VARIATION IN ROOTING AND JUVENILE GROWTH PHENOLOGY OF NARROWLEAF COTTONWOOD IN COLORADO[1]

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Abstract.--Colorado sources of narrowleaf cottonwood (*Populus angustifolia* James) were highly variable with respect to the number and length of roots produced, the length of the 1980 growth period, and measures of total and daily 1980 height growth. Density of roots produced was very uniform among sources. All characters expressed a discontinuous pattern of variation except for growth period length, which seems to be discontinuous between drainages but produced continuous variation patterns within drainages.

Additional keywords: Rooting ability, height growth, phenology, geographic variation, *Populus angustifolia*.

The western United States is experiencing increased environmental impact through residential development and active searches for energy and mineral resources. Narrowleaf cottonwood (*Populus angustifolia* James), an easily-rooted and fast-growing tree found along streams in the foothill-mesa and montane life zones of the Rocky Mountain region, could prove to be an important species in reclaiming disturbed, montane riparian habitats.

Studies with eastern cottonwood (*Populus deltoides* Bartr.) have shown a continuous or clinal pattern of variation in many rooting, morphological, and growth characters (Ying and Bagley 1976, 1977), which influences selection in this species. Rooting ability responds to selection, because variation in rooting ability is under strong genetic control in those poplar species which develop preformed root primordia (Wilcox and Farmer 1968).

Date of bud set and winter hardening in woody plants, which possess an indeterminant growth habit, is under strong genetic control and is primarily a function of adaptation to photoperiod (Pauley and Perry 1954; Mohn and Randall 1971). Other factors may also influence the date of bud set and the initiation of winter dormancy, such as air and soil temperature, soil moisture, and soil nutrients, and therefore predispose the plant to changes in photoperiod (Pauley 1958; Perry 1971). Through selection, breeding, and artificial crosses with other *Populus* species (Schreiner 1970), increases in growth may be realized and result in optimal production of desired characters for a given site.

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Because of the future potential of narrowleaf cottonwood, a study of the geographic variation of this species in Colorado was undertaken (1) to determine the extent of natural variation in rooting, and (2) to quantify the phenology of juvenile vegetative growth.

METHODS

Between January and March of 1979, hardwood branch cuttings were collected from 80 individual winter-dormant narrowleaf cottonwood trees, each at least ten miles apart, along four main latitudinal-drainage transects in Colorado (Figure 1). The cuttings were placed in cold storage until April 12, 1979, when cuttings from 75 of the original 80 ortets 3/ were rooted in a 10 centimeter (cm) deep water bath. The experimental design consisted of three randomized complete blocks, one replication of six cuttings per source per block. Each replication contained three "terminal" (terminal bud present) and three "subterminal" (no true terminal bud present) cuttings. After 12 days, the following measurements were taken: the number of roots; the length of each of the three longest roots; the length of the root zone, measured from the lowermost to the uppermost root on the cutting; and region of maximum root concentration,

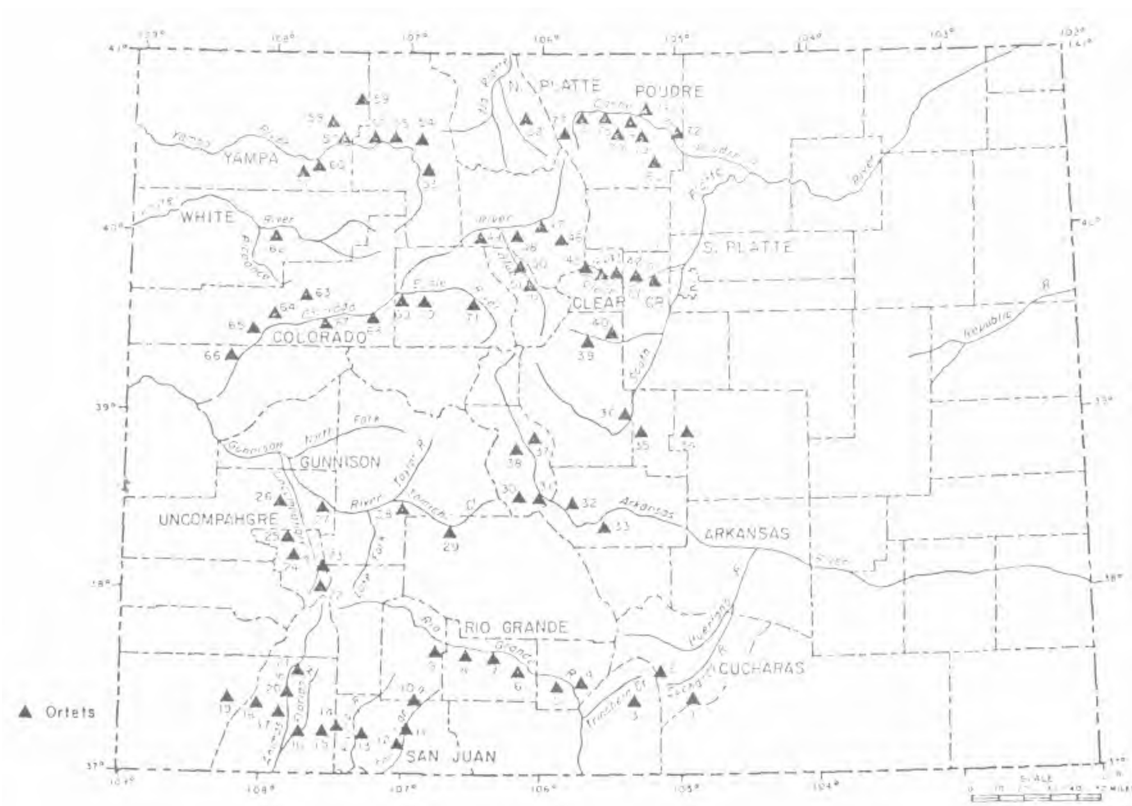

Figure 1.--Locations of narrowleaf cottonwood ortets in Colorado.

3/The number of sources used in different aspects of this study varied due to storage, size of material, and initial survival.

subjectively designated as the top, middle, or bottom of the submerged portion of the cutting. Rooting ability was determined by comparing the number of roots, average root length (the average length of the three longest roots) and density of rooting (the number of roots per cm) among the 75 sources and between terminal and subterminal cuttings of each source.

The rooted cuttings were planted in styrofoam containers. After one month in a greenhouse and two months in a lath house, the trees were outplanted in a randomized complete block design. Each of three rectangular blocks contained three replications per source, each replication consisting of two plants unless insufficient material existed, when only a single plant was used. Growth phenology observations were made on 77 of the original 80 sources/ and included: initial height and date of bud burst, measured in April, 1980; final height and date of bud set, measured during the fall of 1980. Variability in growth characteristics was determined by comparing the length of the 1980 growth period (days from bud burst to bud set), total 1980 height growth, and daily 1980 height growth (millimeters per day of active growth) among the 77 sources.

Analysis of variance was performed to determine the degree of variability in rooting and growth phenology among and within the different sources, the block effects, and also the effect of the position of the cutting on the parent branch on rooting ability. Simple correlation analysis and Duncan·s multiple range test were used to determine the degree of continuity of these factors over Colorado.

RESULTS

Both the number of roots produced and the average root length varied greatly among sources (Table 1), and variation among sources for these two rooting characters was much greater than the variation within sources. The mean number of roots ranged from 19.50 roots for source 76 to 0.22 roots for source 59, while source means for average root length ranged from 45.0 millimeters (mm) for source 46 to 0.0 mm for sources 49 and 72. A small percentage of the sources produced the largest numbers of roots and the longest roots. No clinal trends among the sources across Colorade were evident for either rooting character. Furthermore, when analyzed on the basis of drainage of origin, comparing sources within a common drainage and comparing drainage units, no consistent trends in rooting habit were found.

Table 1.--Summary of rooting and phenological parameters for Colorado sources of narrowleaf cottonwood

Parameter	Mean	Standard Error	Significance[a]
Number of roots	7.46	0.19	0.001
Average root length (mm)	9.9	0.4	0.001
Density of rooting (roots per cm)	2.67	0.07	0.105
Growth period length (days)	151.49	0.53	0.001
Total 1980 height growth (cm)	106.92	1.15	0.001
Daily 1980 height growth (mm per day)	6.9	0.1	0.001

a/ Significance value of the F-ratio testing the variation among sources relative to within source variability as determined by analysis of variance.

The density of rooting did not vary significantly among sources (Table 1). Source means for density of rooting ranged from 4.78 roots per cm for source 51 to 0.70 roots per cm for source 39.

Terminal and subterminal branch cuttings varied greatly in the number of roots produced and in average root length. However, these differences were not consistent from source to source, as indicated by a large source-by-position interaction for the two characters. In other words, some sources produced more roots on terminal cuttings and others produced more on subterminal cuttings. Terminal cuttings produced more roots near their bases, and subterminal cuttings produced more roots near the top of the branch pieces, than was expected by either a normal or a chi-square distribution. No block effects were evident on any of the rooting parameters studied.

The length of the 1980 growth period varied greatly among the sources (Table 1) and a small percentage of the sources had the longest 1980 growth periods. The source means for the length of the 1980 growth period ranged from 183.78 days for source 26 to 128.25 days for source 39. Variability among sources in growth period length was much greater than that within sources, and no block effects were evident for this character. Virtually no differences in date of 1980 leaf flush were observed among the 77 sources, although there were large differences in date of bud set. When the sources were grouped into drainage of origin, the length of the 1980 growth period of the respective sources was found to generally decrease with increasing elevation of the ortet site along a given latitudinal transect, in a given drainage.

Total and daily 1980 height growth varied greatly among sources (Table 1), and variation among sources was much greater than that within sources. Source means for total 1980 height growth ranged from 149.81 cm for source 56 to 57.09 cm for source 37, and source means for daily 1980 height growth ranged from 9.3 mm per day of active growth for source 56 to 4.1 mm per day of active growth for source 37. Block effects were significant for both of these factors. No significant trends existed between total and daily 1980 height growth and the latitude, longitude, elevation, height, or diameter of the ortets.

DISCUSSION

Environmental variability over the range of a species may result in discontinuity of morphological and phenological characteristics (Stebbins 1950). Random variability of neutral characters may also produce discontinuous patterns in natural populations (Dobzhansky et al. 1977). The highly variable and discontinuous variation pattern for the number and average length of roots produced among Colorado sources of narrowleaf cottonwood suggests that the selective pressures and the resulting gene frequencies for these two rooting characters may be quite site specific. This high degree of site specificity seems reasonable due to the environmental heterogeneity of the wont" habitats occupied by this species and the selection pressures that they impose. The discontinuous rooting habit of narrowleaf cottonwood is in contrast to the clinal or continuous geographical trends in rooting habit and other morphological and growth characteristics found for eastern cottonwood (Ying and Bagley 1976, 1977). The different patterns in rooting habit for these two species may be due to the more uniform and gradually-varying environmental conditions over the range of eastern cottonwood relative to the diverse habitats of narrowleaf cottonwood.

The great variability of rooting in narrowleaf cottonwood also suggests that large selective gains can be attained for either character based on the natural variability of the species. In narrowleaf cottonwood, large gains may be expected in rooting ability when selection is focused on the individual tree. The potential to produce greater numbers of and longer roots would be expected to increase establishment and survival of plant materials. Further studies may show that artificial selection for the number and length of roots produced in narrowleaf cottonwood at the stand or family level may result in even greater selective gains. Simultaneous selection for both large numbers of roots and longer roots is possible, based on the variability shown in this study. The uniform pattern expressed for the density of rooting suggests that root primordia in narrowleaf cottonwood are laid down uniformly, the interval probably characteristic of the species.

Apparently, the development of root primordia in narrowleaf cottonwood is similar to that of other species of *Populus*. Bloomberg (1959), working with black cottonwood (*P. trichocarpa* Torr. and Gray), and Ying and Bagley (1977), working with eastern cottonwood, also found that terminal cuttings produced more roots at the base of the stem and subterminal cuttings produced roots more evenly distributed over the stem. In cottonwoods, these differences in root distribution are apparently the result of greater maturity of subterminal stem sections, since they possess greater numbers of, and more developed, root primordia (Smith and

Wareing 1972). Increased maturity of subterminal stem sections creates a more favorable anatomy and nutritional-hormonal balance for differentiation and development of root primordia (Bloomberg 1963; Nanda, Jain, and Malhotra 1971; Haissig 1974).

The lack of variability in date of 1980 leaf flush may have been due to unusual spring weather; extended cool and wet conditions were followed by a period of rapid warming and drying. Therefore, differences among sources for the length of the 1980 growth period were mainly a function of differences in date of bud set. Further observation of the sources in field plots may reveal differences in leaf flush dates.

The strong negative trend between date of bud set and elevation of ortet site within a drainage suggests that the drainage unit may be the common level at which narrowleaf cottonwood has adapted to regulatory mechanisms for initiation of dormancy. The east-west drainages represent geographic units possessing approximately uniform photoperiods. However, these drainages also possess a gradient of differing environmental parameters, such as temperature and moisture, to which the specie! must adapt as a breeding unit. Again, the combined discontinuous pattern in growth phenology of narrowleaf cottonwood between drainages and the continuous pattern within drainages differs from the simple clinal trend found for eastern cottonwood (Ying and Bagley 1976, 1977).

The results of this study indicate that the length of the growth period had only moderate effect on the height growth potential of Colorado sources of narrowleaf cottonwood during the 1980 growing season. This moderate effect of growth period length on height growth potential is further evidenced by the fact that those sources which possessed longer growth periods did not necessarily produce the largest height growth increments. These facts suggest that opportunities exist for increasing height growth through individual tree selection. Further studies may show that even greater increases in height growth are possible through selection at the stand or family level.

Apparently, height growth potential of narrowleaf cottonwood is a function of two factors. First, height growth is dependent on the ability of the genotype to fully utilize the growing season available to it at a given site, due to the indeterminate growth habit of the species. Secondly, the genotype must possess those superior height growth capabilities which are independent of the regulatory mechanisms which control the length of the active growth period of the genotype.

Differences in 1980 growth period length among sources were mainly a function of differences in date of bud set. Under more normal spring growing conditions than were experienced in this study, the length of the growth period in narrowleaf cottonwood may exhibit a higher or lower degree of association with height growth than was observed. Additional years of height growth observation are needed to determine the full relation between growth period length and height growth in this species. The differences observed in height growth among blocks were probably due to plot layout, two of the blocks retaining more soil moisture than the third block due to windbreak shielding.

CONCLUSION

The number of roots produced and average root length in narrowleaf cottonwood are highly variable and discontinuous over Colorado, possibly due to the heterogeneity of the montane habitats that the species occupies. Selective gains for either character to improve establishment and survival may be expected when selection is focused on the individual tree. Simultaneous selection for both large numbers of roots and longer roots is possible. The uniformity in density of rooting found suggests that root primordia are laid down at an interval characteristic of the species.

The length of the 1980 growth period was primarily determined by date of bud set, possibly in response to adaptation to the environmental conditions of the drainage continuum. Growth period length had only moderate effect on 1980 height growth, whereas height growth was highly variable and discontinuous over Colorado. Artificial selection, at the individual tree level, for superior height growth in narrowleaf cottonwood should be focused toward two factors which regulate height growth in this species. First, genotypes which fully utilize the length of the growing season at a given site should be selected. Secondly, the genotypes should possess those superior height growth capabilities which are independent of the adaptive mechanisms that control the length of the growth period. Further studies are needed to determine the effects of selection at the stand and family levels and the full relation between growth period length and height growth in this species.

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