Conclusions

Assuming that clonal gametic contributions to the seed crop are proportional to clonal strobilus numbers, our findings suggest that the gametes of certain clones will dominate the genetic composition of the seed crop, and that both male and female gametes will contribute to this dominance. These findings have several potential genetic consequences for orchard seed production. The genetic diversity of the seed crop is reduced over that expected assuming random mating among clones, and the rate of self-fertilization of certain clones relative to that of others potentially is increased. Both factors will probably lower the expected genetic gain to be made by breeding the clones.

From a management perspective, the problem of reduced genetic diversity in the seed crop may be addressed in a number of ways. Since different clones dominate female strobilus production in different years, the genetic diversity of seeds may be significantly increased by combining the seed crops of two or more years. Alternatively, hormonal treatment of orchard clones (MARQUARD and HANOVER, 1984) may, by increasing male and female strobilus numbers, bring about more equitable production levels.

The potential problem of higher self-fertilization rates in trees and clones producing larger numbers of male strobili is more difficult to solve. It could be addressed by increasing the number of male strobili of other clones, thereby increasing the proportion of non-self pollen in the pollen cloud. Alternatively, clones producing exceptionally high levels of inbred seed could be excluded from use as sources of seed.

Strobilus production levels represent only one factor which potentially influences the mating system of clonal seed orchards. Other factors such as flowering phenology, wind direction, gametophytic selection, clone number, clone mortality, and clone placement probably interact with strobilus production to influence the genetic composition of orchard seed crops. Electrophoretic analysis of the clones and the 1984 and the 1985 seed crops is, therefore, essential to reveal the importance of strobilus production alone on the genetic composition of the seed crop. In particular, it will be important to determine the degree to which clones producing the majority of male strobili contribute the majority of male gametes to the seed crop, and the extent to which such clones self-fertilize at higher rates than those clones which produce less pollen.

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Phenology, Height Increment, and Cold Tolerance of Alnus glutinosa Populations in a Common Environment[1])

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Summary

Progenies of 48 natural populations of black alder [Alnus glutinosa (L.) GAERTN.] were compared on the basis of height increment in the second growing season, date of budburst, date of budset, spring frost injury, winter cold injury, and laboratory-determined freezing tolerance. Budburst occurred in all populations before the beginning of the frost-

free season, and budset occurred well before the frost-free season ended. Variation in spring frost injury appeared to be more closely related to cold tolerance than to time of budburst. About half the variation in height increment was associated with variation in duration of growth, and the rest with differences in rate of growth. However, selection for phenological timing appears relatively unimportant, so that growth increment need not be factored by component. Eight populations from West Germany, Hungary, Ireland, France, Netherlands, and Denmark are identified as potentially useful because of their fast growth and cold hardiness. Several fast-growing populations appear to be climatically unsuited to the test area.

Key words: Alnus glutinosa, phenology, frost injury, winter injury, cold tolerance, height growth, provenance test, geographic variation.

Zusammenfassung

Nachkommenschaften von 48 natürlichen Populationen der Schwarzerle [*Alnus glutinosa* (L.) GAERTN.] wurden auf der Basis des Höhenzuwachses in der zweiten Vegetationsperiode, des Datums des Aufbrechens der Knospen, des Datums der Knospenbildung, der Spätfrostschäden, der Winterfrostschäden und der im Labor festgestellten Frosttoleranz verglichen. Das Aufbrechen der Knospen geschah in allen Populationen vor Beginn der frostfreien Saison und die Knospenbildung gut vor Ende der frostfreien Saison. Die Variation in Spätfrostschäden scheinen enger mit der Kältetoleranz als mit der Zeit des Knospenaufbrechens zusammenzuhängen. Ungefähr die Hälfte der Variation des Höhenzuwachses läßt sich mit der Variation in der Dauer des Wachstums in Zusammenhang bringen und der Rest mit den Unterschieden in der Wachstumsrate. Die Selektion auf phänologische Abstimmung erscheint relativ unwichtig, so daß es keinen Grund gibt, unabhängig von der Phänologie auf Zuwachs zu selektieren. Acht Populationen aus Westdeutschland, Ungarn, Irland, Frankreich, den Niederlanden und Dänemark wurden als potentiell nützlich angesehen, weil sie schnellwachsend und frosthart waren. Mehrere andere schnellwachsende Populationen scheinen jedoch aus klimatischen Gründen für das Testgebiet ungeeignet zu sein.

Introduction

Black alder is one of very few nitrogen-fixing species that can reach commercial timber size in the eastern United States. Black alder has been used in the United States primarily for mine spoil revegetation, but it is also being evaluated for street-tree use, as a "nurse" species for more valuable crops, and for fiber and energy crop management systems (KELLISON and WHITE, 1979; PHARES *et al.*, 1975; PLASS, 1977; SAUCIER, 1977; STEINER, 1983; TARRANT and TRAPPE, 1971). The latter purpose requires rapid height growth and, thus, optimum utilization of the growing reason.

The wide natural range of black alder *(Figure 1)* should provide a large reservoir of variation for selection of populations most suitable for maximum wood fiber yield. Since black alder is not native to the United States, genetic improvement cannot proceed from locally adapted races, and selection for yield must necessarily be combined with selection for climatic adaptation. Timing of budburst and budset potentially affect both (1) growth increment and (2) the timing of events necessary for suitable acclimation to low temperatures.

Previous genetic evaluations of black alder in the United States have emphasized general growth properties of the species. This study describes genetic variation among 48 populations in timing of budburst and budset, and the relationship of these characteristics to population growth increments and cold tolerance.

Materials and Methods

The geographic origins of the 48 populations included in this study are illustrated in *Figure 1,* and a description of their exact location is given by MAYNARD and HALL (1981). Details of the origin of the provenance experiment of which this study is a part are given by ROBINSON *et al.* (1979) and DEWALD *et al.* (1983). The plants for this study were propagated in the greenhouse beginning January 1980 using 1.9-liter containers with a mixture of 1:1:1 peat:vermiculite:granulated kaolinite clay. The seedlings were successfully inoculated three weeks after germination with a nitrogen-fixing actinomycete and were grown under a 16-hour photoperiod with daily irrigation and biweekly fertilization with a nitrogen-free nutrient solution. Additional information on the propagation is provided by DEWALD (1982).
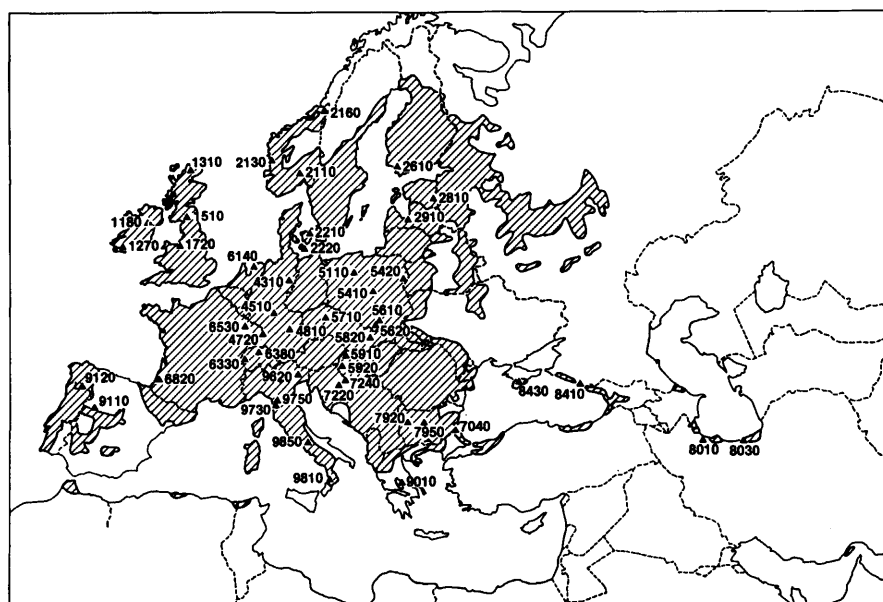

Figure 1. — Natural range of *Alnus glutinosa* and locations of the populations studied (from BORATYNSKI 1980 and ROBINSON *et al.* 1979).

The data reported here were collected on the seedlings outplanted at a 2.1 m² spacing on former agricultural land (silty clay loam, pH 6.5—7.2) near State College, Pennsylvania (latitude 40⁰38' N, longitude 77⁰52' W) that had been plowed, disked, and sprayed with glyphosate herbicide to kill emerging weeds. Weed competition was further minimized by cultivation at 3-week intervals during the first two growing seasons. The greenhouse experimental design, a randomized complete block design with four-seedling row-plots representing each population in each of four blocks, was carried directly into the field when the seedlings were planted on June 12, 1980.

Measurements

Budburst and budset during the second growing season (1981) were measured by visiting each tree in the plantation at 3-day intervals to observe the state of growth. Budburst was recorded as the number of days past March 31 when most of the buds on a tree were completely open with the largest leaves unfolded, reflexed, and about 13 mm long. Budset was recorded as the number of days past June 30 when a tree first had a well-developed terminal bud, all lateral buds were set, and there had been no evidence of growth since a previous observation.

The 1981 growth increment, measured from the point of new stem elongation in 1981 to the top of the terminal bud, was recorded in late October after all trees in the plantation had ceased growth.

Cold injury was evident in the plantation in spring 1981 as a result of freezing temperatures on six days in April during budburst and, apparently, low temperatures of −18⁰ C to −26⁰ C that occurred in January and mid-February. Winter cold injury, based on the presence of twig discoloration and dried inner bark, was measured May 1981 as the proportion of trees injured in each population as well as the population mean percentage of dieback in the 1980 growth increment. The spring frosts caused death of emerging leaves, rated for each tree on a scale of 1 = 1-20, 2 = 21-40, . . . , 5 = 81-100 percent of the young leaves on all shoots injured. There was no injury caused by early autumn frosts in 1981.

Cold tolerance determinations were made on 23 populations in mid-January 1982 using the electrical conductivity procedure described by DeHayes (1977) and Williams (1984). Samples from the fourth or fifth branches below the terminal bud were transported to the laboratory, and 15 mm segments were slowly cooled to one of eight temperatures (unfrozen control, −15⁰ C, −20⁰ C, −25⁰ C, −30⁰ C, −35⁰ C, −40⁰C, −45⁰ C). Each population-temperature combination was replicated twice with two 15 mm segments per replication. After soaking the exposed stem segments in deionized water for 24 hours, the electrical conductivities of the sample solutions were measured to provide an index of the loss of electrolytes from injured cells. The samples were then autoclaved to cause complete death, and their electrical conductivities remeasured after an additional period of soaking. A more complete description of the procedure is given by DeWald (1982). Relative conductivities (RC) were calculated as the before- vs. after-autoclaving conductivity ratio and used as an index of low temperature injury, larger ratios being associated with greater injury.

Data Analyses

Population differences in phenology, 1981 growth increment, cold tolerance, and spring frost injury were tested by analysis of variance. Analyses of covariance were used to examine frost injury differences not explained by budburst timing, and to examine the relationship between growth increment and duration of growth (time in days between budburst and budset).

Relative conductivities of the unfrozen control and two highest test temperatures were averaged for each population and used as an estimate of electrolyte diffusion from uninjured tissue. An estimate of the highest temperature at which statistically detectable injury occurred in the population was calculated by adding the least significant (P = 0.01) difference in RC (based on ANOVA error term) to the estimate of RC for uninjured tissue. The temperature corresponding to this value was interpolated from actual temperature treatment values. "Critical temperatures" calculated in this manner were used as indices of relative cold tolerance for the populations examined.

Geographic variation in phenology and hardiness was examined by regression of population means on latitudes, longitudes, and normal mean temperatures near the population origins for the months of January, March, May, July, September, and November (Wernstedt, 1972).

Results

Phenology

Budburst in the second growing season began the first week of April and was complete on all trees by the end of the fourth week. The first populations to flush were mostly from the Balkan Peninsula and southeastern Europe, and these were followed by populations from progressively farther west and north (*Figure 2*). Thus, trees from Italy burst bud at about the same time as those from the British Isles and Scandinavia. The last trees to flush belonged to populations native to Spain and Iran.

Inspection of *Figure 2* shows a reasonably coherent, non-random pattern of geographic variation, with only a few populations notably different from their neighbors. Nevertheless, the pattern is difficult to decribe statistically with reference to geographic or climatic variables. Regression
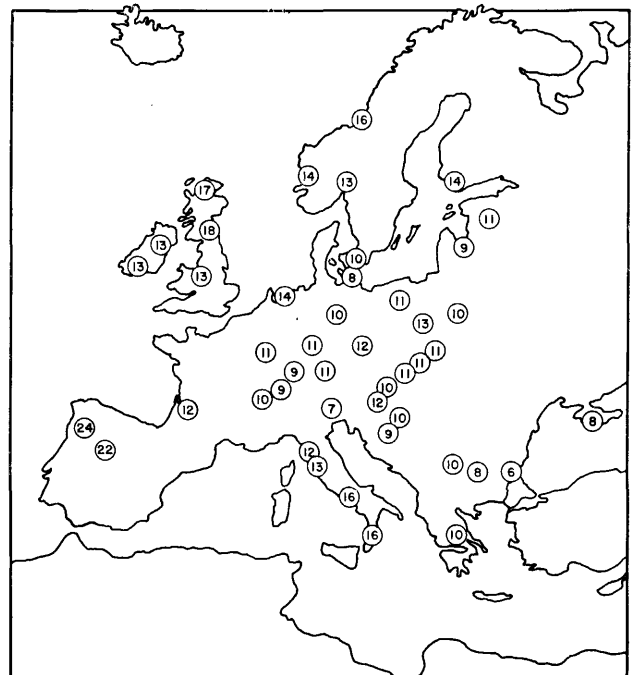

Figure 2. — Population mean dates of budburst (days after March 31, 1981). Not shown in this map are the eastern populations 8010 (mean = 24), 8030 (mean = 23), and 8410 (mean = 16).
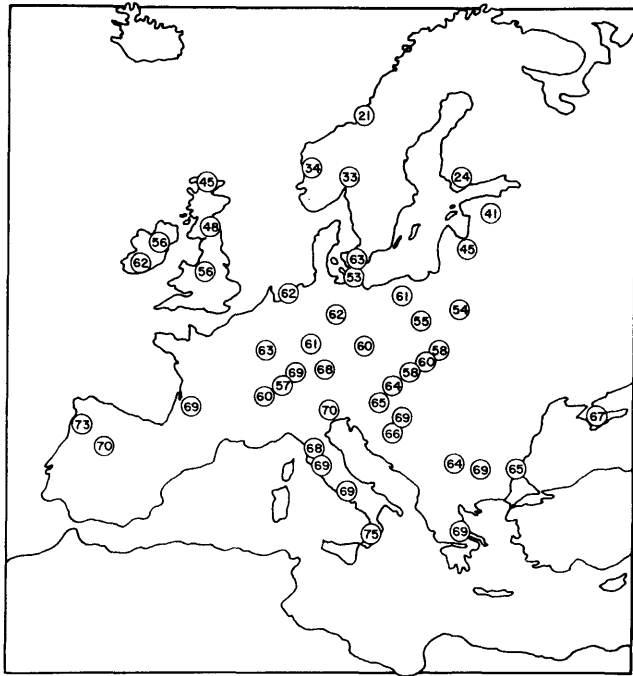
Figure 3. — Population mean dates of budset (days past June 30, 1981). Not shown in this map are the eastern populations 8010 (mean = 83), 8030 (mean = 77), and 8410 (mean = 77).

on a polynomial function of latitude and longitude accounted for 72 percent of the total variation, but simple correlations of budburst timing with latitude or longitude were not significant. Stepwise regression on normal mean monthly temperatures explained a maximum of 44 percent of total variation, for Y = f (January, May, July).

The order in which populations ceased growing was quite different from that in which they burst bud (Figure 3). The first populations to set bud, in late July and very early August, were the most northern populations. Next to set bud were most of the central European populations, in mid- to late August, and last to set bud were

southern European populations, in the first or second week of September.

Time of budset was correlated with latitude, longitude, and monthly temperatures near the population origins. A polynomial function of latitude and longitude accounted for 89 percent of total variation among population means, and latitude alone accounted for 79 percent of the variation. The north-south pattern of progressively delayed budset was remarkably consistent except for a relative late population in Denmark (2210), two relatively early populations in Switzerland (6330, 6380), and a tendency for western populations to be slightly later than eastern populations. A function of March, May, July, and September normal mean temperatures accounted for 88 percent of total variation.

Population mean duration of growth varied from 96 to 155 days (Figure 4), with a plantation mean of 139 days. The eight most northern populations (Scotland, Norway, Finland, Baltic States) had means in the range of 96 to 127 days. All other populations from the British Isles, as well as all those from Spain, The Netherlands, Poland, Czechoslovakia, and Switzerland, had means in the range of 133 to 141 days. All remaining populations (half of the total) grew for 141 days or more, a range of only 14 days.

Height Increment

Population mean height increments varied from 28 to 128 cm. There was no strong geographic pattern to the variation in growth: populations that grew at least 20 percent less than the plantation mean of 81.5 cm included all of those from Scandinavia and the Baltic States, and one from Scotland, but also one population each from Spain, Greece, and Iran. Those that grew at least 20 percent more than the plantation mean included two each from West Germany and Hungary, and one each from France, Denmark, Italy, and Yugoslavia. There was considerable variation in growth among the large number of central European populations.

Analysis of covariance on growth increment with duration of growth as the covariate showed that phenology accounted for a significant portion (47 percent) of the varia-
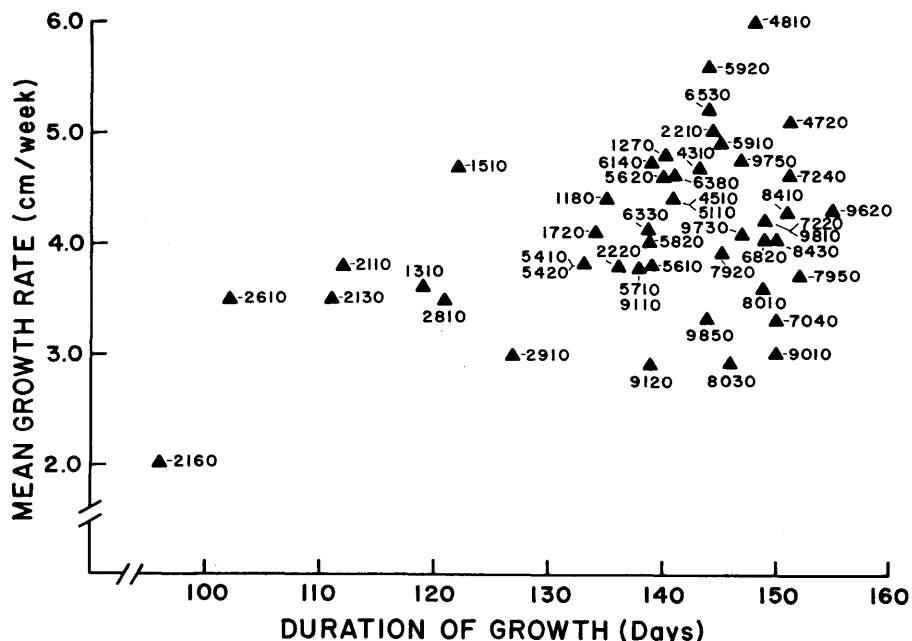

Figure 4. — Relationship between mean weekly height growth and duration of growth in the 1981 season for 48 populations (r² = 0.18).

208

tion in growth; however, populations differed significantly even after accounting for the covariate. Thus, no more than half the variation among populations in growth increment can be attributed directly to differences in phenology; the remaining variation was evidently caused by differences in growth per unit time period. Mean weekly growth (increment ÷ duration in weeks) provides a useful index of such differences, although actual growth rates probably varied over time as temperature changed and, perhaps, as the transition from "fixed" to "free" growth occurred.

Mean weekly growth differed by a factor of 3:1 among populations. *Figure 4* shows rates plotted against duration of growth for the various populations. Growth rate and duration of growth varied more-or-less independently. For example, among those populations that grew for about 150 days, growth rates varied between 2.9 and 6.0 cm/week; and among populations with average growth rates of about 3.5 cm/week, the duration of growth ranged from 102 to 152 days. There was a strong tendency for all southern populations (7000+ numbers, right of *Figure 4)* to have combinations of intermediate growth rate and long duration of growth. Most of the very northern populations (2000+

numbers, left of *Figure 4)* had similarly intermediate rates of growth, but grew for shorter periods of time.

Cold Hardiness

Ten percent of the trees in the plantation suffered dieback as a result of low temperatures in the 1980—81 winter. Of the injured trees, 63 percent were native to the Caspian and Black Sea areas, and 25 percent originated in southern and coastal Europe. In the extreme, both Iranian populations (8010, 8030) sustained injury to 78 percent or more of the 1980 growth increment. Although injury was generally greatest on southern populations, there were exceptions. All Italian and Balkan populations were essentially uninjured, but one Scottish (1510) and one Polish (5110) population lost about 10 percent of their growth increments.

Winter-injured trees produced subsequent height growth from lateral rather than terminal buds, so injury may have affected 1981 height increments. Plots in which all trees were winter injured, irrespective of population, averaged only 80 percent of the height increment exhibited by plots in which no trees were injured. Since the mean duration of growth for injured trees (143 days) was very similar to the plantation mean (139 days), their shorter height incre-
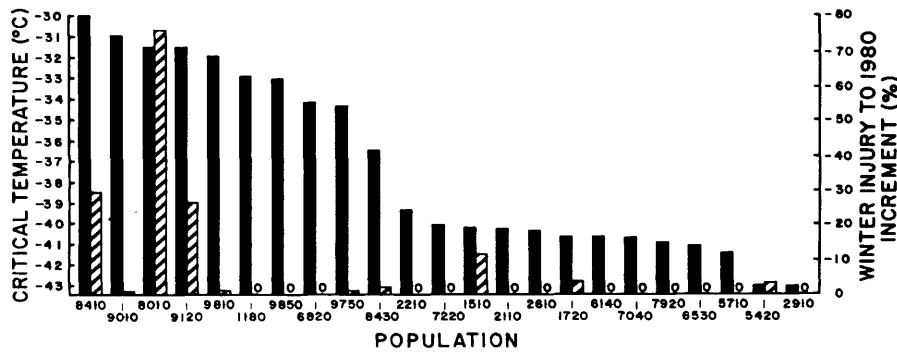

Figure 5. — Population mean January 1982 critical temperatures (solid bars) and winter injury to the 1980 height increments (hatched bars).
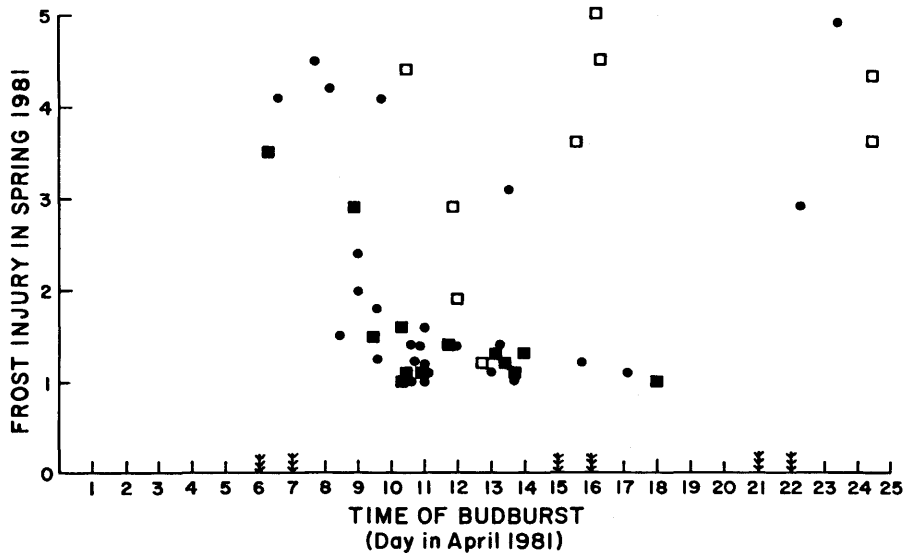
Figure 6. — Relationship between time of budburst and frost injury (5 = most severe) for 48 populations (r^2 = 0.05). Dates with subfreezing temperatures are shown with arrows on the abcissa. Open boxes indicate populations with > −34° C critical temperatures measured in January and closed boxes indicate populations with < − 39° C critical temperatures. Circles represent populations not measured for cold tolerance. Actual times of budburst were about 3 days earlier than shown.

ments were primarily a function of mean weekly growth, which was almost without exception below the average of uninjured trees. However, only six populations (1510, 8010, 8030, 8410, 9110, and 9120) accounted for 8.5 percent of the 10.0 percent of the trees injured in the plantation. Thus, any putative influence of winter injury on 1981 increment has little effect on the overall pattern of growth differences depicted in *Figure 4*.

The 23 populations sampled and exposed in the laboratory to low temperatures differed significantly (P < 0.01) in injury response as measured by RC. Critical temperatures ranged between -30° C and -34° C in most southern European populations, and between -39° C and -43° C in central and northern European populations. *Figure 5* shows January 1982 critical temperatures and 1981 winter injury means for the corresponding populations.

Latitude alone explained 50 percent of the variation in critical temperature. The major deviations from a latitudinal trend occurred in populations from the Balkan Peninsula (except Greece), which were relatively cold tolerant for their latitudes, and in Irish population 1180, which was relatively intolerant. Normal mean monthly temperatures for January and November accounted for 69 to 71 percent of variation in critical temperature.

As *Figure 5* shows, populations with the most injury in the winter of 1980—81 were also the least cold tolerant in January 1982. However, there were major discrepancies between the two characteristics. Several populations with low cold tolerance also had low injury, and a few with high cold tolerance (especially 1510 from Scotland) nevertheless sustained slight injury.

Spring frosts during budburst caused variable amounts of injury, ranging from minimal ($\bar{x} = 1.0$) to almost complete death of all new foliage ($\bar{x} = 5.0$) *(Figure 6)*. Differences among populations in frost injury rating were statistically significant (P < 0.01). Latitude of origin accounted for 61 percent of variation in population mean injury rating. All populations but two (7920, 9750) with origins south of latitude 46°30' (about that of population 6380) had mean injury ratings greater than 2.8, and all populations north of that latitude had mean injury ratings less than 2.4. As *Figure 6* suggests, there was no statistical relationship between time of budburst and injury. Frost injury, which affected only a tiny fraction of the foliage produced in 1981 and did not kill shoots, had no perceptible effect on height increment. The mean increment of trees with the highest frost injury score was identical to that of trees with the lowest score.

Discussion

The results for budburst timing are remarkable in two respects: first, in the uniformity displayed by populations over most of the range, from Ireland and France to Greece and Estonia. The means for almost all these populations varied by no more than 4 days. In this, black alder resembles Scots pine *(Pinus sylvestris* L.), which is also relatively uniform in budburst timing over the central European portion of its range (STEINER, 1979). The other notable result is that most populations outside this region were later to burst bud, so that trees from such climatically diverse locations as Italy, Scotland, Norway, and southern Russia burst bud at almost the same time. This is different from Scots pine, in which geographic variation in budburst timing followed a clear pattern of climatic differences (STEINER, 1979).

Our results for budburst timing agree in most particulars with those of MAYNARD and HALL (1981) for an Iowa plantation of the same material. The main exception is that in their plantation the far northern populations 2130, 2160, and 2610 were early rather than late. Since they studied the same populations at the same age, it is possible that this discrepancy is an indication of genotype × environment interaction.

The apparently clinal relationship between time of budset and latitude is typical of forest trees of temperate regions (WRIGHT, 1976). Extension growth in black alder occurs first from bud primordia and then from primordia developed during the current growing season, and it evidently proceeds until decreasing daylength triggers growth cessation in the manner described by PERRY (1971). VAARTAJA (1959) has discussed in detail the ecotypic response of forest trees to photoperiod, particularly in regard to growth cessation. For each species in his study, there was typically a daylength at which northern origins ceased growing while southern origins continued. Early growth cessation is undoubtedly an adaptation to cold climates, as the relationship of this character with latitude suggests. However, the strength of such a relationship in a common garden study is probably exaggerated by the fact that the very expression of the character is photoperiodically (i.e., "latitudinally") induced. McVEAN (1953) and MAYNARD and HALL (1981) also found earlier budset in northern vs. southern populations of black alder grown in common environments.

Time of budset and winter cold tolerance were both correlated with latitude of origin and hence with one another. Winter cold tolerance corresponded less well with latitude than did time of budset, but the greatest anomalies can be explained by reference to climate of origin. For example, the relatively cold tolerant and relatively southern Bulgarian populations 7040 and 7920 are native to areas that are about 4° C colder in January than even northern Scotland (WERNSTEDT, 1972).

We have no good explanation as to why there was not better correspondence between 1981 winter injury and 1982 cold tolerance. Clearly, the single determination of cold tolerance in mid–January 1982 was an inadequate estimator of the relative tolerance that existed at the time (or times) when injury occurred in the first winter. For example, it is possible that discrepancies originated from injury that happened during autumn acclimation, rather than in mid-winter, and were perhaps complicated by stresses resulting from the recent establishment of the plantation in June 1980.

To what degree late budset in the climate of Pennsylvania may have affected the cold tolerance of southern populations is of course unknown. Since growth cessation is a neccessary precursor of acclimation (WEISER, 1970), its timing can presumably affect the level of tolerance achieved at a given time. However, the fact that Bulgarian populations set bud relatively late but nevertheless developed high tolerance suggests that other factors were involved. All populations set bud 22 to 84 days in advance of the normal date of the first autumn frost at the plantation site (October 14). Thus, the timing of budset did not (and normally would not) directly expose any of the populations to autumn frost injury in central Pennsylvania.

Date of budburst had little or no effect on susceptibility to injury by spring frosts, probably because frosts occurred almost throughout the period over which budburst occurred. Growth initiation in all populations occurred 2 to 20

days in advance of the average date of the last spring frost (April 27). Although spring phenological events for most plants in the area were one to two weeks in advance of normal in 1981, it is likely that in most years black alder would be growing before the danger of frost is past. Thus, selection for avoidance of injury through late budburst (e.g., NIENSTAEDT and KING, 1969) is probably out of the question.

Although all populations were exposed to frosts in spring 1981, many escaped with only minor injury. Many of these latter were populations which exhibited a high degree of cold tolerance in January 1982 (only 23 of the 48 populations were evaluated for cold tolerance). Almost all the populations which had low cold tolerance suffered high frost injury *(Figure 6)*. The relationship must be considered tentative at best; but, strengthened by the lack of correspondence between phenology and injury, it suggests that population differences in spring frost injury were more a function of tolerance than avoidance.

The populations which grew the most tended to come from the central part of the natural distribution, although there was no clear pattern to geographic variation in this characteristic. About half the variation in height increment could be attributed to differences in rate of growth and about half to differences in duration. No population made full use of the normal 170-day frost-free season for the area, and indeed all began growing before the danger of frost was past. Since tolerance appeared to have more of an effect on spring frost resistance than avoidance, and since all populations ceased growth well in advance of autumn frosts, there appears to be no good reason to select for rate of growth independently of duration (phenology), although it would be possible to do so.

Predicting future performance can be risky even for a relatively short-rotation crop such as black alder. Assumptions about the choice of black alder provenances for the eastern United States have been based largely upon the superior growth to age 6 years of stock from southern West Germany in a single, limited-range provenance test of the species (FUNK, 1973). By age 16, several of the previously superior provenances were below-average in survival or diameter, and one had declined drastically in relative height (FUNK, 1979). Such genotype × age interactions are evidence of climate or edaphic maladaptation. In our study, eight populations were among the best 25 percent with respect to height increment (mean > 0.92 m), had minimal frost injury (mean < 1.5), and had no winter injury. In order of decreasing height increment, these were 4810 (West Germany), 5920 (Hungary), 6530 (France), 2210 (Denmark), 5910 (Hungary), 1270 (Ireland), 4310 (West Germany), and 6140 (Netherlands). Several others (4720, 7240,

9620, 9750) exhibited very good growth but also evidence of climatic maladaptation. We will watch with interest the development of these two groups of populations with respect to one another.

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