Variation in Distribution of Assimilate among Plant Parts in Three Populations of Populus deltoides

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Abstract

Cloned seedlings of three populations ob Populus *deltoides* BARTR. ex MARSH. from Wisconsin, Illinois, and Louisiana were grown outdoors at Urbana, Illinois and sampled periodically over the first growing season for differences in dry matter distribution to root, stem, and leaves. Allometric analysis of the data indicated little genotypic variation in relative rate of shoot growth compaxed to root growth. However, the Wisconsin population had a greater proportion of dry matter allocated to stem growth than the other two and grew taller. This was associated with a higher specific leaf area in the Wisconsin plants. By producing thinner leaves, seedlings of this source are able to have more leaf area for the same amount of leaf biomass. Enhanced food production results in more photosynthate being allocated to stem growth.

Net photosynthesis and transpiration for the Wisconsin and Illinois populations measured over a range of light intensities revealed no differences in light saturated carbon fixation, but greater rates of water loss for the Wisconsin seedlings. Wisconsin plants with their thinner leaves had a lower water use efficiency than plants of the Illinois population. Although the Wisconsin seedlings show superior early height growth potential this advantage is not maintained in older plantations.

Key words: Populus, Photosynthesis, Transpiration, Resource allocation, Allometric analysis, Biomass, Ecotype, Growth.

Zusammenfassung

Aus Sämlingen hervorgegangene Stecklingsklone von Populus deltoides aus 3 Herkunftsgebieten in Wisconsin, Illinois und Louisiana wurden in Urbana (Illinois) versuchsmäßig angebaut und dort in Abständen auf den Trockensubstanzgehalt der Wurzel, des Stammes und der Blätter hin untersucht.

Die Klone aus Wisconsin zeigten gegenüber denjenigen aus Illinois und Louisiana einen proportional größeren Anteil an Trockenmasse im Stamm. Die Blätter dieser Pflanzen waren zugleich dünner und hatten eine größere Oberfläche, wobei jedoch im Vergleich zu den Klonen aus Illinois und Louisiana eine geringere Waseraufnahmefähigkeit beobachtet wurde.

Introduction

Eastern cottonwood (Populus deltoides BARTR.) ranges over much of the east and midwestern United States occurring typically in bottomlands along streams and river valleys (FOWELLS, 1965). Because of rapid growth rate and ease of vegetative propagation the species has become commercially important particularly in the southern United States along the Mississippi River valley. Cottonwood plantations have been established to provide high quality wood pulp for the paper industry as well as sawlogs and veneer. The high degree of genetic variability and good hybridizing qualities of cottonwood make it a potentially useful species on which to focus efforts in breeding and tree improvement.

Racial variation in phenology (PAULEY and PERRY, 1954; ROCKWOOD, 1968; ELDRIDGE et al., 1972), bark thickness, branching habit, height, and diameter growth (YING, 1974; YING and BAGLEY, 1976), and leaf morphology (MARCET, 1961; YING and BAGLEY, 1976) is well documented in the species. We have examined populations of P. deltoides ranging over the north-south distribution of the species along the Mississippi River in an effort to identify further sources of variability in phenology and growth rate. Our attention has focused on proportionate distribution of photosynthate between plant organs and associated changes in rates of distribution over time. Population differences in allocative growth may be either clinal or ecotypic. When expressed mathematically as parameters of growth equations, differences in growth allocation of populations provide useful input for general models (LEDIG, 1969; PROMNITZ, 1975) or as a basis for selection of superior phenotypes in tree improvement work. HUXLEY (1924) was the first to study allometry, or the relative growth rates of different plant parts. Using the allometric equation, log Shoot Dry Weight = a + B log Root Dry Weight, the relative growth of shoot versus root systems becomes comparable. The allometric coefficient, B, expresses this balance as a constant relative growth rate.

Recent attempts have been made to assess the relative growth rates of shoot and root in provenances of Populus *trichocarpa*, Picea sitchensis, and Pinus contorta (CANNELL and WILLETT, 1976), and in different sources of Pinus taeda (LEDIG and PERRY, 1965; DREW and LEDIG, 1975). These studies indicate that little genotypic variation in relative shoot/root growth is present, and that the allometric coefficient for shoot and root growth is unusually stable, even over successive years. Techniques of allometric analysis have been employed to further knowledge of assimilate distribution in populations of Populus deltoides.

Materials and Methods

In early March of 1976, one-year-old branches were removed from selected individuals of P. deltoides in a 6-year-old Urbana plantation (North Central Regional Project, NC-99) and cut into 18 cm sections excluding terminal portions. The cuttings represented three populations along a latitudinal gradient, viz., Diamond Bluff, Wisconsin (45°), Fulton, Illinois (42°), and Baton Rouge, Louisiana (31°). Each cutting was weighed, labeled, and stored in the dark at 4° C until late April when placed outdoors. Just prior to insertion of each cutting into soil in 22 cm diameter and 20 cm deep clay pots, all the buds except the most distal were removed. The cutting was then inserted as deeply as possible in a soil mixture of 3 parts loam, 1 part sand, 1 part peat moss, and 1 part "Perlite" leaving the one bud exposed, and watered daily.

Each pot had a cork placed in its basal hole to prevent root loss. The pots were sunk into soil to ground level in a randomized design out-of-doors in Urbana, Illinois. A separate sample representing the northern Illinois source was oven dried, weighed, and a regression established which was later used to predict cutting dry weight from fresh or wet weight.

A week after setting cuttings, buds began to open. When new shoots were about 40 cm long, a sample of from 5 to 8 plants was randomly selected for dry weight analysis, and continued at three week intervals into September when supply of plants ran out and abscission began in the Wisconsin provenance. Due to staggered rates of shoot development and differences in numbers of developing cuttings, plants from Wisconsin were sampled five times, those from Illinois four times, and the Louisiana source only three times for a total of 40, 26, and 16 plants per source, respectively. These data are presented as a mean for each sampling date.

Additionally, a sample of six plants from each provenance was selected for studies of photosynthetic response to temperature which is to be reported later. These plants were sampled weekly for height growth and in late September the plants from Illinois and Lousiana were harvested and included along with plants from regular harvests in studies of assimilate distribution. A few very small plants from the latter were deleted.

Photosynthetic response to light intensity (photosynthetically active radation) was also measured simultaneously with transpiration for seedlings of the Wisconsin and Illinois populations to determine if any differences in photosynthetic rate or water use efficiency existed. Louisiana seedlings were not measured as this work was done during a second year when severe winter injury inhibited rooting of the southern source.

All plants harvested were sampled for leaf, stem with petioles, original cutting, and root dry weight as well as total leaf area and plant height. By regression equation, original as well as final ramet wet weights were converted to dry weights, and the difference due to growth added onto stem dry weight.

Logarithmic regressions of shoot, leaf, and stem dry weight on root dry weight were developed for each of the three sources. In this manner, relative rates of growth of plant organs may be compared. Allometry (Huxley, 1924) allows for quantitative expression of the asymptotic decline in shoot relative to root growth experienced by many tree seedlings over their first year of growth (Ledig *et al.*, 1970; Drew and Ferrell, 1977). The allometric equation, log Shoot Dry Weight = a + B log Root Dry Weight expresses this change through B, the allometric coefficient. When B is less than 1.0, the rate of shoot growth is less relative to rate of root growth, and when greater than 1.0, the opposite trend in ontogeny occurs. The same trend is further examined through analysis of leaf and stem growth relative to root growth.

Results

Bud burst in the Wisconsin source, centered around May 5, preceded that of the Illinois source by two days and that of the Louisiana source by three days. The first leaves to emerge, having been preformed in winter buds, are small in size. In this study there was a growth cessation immediately following their emergence which persisted for a month or more prior to vigorous shoot development. During this time, presumably, roots were being formed on ramets. Success of rooting varied among the populations. Some ramets never rooted. The Wisconsin population had 90 percent rooting success followed by 60 percent for Illinois and only 40 percent for the Louisiana source. Finally, by late June when the Wisconsin plants were about 40 cm tall, the first plants were harvested *(Fig. 1)*. Rapid early growth in June and July occurred in the Wisconsin and Illinois plants whereas the Louisiana plants surged later and over a longer period throughout July and August. Total height was greatest in the Wisconsin source. Bud set and cessation of shoot growth occurred in late July in both Wisconsin and Illinois plants, but not until early September in the Louisiana source. Plants of the Wisconsin population showed yellowing of lower leaves in late August leading to abscission in September.

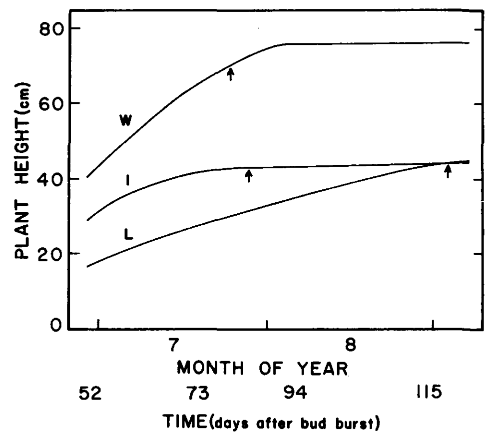

Figure 1. — Increase in seedling height (cm) over the study period based on mean of six plants each for populations from Wisconsin (W), Illinois (I), and Louisiana (L) measured weekly.

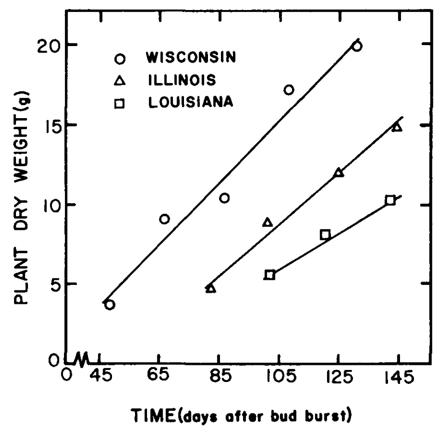

Figure 2. — Regressions of plant dry weight (g) on time after bud burst for three populations of *Populus deltoides* Bartr. Mean dry weight for 5—8 seedlings per sample are shown.

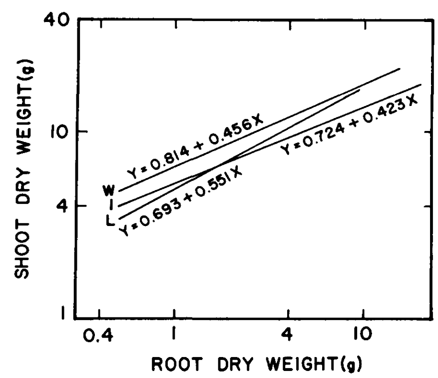

Figure 3. — Regressions of shoot on root dry weight (g) for three populations of *Populus deltoides* Bartr. from Wisconsin (W), Illinois (I), and Louisiana (L).

Differences in timing of height growth of the sources were also reflected in total dry weight *(Fig. 2)*. Regression analysis of rates of dry weight increase for the three populations revealed no differences although variability in size at each harvest time was large.

Allometric analysis of shoot and root development revealed similar rates for the three populations *(Fig. 3)*. Allometric coefficients although not significantly different ranged from 0.551 for Louisiana plants to 0.423 for Illinois plants with Wisconsin plants intermediate. However, statistically significant differences in intercept of the allometric equation were found.

The intercept, a, for the Wisconsin population, 0.814, differed from that of the Illinois population, viz., 0.724, at the 1 percent level. Intercepts of Wisconsin and Louisiana populations differed at the 5 percent level. Plants of the Wisconsin population were therefore allocating more dry matter to shoot growth relative to root growth than the more southerly populations, but the rate of relative growth as evidenced by allometric coefficients, B, was not different for the three.

A further breakdown of shoot development showed that it was not increased dry matter allocation to leaf growth that was responsible for higher shoot/root ratios in the Wisconsin population *(Fig. 4)*, but rather increased allocation to stem growth *(Fig. 5)*. The intercept, 0.539, for Wisconsin differed from 0.363 for Illinois and from 0.354 for Louisiana (not shown) at the 1 percent level.

Although leaf biomass was proportionally the same for all three sources, the ratio of leaf area to weight, specific leaf area, was greater in the Wisconsin population than in either of the other two *(Fig. 6)*. Specific leaf area declined over the growing season in all three sources, but its greater magnitude in the most northerly population reflected thinner leaves in that source. The implication is that the Wisconsin plants had either more leaves per plant or leaves of greater area than either Illinois or Louisiana. *Table 1* shows that leaf size as well as internode length did not differ between the populations for plants 3—12 grams in weight. Leaf area is represented here as a mean of the 4th through 8th leaves back from the top. Both parameters tended to increase slightly as plant dry weight got larger.

Thus more leaves mean greater stem growth when internode length is constant; in the Wisconsin population this should be reflected in taller plants. As *Figure 7* indicates, this was true at comparable dry weights.

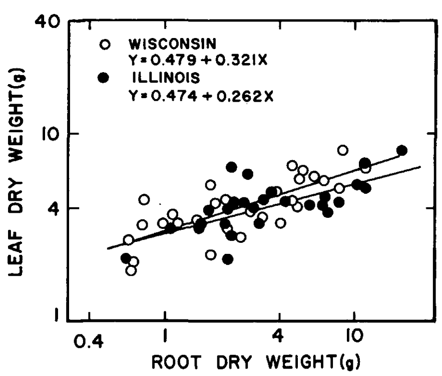

Figure 4. — Regressions of leaf on root dry weight (g) for two populations of *Populus deltoides* Bartr. from Wisconsin and Illinois.

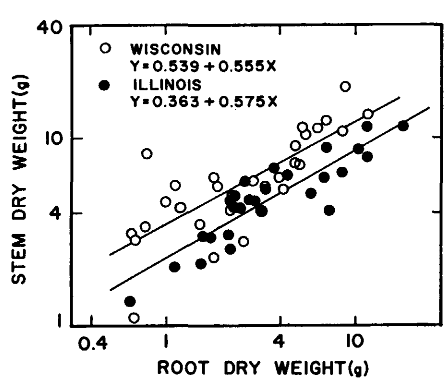

Figure 5. — Regressions of stem on root dry weight (g) for two populations of *Populus deltoides* Bartr. from Wisconsin and Illinois.

Table 1. — Mean leaf area (cm^2) and mean internode length (cm) for three populations of *Populus deltoides* Bartr. based on total number of seedlings sampled per population.

Source	Mean Leaf Size cm^2*	Mean Internode Length cm*
Wisconsin	33.0	2.52
Illinois	33.3	2.25
Louisiana	34.9	2.33

*Plants 3-12 g dry weight

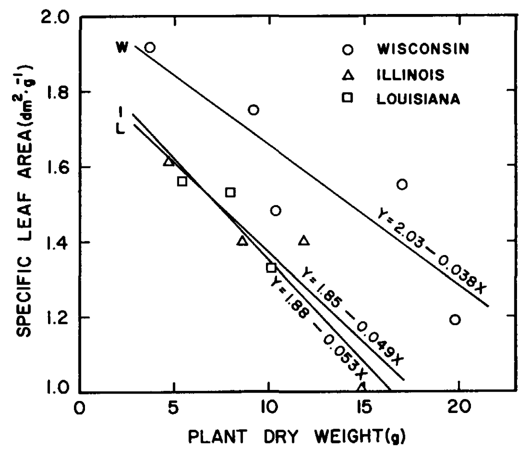

Figure 6. — Regressions of specific leaf area ($dm^2 \cdot g^{-1}$) on dry weight (g) for three populations of *Populus deltoides* Bartr. from Wisconsin (W), Illinois (I), and Louisiana (L). Each data point represents a mean of from 5—8 seedlings per sample.

No differences in photosynthetic response to light intensity were apparent between the Wisconsin and Illinois populations *(Fig. 8)*. However, at high light intensity, seedlings from Wisconsin had a significantly higher transpiration rate. At light intensity above 300 $\mu E \cdot m^{-2} \cdot sec^{-1}$, the ratio of photosynthesis/transpiration was uniformly lower in the Wisconsin population. In prior work the light-saturated photosynthetic rate of seedlings from the Louisiana population did not differ from that of the other two (Bazzaz and Drew. unpublished data.).

Discussion

Early bud break in spring in northern populations when grown at northerly latitudes is expected as such plants are adapted to lower early season temperatures and longer photoperiods (Kaskurewicz and Fogg, 1967) than more southerly populations. As Wilcox and Farmer (1967) have pointed out, date of flushing in *P. deltoides* is associated with a high heritability. Not only were there wide differences in rates of early season growth among the populations studied here, but in later season growth as well. Working with the same populations grown in Mississippi, Rockwood (1968) found that rate of growth during the first part of the growing season was greater for northern sources, but during the last part of the year, surpassed by southern sources as in this study.

Earlier decline in growth in the Wisconsin and Illinois sources than in the Louisiana source fits into the broad pattern of response noted by Pauley and Perry (1954) in *P. deltoides* where date of height growth cessation correlated negatively with latitude of origin of the source. Early abscission in northern sources has also been observed by Ying and Bagley (1976) and Eldridge *et al.* (1972).

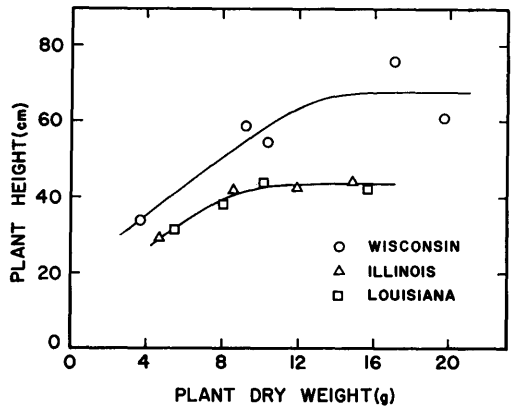

Figure 7. — Plant height (cm) graphed against dry weight (g) for three populations of *Populus deltoides* BARTR. Each data point represents a mean of from 5—8 seedlings per sample.

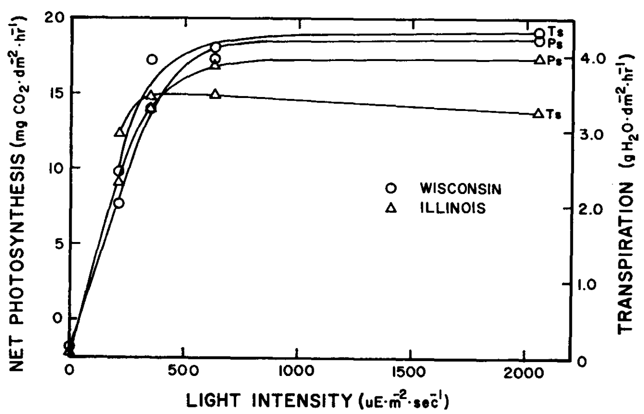

Figure 8. — Net photosynthesis and transpiration rate graphed as a function of light intensity for two populations of *Populus deltoides* BARTR. from Wisconsin and Illinois. The Wisconsin data is based on a sample size of 4 leaves from 2 seedlings, and the Illinois data, 6 leaves from 3 seedlings.

Had it not been for the long delay between bud burst and rooting of the Louisiana source, total height growth for the southerly population would probably have been higher as a consequence of adaptation to longer growing seasons in the south and later budset. Poor survival of ramets from a southern population is consistent with work of SEKAWIN (1974). YING (1974) and ROCKWOOD (1968) also found best survival among northern populations.

The variation in height growth potential displayed among the three populations represented did not vary uniformly with latitude. The northern Illinois ecotype showed none of the adaptive response for enhanced stem growth shown by the Wisconsin ecotype although separated by only 3 degrees. Apparently selective pressures of a local nature have been involved in differentiation within the Diamond Bluff, Wisconsin population.

The Wisconsin ecotype has evolved a "shade-leaf" morphology in contrast to the more "sun-leaf" morphology of the Illinois and Louisiana sources. Obviously, in this case, the "shade-leaf" adaptation results in enhanced productivity. By producing more leaf area with the same amount of dry matter these plants become more effective photosynthesizers. In this case the more photosynthate appears to be "channeled" into stem growth rather than into further leaf production. This should lead to a greater rate of dry weight increase over time in the Wisconsin population. *Figure 2* would support this although high sample variation probably obscured real differences. The constancy of allometric coefficients for the three sources shows that the relative growth of leaf and stem versus root is the same reflecting what may be little or no genetic variation throughout the species with regard to these parameters. However, relative growth when combined with assessment of differences in photosynthetic and respiration rates by growth modelling (LEDIG, 1969) may explain differences in productivity of different genotypes.

In detached *P. deltoides* shoots a thin leaf or one of high specific leaf area was less able to maintain photosynthesis and photorespiration under moisture stress than a thicker leaf (FURUKAWA, 1972). This may imply that the Wisconsin ecotype evolved under conditions of high moisture availability throughout the growing season, and may not be very drought resistant. Selective pressures favoring the type of adaptation observed in the Wisconsin population may be due to a particular combination of short growing season and high moisture availability.

This hypothesis is supported by the high transpiration rates at high saturating light intensities apparent in the Wisconsin seedlings. For the same rate of net CO_2 uptake a higher transpiration rate suggests lower water use efficiency and is possible related to the presence of high available moisture throughout the growing season. Under drought, the Wisconsin population might be at a physiological disadvantage in its ability to photosynthesize compared to the Illinois population. Higher rates of water loss from thinner leaves could result in more rapid decline in leaf water potential to levels ultimately limiting carbon fixation and cellular growth processes.

The height advantage attained by the Wisconsin population over one year is not maintained, however, in stands established at Urbana, Illinois (40° N). After 5 years of growth, the mean height of progeny of the three populations in terms of percentage of an average of the population mean of six sources was 95 for Wisconsin, 98 for northern Illinois, and 93 for Louisiana. Diameter growth followed a similar trend (JOKELA and MOHN, 1977). The Wisconsin source with its superior potential for height growth does not grow taller in stands in Urbana, Illinois than the northern Illinois source. Similarly, YING and BAGLEY (1976) report that a Minnesota-Wisconsin provenance from the same geographical area and the same seed source as that in this study showed rapid height growth early in the life of a 7-year-old plantation near Mead, Nebraska (40° N). However, the provenance lost that early growth advantage in later years to other provenances.

Growth reductions in the Louisiana population can be explained by winter injury and dieback, an annual occurrence since plantations were established here in 1970. Apparently other factors such as climate, soils, or pathogens not assessed in this study, act to reduce growth of the Wisconsin population in a plantation 5° south of its indigenous habitat. JOKELA *et al.* (1976) report earlier and more premature defoliation by *Marssonina* leaf spot disease in *P. deltoides* from northern as compared to central and southern origins. Alternatively, full expression of genetic potential in the Wisconsin population may not be possible outside of a limited geographical area or narrow range of conditions.

We know very little about factors controlling stem form and branching habit. The Wisconsin population shows superior height growth over the first year where no branching occurred. With branching in later years crown shape begins to form and other factors not possible to assess over the first year take effect. YING and BAGLEY (1976) noted prevalence of a dense crown with small, short branches in northern and western provenances, but more of a spreading crown with long, large branches in eastern provenances.

In addition, height and diameter growth in *P. deltoides* are subject to large genotype × environment interactions (MOHN and RANDALL, 1973) so that ecotypic variation observed under experimental conditions may not readily extrapolate to the plantation environment. Knowledge of the existence of a population with the genetic potential for superior early height growth, however, should be of interest to tree breeders trying to produce improved phenotypes. Further exploratory work is necessary to delineate the boundaries of the observed population response and nature of selective pressures involved as well as factors influencing extrapolation of first year experimental results to older plantations.

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Early growth of some progenies from two phenotypically superior white spruce provenances in Central Newfoundland

II. Heritability and genetic gain

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Summary

The nursery phase of the study started in 1971 to verify the genetic superiority of phenotypically superior trees of white spruce (*Picea glauca* (MOENCH) VOSS) from two locations in central Newfoundland, Canada, was completed in 1975. Although statistically significant differences in four-year growth between the two locations were detected there were no such differences between the progenies of "plus" and "ordinary" trees at either location. The superiority of "plus" trees over "ordinary" trees may be due to more outbreeding in the former than in the latter class of trees. Heritability studies show the possibility of more genetic gain by selection from "plus" trees than that from "ordinary" trees. Establishment of a seed orchard of "plus" trees from each location is recommended.

Sommaire

L'étape de l'étude en pépinière amorcée en 1971 pour vérifier la supériorité génétique d'Épinettes blanches (*Picea glauca* [MOENCH] VOSS) phénotypiquement supérieures et provenant de deux endroits du centre de Terre-Neuve, Canada, fut complétée en 1975. Bien que des différences statistiquement significatives entre les deux endroits fussent décelées pour une période de croissance de 4 ans, il n'y a pas eu de telles différences entre les deux descendances d'arbres «plus» et «ordinaires» à l'un ou l'autre endroit. La supériorité des arbres «plus» sur les arbres «ordinaires» est peut-être due à un croisement libre plus intense chez le premier groupe que chez le second. Des études sur l'héritabilité démontrent la possibilité d'une meilleure amélioration génétique par la sélection d'arbres «plus» que par celle