SEED TRANSFER AND GENECOLOGY IN LONGLEAF PINE

R.C. Schmidtling and E.R. Sluder[1]

Abstract.--Twenty seed sources of longleaf pine *(Pinus palustris* Mill.) were grown in seven locations in Georgia and Florida for 25 years. The plantings and seed sources approximated a north-south transect of the entire species range through Georgia and Florida, with plantings and seed sources representing all physiographic provinces. Tree heights were related to latitude and climatic variables with polynomial regression models. The most important climatic variable associated with north-south variation was average annual minimum temperature at the seed source. Results of different plantings were combined by expressing growth as a percent deviation from the local source and by expressing temperature at the source as a deviation from that of the planting site. The combined analysis using minimum temperature difference between the seed source and the planting site and the square of this value accounted for 58.9% of the total variation. The regression equation predicts that moving seed sources northward from areas with minimum temperatures 3° F warmer (approximately 100 km in central Georgia) than the planting site results in the maximum gain in height over local sources. Moving seed sources northward more than 6° F results in less growth than that of the local source. Ecotypic differentiation did not appear to be an important factor in geographic variation.

Keywords: *Pinus palustris,* provenance, geographic variation

INTRODUCTION

The area of longleaf pine *(Pinus palustris* Mill.) in the Southern United States has declined from 12.2 to 3.8 million acres over the past 30 years (Kelly and Bechtold 1990). In many ways, longleaf is the most valued of the southern pines (Croker 1990), and there is now a concerted effort to restore longleaf to its historical and ecological prominence.

Restoration of longleaf pine will necessarily require a great deal of planting (or perhaps direct seeding). Choosing the proper seed source will be essential to ensure long-term success. It is necessary to define geographic variation in longleaf pine precisely to identify suitable seed sources for restoration planting.

The most effective way to measure the *range of genetic* variation *and limits* to *germplasm movement is to establish seed source studies or* provenance tests. Ideally, long-term experiments are established using seed collected from natural stands, sampling from the entire natural distribution of the species and planted in common gardens in many locations representing the

[1]Principal Geneticists, USDA Forest Service, Southern Research Station, Saucier, MS 39574 and Dry Branch, GA 31020

full range of climatic and edaphic variation. Growth of the trees is measured over a period of time, preferably to rotation age, since stress increases with age. Such provenance tests have been used for more than 200 years to examine geographic variation and genecology in forest tree species (Langlet 1971).

A major factor in the performance of a seed source in a particular location is the difference in climate between the planting site and the seed source. Seeds moved a modest distance northward often out-perform seeds from the local source (Wells and Wakeley 1966). If moved too far to the north, however, they suffer cold damage and do not perform as well as the local source. If moved to the south, they also do not perform as well as the local source. These results suggest a curvilinear relationship between growth and climatic differences between seed source and the planting location.

Differences in temperature are certainly important, and yearly average minimum temperature at the seed source was the best variable found to predict effects of seed transfer in loblolly pine *(Pinus taeda* L.) (Schmidtling 1994). In the present study, results of a provenance test established in Georgia and Florida were used to explore the genecology and to predict the effects of seed movement on the growth of longleaf pine.

MATERIALS AND METHODS

The study is unique in that intensive sampling was conducted on the entire north-south distribution of longleaf pine in Georgia and Florida (Fig. 1), as well as all the physiographic provinces where the species occurs. This test was established in 1970.

Plots representing single seed sources contained five rows of five trees at 2.5-m by 2.5-m spacing. These plots were replicated six times. Trees from 20 sources were planted at each site. Kraus and Sluder (1990) completely described the study. Climatic and other location data, in addition to those in Wells and Wakeley (1970), were obtained from USDA Forest Service (1969), USDA Agricultural Research Service (1990), and NOAA (1991).

In an initial examination, 15-year data from each of the seven plantings was reanalyzed separately. Mean heights and survival of the provenances were used as dependent variables. Independent variables included each seed source's latitude, mean temperature, yearly average minimum temperature, frost-free period, and the squares of these. The variables were included in step-wise multiple regressions to determine the most important variables. Overall, mean temperature and minimum temperature are probably the most useful, apparently because they integrate the effects of latitude, elevation, and maritime effects into a single variable. It also is important, however, to know what other variables are affecting growth.

In the spring of 1995, height and DBH were measured in four of the plantings (111 through 114), and DBH only was measured in the southernmost planting, number 115 (Figure 1). Plot volumes or basal areas were analyzed in the same manner as the 15-year data.

In the regression analysis of combined data, the percent survival and the percent deviation in height or volume from the local source were the dependent variables. Independent variables

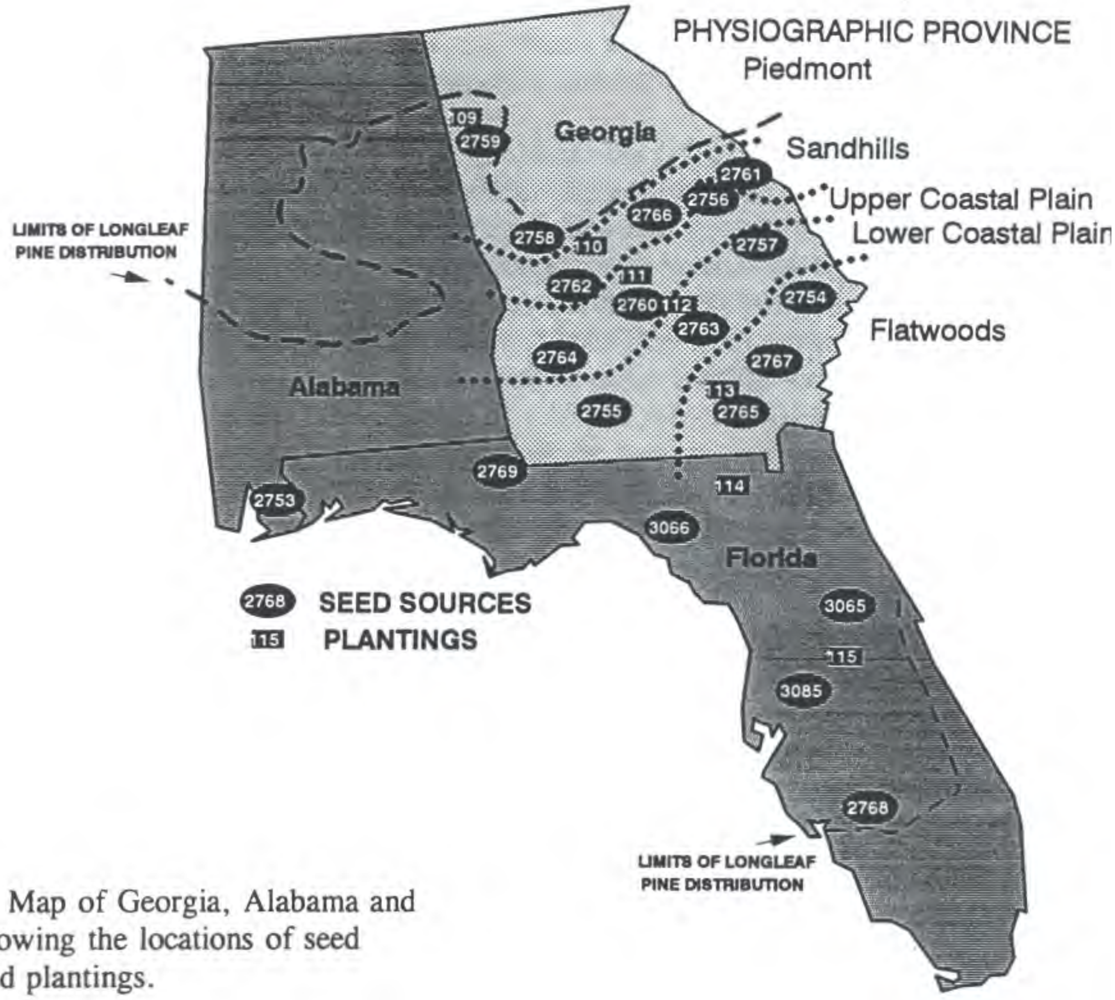

Figure 1. Map of Georgia, Alabama and Florida showing the locations of seed sources and plantings.

were the differences between the location and the seed source for latitude, minimum temperature, mean temperature, frost-free period and rainfall, and the squares and cross-products of these variables. Differences among physiographic provinces (Figure 1) were examined by plotting residuals from the regression models.

RESULTS AND DISCUSSION

In the original analysis of the study, there was a strong interaction between planting location and seed source (Kraus and Sluder 1990). Their analysis showed that the relative performance of the seed sources depended on the planting location. This result is common, and even expected, in seed source studies, and is evident when comparing height growth with temperature in Figures 2a-c.

Consistently, the best single predictor for height growth was average annual minimum temperatures at the seed source. In only one of seven plantings, planting 111 (Figure 1), was no relationship found between height and any independent variable. In the other six

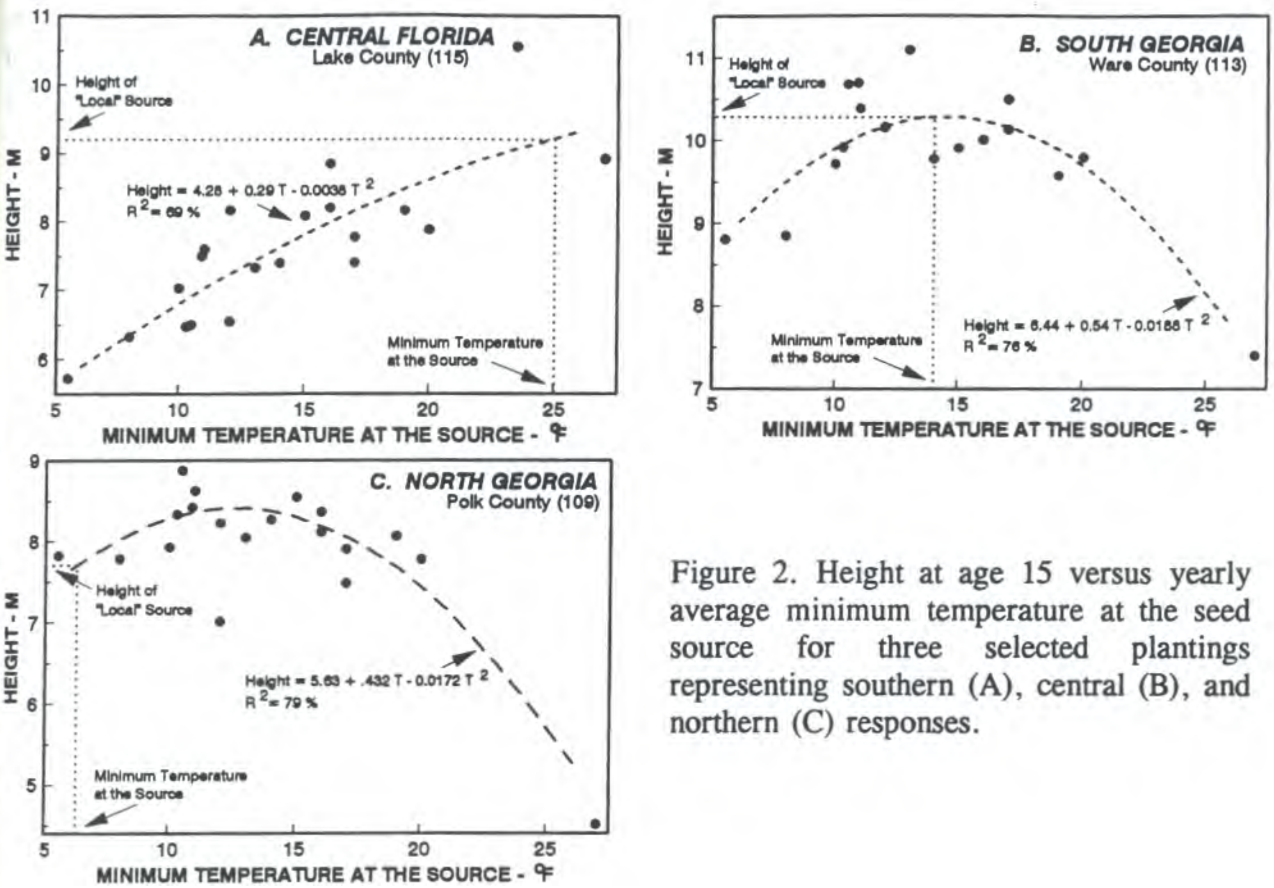

Figure 2. Height at age 15 versus yearly average minimum temperature at the seed source for three selected plantings representing southern (A), central (B), and northern (C) responses.

plantings, from 51 to 79 percent of the variation in height at age 15 years was explained by a quadratic relationship with minimum temperature at the seed source. Latitude, mean temperature, frost-free season, and the squares of these variables also were significantly related to height in individual analyses.

The relationship between height and minimum temperature at the source was nearly linear in the most southern planting (Figure 2a). The sources from areas with the highest minimum temperature, those from the southernmost collection points, were the tallest, up to 10.6 m, and those from area of the lowest minimum temperature averaged less than 6 m. The climate in this southern planting was not cold enough to adversely affect the growth of any source.

A curvilinear relationship between minimum temperature at the source and growth is apparent in a mid-latitude planting (Figure 2b). The linear regression with minimum temperature explained 36 percent of the variation in height; adding the square of minimum temperature improved the fit to 76 percent. The sources with the tallest trees at age 15 were those that were collected from areas with minimum temperatures somewhat above that of the planting location--those from south of the planting location. Seed sources from climates colder than the planting location, as well as those from climates much warmer than the planting location, did not grow as well as the local stock.

The curvilinear relationship also can be seen in a plot of height versus minimum temperatures in one of the northern plantings (Figure 2c). A linear fit with minimum temperature at the seed source explained 36 percent of the variation; addition of minimum temperature squared improved the fit to 79 percent. In this planting, the poor performance of sources from far south of the planting site is more evident than in the mid-latitude planting (Figure 2b).

Differences in site index present difficult problems in combining data from different locations (Matyas and Yeatman 1992). The approach used in the present study was to first express growth as a percent deviation from the local source, and then combining the data from the different plantings.

The definition of the "local source" is often problematical, and in this study, exact local sources do not exist for many of the plantings. There may be one or more sources from nearby areas that could be used. In this analysis, the height of the "local" source was determined by regression (Figure 2a-c). As Matyas and Yeatman (1992) have pointed out, the height of the local source is not known without error. Using a regression model to determine this height may result in less error than using any one particular source.

When combining studies from different locations, the differences in latitude, temperature, precipitation, etc., between the planting location and the seed source are probably more important than the absolute values of these variables. Giertych (1977) used "latitude displacement" to combine seed source data from several nurseries. In developing their seed transfer model in jack pine *(Pinus banksiana* Lamb.), Matyas and Yeatman (1992) used the difference in latitude and the difference in heat sums between the planting location and the seed source to define "ecological distance."

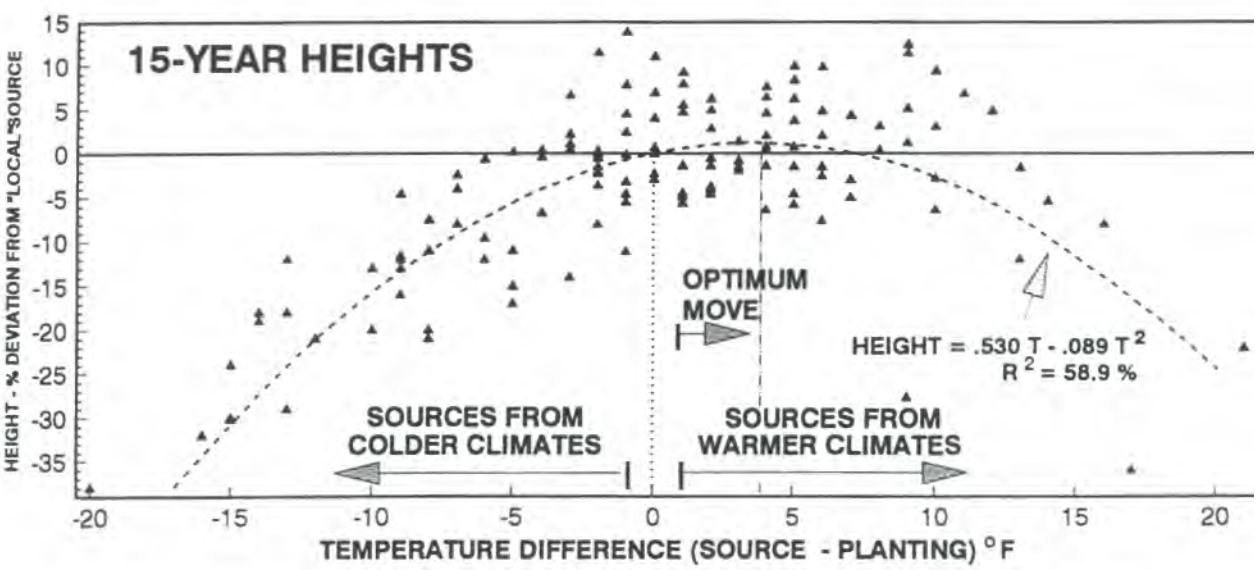

Figure 3. Height at age 15 versus minimum temperature for the combined data. On the vertical axis, heights are expressed as deviations from the local source. On the horizontal axis yearly average minimum temperatures are expressed as differences between the seed source minimum temperature and the planting location minimum temperature.

Minimum temperature difference and minimum temperature difference squared were the most important variables when the data from the seven plantings were combined (Figure 3). This combination accounted for 58 percent of the variation in height deviation from the local source. No other independent variables were significantly related to height deviation in the multiple regressions in this study, after effects of temperature were accounted for.

The analyses that are summarized in Figure 3 show that moving seed sources northward from areas with minimum temperatures of 3 °F warmer than the planting site result in the maximum gain over local sources. Moving seed sources southward or northward more than 6 °F results in less growth than that of the local source.

Survival at age 15 years varied significantly by seed source, but the seed source by planting interaction was minimal (Kraus and Sluder 1990). There was very little additional mortality in any of the measured plantings at age 25. In general, the sources from the coldest climates survived better. The sources from colder climates are adapted to colder winter temperatures and shorter growing seasons. Dormancy is longer and deeper, allowing them to survive adverse conditions. As a result of the shorter active growing season, they generally grow slower than sources from warmer climates. However, there is a tendency for lower than expected survival when northern sources are moved very far south. If survival is analyzed in the same manner as height, the combined data predicts that survival will be reduced if seed sources are moved from a warmer to a colder climate, and enhanced if seed sources are moved in the opposite direction (Fig. 4). For survival, the optimum movement is farther, and in the opposite direction as for height (Fig. 3).

Both height and survival are important components of plot volume (quantity of wood produced on a given area of land). Plot volume is often more variable than height because of large variation in early survival (Wells 1983). In regressions using the deviation in plot volume from the local source as the dependent variable, only 24 percent of the variation in plot volume was explained by minimum temperature and its square (Figure 5). Plot volumes for the "local" sources were determined by regression in a manner identical to those used for heights in Figure 2 and combined as in Figure 3.

As with heights, the most important independent variables in the step-wise regressions were mean annual minimum temperature deviation and its square. No other independent variables were significantly related to volume. The regression formula predicts a decrease in volume for any movement away from a mean annual minimum temperature different than that of the source (Figure 5). The volume data is undoubtedly biased by differences in early survival. With time, lower survival is compensated for by greater diameter growth of the surviving trees on poorly-;tocked plots, and self-thinning due to competition on the better-stocked plots. Little, if any, ;elf thinning has occurred in this study, and the relationship between volume and seed movement ;hown in Figure 5 may change with time. Analysis of 25-year volumes from the Southwide southern Pine Seed Source Study (Schmidtling 1994) showed a relationship similar to that found For height in Figure 3, that is, some gain in volume could be expected for a movement of seed ;ources from a warmer to a colder climate.

In the analysis of the 15-year data, effect of physiographic province of the seed source was not statistically significant (Kraus and Sluder 1990). Examination of residuals from the minimum-temperature model also failed to show any consistent seed source differences among physiographic provinces. There also were no consistent interactions between physiographic province of the seed source and planting site, e.g., the seed sources from the Piedmont did not grow or survive in the Piedmont significantly better than sources from the Sandhills, or vice-versa.

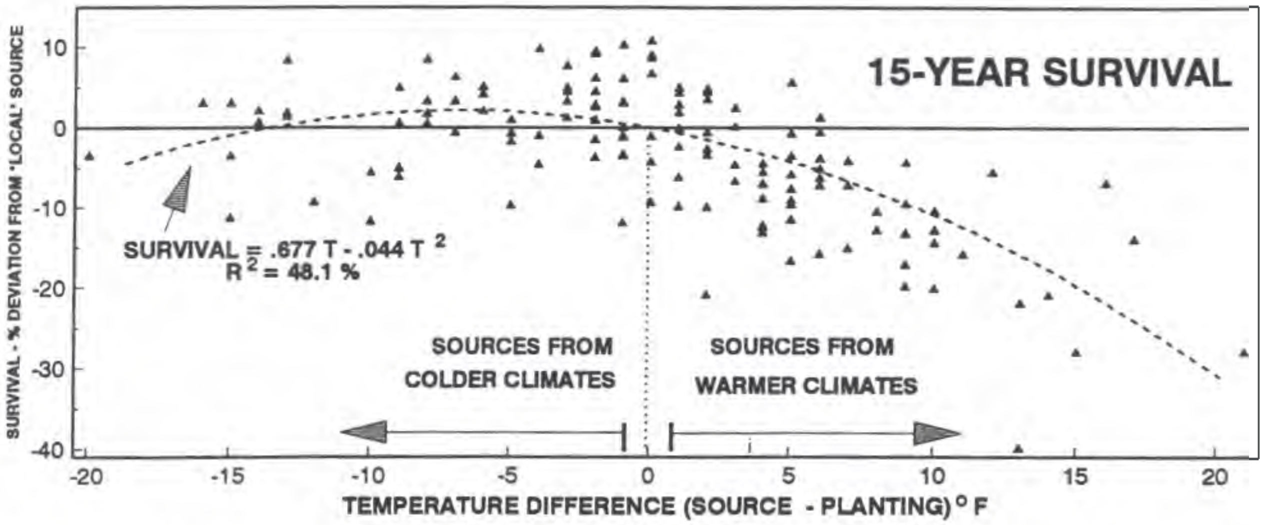

Figure 4. Survival at age 15 versus minimum temperature for all seven plantings combined. On the vertical axis, survival is expressed as deviations from the local source. On the horizontal axis, yearly average minimum temperatures are expressed as differences between the seed source minimum temperature and the planting location minimum temperature.

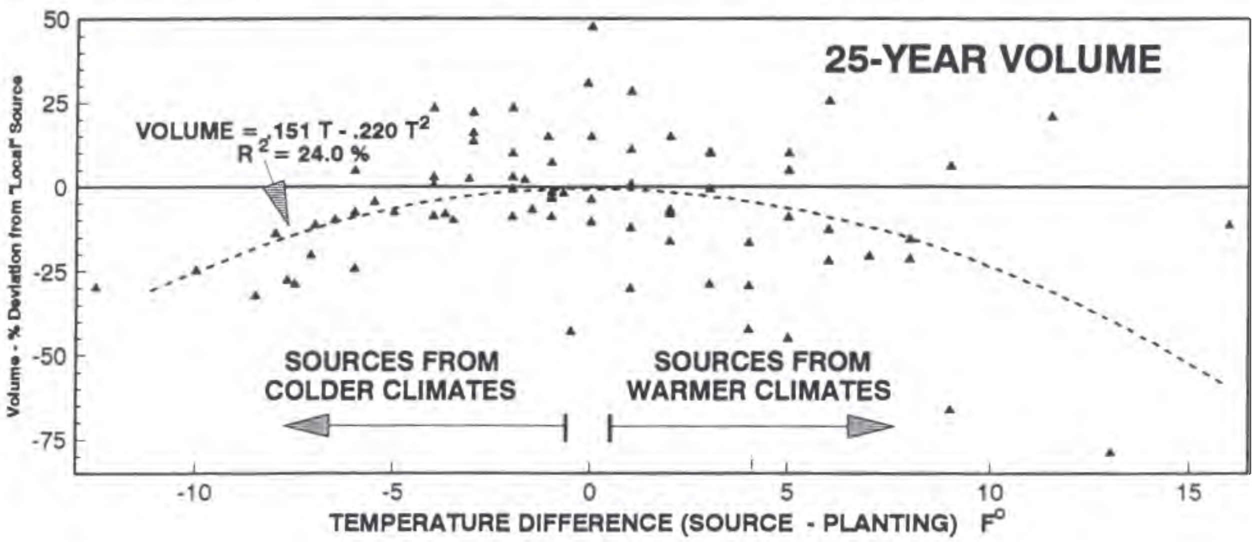

Figure 5. Volume at age 25 versus minimum temperature for plantings 111 through 114 combined. On the vertical axis, volumes is expressed as a deviation from the local source. On the horizontal axis yearly average minimum temperature is expressed as a difference between the seed source minimum temperature and the planting location minimum temperature.

CONCLUSIONS

Provenance tests are often analyzed planting by planting, to determine which seed source is best at a given planting location. That approach is a simple way to deal with the strong and complex interactions between seed source and planting site. The approach described here provides an overall picture. Growth variables are related to climatic factors at the seed source by regression. Performance in different plantings is combined by expressing growth as a percent deviation from the local source. Temperature or other climatic factors at the source are expressed as deviations from conditions of the planting site. The result is a general picture of the effects of seed transfer.

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