

ALTITUDINAL VARIATION IN GROWTH, BUDBREAK AND SUSCEPTIBILITY TO
BALSAM TWIG APHID DAMAGE OF BALSAM FIR FROM 6
VERMONT SEED SOURCES

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ABSTRACT

Differences in 10-year heights, 4-year growth from 1987 through 1990, relative timing of budbreak and damage by the balsam twig aphid (Mindarus abietinus Koch.) among balsam fir (Abies balsamea (L.) Mill.) from 6 Vermont seed sources originating from different elevations were examined. Height differences among seed sources were highly significant and trees from high elevation seed sources tended to be the shortest. Differences in 4-year growth among seed sources were also highly significant and followed the same trend as total height. Although differences in the amount of twig aphid damage (1990) among seed sources were highly significant, there was no consistent pattern of damage associated with elevation of origin. Trees from the 872 m seed source on Mount Mansfield had considerably more aphid damage than trees from any other seed source including those from 1173 m on the same mountain. Differences in budbreak (1991) among seed sources were highly significant. Seed sources were segregated into 3 groups. Low elevation seed sources had the earliest average budbreak, high elevation sources had the latest average budbreak and mid elevation sources were intermediate. The correlation between seed source means in percent aphid damage (1990) and relative budbreak (1991) was significant, but the biological interpretation of this statistic is complicated by the fact that measurements of these variables were made in different years. Although differences in the relative timing of budbreak between seed sources may partially contribute to differences in aphid damage, data from the two highest elevation seed sources suggests that factors other than budbreak timing alone can greatly affect seed source susceptibility to damage.

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INTRODUCTION

Balsam fir (*Abies balsamea* (L.) Mill.) is a prominent component of coniferous forests of eastern North America, and it is a species commonly harvested for pulp and paper production. Within New England, balsam fir is also the most common species used for Christmas trees. Even though balsam fir is already economically important, genetic selection for traits such as faster growth rate and resistance to insect damage could significantly increase balsam fir's value. But, before meaningful selection can occur, genetic variability must be identified. Most studies of genetic variation within a species have focused on seed sources from many geographically distant regions. Range-wide provenance tests of balsam fir in New England and the Lake States have revealed genetic variability in several economically important traits (Lester 1970, Lester et al. 1976, Lowe et al. 1977, DeHayes 1981).

Significant genetic variability can also exist within more geographically limited areas, and is sometimes associated with ecotypic adaptation of populations to differences in physiographic features such as elevation. In addition to being of scientific interest, an understanding of genetic variability within more limited geographic areas could be of immediate utility to commercial operators. For example, the Vermont Department of Forest, Parks and Recreation grows balsam fir seedlings for sale to local Christmas tree growers. Most of the seed for this program is collected from Vermont sources, but little is known about how these sources vary regarding traits important to growers. If Vermont seed sources differed significantly in important traits such as growth rate, then seed collection could be directed to take advantage of these differences.

In addition to growth, potential differences in balsam fir's susceptibility to damage by the balsam twig aphid (*Homalodendrum abietinus* Koch.) would be of interest to Christmas tree growers. Although severe infestations in any one plantation seem to be cyclic, with peaks on 4 to 5 year intervals (Varty 1966),² infestation levels in Vermont as a whole have been heavy for the past 6 years.² Feeding by the balsam twig aphid causes twisting and deformation of needles, which disrupts normal phyllotaxy and changes needle orientation to sunlight, wind and atmospheric gases. Because this damage is unsightly, it can greatly reduce the value of Christmas trees in years following infestation (Saunders 1969). Although regional differences in the susceptibility of balsam fir to twig aphid damage have been documented (DeHayes 1981), possible within-region differences have not been fully examined.

This paper documents differences in growth, susceptibility to balsam twig aphid damage and relative timing of budbreak among balsam fir from 6 Vermont seed sources originating from different elevations.

² Personal communication with Ronald Kelly, Forest Protection Specialist, Vermont Department of Forests, Parks, and Recreation, Morrisville, VT.

MATERIALS AND METHODS

In June 1985, 5-year-old nursery grown balsam fir seedlings representing 6 Vermont seed sources (Table 1) were planted at the USDA Forest Service Northeastern Forest Experiment Station, South Burlington, VT. Seed sources ranged in elevation from 244 m (Groton, VT) to 1173 m (Mount Mansfield, Stowe, VT). The plantation is a randomized complete block design with one 4-tree plot from each seed source in each of 32 blocks. Trees were planted on a 1 x 2 m spacing with a border row surrounding the plantation and 4 east-west oriented border rows separating blocks within the plantation.

Table 1. Location and elevation of parental stands for the 6 Vermont seed sources.

Seed Source locations	Elevation (m)
Groton, VT	244
Maidstone, VT	317
Victory, VT	366
Granville, VT	597
Mount Mansfield, Stowe, VT	872
Mount Mansfield, Stowe, VT	1173

Heights (cm) of all trees were measured in March 1987 and again in October 1990. Four-year height growth (cm) was calculated for each tree by subtracting 1987 measurements from corresponding 1990 measurements. In spring 1990, the plantation was infested with the balsam twig aphid. In April 1991 (before budbreak), 1990 twig aphid injury was evaluated. Percent of current-year growth damaged by aphids was estimated to the nearest 10% for each tree. Beginning in April 1991 the date of budbreak for individual trees was recorded using the protocol established by Wilkinson (1977). The date of budbreak was defined as the day when buds in the upper 1/3 of the crown showed green needles under the cap of bud scales; data was recorded as the number of days after April 28 - the day before the first tree flushed. Data for individual trees were averaged by plot and analyses of variance were used to determine significance of seed source differences in height (1990), 4-year growth, percent aphid damage (1990) and relative timing of budbreak (1991). Differences among specific seed sources were determined using Duncan's multiple range procedure. Correlation analyses were used to assess relationships among seed source elevation, aphid damage (1990) and budbreak (1991).

RESULTS AND DISCUSSION

Height differences among seed sources were highly significant. In general, trees from high elevation seed sources tended to be shortest (Figure 1). Trees from the highest elevation seed source (1173 m) were, on average, 43% shorter than trees from the two lowest elevation seed sources. Trees from seed sources at the 872 m and 597 m elevations were not significantly different from each other in height, but were significantly shorter than trees from low

elevation sources. Their average height was 12% shorter than trees from the two lowest elevation seed sources. Trees from the Victory seed source (366 m) were unusual in that they were on average 8% taller than trees from the two lower elevation seed sources. Differences in growth from 1987 through 1990 among seed sources were also highly significant. Relative amounts of growth and differences between seed sources followed the same pattern outlined for 1990 heights (Figure 2).

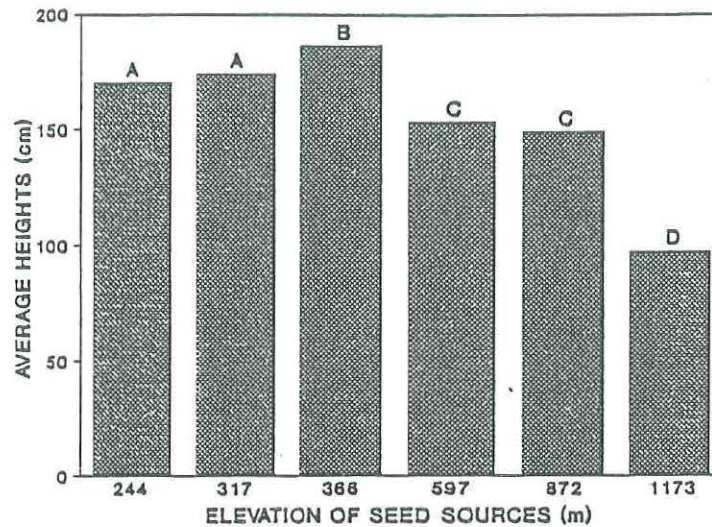


Figure 1.--1990 heights of balsam fir from 6 Vermont seed sources. Seed source means with the same letter are not different ($P \leq 0.05$) based on Duncan's Multiple range test.

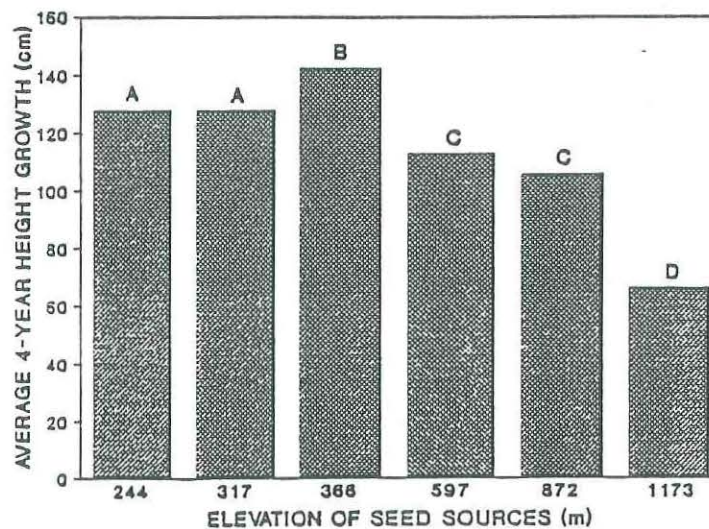


Figure 2.--Four-year height growth of balsam fir from 6 Vermont seed sources. Seed source means with the same letter are not different ($P \leq 0.05$) based on Duncan's Multiple range test.

A negative relationship between tree height and elevation has been noted for balsam fir in the White Mountains of New Hampshire (Reiners and Lang 1979). This relationship has also been observed for other conifers grown in common garden (Callaham and Liddicoet 1961, Conkle 1973, Rehfeldt 1986). In a greenhouse study of balsam fir seedlings from 5 different elevations on Mt. Moosilauke in New Hampshire, there was a significant negative correlation between seedling dry weight and seed source elevation (Fryer and Ledig 1972). In fact, in this last study, seedling dry weights followed a pattern similar to that for tree heights in our study; they first increased slightly with seed source elevation but decreased with elevation thereafter.

It is not surprising that trees from the highest elevation seed source are the shortest. A prominent characteristic of high elevation balsam fir within New England is its short stature and prostrate form. In fact, these trees are unique enough in a number of characteristics that some consider them to be a separate variety of fir called bracted balsam fir (Abies balsamea var. phanerolepis Fern.) (Bakuzis and Hansen 1965). There is also additional evidence that at least some of bracted balsam fir's growth habit is inherent. As part of a hybridization study among several North American firs, Hawley and DeHayes (1985a) found that after 24 weeks of growth in a controlled environment bracted balsam fir seedlings were significantly shorter than eastern balsam fir of the same age.

It is possible that the slightly shorter stature of fir from the 872 m and 597 m seed sources reflects some genetic mixing of balsam and bracted balsam fir. For example, in their study of certain cone and needle characteristics of fir on Mt. Washington in New Hampshire, Myers and Borman (1963) found forms resembling bracted fir at high elevations and forms resembling balsam fir at low elevations with a regular gradient of forms in between. However, Hawley and DeHayes (1985a) note that eastern balsam female parents do not appear to be fully crossable with bracted balsam males. They suggest that this incomplete compatibility may reflect a partial isolation mechanism responsible for the continued existence of these two varieties.

Differences among seed sources in the percent of current-year growth damaged by the balsam twig aphid in 1990 were highly significant. Although there were some significant differences in aphid damage among seed sources from lower and mid elevations (Figure 3), differences in the amount of damage were not great, and there was no consistent pattern of damage associated with the elevational origins of seed sources. In contrast, aphid damage on trees from the lower Mount Mansfield seed source (872 m) was considerably higher than that of trees from any other source. In fact, the average percent of foliage damaged on trees from this source was more than double the average of the two lowest elevation seed sources. Trees from the highest Mount Mansfield seed source (1173 m) had significantly more aphid damage than all sources except the 872 m source. Although damage on trees from the 1173 m seed source averaged 56% greater than damage on trees within the two lowest elevation seed sources, damage was still 25% less than the average damage on 872 m seed source trees. The correlation of seed source elevation with percent aphid damage was not significant (Table 2), suggesting an overall lack of linear association between these parameters.

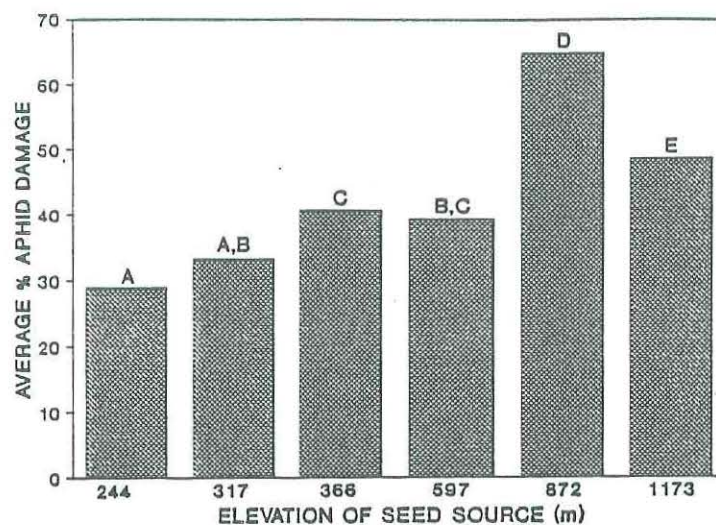


Figure 3.--1990 balsam twig aphid damage on balsam fir from 6 Vermont seed sources. Seed source means with the same letter are not different ($P \leq 0.05$) based on Duncan's Multiple range test.

Table 2. Correlations of seed source means in elevation, percent aphid damage (1990) and relative budbreak (1991).

Parameters correlated	Correlation coefficient ----(r)----
Seed Source Elevation and % Aphid Damage (1990)	.7497
Seed Source Elevation and Relative Budbreak (1991)	.9496**
% Aphid Damage (1990) and Relative Budbreak (1991)	.8868*

* Correlation coefficient significantly different from zero at the 5 percent level of probability.

** Correlation coefficient significantly different from zero at the 1 percent level of probability.

The relative timing of both twig aphid development and balsam fir shoot development is apparently important in determining the extent of visible damage on foliage. Although the balsam twig aphid's life cycle includes several stages, it is the sexupara stage which causes the majority of the visible feeding damage (Varty 1966). Although older needles and hardened shoots can be fed upon, visible damage results only from feeding on new growth prior to hardening (Schneski³). Maximum feeding damage would presumably occur when a large sexupara population developed in a balsam fir stand with many newly expanded shoots. Considering this, the relative timing of budbreak could be one factor influencing the amount of damage.

³ Schneski, Wm., unpublished report, Cornell University, Ithaca, NY.

Differences among seed sources in the relative timing of budbreak in 1991 were highly significant. Although there were significant differences in the timing of budbreak of trees from the two lowest elevations (Figure 4), the seed sources segregated into 3 groups which differ significantly in their relative timing of budbreak; a low elevation group (244 m and 317 m seed sources), a mid elevation group (368 m and 597 m seed sources) and a high elevation group (872 m and 1173 m seed sources). Despite the significant differences in the timing of budbreak between elevational groups, differences in terms of days were not large. For example, the average date of budbreak for trees from 244 m and 317 m seed sources was May 2 whereas the average date of budbreak for trees from the 872 m and 1173 m seed sources was May 9, a difference of just 7 days. The apparent positive relationship between seed source elevation and the relative timing of budbreak was supported by a highly significant correlation between these two variables (Table 2).

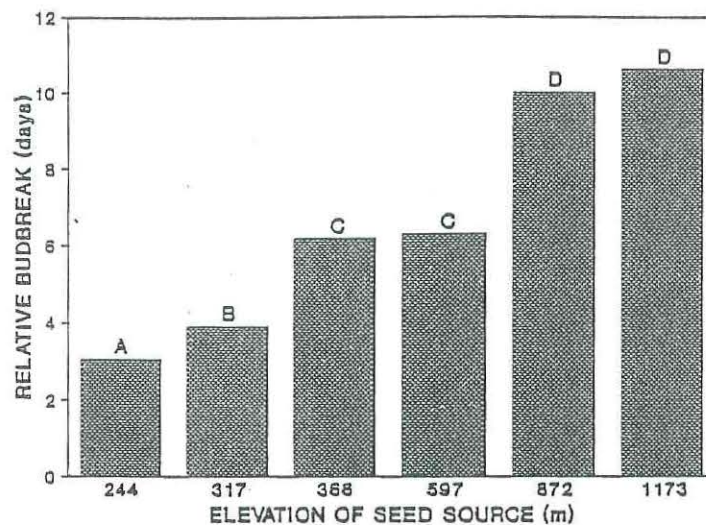


Figure 4.--1991 relative timing of budbreak among balsam fir from 6 Vermont seed sources. Seed source means with the same letter are not different ($P < 0.05$) based on Duncan's Multiple range test.

Correlation analysis was used as a first step in evaluating the possible relationship between the timing of budbreak and the extent of twig aphid damage. Seed source means of percent aphid damage (1990) and relative budbreak (1991) were significantly correlated (Table 2), however, the biological interpretation of this statistic is complicated by the fact that measurements of aphid damage and budbreak are from different years.

Budbreak is under strong genetic control in some conifers (Wilkinson 1977). In fact the relative timing of budbreak was one of the phenologic characteristics that Hawley and DeHayes (1985b) used to verify fir hybrids. Assuming that budbreak is under reasonably strong genetic control in balsam fir, then a relative measure of budbreak among balsam fir seed sources should not vary greatly from year to year. With this in mind, the significant positive correlation of budbreak timing with percent aphid damage would suggest that, on average, seed sources which broke bud later also experienced greater aphid damage in 1990. Although this may be a general trend, a notable

exception to this occurred with the two higher elevation seed sources (Figure 5). Although these seed sources did not differ significantly in their relative timing of budbreak, trees in these sources had substantially different levels of aphid damage.

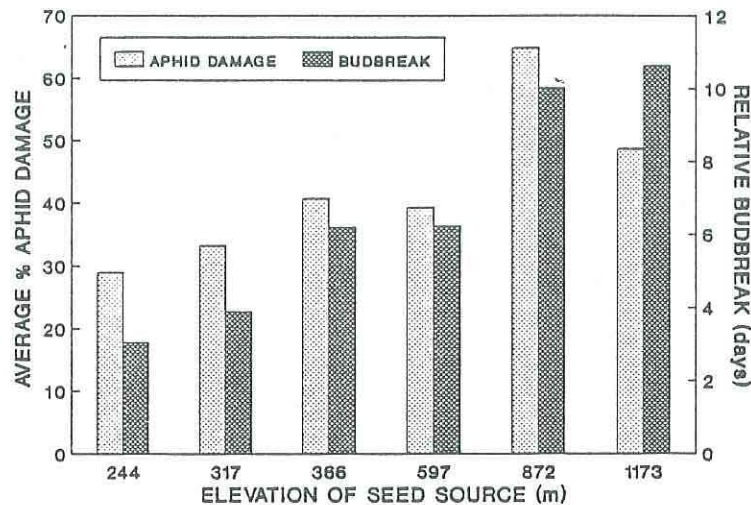


Figure 5.--Balsam twig aphid damage (1990) and relative budbreak (1991) for balsam fir from 6 Vermont seed sources.

For trees within individual seed sources, there was no consistent association between twig aphid damage (1990) and the relative timing of budbreak (1991) (Table 3). For trees within two seed sources (244 m and 597 m) there were significant positive correlations between percent aphid damage and budbreak, suggesting that within these sources trees that flushed later tended to be more heavily damaged by the balsam twig aphid in 1990. However, this apparent relationship did not exist for the other 4 seed sources examined.

Table 3. Correlations between percent aphid damage (1990) and relative budbreak (1991) among individual trees within each seed source and all seed sources combined.

Seed source elevation (m)	Correlation coefficient
	---r---
244	.349**
317	.144
366	.153
597	.220*
872	-.013
1173	-.028
All sources	.355**

* Correlation coefficient significantly different from zero at the 5 percent level of probability.

** Correlation coefficient significantly different from zero at the 1 percent level of probability.

Although differences in the relative timing of budbreak between seed sources may partially contribute to differences in aphid damage, data from the two highest elevation seed sources suggests that factors other than budbreak timing alone can greatly affect seed source susceptibility to damage. In a study of genetic variation in susceptibility of balsam fir to the balsam twig aphid, DeHayes (1981) noted that none of the traits he measured (including date of budbreak) conclusively explained variation in twig aphid susceptibility among the provenances studied. However, DeHayes (1981) suggested that certain monoterpenes (most notably B- phellandrene) may impart partial chemical resistance to twig aphid damage, but that conclusion was based on monoterpene data from the same provenances grown at another location. As part of an ongoing examination of the differential susceptibility of balsam fir to balsam twig aphid damage, we will conduct a quantitative survey of monoterpene concentrations in trees within the balsam fir plantation described in this paper. By relating ongoing measures of differential susceptibility to aphid damage with direct measures of monoterpene concentrations, a more direct understanding of any chemical resistance mechanism may be obtained.

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