Early root and shoot growth of Populus clones[1]

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Summary

A greenhouse study was conducted to observe early patterns of shoot growth, root elongation, and leaf area growth of rooted leafy tip cuttings of 4 Populus clones of varied growth rate. Clones differed in total plant dry weight, dry weight distribution among plant parts, and estimated net assimilation rate (NAR) after 5 weeks growth. Rapidly growing clones had more root weight per unit leaf area and greater rates of root elongation after transplanting compared with a very slowly growing clone, suggesting better potential water balance and drought avoidance, at least in early growth. More rapidly growing clones also exhibited higher NAR, indicating greater carbon assimilation per unit leaf area in early growth. Although NAR differed by only 20% among clones over the 5 weeks of the experiment, total yield differed more than 2-fold because of the compounding of weekly differences in NAR.

Key words: Populus, dry weight distribution, water relations, growth patterns, genetic variation.

Zusammenfassung

Eine Gewächshausstudie wurde durchgeführt, um Jugend-Muster des Sproßwachstums, der Wurzelstreckung und des Blattflächenwachstums bewurzelter, beblätterter Kopfstecklinge von vier Populus-Klonen mit unterschiedlicher Wachstumsrate zu beobachten. Die Klone unterschieden sich nach fünfwöchigem Wachstum im Trockengewicht der ganzen Pflanze, in der Trockengewichtsverteilung zwischen Pflanzenteilen, und in der geschätzten Netto-Assimilationsrate (NAR). Schnellwüchsige Klone hatten ein höheres Wurzelgewicht je Blattflächeneinheit und eine höhere Geschwindigkeit im Wurzelwachstum nach dem Verpflanzen als sehr langsam wachsende Klone, was ein besseres Potential im Wasserhaushalt und Trockniswiderstand, zumindest im frühen Wuchsstadium annehmen läßt. Schneller wachsende Klone wiesen höhere NAR auf und bewiesen dann im frühen Wachstum eine größere Kohlenstoffassimilation pro Blattflächeneinheit. Obwohl sich die geschätzten NAR zwischen Klonen in dem fünfwöchigen Experiment nur um 20% unterschieden, unterschied sich die Gesamtausbeute um mehr als das doppelte, weil sich die wöchentlichen Unterschiede in der NAR vervielfältigten.

Introduction

Rapid establishment of a root system is important in the growth of young trees (PARKER, 1968). The roots must absorb and transport water and minerals to supply the young plants. Later, the root system of an older plant must supply sufficient water to meet high transpirational demands induced by large leaf areas, intense radiation, and substantial vapor pressure gradients. At any stage of its development, the failure of a plant to maintain a favorable water balance results in declining leaf water potential (Y) and, ultimately, in reduced photosynthesis caused by stomatal closure. Additionally, some studies show that low Y has a direct nonstomatal inhibitory influence on photosynthesis (BOYER, 1971; O' TOOLE et al., 1976; KRIEDEMANN et al., 1975).

The extensive utilization of leafy softwood cuttings of Populus as a source of planting stock for intensively managed plantations (PHIPPS, 1976) may present special water relations problems. LOACH (1977) and GAY and LOACH (1977) have shown that poor water balance and restricted gas exchange capacity are related to slow root system establishment after propagation of leafy cuttings of Rhododendron and Cornus. The initial presence of a large leaf surface area and limited root system predisposes such cuttings to water stress, especially immediately after transplanting to the field. Establishment of an extensive, ramifying root system would assure an adequate water supply for high rates of photosynthesis and leaf expansion. The findings of BOYER (1970) that $\Psi \leqslant -4$ bars caused cessation of leaf expansion in sunflower leaves emphasizes the deleterious effects of even moderately low Y on leaf expansion.

Study of the allometric distribution of photosynthate relates to potential water balance of plants and, additionally, to potential increase in wood production of forest trees. The area of leaf surface in relation to root surface area can influence the water balance of plants, and differential distribution of photosynthate among plant parts can affect the yield of the utilizable fraction. With these considerations in mind an experiment was conducted to compare root, stem and leaf growth patterns of young rooted tip cuttings of 4 Populus clones after transplanting. Large, clear acrylic resin tubes were used as plant containers to present a large volume of soil to the plant, to minimize root binding, and to allow monitoring of root growth. Of particular interest were clonal variations in total dry weight increment in the first month after transplanting, dry weight distribution among plant parts, potential water balance as inferred from the leaf area-root weight ratio, and net assimilation rate (NAR).

Materials and Methods

Plant Material. Tip cuttings of 4 Populus clones were rooted under mist in a medium of perlite and peat. United States Forest Service clone identifying numbers assigned to the material were as follows: 5262, Populus candicans AIT. X P. berolinensis DIPP.; 5272, *Populus* nigra L. X P. laurifolia LEDEB.; 5258, *Populus* sp. (a clone of unknown parentage); and 5267, Populus deltoides BARTR. X P. *caudina* (TEN.) BUCALA. General growth rates of the experimental clones were: 5267, low; 5272, low to intermediate; 5262, intermediate to high; and 5258, high (WRAY and PROMNITZ, 1976).

Experimental Procedure. Twenty healthy plants per clone were randomly divided into 3 groups. One group of 10 plants was transplanted to acrylic resin tubes (90 cm deep, 10 cm inside diameter). This method (BILAN, 1964; PEREIRA and KOZLOWSKI, 1976) allows a large volume of soil to be presented to the plant and also permits monitoring of root growth through the transparent sides of the tubes. Although at least one investigator described an inhibitory effect of the tube on growth of roots at the soil-plastic interface (VOORHEES, 1976), the method should be useful for comparative studies. Prior to planting the tubes were filled with an

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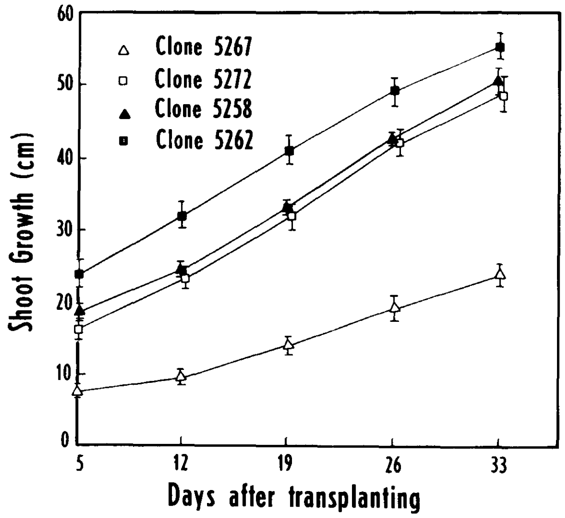

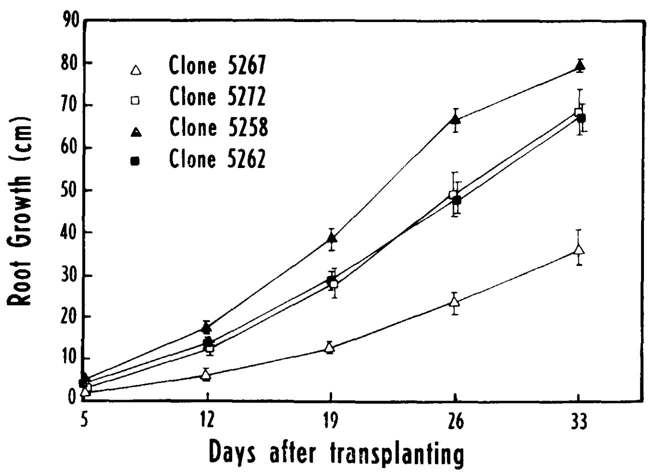

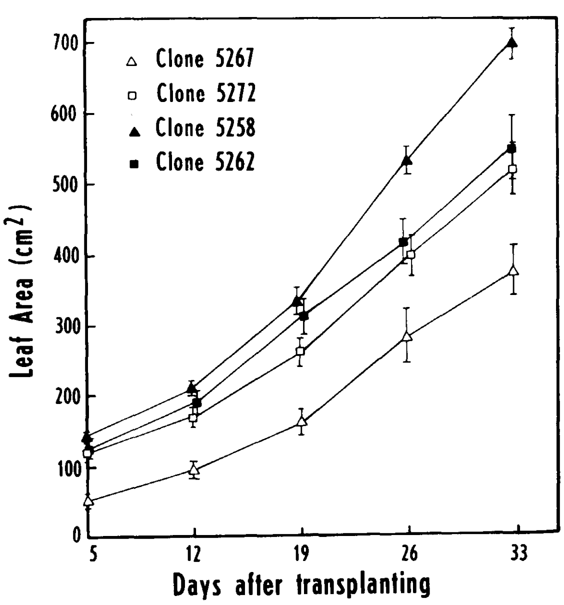

Figs. 1—3. — Shoot height, root elongation, and leaf area growth of 4 *Populus* clones grown in acrylic resin tubes. Bars denote 1 standard error of the mean. Fig. 1 — Shoot height growth. Fig. 2 — Root elongation. Fig. 3 — Leaf area growth.

autoclaved mixture of soil (3 parts sand : 2 parts loam). The upright tubes were then watered daily for one week to allow wetting and settling of the soil. After transplanting the tubes were placed in racks in the greenhouse at a 45° angle and, except for the extreme upper portion, covered with black polyethylene sheeting to exclude light. Geotropism and tube angle forced plant roots to grow against the lower sides of the tubes.

A second group of 5 plants per clone was transplanted to 15 cm pots containing the same soil mixture that was used in the tubes. Leaves from these plants were destructively sampled periodically during the experiment for determination of regressions of leaf area on leaf dimensions. A third group of 5 plants per clone was harvested immediately to provide initial leaf area and dry weight data for subsequent calculation of net assimilation rate.

The forty plants in tubes were placed randomly on racks in the greenhouse. Natural light was supplemented by fluorescent lighting (Sylvania Cool-White) to provide a total photoperiod of 16 hours. Temperature in the greenhouse during the experiment was 19—30° C. Relative humidity varied between 20—80%. Plants were watered daily and given full-strength Hoagland's solution weekly.

Root growth, shoot height, and leaf area were measured on each tube-grown plant weekly for 5 weeks. Root growth was measured by turning the tube of each plant over, marking the depth on the tube to which the 2 most rapidly growing roots had penetrated (from which the mean was calculated), and then returning the tube to its original position.

Leaf area was determined by linear regressions relating the product of leaf length and width to leaf area. Three times during the course of the experiment 10 leaves of each clone were selected from potted plants. Leaf dimensions were measured and leaf area determined by weighing photosensitive paper images of the leaves and relating the image weight to the area-weight ratio of the paper. One equation was developed for each clone at each measurement time. Coefficients of determination (R^2) for the regressions were generally greater than 0.99. Leaf length and width were measured for all leaves of the tube-grown plants and leaf area calculated by the appropriate regression equation. Areas for individual leaves were summed over each plant.

At the end of the 5th week of the experiment the soil was carefully washed from the roots of each tube-grown plant with a gentle stream of water. Plants were separated into stems, leaves, and roots and dried at 70° C for 48 hr. Estimates of NAR ($mg \cdot cm^{-2} \cdot week^{-1}$) were calculated from dry weight and leaf area data taken at initial and final harvests after Gregory (1926).

Results

Shoot height growth, root elongation, and leaf area growth over the course of the experiment are shown in *Figs. 1—3*. Analyses of variance for weekly data revealed significant differences among clones (1% level) at each measurement time for stem height, leaf area, and total root growth. Clone 5262 exhibited the greatest height growth of all clones; 5267 the least height growth. Clones 5272 and 5258 were similar and intermediate in height growth. Clone 5258 had the greatest leaf area growth during the experiment. Clone 5267 had the least leaf area growth and clones 5262 and 5272 had intermediate and similar leaf area growth. Total root growth of clone 5258 was highest during the experiment, with clone 5267 having a much slower root growth rate. Root growth of clones 5262 and 5272 was intermediate and similar.

At final harvest significant differences among clones were found in dry weight distribution among plant parts (*Table 1*). In particular, clone 5267 had significantly higher leaf weight as % of total plant weight, and significantly higher ratio of leaf area to root weight (except for 5272). On the other hand clone 5267 had significantly lower stem, leaf, root, top and total dry weight, and lower stem weight as % of total plant weight. Clones 5262 and 5272 were similar and intermediate to high in stem, leaf, root, top, and total dry weight. Clone 5258 was highest of all clones in leaf, root, top, and total dry weight and lowest in ratio of final leaf area to root weight. Relative total dry weight production among the 4 clones followed stem and leaf productivity ratings previously described by WRAY and PROMNITZ (1976). Trends in NAR *(Table 1)* indicated that clones 5267 and 5272 had relatively low and 5262 relatively high NAR, with NAR of clone 5258 being intermediate.

Table 1. — Growth characteristics of 4 *Populus* clones at final harvest. Except for NAR, means not superscripted by the same letter are significantly different at the 5% level.

Growth Characteristic	Clonal Means 5267	5272	5258	5262
Calculated NAR over the duration of experiment ($mg \cdot cm^{-2} \cdot week^{-1}$)	4.8	4.9	5.3	5.7
Total weight (gm)	3.7^a	6.6^b	8.8^b	7.8^b
Stem weight as % of total weight	23^a	36^b	32^c	37^b
Leaf weight as % of total weight	49^a	36^b	38^{bc}	38^b
Root weight as % of total weight	29^a	27^a	30^a	24^b
Top weight as % of total weight	71^a	73^a	70^a	76^b
Ratio of leaf area to root weight ($cm^2 \cdot gm^{-1}$)	371^a	314^{ab}	269^b	296^b
Root-shoot ratio	0.40^a	0.38^{ab}	0.43^a	0.32^b

Analysis of variance for weekly root growth rate data in a 2-way design with clones and weeks as factors (analysis not shown), indicated significant differences among clones and weeks, and a significant clone × week interaction. The rate of root growth was much lower in clone 5267 than in other clones *(Fig. 2)*. Rates of root growth were very similar in clones 5262 and 5272 throughout the experiment. Clone 5258 had the highest rate of root growth. In the first week after transplanting, roots of clone 5258 grew almost 3.5 times as fast as those of clone 5267. Root growth of clone 5258 was rapid throughout the experiment. Root growth during the last week for clone 5258 *(Fig. 2)* is questionable because roots of several plants of this clone had reached, and were restricted by, a perforated plastic plate used to contain the soil at the bottom of the tubes.

Discussion

Large differences among clones were found in total dry weight and dry weight distribution. Allocation of photosynthate is important in evaluating clone productivity from the standpoint of wood utilization. In this study, clone 5267, in addition to being a poor overall producer, was also a poor stem producer.

Root-shoot ratios showed no consistent relationship with productivity. The implications of root-shoot ratio as they relate to potential water balance must be examined with caution. High root-shoot ratio may suggest a large amount of root surface absorbing area per unit leaf area, but the rate of root growth, which need not be closely correlated with root-shoot ratio, can also be of equal or greater importance in water relations. In addition distribution of shoot weight between stem and leaves can vary widely (as was the case in this study) and thus plants with similar root-shoot ratios can have very different absorption-transpiration relations.

Comparison of final leaf area with root weight and root growth rate suggested the predisposition of clone 5267, and possibly clone 5272, to water deficits. Both of these clones had high leaf area per unit of root weight. In clone 5267 the high leaf area-root weight ratio was combined with a slow rate of root growth. In clone 5272 the leaf area-root weight ratio was higher than in the more productive clones, but the rate of root growth of 5272 was also higher. Both clones, but particularly 5267, might have water balance problems because of their poor absorption capacity-potential transpiration characteristics.

Clone 5258 showed very vigorous root penetration of the soil and the least amount of leaf area per unit of root weight. Several studies have emphasized the importance of root growth into unexplored soil in establishment and growth of plants, especially when plants are exposed to environmental stress (PEREIRA and KOZLOWSKI, 1976; MORROW and MOONEY, 1974; MCWILLIAM and KRAMER, 1968; HEINER and LAVENDER, 1972; PIGGIN, 1976; HARRIS and WILSON, 1970). Working with Douglas-fir ecotypes of xeric and mesic origins HEINER and LAVENDER (1972) found depth of seedling root systems to be directly related to drought survival and early shoot growth. PIGGIN (1976) found that establishment and survival of certain weed species were related to the ability of the roots to penetrate the soil. PEREIRA and KOZLOWSKI (1976) reported that the greater drought avoidance of *Eucalyptus camaldulensis* over *Eucalyptus globulus* was at least partially related to the capacity of the former species to establish a deep and ramifying root system, enabling it to absorb more water from greater soil depths as the upper soil dried. Thus the vigorous root growth rate and low leaf area-root weight ratio shown by clone 5258 suggest that it may best be suited to resist drought after transplanting, despite its tendency to project a large leaf surface area.

Net assimilation rate, which because of the length of the experiment must be viewed as approximate, revealed that the more slowly growing clones, particularly 5267, did in fact appear less efficient in dry weight gain per unit leaf area than the more rapidly growing clones. There was a difference of approximately 20% between clones with the highest and lowest NAR, but because the rate was compounded over 5 weeks, total dry weight increment differed by a factor of more than 2. Hence, small differences in NAR, when compounded over time can result in large total weight differences. It must be cautioned that, theoretically, NAR is an instantaneous measure of net assimilation per unit leaf area. The values given here represent average NAR over several weeks and are only approximate. However, the data are useful in studying relative efficiency of early growth of clones after transplanting. Differences in NAR may be caused by variation in biochemical fixation rate, variation in modulation of photosynthetic fixation by the environment, and by leaf anatomy, among other factors.

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Genetic control of 1,5-year-old traits in Pinus patula Schiede et Deppe and a comparison of progeny test methods[1])

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Summary

The *Pinus patula* Schiede et Deppe breeding population in Zimbabwe Rhodesia is based on plus trees selected in stands which may be up to fourth generation since the species' first introduction as an exotic. Polycross, factorial and diallel mating plans have been used in progeny tests designed to elucidate the genetic structure of the population, to investigate genotype-environment interaction, to identify the best general combiners and to provide information on the efficiency of mating and environmental designs. At 1.5 years from planting, a large number of morphological characteristics were assessed. Statistical analysis showed a portion of the considerable variability expressed in all these traits to be under additive genetic control. Individual tree heritabilities were as high as 0.60 for branch traits. Specific combining ability was of little practical significance, nor were maternal or reciprocal effects important. Genetic correlations were generally favourable both in sign and magnitude. Genotype-environment interaction did not seriously affect ranking of parents but variation between sites in the scale of family differences contributed to large discrepancies in heritability estimates, for example 0.12—0.55 for height. There was evidence that the polycross test is reliable and the assumption of half-sib relationship within families is valid. The precision of component estimation was satisfactory (CV $< 50\%$) where individual tree heritability was over 0.10 and family heritability over 0.50; at the same time, an increase in the number of parents under test would lead to a proportionately greater improvement in precision where heritabilities are low. Although the triple lattice structure provided blocking efficiencies of up to 201 per cent, the design had only a small effect on parent ranking and therefore was of little practical use to the breeder. There were indications that within- and between-plot variances stabilized at three to five trees per plot; greater precision of ranking might have been accomplished had plots of this size and more replications been used.

Key words: *Pinus patula* Schiede et Deppe, progeny tests, diallel, NCM II, polycross, general combining ability, specific combining ability, maternal effects, reciprocal effects, heritability, genotype-environment interaction, genetic correlations, triple lattice design.

Zusammenfassung

Die Züchtungspopulation von *Pinus patula* Schiede et Deppe in Zimbabwe Rhodesien basiert auf in Beständen selektierten Plus-Bäumen, die z. T. bereits die vierte Generation seit Einführung dieser Exotenbaumart erreicht haben. Kontrollierte Mehrfachbestäubungen, sowie faktorielle und diallele Kreuzungspläne kamen bei der Nachkommenschaftsprüfung zur Anwendung, um die genetische Struktur der Population zu klären, das Bestehen von Interaktionen zwischen Genotyp und Umwelt zu untersuchen, die Bäume mit der besten allgemeinen Kombinationseignung auszulesen und Informationen über die Effizienz verschiedener experimenteller Ansätze bei der Prüfung von Kreuzungs- und Umwelteffekten zu erhalten.

Aus den 1.5 Jahre nach der Pflanzung gewonnenen Daten geht hervor, daß ein Großteil der Variation in vielen morphologischen Eigenschaften von allgemeiner Kombinationseignung gesteuert wird, wobei die Heritabilität in manchen Fällen 0.60 erreicht. Weder spezifische Kombinationseignung noch reziproke oder mütterliche Effekte erwiesen sich als signifikant. Die Genotyp/Umwelt-Interaktion war nur in Bezug auf ihre Wirkung auf die Heritabilitätsschätzung von Bedeutung.

[1]) The paper is adapted from part of the senior author's Ph. D. thesis (1973).

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