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Inheritance of the Photoperiodically Induced Cold Acclimation Response in *Cornus sericea* L., Red-Osier Dogwood*

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Summary. Cold acclimation responses of latitudinal ecotypes of *Cornus sericea* L. (*C. stolonifera* Michx.) and F_1, F_2 and BC_1 hybrid progenies were measured under natural photoperiod conditions in St. Paul, MN and artificially shortened photoperiods in the glasshouse. The 65 °N and 62 °N ecotypes (Alaska and Northwest Territories, respectively) were characterized by a short night length for hardiness induction, the 42 °N ecotype (Utah A and B) by a long night length for hardiness induction, while the F_1 was intermediate to the parents. Results from reciprocal crosses indicated there was no significant unilateral maternal influence on cold acclimation. Acclimation responses of the F_2 were highly variable but generally ranged between the parental extremes. However, three individuals from the 42°×62 °N crosses exhibited greater cold resistance than the northern parent on two successive freezing test dates. F_2 plants were also found with less freezing resistance than the southern parent. Backcrosses to the southern parent produced progeny with acclimation patterns resembling that of the southern parent and were significantly less hardy than the F_2 in early freezing tests.

Key words: Cold hardiness – Photoperiod – *Cornus stolonifera* – Acclimation – Freezing resistance

Introduction

Survival of woody perennial plants native to the temperate zone depends upon the timing of vital physiological processes with favorable and unfavorable environmental cycles. Cold temperature is one of the most important environmental factors limiting plant distribution. Individual plant resistance to cold stress changes dramatically during the year. Plants killed at temperatures a few degrees below zero during the summer may survive temperatures as low as −196 °C during the winter. The change from a cold-susceptible (tender) to a cold-resistant (hardy) state is called acclimation.

Based on work done with *Cornus sericea* L., Weiser (1970) divides the natural acclimation response into a two stage pattern typical of woody plants native to the temperate zones. The first stage of acclimation is induced by decreasing photoperiods in autumn. Cold resistance in *C. sericea* plants increases from −5 °C to about −22 °C during this phytochrome mediated first stage (Van Huystee et al. 1967; Williams et al. 1972; McKenzie et al. 1974a). The second stage of acclimation is induced by low temperatures, in nature by the first frost. Weiser postulates a third stage of acclimation in hardy woody species which is induced by low temperatures (−30 to −50 °C). Exposure to temperatures in this range can cause hardened plants to attain freezing tolerance levels of at least −196 °C, the temperature of liquid nitrogen (Sakai 1960). However, acclimation is a complex process. Other environmental factors such as temperature, and nutrient and water availability interact with photoperiod to increase the complexity (Van Huystee et al. 1967; McKenzie et al. 1974b; Parsons 1978).

There are two phases involved in the photoperiodically induced first stage of acclimation: a critical night length requirement which actually triggers growth cessation and acclimation, and a rate of development of cold tolerance once acclimation has been initiated. Acclimation is but one component of whole plant cold hardiness however. Essentially, whole plant cold hardiness can be classified into three main components: 1) acclimation 2) ultimate midwinter hardiness and 3) deacclimation. Ultimate midwinter hardiness refers to the maximum potential freezing tolerance the plant is capable of developing at its hardiest level. Deacclimation refers to the timing and rate of loss of freezing tolerance in response to warm temperatures and the ability to regain freezing tolerance if temperatures should drop suddenly. Any one of these components may be the limiting factor in winter survival. Cold hardiness is further complicated by the fact that adjacent tissues and/or organs of a plant may simultaneously have different hardiness levels (Weiser 1970).

The timing of acclimation in response to decreasing fall photoperiods is genetically controlled. Whenever several ecotypes of a single species are grown in a uniform environment, there are differences in the timing of acclimation,

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although the overall pattern of cold hardiness development is similar. Plants from high latitude or altitude regions cease growth and acclimate at shorter night lengths than plants from low latitude or altitude regions (Pauley and Perry 1954; Vaartaja 1959; Smithberg and Weiser 1968; Dormling et al. 1968). Smithberg and Weiser (1968) found that climatic races of *C. sericea*, collected throughout North America and grown at one location, exhibited marked differences in the timing of acclimation. Races from northern sites acclimated to cold stress earlier in the fall than those of southern or coastal origin. However, all races possessed the same ultimate midwinter hardiness level (−196 °C). Temperate zone woody species have become genetically differentiated into populations adapted to the climatic conditions at different latitudes and altitudes. A primary factor in this adaptation is the ability to respond to decreasing photoperiods (Ekberg et al. 1976).

Many economically important woody species possess an adequate ultimate midwinter hardiness level but the photoperiodically induced acclimation response is improperly timed and they cannot be successfully grown in high latitude or altitude regions. For example, the ultimate hardiness level (−40 °C) of commercial highbush blueberry cultivars was the same as the wild lowbush species, *Vaccinium angustifolium*, native to Canada and the Northern United States (Quamme et al. 1972). However, the highbush cultivars failed to acclimate before the autumn frost and thus sustained freezing injury in Minnesota. The authors recommended selection for more rapid induction of acclimation rather than for maximum freezing tolerance as the most suitable breeding approach.

Studies aimed specifically at elucidating genetic control of cold hardiness in woody plants are scarce. The literature that does exist is often aimed at components other than acclimation. Because of the paucity of information on the genetics of woody plant cold acclimation, the present investigation was undertaken to compare the photoperiodically induced cold acclimation behavior of *Cornus sericea* L. latitudinal ecotypes and their F_1, F_2 and backcross progeny in a uniform environment. The information to be gained from such an investigation is of both theoretical and practical value. To the geneticist, the information will add to the knowledge of genetic systems controlling physiological responses of adaptive significance in woody plants. To the woody plant breeder, the information will demonstrate the feasibility of using a breeding approach whereby diverse ecotypes are crossed and selection for desirable physiological and morphological traits is practiced on a segregating F_2 population.

Materials and Methods

Field Experiments

Four F_1 hybrid families were produced from controlled pollinations between three latitudinal ecotypes of *Cornus sericea*. Figure 1 indicates origins of the latitudinal ecotypes while the mating pattern, family codes and number of individuals per F_1 family appear in Table 1. Pollinations were made during April of 1976 on plants forced into bloom in a warm, long day glasshouse. After ripening, seeds were acid scarified, cold stratified for 3 months and, in the fall of 1976, sown in 8 cm pots. F_1 seedlings were grown over winter in the glasshouse and transplanted to the field in the spring of 1977.

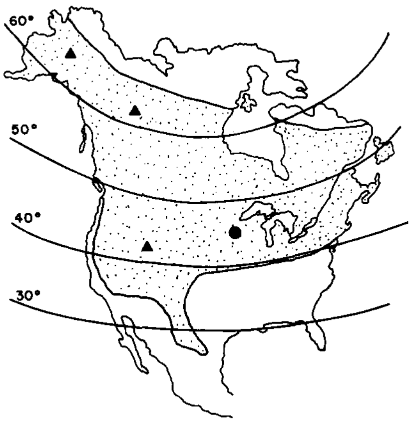

Fig. 1. The natural range (stippled area) and collection sites (triangles) of the Alaska, Northwest Territories and Utah *Cornus sericea* clones. The uniform environment test plot was located at Excelsior, Minnesota (circle). (Map adapted from Smithberg and Weiser 1968)

Because of inadequate spacing, the F_1 was dug in the fall of 1977 and placed in bare-root storage over winter. In April of 1978, the F_1 along with 10 to 13 ramets of each of the parent plants were lined out in a permanent field site at Excelsior, Minnesota (Fig. 1). It was not necessary to irrigate or fertilize the field plot, however, insect and weed control were practiced as needed.

Acclimation responses of the latitudinal ecotypes and the F_1 progenies to the naturally decreasing photoperiod of the Excelsior, MN, location were determined over two consecutive years. Cold acclimation levels were measured at approximately 2-week intervals starting on August 22, 1978, and August 8, 1979. Ultimate midwinter hardiness of the field grown plants was tested February 20, 1979, and a midsummer freezing test was done July 17, 1979. On each 1978 freezing test date, uniform stems of the current season's growth were taken from randomly selected plants; 1 plant of each parental clone and cross 76-3, and 3 plants of each cross of the 76-1, 76-2, and 76-4 populations were frozen. Parents and 76-3 plants were large enough to permit sampling of 2 plants on 4 of the 6 freezing test dates in 1979.

Internodes from the middle portion of each stem were cut into 2 cm long segments with care being taken to insure that stem diameter was uniform. Segments were placed in plastic

Table 1. Mating pattern for the production of reciprocal F_1 hybrids from latitudinal ecotypes. Two clones from the Utah location, labeled A and B, were used. F_1 family codes include the year seeds were planted. When referring to a single F_1 plant, the year is dropped, the F_1 sibling number added and a three digit code produced

Crosses	F_1 family code number	Number of siblings per F_1 family
UtahA (42°N) × Alaska (65°N)	76-1	44
Alaska (65°N) × UtahA (42°N)	76-2	46
UtahB (42°N) × NWT (62°N)	76-3	10
NWT (62°N) × UtahB (42°N)	76-4	44

bags in direct contact with an ice nucleating agent (wet paper toweling) and frozen at a rate of 9 °C per hour. The bags were placed flat on an aluminium plate suspended inside an insulated chamber which was placed in a modified Revco low temperature freezer as described by Gusta et al. (1978). Stem temperatures were measured with thermocouples inserted into the pith of a representative stem segment in each bag. Bags were removed from the freezer at successively lower 3 °C intervals. A control bag was prepared but not frozen. Every bag contained 3 stem segments from each plant sampled, thus each genotype was replicated 3 times at each temperature.

After thawing for 12 h at 0 °C, bags containing stem segments were incubated at 21 °C and 100% RH for 7 days. Then stems were dissected and visually evaluated for tissue injury with the aid of a dissecting microscope. Segments showing brown discoloration and breakdown of cells in the cambium and phloem were rated as dead. The percentage of the stems surviving at each temperature was recorded, and from these data, a T_{k50}, the freezing temperature required to kill 50% of the samples (Proebsting and Fogle 1956; Levitt 1980), was calculated for each plant on each freezing test date. The nonparametric Mann-Whitney test (Snedecor and Cochran 1967) was used to evaluate differences in acclimation patterns between crosses.

Stem segments were color coded before freezing so that injury evaluations could be made without knowledge of genotype. This was done to eliminate bias associated with visual observation methods (Stergios and Howell 1973). Even though visual observation of tissue browning is slow and quantitative, this method has been used extensively with *C. sericea* (Van Huystee et al. 1967; Smithberg and Weiser 1968; Fuchigami et al. 1971 a, b; McKenzie et al. 1974 a, b; Parsons 1978), and has been found to be consistent with regrowth tests (Van Huystee et al. 1967). Stergios and Howell (1973) found visual browning more reliable than specific conductivity, TTC reduction, or multiple freezing points on several woody fruit species.

Glasshouse Experiments

Flowering of the F_1 population in the field was expected during the summer of 1978. F_2 seed would have been produced at that time. However, the F_1 did not bloom due to juvenility. In an effort to induce flowering, softwood cuttings were taken from the parents and F_1's in mid-July 1978, rooted under mist, transplanted to 15 cm pots September 15, and then grown under 22 h of light and 24 °C/21 °C (day/night) temperatures. Whenever photoperiods were extended, supplemental light levels of 10.5 $\mu Em^{-2} sec^{-1}$ 1-m above the soil line were provided by 100 watt incandescent bulbs. Fertilizer treatments of 200 ppm Peters 20–20–20 were applied every 2 weeks. The F_1 began flowering on February 1, 1979. *C. sericea* is a self-incompatible species (Hummel 1981), therefore the F_2 could only be obtained by sib crosses. Controlled pollinations were made on randomly chosen siblings within each F_1 population. F_2 progeny resulting from the sibling diallels were assigned a numerical code as shown in Fig. 2. A backcross of several 76-1 plants to the Utah A parent was obtained. However, flowering of the northern parents was such that they were unavailable for backcrosses.

ALASKA – UTAH A.
crosses

♀ ♂	76-1	76-2
76-1	41 42 43 44 46 53 56 60 63 68	45 70
76-2	38 64	47 55 62 65

NWT. – UTAH B.
crosses

♀ ♂	76-3	76-4
76-3	72	35 52 69
76-4	32 36 75	30 34 54 59 73 74 76 81

Fig. 2. Crossing scheme and coding system for the F_2. F_1 reciprocals were crossed in diallel to produce the F_2. Numbers 30 – 81 are the identification numbers of the F_2 families produced from these crosses and used in the acclimation study

The F_2 seed was harvested, acid scarified, cold stratified, and in mid-September, 1979, germinated in peat moss. After 4 weeks, 500 F_2 seedlings were transplanted to 13 cm pots in a 1 soil : 1 peat : 1 perlite potting mix, placed in a 24 °C/21 °C (day/night) glasshouse under 22 h light, and fertilized as previously indicated. At the same time, representative F_1 parents which had been kept in pots in the glasshouse over the summer were cut back to 5 cm above the soil line, eight rooted cuttings of each latitudinal ecotype were transplanted into 13 cm pots, and all were placed under the same environmental conditions as the F_2 seedlings. This was done to insure that all stem materials used in the greenhouse acclimation study were the same physiological age.

Plants were given a constant 24 h of light for 1 month prior to the start of acclimation. Acclimation was begun on March 17, 1980 when plants over 75 cm tall were chosen and randomly spaced 5 cm apart on the glasshouse bench under a 20 h photoperiod and 18 °C/13 °C (day/night) temp. Starting March 20, the photoperiod was decreased 30 min every 3 days. When the experimental photoperiod coinciding with the natural photoperiod was reached, black shade cloth was pulled to further shorten the daylength. A 7½ h light period was reached on May 31 and was held constant throughout the remainder of the experiment.

The first freezing tests were performed March 20 and 24, on rapidly growing, unacclimated plants. The next freezing tests were performed approximately 1 month later on April 14 and 15 and subsequent freezing tests were performed at approximately 2 week intervals, the last on July 20. However, NWT, UtahB and their F_2 progeny remained under the 7½ h photoperiod until November 5, when an additional freezing test was performed. On each freezing date, the parents, several representative F_1 and up to 29 F_2 plants were randomly selected for freezing. Freezing techniques and evaluation of data were the same as for field experiments.

Results

Parental Ecotypes and F_1's-Field and Glasshouse Experiments

Acclimation patterns of parental ecotypes and F_1 progenies in both field and glasshouse environments appear in Fig. 3. Field results (Fig. 3 A–D) indicate that the acclimation process was similar from year to year. Parental ecotypes from northern latitudes acclimated earlier, in response to shorter nights, than did parents from southern latitudes. F_1 populations exhibited an acclimation pattern intermediate to that of the parents. F_1's and parents in the glasshouse (Fig. 3 E, F) exhibited a pattern similar to the acclimation pattern of

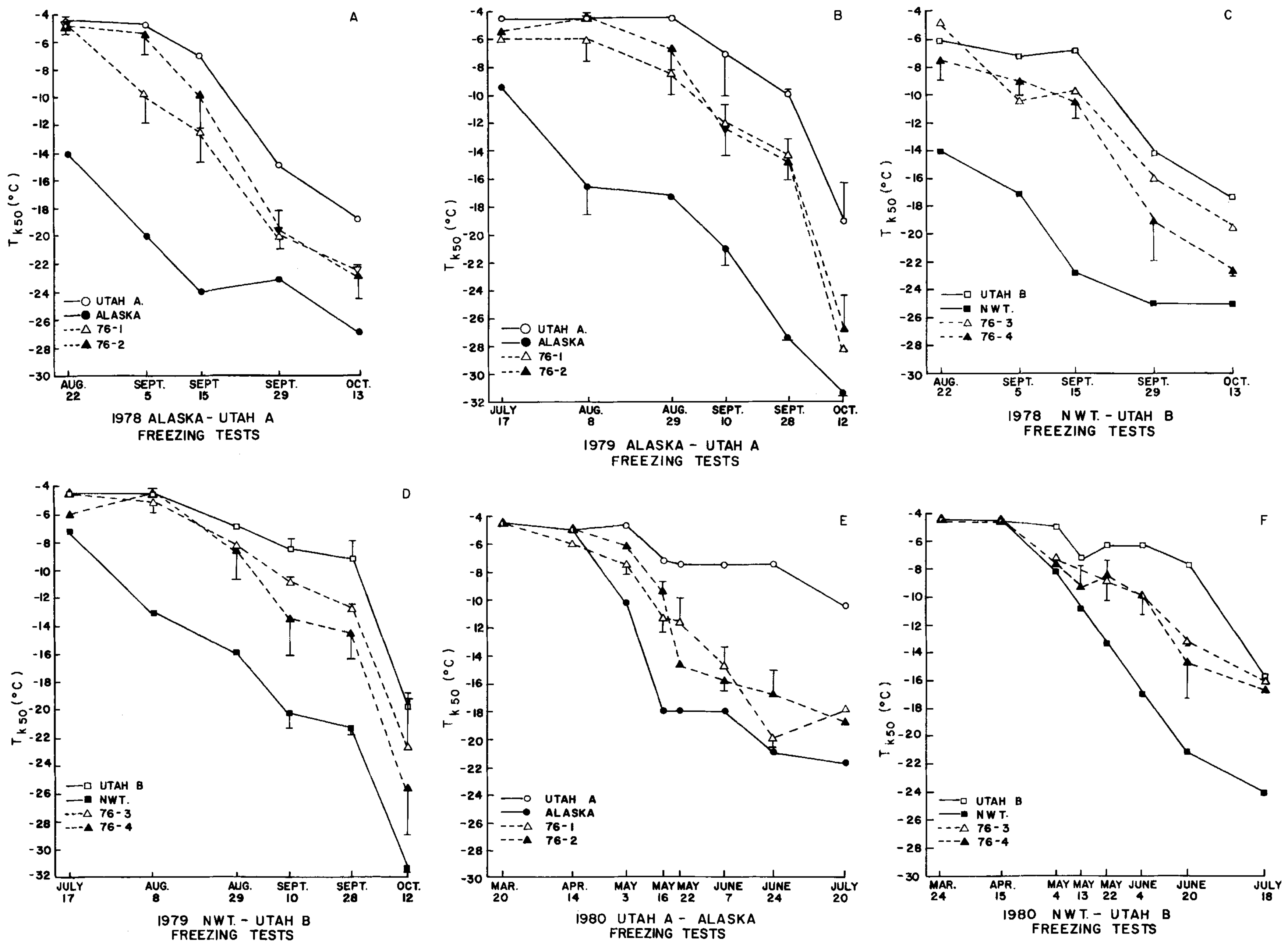
A
T k50 (°C)
—○ UTAH A.
—● ALASKA
---△ 76-1
---▲ 76-2
AUG. 22
SEPT. 5
SEPT 15
SEPT. 29
OCT. 13
1978 ALASKA - UTAH A
FREEZING TESTS
B
T k50 (°C)
—○ UTAH A.
—● ALASKA
---△ 76-1
---▲ 76-2
JULY 17
AUG. 8
AUG. 29
SEPT. 10
SEPT. 28
OCT. 12
1979 ALASKA - UTAH A
FREEZING TESTS
C
T k50 (°C)
—□ UTAH B
—■ NWT.
---△ 76-3
---▲ 76-4
AUG. 22
SEPT. 5
SEPT. 15
SEPT. 29
OCT. 13
1978 NWT. - UTAH B
FREEZING TESTS
D
T k50 (°C)
—□ UTAH B
—■ NWT.
---△ 76-3
---▲ 76-4
JULY 17
AUG. 8
AUG. 29
SEPT. 10
SEPT. 28
OCT. 12
1979 NWT. - UTAH B
FREEZING TESTS
E
T k50 (°C)
—○ UTAH A
—● ALASKA
---△ 76-1
---▲ 76-2
MAR. 20
APR. 14
MAY 3
MAY 16
MAY 22
JUNE 7
JUNE 24
JULY 20
1980 UTAH A - ALASKA
FREEZING TESTS
F
T k50 (°C)
—□ UTAH B
—■ NWT.
---△ 76-3
---▲ 76-4
MAR. 24
APR. 15
MAY 4
MAY 13
MAY 22
JUNE 4
JUNE 20
JULY 18
1980 NWT. - UTAH B
FREEZING TESTS
-4
-6
-8
-10
-12
-14
-16
-18
-20
-22
-24
-26
-28
-30
-32

Fig. 3A–F. Cold acclimation of *Cornus sericea* latitudinal ecotypes and their F_1 progeny under field and greenhouse conditions. Dates indicate when freezing tests were performed. Southern parents and the F_1 with the southern parent as the female are represented by open symbols. Northern parents and F_1 progeny with the northern parent as female are represented by solid symbols. Bars representing one standard deviation have been placed above or below those symbols where two or more ramets of one ecotype or individuals of the same cross were sampled on the same freezing test date. Graphs **A**, **B**, **C**, and **D** show the acclimation response of plants under field conditions. Graphs **E** and **F** indicate the acclimation response of plants under artificially shortened photoperiods in the greenhouse

field grown plants. The glasshouse data are also presented as a frequency distribution (Fig. 4A, B) to enable the reader to pursue the acclimation pattern, over time, of particular F_1 clones. For example, F_1 clones 303 and 421 (Fig. 4B) were tested on several different dates during the greenhouse acclimation experiment; both clones exhibited a consistent acclimation response intermediate to the parents.

From observation and comparison of the graphically depicted patterns (Fig. 3), it appears that acclimation of the reciprocal crosses was not unilaterally influenced by the maternal parent. This visual evidence was corroborated by Mann-Whitney analysis (1% level) of T_{k50} values for the F_1 reciprocal acclimation patterns shown in graphs A, B, D, and E. Thus there was no significant unilateral maternal effect on the inheritance of the photoperiodically induced cold acclimation response in *C. sericea*.

The first fall frosts occurred October 13, 1978 and October 9, 1979. A freezing test done on field grown parents and F_1's November 12, 1979 indicated all plants were hardy to at least –43.5 °C. Ultimate mid-winter hardiness, tested February 20, 1979, was at least –196 °C for both parents and progeny. No effect due to latitude of origin was found on mid-winter hardiness in *C. sericea*.

Results of the July 17, 1979 freezing test (Fig. 3B) reveal that the Alaska ecotype had acclimated to –9.4 °C. Observation of Alaska plants in the field

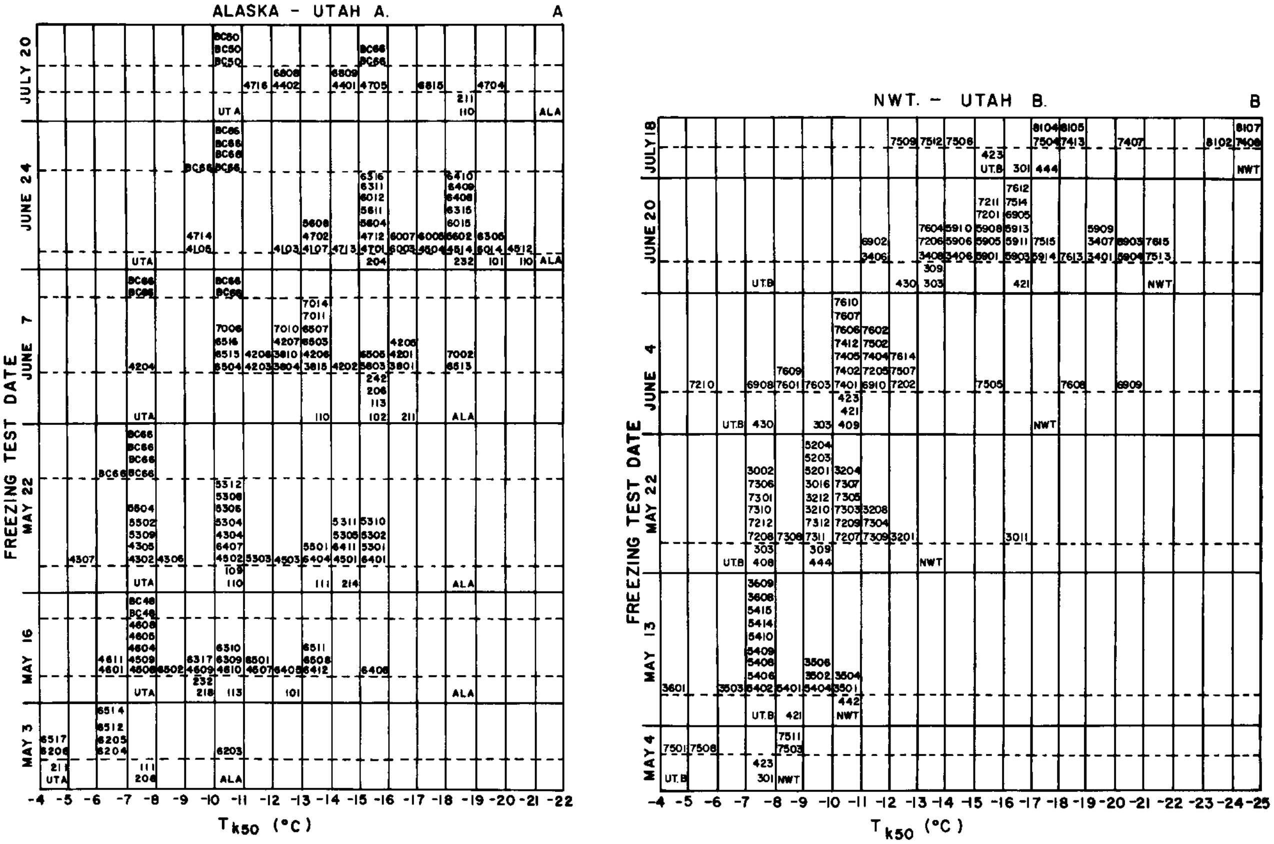

Fig. 4A and B. Frequency distributions of parents, F_1 reciprocals and F_2 progenies for T_{k50} values in the 1980 greenhouse acclimation experiment. Freezing test dates are separated by solid lines. Dashed lines within a freezing test data separate the parents and F_1's from the F_2's. The origin of F_1 code numbers is described in Table 1. A 4 digit code is used to describe a single plant: the first 2 digits or letters designate a particular F_2 population (Fig. 2) or backcross and the second two digits refer to a particular sibling within a population. Graph **A** shows the acclimation results for the Alaska-UtahA group. An additional dashed line separates the backcross from the F_2. Graph **B** shows the acclimation results for the NWT-UtahB group indicated growth cessation and terminal bud set also occurred by this date. At its latitude of origin (65 °N), the day length (based on time of sunrise and sunset) at the time of the summer solstice is ca. 22 h and day lengths greater than 20 h prevail from May 27 to July 17. At the Excelsior, MN, latitude (45 °N), the day length at the time of the summer solstice is ca. 15.5 h. The great disparity in summer day lengths between the native latitude and the test garden latitude coupled with the observation that propagation of the Alaska plant is successful only when cuttings are given at least 20 h of light lead to the conclusion that the Alaska ecotype, when grown in the field in Minnesota, always receives a night length longer than that necessary to trigger acclimation.

F_2's and Backcrosses – Glasshouse Experiments

Freezing tests done March 20 and 24, at the beginning of the glasshouse acclimation sequence, and in mid-April indicated that no acclimation had occurred. By May 3 and 4, when the night was 12 h long, acclimation had already been triggered in the Alaska (– 10.2 °C) and NWT (–8.0 °C) parents and several F_1 and F_2 plants (Fig. 3 E, F). Acclimation had been initiated and had progressed to –7.2 °C in both Utah parents on the May 13 and 16 freezing dates.

Figure 4 A and B show the T_{k50} for each genotype sampled on each freezing test date in the glasshouse acclimation experiment. T_{k50}'s of individual F_2 plants rather than sibling averages are presented so that the reader can readily assess the range in acclimation response within the entire F_2 population as well as with F_2 sibling groups. T_{k50} values for each parent and F_1 tested on each freezing test date are also indicated in the figure.

The F_2 of both reciprocal-cross sets exhibited a highly variable acclimation response. The range in T_{k50} values became progressively wider as acclimation proceeded. A minimum range of 7 °C on May 3 and a maximum of 12 °C on June 7 was observed for the Alaska-UtahA F_2 population. The NWT-UtahB F_2 population had a 5 °C minimum range on May 4 and a 19 °C maximum range on June 4. This concommitant increase in T_{k50} range and length of the dark period would be expected if the F_2 were segregating for the critical night length response which initiates acclimation. There is no doubt that segregation for the rate of development of acclimation after initiation could also occur. However, in this study, initiation and the rate of development are confounded. A wide range in T_{k50} values appeared not only in the F_2 population as a whole but also within F_2 full-sib families. For example, F_2 full-sib family 4,200 of the Alaska-UtahA group has a 10 °C range in T_{k50} values on June 7 (Fig. 4 A) and the NWT-UtahB F_2 full-sib family 6,900 has a 14 °C T_{k50} range on June 4 (Fig. 4 B).

On 12 different dates, an F_2 full-sib family and both of its F_1 parents were frozen. The T_{k50} results of plants 409 and 430 and their progeny (F_2 full-sib family 7,600) on June 4 serve to illustrate that the range of the F_2 progeny was much wider than the range of its F_1 parents. This was also true for the 11 other dates. The F_1 always exhibited T_{k50} values intermediate to the latitudinal ecotypes and much less variable than the T_{k50} values of the F_2. On several freezing test dates, some F_2 plants were as hardy as, if not hardier than, the northern parent. Conversely, other F_2 plants were only as hardy as, or less hardy than, the southern parent. The instances where an F_2 segregant appeared to be more hardy than the northern parent were limited to the NWT-UtahB crosses. F_2 plants were judged as hardy as the Alaska parent on several freezing test dates, but F_2 plants were never judged to be hardier than Alaska.

Although the data are not included in this paper, results of a freezing test done November 5, on 2 NWT, 2 UtahB and 8 F_2 plants that remained under 7½ h days indicated all plants except one F_2 were hardy to at least –28.5 °C. Thus, acclimation had proceeded during the summer and early fall. For example, the UtahB ecotype which had a T_{k50} of –15.8 °C on July 18, had a T_{k50} of –28.5 °C seventy days later on November 5. The plants were not frozen to lower temps. Therefore, if genotype differences existed, they were not detected.

T_{k50} results for progeny from the UtahA × 76-1 backcrosses are included in Figure 4 A. Individuals of BC66 along with both parents (UtahA × 110) were tested May 20, June 7, June 24 and July 20. In the early freezing tests, backcrosses had the same hardiness level as the recurrent parent, UtahA. Acclimation of the backcross progeny was similar to that of the UtahA parent on later freezing test dates. A comparison of backcross progeny and F_2 progeny using the Mann-Whitney test indicated the backcross was significantly less hardy (1% level) than the F_2 on all but the last (July 20) freezing test date. Although the sample size is small, it would appear that backcrossing to the parent requiring a longer night length to acclimate slows acclimation.

Discussion

The glasshouse acclimation experiment described in this paper was done during a time period, March to July, when artificial induction of acclimation in *C. sericea* was thought to be impossible (Van Huystee et al. 1967;

Fuchigami et al. 1971 b). However, previous acclimation work was done on plants that were grown out-of-doors under normal conditions, while plants used in our experiment were grown in the glasshouse under warm, long day conditions for at least 6 months prior to the start of acclimation. These plants, though actively growing, were able to perceive the photoperiod signal and acclimate (Hummel 1981). A preliminary experiment was also performed to test the validity of comparing acclimation patterns of *C. sericea* plants from seeds and cuttings; the results indicated that plant source did not significantly effect acclimation (Hummel 1981). Based on our studies, it seems possible that the glasshouse acclimation method can be used at any time of the year to speed progeny testing in *C. sericea.*

Because of the problems associated with using woody plants, very little is known about their genetic systems. The long juvenile periods of many woody species make the rapid production of successive generations impossible. Thus the investment in space and time required to study a woody plant system is much greater than for an herbaceous system. However, our results indicate that *C. sericea* would make an ideal model system with which to study woody plant genetics. It is a wide ranging North American species and therefore has produced numerous ecotypic variants. *C. sericea* has a short juvenile period and experience has shown it possible to go from seed to bloom in seven months when plants are grown under photoperiods of 20 h or more. It is easy to clonally propagate, grows rapidly and can be trained to a multiple branch system thereby increasing the amount of plant material available for experimental purposes without greatly increasing the amount of space needed to grow the plant.

An ideal study of the acclimation response would separate the critical night length which initiates acclimation from the subsequent rate of development of cold tolerance. Our study was not designed to provide this separation. However, several researchers studying either photoperiodically controlled acclimation or flowering responses have made this separation. Concerning the photoperiodically induced growth cessation and bud set necessary for the development of cold tolerance, Swedish researchers found differences in populations of *Picea abies* from different latitudinal origin (Dormling 1973; Dormling et al. 1974; Ekberg et al. 1976). The critical night length of *P. abies* populations from ca 68 °N was 2 h while a population from 52 °C had a critical night length of 7 h. However, the rate of development of visible buds was the same, 15 to 20 days, in all provenances tested. In contrast to *P. abies,* both the critical night length that induces flowering and the rate of development of visible flower buds after induction varied with latitude of origin in wild populations of *Xanthium strumarium* (Ray and Alexander 1966; McMillan 1969, 1970). Critical night lengths ranged from 7.5 h in plants from 45.5 °N to nearly 11 h in plants from 21.3 °N. Under a constant 11 h dark period, populations with shorter critical night lengths developed buds faster (7 to 11 days) than did populations with longer critical night lengths (14 to 21 days). The data in Fig. 3 indicate the *C. sericea* F_1 acclimation pattern was intermediate to the parents. Graphically it appears the F_1 was closer to the southern parent. However, the graphic picture is somewhat misleading because an F_1 with a critical night length for acclimation exactly halfway between the parents would appear to resemble the southern parent on early sampling dates. Determination of the critical night length and the subsequent rate of development of cold hardiness in the *C. sericea* ecotypes, F_1 and F_2 populations would provide a better understanding of both the physiology and genetics of acclimation and is suggested as an area for future research.

Because reports in the fruit breeding literature indicated the possibility of a unilateral maternal influence on cold hardiness (Stushnoff 1972), we decided to investigate the role of the maternal parent in the acclimation behavior of *C. sericea.* The first reported maternal effect on cold hardiness resulted from the Minnesota test winter of 1917–1918 (Dorsey and Bushnell 1925). Cold injury to interspecific *Prunus* progenies was rated and 58 of 72 seedlings were hardy when the hardy species, *Prunus americana,* was the female parent but when the tender species, *Prunus salicina,* was the female only 39 of 85 seedlings were hardy. Based on this evidence, Dorsey and Bushnell suggested that the hardier plant should be used as the pistillate parent. The other evidence for a maternal influence on cold hardiness comes from breeding work with apple. Thiele (1957) found a significant effect of the maternal parent on the capability of germinating apple seeds to withstand freezing and Wilner (1965) and Harris (1965) found crosses in which the hardier apple variety was used as the female parent produced hardier progeny than the reciprocal cross. Although Harris stated he would expect to obtain the same results with most apple varieties and with trees of all ages, Quamme (1978) detected no reciprocal difference in the hardiness of progenies from crosses between apple cultivars of different cold hardiness levels. No evidence of a maternal effect can be detected in Eriksson et al.'s (1978) data on critical night length for bud set in reciprocal crosses between Swedish and French *Picea abies* provenances. Our results indicated that there was no unilateral maternal effect on the inheritance of the photoperiodically induced cold acclimation response in *C. sericea.*

In addition to the *C. sericea* F_1's produced in this study, several other woody species have been shown to produce an

F_1 with an intermediate response for photoperiodically controlled characters when northern and southern ecotypes were crossed. Pauley and Perry (1954) crossed *Populus trichocarpa* provenances from 58 °N and 47 °N and produced an F_1 with a date of height growth cessation intermediate to the parents. F_1 *Populus tremula* hybrids between different latitude populations were observed by Johnson (1956) to be intermediate in height growth cessation to their respective intraprovenance half-sibs. Dormling et al. (1974) found that the critical night length for bud set of *Picea abies* progenies from French × Swedish interprovenance crosses was intermediate to the critical night lengths of progenies from French × French and Swedish × Swedish intraprovenance crosses.

Two recent reports indicate the importance of additive genetic effects on the control of traits related to cold hardiness in woody plants. With *Picea abies* F_1's from inter- and intraprovenance crosses, Eriksson et al. (1978) concluded that the photoperiodic bud set response was determined by a considerable number of genes and/or alleles with small additive effects. Based on his analysis of F_1 hybrids from crosses between the coastal and interior varieties of *Pseudotsuga menziesii,* Rehfeldt (1977) also concluded the inheritance of traits controlling adaptation, such as bud set and freezing tolerance, was somewhat dependent on additive effects.

Because little information is available on the winter survival characteristics of F_2 progeny from crosses between woody plants of different hardiness levels, the literature that does exist will be discussed. In the forestry literature, the two examples that can be found involve interspecific *Pinus* crosses. Rudolph and Nienstaedt (1962) examined winter injury in small F_1, F_2, and BC_1 populations of *Pinus banksiana – Pinus contorta* hybrids after the 1958–1959 test winter in northeastern Wisconsin. The native *P. banksiana* was not injured while *P. contorta* suffered injury to more than two-thirds of its foliage. F_1 hybrids had injury levels intermediate to the parents. The backcross to *P. banksiana* showed injury intermediate to that of the F_1 and the recurrent parent. Greater average injury than was expected occurred in the F_2, as it was intermediate in injury to the F_1 and less hardy parent. The authors concluded that the inconsistency in the results may have been due to chance because of the small number of F_2 trees observed. No discussion of the range of injury in the F_2 was included but Rudolph and Nienstaedt concluded that winter injury was governed by multiple factor inheritance. Since the early 1950's, Korean forest tree breeding efforts have focused on incorporating the growth rate and timber quality of the tender *Pinus taeda* with the winter hardiness of the slower growing *Pinus rigida* (Hyun 1956; Hyun and Hong 1969; Hyun 1972; Hyun et al. 1972). Tests at four plantation sites (Hyun 1972), with successively more severe climates, have shown the F_2 from *P. rigida* × *P. taeda* crosses was slightly more susceptible to cold damage than the F_1. The author attributed this increased cold damage to the segregating component of the F_2 which was close to *P. taeda,* the cold susceptible parent. Here again, no mention was made of the cold tolerance variability in the F_2.

Fruit breeders in Poland (Zagaja 1974) crossed very hardy Chinese peaches to commercial cultivars, screened the F_1 for winter hardiness and fruit size and either selfed or backcrossed the most promising selections to the commercial cultivars. The F_2 seedlings were screened for hardinesss by the electrolyte conductivity method. Results indicated that the hardiness level of backcross seedlings resembled the recurrent parent, however, individuals were found among the F_2 hybrids that were as hardy as the original Chinese ancestors. The majority of F_2 hybrids produced larger fruit, average weight 60 gm, than the very hardy parent, average weight 35 gm.

Genetic systems that control complex characters, particularly those related to survival, in wild species have been shown to be governed by complex gene interactions considered to be coherent, balanced and buffered (Clausen 1958, 1959; Clausen and Heisey 1960). In their examination of segregation and coherence in two hybrids from four contrasting altitudinal races of *Potentilla glandulosa,* Clausen and Heisey measured survival as the ability to live a period of years at three altitudinal transplant stations. They observed transgressive segregation for many morphological and physiological characters in the F_2. Of particular interest was their finding of a slight transgression toward frost resistance in the F_2 progeny from a cross between a frost resistant and a frost susceptible race (Clausen and Heisey 1958). They estimated at least 4 pairs of genes governed frost suceptibility in *P. glandulosa.* In the context of Clausen and Heisey's work, survival encompassed the entire sum of environmental factors to which a plant must adapt if it is to be successful. In our study with *C. sericea* ecotypes, survival was limited to the ability to respond to shortening photoperiods and acclimate before the onset of freezing temperatures.

The difference between *C. sericea* NWT-UtahB and Alaska-UtahA F_2 progenies relative to variation beyond the parental limits in freezing resistance may reflect the northern distribution limits of *C. sericea.* According to Hulten's (1968, 1970) distribution maps, *C. sericea* follows the Koyukuk and Yukon river valleys as far north as ca. 67 °N and thus the Alaska parent was collected from very near the northern limit of *C. sericea.* Therefore, the Alaska ecotype may represent the species potential for adaptation to northern latitudes and, as such, may have no further releasable genetic variability. It may not be possible to create an ecotype adapted to more northerly conditions from the Alaska ecotype. If the NWT ecotype (62 °N) has not been as intensively selected in nature it may be possible, through recombination, to release the potential for northward movement from this ecotype. However, it was not possible to obtain a measurement of the variability in acclimation responses of individual plants within an ecotype. In the absence of such a measurement, and because F_2 sample sizes were small, it cannot be concluded that the observed differences between Alaska-UtahA and NWT-UtahB progeny populations are biologically significant.

Current efforts at improving hardiness in woody ornamental species involve collecting seed from trees at the northern limit of distribution for the species. Northern nurseries are cautioned to pay strict attention to provenance source when shipping in liner plants or buying seed. A more productive approach to obtaining hardy genotypes with favorable ornamental characters may be to cross northern and southern ecotypes, and intermate promising F_1 plants to produce a large F_2 population from which desirable recombinant types can be selected. Clausen and Hiesey (1960) demonstrated that interracial crosses of two differentially coadapted (*Potentilla glandulosa*) genotypes produced a segregating F_2 population with many recombinations that exhibited new growth patterns, a widely increased range of tolerance, and presumably would fit new ecological niches. A wide range of acclimation responses was also observed in segregating F_2 progeny derived from crosses of northern and southern latitudinal *C. sericea* ecotypes. Fruit breeders Cain and Andersen (1980) studied the inheritance of wood hardiness in the F_1 of crosses between wild-hardy and commercial peach cultivars and recommended intermating selected F_1 plants, producing large F_2 populations and then backcrossing desirable recombinants to elite commercial cultivars in order to obtain wood hardy commercial genotypes. They predicted backcrossing F_1 hybrids directly to commercial peach types would rapidly produce a commercial type but would give minimal opportunity for increased hardiness. Commercial types are almost always the less hardy genotypes in fruit breeding programs. Cain and Andersen's prediction would appear to be borne out by the results obtained in this study where backcrosses of *C. sericea* to the less hardy parent produced BC_1 progeny with T_{k50} values very much like those of the less hardy southern parent.

Problems associated with long life cycles, large sizes, and small progeny numbers hamper investigations of quantitative characters in woody plants. Our work indicates *C. sericea,* with its short juvenile period and small size, can be used to overcome some of these problems. Howell and Weiser (1970) pointed out the environmental and physiological similarities between cold acclimation and flowering and suggested that traditional techniques for studying flowering could be used to study cold acclimation. Information concerning the genetic control of the photoperiodic flowering response may also be useful in attempting to understand the genetics of the photoperiodically induced cold acclimation response. Whenever a photoperiodically controlled character is studied, the researcher must decide whether the response will be evaluated under a selected photoperiod or a continually changing photoperiod. Environmental conditions which maximize the effect of particular genetic differences provide a window through which a direct Mendelian view of quantitative characters may be obtained (Murfet 1977). In the research with *C. sericea,* we chose the continuum approach of looking at acclimation in response to gradually decreasing photoperiods rather than the window approach. However, a large number of *C. sericea* genotypes sampled on a single, carefully chosen, freezing test date might produce the appearance of qualitative segregation.

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