nances on sites where both were planted together (LIEGEL, 1983).

Conclusions

Good growth and performance of known *P. oocarpa* sources in 5- to 6-year-old CFI trials in Puerto Rico paralleled similar performance for fewer but unknown provenances used in adaptability trials a decade earlier. Even the poorest provenances averaged 1.0 m or better in mean annual height growth on diverse soils ranging from deep clays to sandy clay loams. Genetic variability of tested provenances appears high because good growth occurred on sites in Puerto Rico that are much lower in elevation and have two to three times more annual rainfall than do the seed origin sites. However, generalizations or implications about this variation for reforestation or tree improvement programs, locally or elsewhere, seem premature until additional data are collected and analyzed. Data from the Ivory Coast and Sri Lanka (OJO, 1978) indicated changes in overall rankings for top *P. oocarpa* performers between 0.5 and 4.0 years.

Although the three Nicaraguan sources and that from Mt. Pine Ridge grew best, more extensive testing is needed before embarking on a reforestation program. Quantitative wind damage data must be obtained from other countries to determine *P. oocarpa*'s species and provenance damage susceptibility levels more accurately, and to ascertain under what conditions severe damage occurs. Wider assessments of form and wood quality traits, such as specific gravity and fiber lengths, are needed for local *P. oocarpa* trials, now 9- to 10-years-old. Using new and existing data, juvenile-to-mature correlations will be possible for all provenances regarding overall growth performance, growth traits and form, wood quality, and wind damage susceptibility.

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Seedling Growth Variation Among Rocky Mountain Populations of Lodgepole Pine

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(Received 16th March 1984)

Summary

One-hundred fifty-three lodgepole pine trees *(Pinus contorta* var. *latifolia)* from 34 natural populations representative of the latitudinal and elevational range of the species in Montana, Wyoming and Colorado supplied seedlings for a provenance test in Colorado. Growth models were developed for each population based on periodic height growth through the 1982 growing season. Results revealed clinal latitudinal effects of seed source on growth patterning, but the effect of elevational differences was unclear. Progeny from southern seed sources started growth earliest, had a gradual increase in growth rate, and then a gradual decrease in growth rate to the end of the season. Progeny from high latitude sources grew slowly at first, had a rapid increase in growth rate at mid season, and had the greatest overall incremental growth for the season. No sharp distinctions between the populations were evident from the growth models. Rather, the models described a gradual change in character along a latitudinal gradient.

Key words: geographic variation, lodgepole pine, phenology, seedling growth.

Zusammenfassung

153 Einzelbäume von *Pinus contorta* var. *latifolia* aus 34 natürlichen Populationen, die nach Breitengrad- und Höhenlage für das Verbreitungsgebiet der Art in Montana, Wyoming und Colorado repräsentativ sind, lieferten die Sämlinge für einen Herkunftsversuch in Colorado. Für jede Population wurden auf der Basis des periodischen Höhenwachstums während der Vegetationsperiode 1982 Wachstumsmodelle entwickelt. Die Ergebnisse zeigten, auf den Breitengrad der Herkunft bezogen, klinale Effekte im Wachstumsmuster; der Effekt der Höhenunterschiede war jedoch unklar. Nachkommenschaften aus südlichen Herkunftsgebieten begannen mit dem Wachstum am frühesten. Sie zeigten einen graduellen Anstieg in der Wachstumsrate und dann zum Ende der Vegetationsperiode hin einen graduellen Rückgang der Wachstumsrate. Nachkommenschaften von Herkünften höherer geographischer Breite wuchsen zunächst langsam, wiesen jedoch zur Mitte der Vegetationsperiode hin einen rapiden Anstieg in der Wachstumsrate auf und hatten den größten Gesamtzuwachs in der Vegetationszeit. Zwischen den Populationen war keine scharfe Unterscheidung bei den Wachstumsmodellen zu erkennen. Die Modelle beschrieben vielmehr einen graduellen Wechsel der Merkmale entlang eines auf den Breitengrad bezogenen Gradienten.

Introduction

Lodgepole pine *(Pinus contorta* Doug.) has one of the widest ranges of any coniferous tree species in North America. The species' natural distribution spans 32° of latitude, from 31° North in the southern Sierra Nevada mountains to 63° North in the Yukon, and it grows from sea level on the Pacific coast to 3350 meters elevation in the Colorado Rockies (Critchfield, 1980; Critchfield and Little, 1966). Studies of geographic variation in morphology and growth-related traits suggest that sufficient differentiation has occurred to enable recognition of several subspecific divisions of lodgepole pine (Critchfield, 1980). Of these divisions, the Rocky Mountain-Intermountain race *(P. contorta* var. *latifolia* Engelm.) is the most widely distributed and is found in most western North American mountains.

Provenance variation studies with lodgepole pine of Rocky Mountain origin have emphasized Canadian and northern United States populations. Many of these past studies have revealed clinal variation along latitudinal and elevational gradients for traits related to growth and phenology (Illingworth, 1975; Rehfeldt and Wycoff, 1981; Sweet and Waring, 1968). In British Columbia, provenance research shows that seed sources from low elevations and low latitudes grow for a longer period of time than high elevation and high latitude seed sources (Illingworth, 1975). Cannell's (1974) analysis shows that leader growth of lodgepole pine often decreases with an increase in the origin of seed source's latitude or elevation. This trend reflects adaptive differences in the several shoot and needle meristems responsible for such growth. Rehfeldt and Wycoff's greenhouse study (1981) of growth periodicity in northern Rocky Mountain populations of lodgepole pine concludes that, compared to seedlings from higher elevation provenances, those from lower elevation populations elongate more, cease elongation later, and produce greater shoot growth per day during the period of greatest growth rate.

Many past studies show a great deal of interpopulation variation in growth-related traits of lodgepole pine. This is not unexpected for a species of such extensive latitudinal range (Vaartaja, 1959). But, few studies have included provenances representative of lodgepole pine distribution in the central Rocky Mountains. The current study reports on provenance variation in seedling terminal shoot growth in a plantation of three-year-old trees. The provenances included in the study represent the latitudinal and elevational ranges of lodgepole pine in Montana, Wyoming, and Colorado.

Materials and Methods

In the late summer and early autumn of 1979, I selected 153 individual trees from 34 natural populations for inclusion in a study of the geographic variation of lodgepole pine in the central Rocky Mountains (Moore, 1981). To adequately represent the variability of lodgepole pine in this region, population sampling occurred along latitudinal and elevational gradients. From La Veta Pass, Colorado north to Marias Pass, Montana, I collected several groups of population samples with the groups separated by roughly one degree of latitude. Up to three population samples appeared in each group, and the samples represented the low, mid, and high elevation where lodgepole pine occurred in a given area. Five trees normally made up an individual population sample *(Figure 1).*

In the spring of 1980 I greenhouse-sowed seed from each of the 153 single-tree collections. The resulting seedlings were transferred to lathehouse conditions that summer and remained there until outplanting in spring of 1981.

The study site is in the Colorado State Forest approximately three miles northeast of Gould, Colorado. This location corresponds to 106° 00' W longitude, 40° 34' N latitude, at an elevation of 2868 meters. The plantation site is characterized by summer temperatures of 5° C to 18° C and winter temperatures of −3° C to 1° C with about 56 cm annual precipitation. The soils in the area are predominantly light-colored, well-drained, acidic, Gray Wooded soils (Johnson and Cline, 1965).

The plantation consists of a completely randomized block with three replications of wind-pollinated progeny for each seed parent. Some mortality did occur after planting (summer, 1981), and replacement seedlings were established as available. No further replacement planting occurred after the 1981 growing season.

Height measurements began on June 30, 1982 and continued on a generally weekly basis throughout the growing season. The height data provided the basis for development of growth models for each of the 34 natural populations represented in the plantation. The basic regression model which describes growth over a growing season is (Rehfeldt and Wycoff, 1981):

$$LN\,(1/Y-1) = -a + b(c/X),$$

where

Y = amount of growth at a given time relative to the total amount of growth in the season.

X = time period; days after January 1, 1982

a, b, and c = coefficient for regression.

The major question addressed by this study is whether or not a difference exists among the 34 populations on the basis of the growth models. Analyses of variance provide some insight into the question, and multiple linear regression techniques reveal how much of the variability in seedling growth the latitude and elevation of the parent tree seed sources might explain.

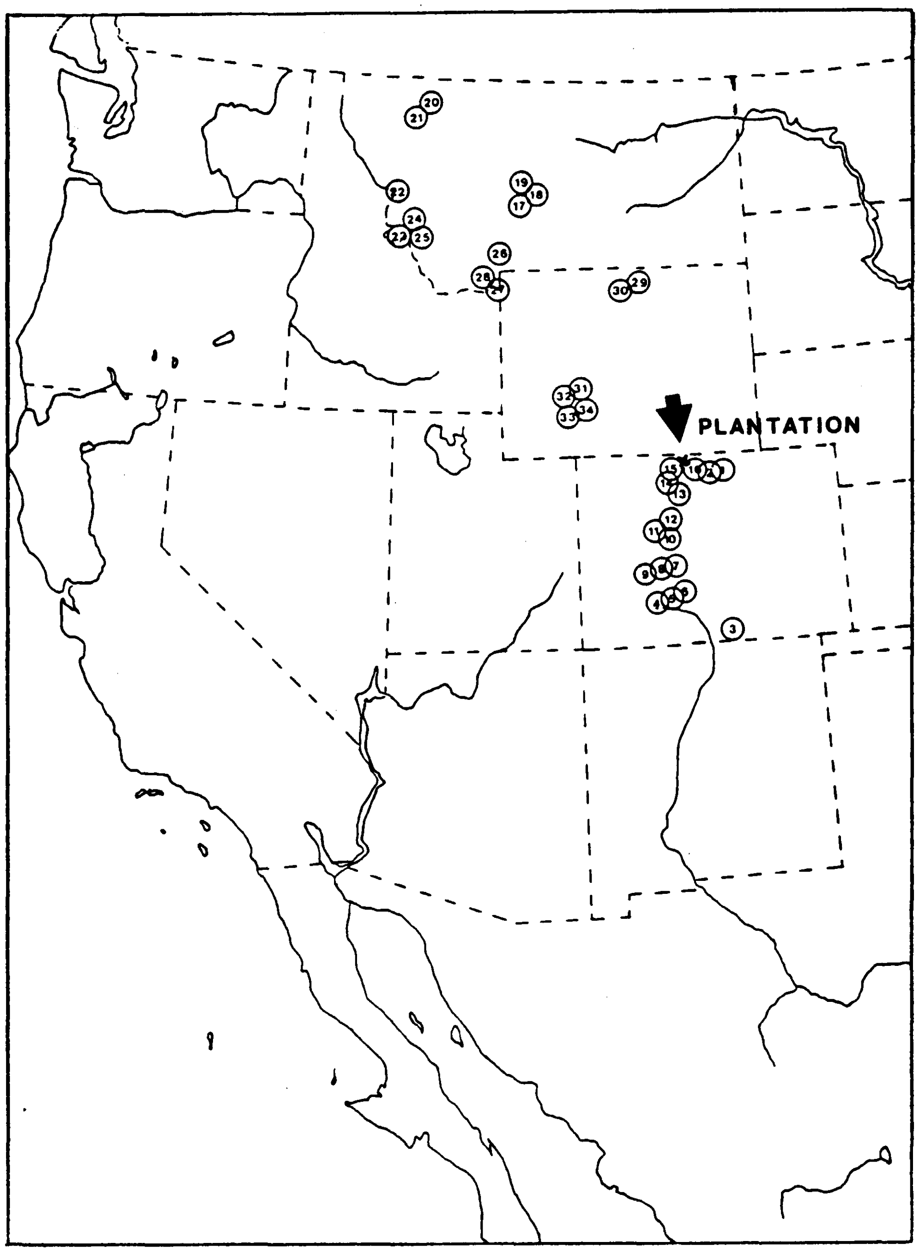

Figure 1. — Location of the 34 natural population samples and of the provenance test plantation site.

Results

Total terminal shoot growth ranged from 2.3—6.6 cm for populations 19 and 22, with a mean value over all populations of 4.4 cm *(Table 1)*. Given the range of 4.6 cm in the amount of growth attained by the progeny of the 34 populations, analyses of variance do not indicate statistically significant differences among the populations on the basis of amount of terminal shoot growth over the growing season. Evidently, substantial variability exists within the populations, masking between-population differences.

Next, I developed growth models for each of the populations with the regression techniques discussed above. Describing these models graphically revealed some interesting patterns. *Figures 2, 3,* and *4* illustrate the modelled growth patterns for several of the 34 populations. While these figures typify all populations, they specifically depict the growth patterns of seedlings from natural populations at several elevations in the southernmost, middle and northernmost latitudes studied, respectively.

The graphs show a gradual transition from an elongated, gradual "S" shape for the southerly populations to a more distinct and abrupt "S" for the northerly sources. In other words, southern populations start noticeable terminal shoot growth early in the season, slowly increase their growth rate, and slowly stop growing. The northern sources begin noticeable shoot growth later in the season and then rapidly increase growth before tapering off. Mid-latitude sources fall somewhere in between. Furthermore, it seems the populations begin to decrease their growth rates at about the same time, regardless of the total amount of growth. No consistent pattern related to elevation of seed sources within similar latitudinal locations is evident.

Table 1. — Mean total shoot elongation for the 34 populations of lodgepole pine.

Population	Latitude (°North)	Longitude (°West)	Elevation (Meters)	Total Mean Increment (CM)
1	40.6	105.4	2378	5.2
2	40.6	105.5	2588	3.9
3	37.6	105.2	2805	5.1
4	38.4	105.4	2744	4.0
5	38.5	105.4	3049	5.3
6	38.5	106.3	3338	4.5
7	38.8	106.3	3003	3.8
8	38.8	106.4	3079	4.1
9	38.8	106.4	3506	3.7
10	39.4	106.3	3178	4.3
11	39.4	106.3	3201	4.3
12	39.5	106.4	2652	3.5
13	40.3	106.1	2652	4.1
14	40.4	106.1	2835	5.3
15	40.4	106.1	2683	4.6
16	40.6	105.5	2805	4.0
17	46.8	110.8	1875	4.7
18	46.8	110.7	2165	4.5
19	47.0	110.8	1561	2.3
20	48.3	113.4	1555	4.7
21	48.3	113.4	1524	5.0
22	46.7	114.5	1372	6.6
23	45.7	114.0	2134	4.0
24	45.7	114.0	2210	5.3
25	45.7	113.9	1951	4.8
26	45.4	111.2	1783	5.4
27	44.8	111.2	2012	4.1
28	44.9	111.4	2287	4.7
29	44.8	107.4	2287	4.0
30	44.8	107.5	2591	2.9
31	42.7	108.9	2439	4.7
32	42.7	108.9	2591	3.4
33	42.7	108.9	2920	6.2
34	42.6	108.8	2668	3.7
Plantation Mean				4.4
Standard Deviation				3.0

To test whether or not the latitudes and elevations of the populations could explain the variation in amount of growth between the several measurement dates, I performed multiple regression analyses (*Table 2*). The multiple regression correlation coefficients suggest that very little of the variability in the amount of growth between measurements, as well as the amount of growth for the entire season, is explained by the model including latitude and elevation as independent variables. However, the regression of latitude and elevation on seedling growth is

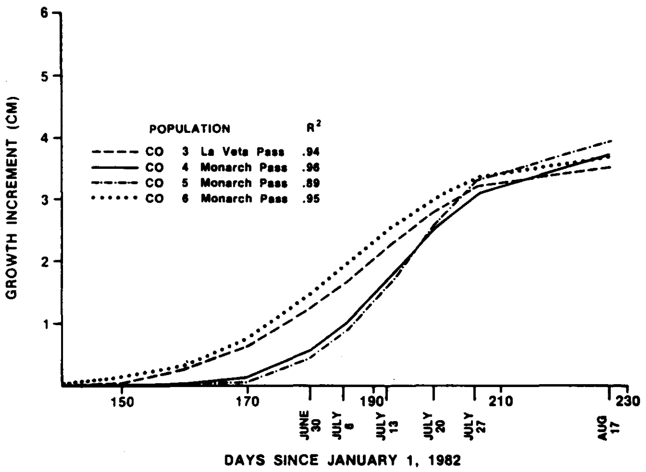

Figure 2. — Graphical representations of growth models of southern Colorado populations. R^2 values for this and subsequent figures indicate the percentage of variability in growth measurements explained by the model for any given population.

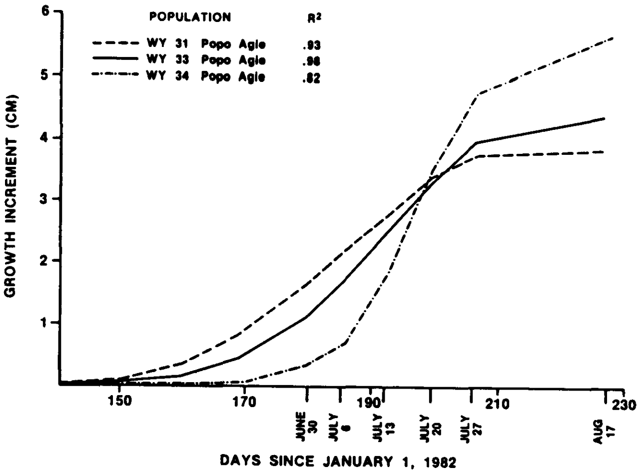

Figure 3. — Graphical representations of growth models of southern Wyoming populations.

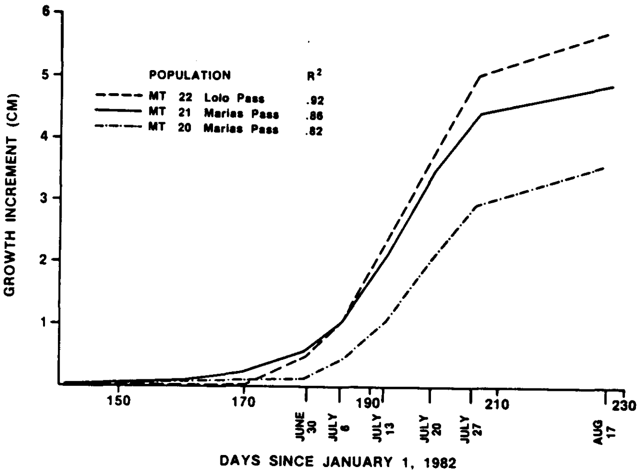

Figure 4. — Graphical representations of growth models of northern Montana populations.

Table 2. — Regression analysis relating amount of incremental shoot growth between measurement dates to the independent variables of latitude and elevation of seed source origin.

Growth Period	Mean Response (CM)	Regression Coefficients: Constant	Latitude	Elevation	R^2
1/1/82-6/30/82	0.6	3.06	-0.059	0.00002	0.01
6/30/82-7/6/82	0.2	2.96	-0.038	-0.00046	0.02*
7/6/82-7/13/82	0.5	3.85	-0.054	-0.00044	0.01
7/13/82-7/20/82	0.5	2.11	-0.024	-0.00023	0.01
7/20/82-7/27/82	0.2	0.13	0.007	-0.00008	0.01
7/27/82-8/17/82	0.3	-3.03	0.060	0.00033	0.01
Season	4.4	11.07	-0.107	-0.00085	0.01

significant ($P < 0.05$) between June 30 and July 6, the period between the first two measurements of the growing season. Evidently, for the progeny of the Gould plantation during the 1982 season, latitude and elevation of the parent seed source differentially affected growth only early in the season.

Discussion

Experiments can show that seedlings from provenances of varying geographic origin often display characteristic patterns of shoot growth when grown under common environmental conditions (DORMLING, 1979; REHFELDT and WYCOFF, 1981; SORENSEN, 1979). However, what is not always easy to show is that such differences reflect genetically based adaptations to, presumably, the environment of the parent seed source origin. In fact, the analysis of variation in growth-related traits of some species may indicate that adaptive differentiation into distinct populations may not be as successful a strategy as phenotypic (including phenological) plasticity (REHFELDT, 1979). Nevertheless, evidence from past studies supports the view that tree populations develop adaptations that synchronize phenology with the annual environmental changes determining growth season characteristics (HESLOP-HARRISON, 1964).

Temperature and photoperiod are two critical factors associated with annual cycles which probably exert strong selective pressure on tree populations (CAMPBELL and SORENSEN, 1978). While photoperiod differences between seed source origins included in the present study can be envisioned to change gradually from north to south, the temperature factor could vary dramatically over short distances. In general, as one goes higher in elevation in the central Rockies, temperatures decrease. But the abrupt topography of this area can create a myriad of micro-climates that can mask the general trend.

Other environmental factors which can change dramatically over short distances in the Rocky Mountains include: soil moisture and temperature; precipitation types, timing, and amounts; and precipitation/evaporation ratios. In light of the changeable and often unpredictable conditions associated with elevational changes in the central Rockies, the lack of a discernable trend in differential growth of the seedlings in this study related to the elevation of the seedling's origin is not entirely unexpected. Another study, however, implicates elevation of seed origin as a good predictor of seedling growth periodicity (REHFELDT and WYCOFF, 1981).

The analyses used in this study do not support the case for significant differences in growth between populations of lodgepole pine from different latitudes when planted in a common plantation about midway between the extremes of the sampled latitudinal range. But, a gradual change in the shape of growth models typifying the populations is evident. This change suggests clinal variation in growth in a latitudinal context. Furthermore, the generalizations that southern seed sources, when compared to northern sources of the same species, grow faster, break bud later in the spring, and grow later into the fall (WRIGHT, 1976) are not substantiated here.

Overall, a great deal of variation in growth characteristics is seen for the seedlings of the Gould plantation. Very little of that variation can be explained by the latitude or elevation of seed source origin, alone. However, the lack of great differences among the populations may be an indication of phenotypic plasticity of lodgepole pine. Such plasticity would be of adaptive value in the heterogeneous environments of the species' range in the central Rocky Mountains.

Subsequent evaluations of the trees at Gould, as well as other plantings of similar material, should help to quantitatively and qualitatively characterize the genetic structure of lodgepole pine in the central Rocky Mountains, and allow for more informed management decisions concerning the growth of lodgepole pine in this region.

Acknowledgement

This study was partially supported through the cooperation of the Colorado State Forest Service and the Department of Forest and Wood Sciences, Colorado State University, Fort Collins, Colorado 80523.

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