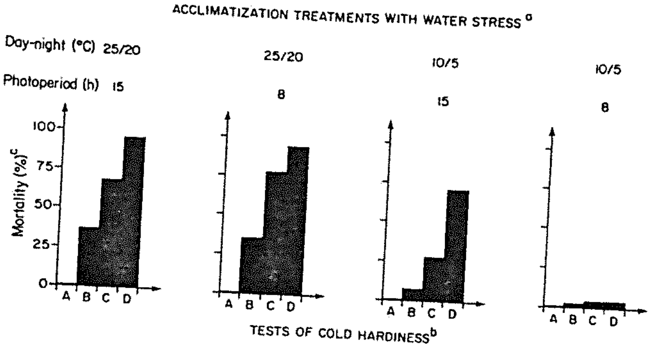

Figure 6. Effects of different acclimatization treatments with water stress on the cold hardiness of 14-week-old black spruce seedlings.[7]

The only exception was the actively growing control material which acquired a mild cold tolerance (compare Fig. 5 and 6 for treatment at 25°/20°C and 15 hr).

Seedlings were also treated with PK or NPK at the end of the production period, and submitted to cold stress. Seedlings deprived of nitrogen (PK treatment) did not appear to

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[5] a) Seedlings were treated at high or low temperatures under short- or long-day conditions for 4 to 6 weeks.
b) A cold hardiness test was carried out in cold rooms; 24 hr at 4°C (A); 24 hr at 4°C and 4 hr at -4°C (B); 24 hr at 4°C and 8 hr at -4°C (C); 24 hr at 4°C and 24 hr at -4°C (D). For each interaction (acclimatization x cold period) 10 seedlings were sampled and transferred to a growth chamber for evaluation of their cold tolerance.
c) After 2 weeks of normal care, the seedlings were evaluated visually as either tolerant or severely damaged and dead. The histograms represent average values for five replicates.

[6] Ice formation in the rooting medium was noticed after 4 hr at -4°C and a solid ice block was present after 8 hr at -4°C.

[7] a) Seedlings were treated at low or high temperatures under short- or long-day conditions for 4 to 6 weeks and watering was withheld until wilting was evident.
b) Cold hardiness was induced in cold rooms; 24 hr at 4°C (A); 24 hr at 4°C and 4 hr at -4°C (B); 24 hr at 4°C and 8 hr at -4°C (C); 24 hr at 4°C and 24 hr at -4°C (D). For each interaction (acclimatization x cold period) 10 seedlings were sampled and transferred to a growth chamber to evaluate their cold tolerance.
c) After 2 weeks of normal care, the seedlings were evaluated visually as either tolerant or severely damaged and dead. The histograms represent average values for three replicates.

be hardier than those fertilized with NPK during the entire rearing period (data not shown).

FIELD SURVIVAL

Preliminary field tests with limited numbers of seedlings have yielded promising results. Survival has been assessed after one year on seedlings subjected to four cold acclimatization regimes prior to outplanting in spring and fall (Table 2).

Table 2. Mortality rates of transplanted seedlings after one year in the field.

	Acclimatization conditions			
Day/night temp. (°C):	25°/20°	25°/20°	10°/5°	10°/5°
Photoperiod (hr):	15	8	15	8
Spring planting	18%	5%	9%	1%
Fall planting	48%	21%	5%	15%

Mortality after one year in the field indicates that spring planting is superior to fall planting and that seedlings subjected to short-day or cold treatments survived better than did untreated seedlings.

CULTURAL APPLICATION

The similarity in response of black spruce to various inductive factors suggests that the same general prescriptions proposed for other species (Tinus and McDonald 1979) may be used in container nurseries. More precise recommendations concerning treatment manipulation to optimize the rate and/or depth of cold hardening are unavailable.

Indeed, it is necessary to be cautious with our conclusions since the material used originated from a single provenance and was treated under strict environmental control. Furthermore, the cold hardiness assays have used only mild cold stresses (-4°C), and subsequent evaluation was carried out under artificial conditions. However, evaluation of correlations between cold acclimatization conditions and field performance on the basis of so few experiments requires care. Field conditions may have been atypical, and the variation in results observed in the initial trial is sufficiently great that we must be cautious. Even so, some guidelines specific to this species seem applicable.

Bud formation as a morphological indicator of cold hardening may be inappropriate, since long days at low temperatures do not produce visible buds, but freezing tolerance similar to that observed by Timmis and Worral (1975) for Douglas-fir *(Pseudotsuga menziesii* [Mirb.] Franco) has been recorded (Fig. 5 and 6).

The short-day/low temperature combination induces the greatest cold hardiness (Fig. 5 and 6) although it is not always easily achieved operationally. Short days in the greenhouse can be obtained by opaque shade covering, and low temperature by proper ventilation. However, in late spring or early fall ventilation may not be sufficient, because of warm outdoor temperatures. Presumably, during such conditions only the short-day component would be effective. Active short-day imposition using shading with black spruce (as opposed to simply discontinuing supplementary lighting) is not practised, to our knowledge, although the inductive effects on growth cessation have been well documented (Vaartaja 1959, Morgenstern 1969, D'Aoust 1981). In addition to accelerating the rate of growth cessation, short days can decrease the shoot:root ratio at the end of the production period (Fig. 4), a modification generally regarded as being beneficial to the survival of transplanted seedlings.

Cold hardiness induction is possible with a shadehouse. If the seedlings are moved out of the greenhouse in spring or fall, low outdoor temperatures will induce hardening off, although frost damage may be prevented by irrigation or supplemental heat. The risk of frost in both seasons and the lengthening photoperiod in spring may require that initiation of dormancy induction be done in the greenhouse before transfer to a shadehouse for further hardening. It was once thought that, since seedlings needed short days and low temperatures for maximum cold hardiness; the two processes could be culturally separated by beginning with the short-day treatment followed by cold storage. However, our results indicate that this method does not work and therefore, like Weiser (1970), we believe that the low temperature treatment, to be effective, must be carried out concurrently with short-day treatment.

As with other species (Tanaka and Timmis 1974, Timmis 1974) neither moisture stress nor nitrogen deprivation at the end of the production period appear to affect the cold hardening process in black spruce. However, leaching followed by moderate water stress cannot be discounted as a potential preliminary treatment applied prior to dormancy induction. Aside from the shock-stress value in growth cessation (Tinus and McDonald 1979), some evidence (compare Fig. 5 and 6) indicates that slight cold hardiness can be induced by moisture stress during the active growth phase (Tanaka and Timmis 1974, Blake *et al.* 1979).

CONCLUSIONS

It is possible to modify growth behavior of containerized black spruce substantially so as to affect the cold hardiness of seedlings. A reduction of photoperiod with low temperatures, at the end of the production period, is the best acclimatization treatment, but short days or low temperatures alone can also stimulate cold hardening. Such flexibility must be considered a cultural advantage. Cold hardening influences survival, but additional factors, such as bud size and response to other types of stress, determine subsequent field performance. Detailed outplanting performance assessments may show that a regime tailored to produce maximal cold hardening may have to be modified to optimize other quality indices (Tinus 1974, Christersson 1978). Obviously, extensive, carefully planned field trials will be required to define a precise prescription. However, one positive aspect of cold hardiness induction is that, as far as environmental stresses are concerned, it appears that the plant does not have many ways of surviving adverse conditions. Tolerance of stresses other than cold--namely, heat, drought and salt--can be induced by the same acclimatization process (Levitt 1972, Christersson 1976, Vieira da Silva 1978). The container nurseryman should be aware that the processes involved in hardening crops to withstand various stresses are related, and therefore inducing tolerance of one may affect response to others beneficially.

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