

## YIELD PHYSIOLOGY OF SHORT ROTATION INTENSIVELY CULTURED POPLARS

J. G. Isebrands  
N. D. Nelson  
D. I. Dickmann  
D. A. Michael<sup>1/</sup>

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Abstract.--An integrated research approach is described for studying yield physiology of short rotation intensively cultured (SRIC) poplar plantations. Branch architecture differs with clone and stand density, but the clonal ranking of important branch characteristics does not change with spacing. Crown morphological variables have a distinct effect on physiological properties of leaves within the crown. Such variables as leaf age, position, shoot type, and distance to the main stem are all important. Leaf area is linearly related to biomass production in the first 5 years of SRIC plantations. Photosynthetic rate (PgA) is strongly influenced by differences in leaf orientation in the crown. Diurnal patterns of PgA also differ with position in the crown and light climate. PgA is high in clones that exhibit significant autumnal green leaf retention. Clones differ distinctly in photosynthate distribution patterns. Both timing of budset and leaf fall are important factors determining these patterns. Current terminal leaves provide most of the photosynthate used for height growth; mature leaves on the upper branches contribute primarily to stem diameter and root growth. Clones with high late-season PgA's also show substantial production of photosynthate, which is exported to the stem and roots. Growth analysis conducted in conjunction with photosynthesis and photosynthate distribution studies led to a better understanding of growth patterns. Stem dry matter production paralleled leaf production during the course of the season. Clones differ in root/shoot ratio during the establishment year so both above- and below-ground growth data are needed to evaluate clonal performance in that year. Silvicultural and genetic implications of the data are discussed and recommendations are given for practical applications of the results. The current understanding of a superior "ideotype" for a SRIC poplar tree is also given.

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<sup>1/</sup> Wood Scientist and Plant Physiologist, Forestry Sciences Laboratory, P. O. Box 898, Rhinelander, WI 54501; and Professor and Research Assistant, Department of Forestry, Michigan State University, East Lansing, MI 48824.

Basic physiological and genetic investigations of yield have allowed agronomists and horticulturists to improve the productivity of several important crops (Coyne 1980; Evans 1980; Boyer 1982). Fundamental research information has been used to identify which physiological characteristics (or criteria) of the crop are important in determining the efficiency of energy conversion to harvestable yield. Those criteria with high heritability are then used by the plant breeder to choose parents for a breeding program.

Physiological data have also been successfully used to identify the critical stages of plant development; then plant varieties can either be identified or developed that perform well at those critical stages (Freeman 1975). Unfortunately, the complex physiological characteristics correlated with crop yield are often interrelated (Nasyrov 1978) and controlled by multigene systems (Wallace et al. 1976). As a result of this complexity the most successful programs for improving crop yield have been those that utilized the cooperative talents of plant breeders, crop physiologists, and plant biochemists.

The most common approaches to increasing productivity in crops are: 1) optimizing canopy structure, 2) improving photosynthetic rates, and 3) partitioning a large proportion of the total assimilates into yield (harvest index) (Nasyrov 1978). These approaches can also be applied toward increasing productivity of trees because many of the theoretical and conceptual principles of yield are fundamentally similar between cultivated crops and trees (Larson 1969; Ledig 1975; Borlaug 1977).

In 1978 we began a research program designed to provide physiological criteria for improving short rotation intensively cultured (SRIC) poplars. Our goal was to obtain baseline morphological and physiological information on poplar trees grown in the field. An integrated research approach was selected to obtain the baseline information on similar trees. Integrated studies of crown morphology, photosynthesis, and photosynthate distribution were conducted in relation to biomass yield as expressed by traditional growth analysis (see Evans 1972). Studies in each scientific discipline were coordinated so that resultant information would be compatible. Research was conducted each year for 4 years on several clones, beginning with the establishment year. Our philosophy was that detailed physiological data on a few representative clones would be more valuable at the early stages of the research program than scattered data on many clones. We believe that such baseline information can also eventually be applied (within limits) toward the understanding of the physiology of some other promising clones. Studies of the few selected clones were also designed to extend baseline physiological data developed on trees grown in controlled environments and in the greenhouse to trees grown in the field. Information from the field experiments was used to plan further laboratory studies. We hoped that an understanding of baseline physiological mechanisms in field-grown poplars would help explain results of various field tests of establishment and growth. We also hoped that a biological explanation of yield would

give forest managers more confidence in selecting clones and choosing cultural practices (Ledig 1975).

The objectives of this paper are to summarize and explain the results to date of our integrated research and to discuss the silvicultural and genetic implications of these results. These morphological and physiological data will also be used to describe what the "ideal" poplar clone (i.e., ideotype; Donald 1968) might be for certain SRIC systems.

The following clonal materials were studied: 1) Populus tristis x P. balsamifera cv. 'Tristis #1' (NC-5260) and P. x euramericana cv. 'Eugenei' (NC-5326)<sup>2/</sup> trees grown in pots for one growing season in both controlled environments and the field (Nelson and Ehlers 1981; 1982); 2) the same two clones grown under SRIC at 0.6 m spacing for 4 years; 3) Tristis grown at 1.2 m and 0.6 m spacings for 5 and 6 years (Isebrands and Nelson 1982); 4) P. nigra cv. betulifolia x P. trichocarpa (NE-298) and NC-9922, (probably P. deltoides x P. trichocarpa) grown for 4 years at 1.2 m spacing under a gradient of cultural practices; and 5) P. nigra x P. laurifolia cv. 'Strathglass' (NE-1) grown under SRIC at several spacings for 2 years (Nelson et al. 1980 b,c). Details of the establishment and culture of the SRIC poplar clones are given elsewhere (Nelson et al. 1981, Isebrands and Nelson 1982, Nelson and Michael 1982, Nelson et al. 1982).

#### CROWN ARCHITECTURE AND CANOPY DENSITY

Solar energy is the driving force of all photosynthetic processes. Thus, biological yield is intimately related to the light-intercepting characteristics of a crop (Wilson 1979). In trees, as in other crops, light interception is strongly influenced by crown architecture and canopy density. Photosynthetic capacity of leaves is also affected by such variables as position in the crown (Michael et al. 1980), shoot type (Nelson and Michael 1982), and specific leaf weight (Nelson and Ehlers 1981, 1982). Moreover, the economic yield of tree crops such as SRIC poplars is strongly influenced by crown characteristics because of their effects on the utilization potential of the raw material (Crist et al. 1979, Isebrands et al. 1979, Phelps et al. 1982a, 1982b). Therefore, the variables we collectively define here as crown architecture and canopy density (i.e., branch architecture, leaf morphology and distribution, leaf area, and leaf orientation) have a major impact on the quantity and quality of yields

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<sup>2/</sup> Hereafter Tristis and Eugenei.

from SRIC poplar plantations.

**Branch Architecture.**--Many factors affect the sequential growth pattern of a poplar crown. Some of these factors are amenable to genetic and/or silvicultural manipulation whereas others are not (Isebrands 1982). For example, branch characteristics of SRIC poplars differ greatly with clone and stand density (Dawson *et al.* 1976, Isebrands *et al.* 1977, Nelson *et al.* 1980a, 1981). However, the ranking of poplar clones for most branch characteristics does not change significantly at different plantation spacings. This lack of a clone-spacing interaction for branch properties (i.e., branch angle) greatly simplifies genetic selection and breeding for crown architecture in poplar (Nelson *et al.* 1980a, 1981). One illustration of this point is that selected fastigiate genotypes will probably maintain their acute branch angle for a wide range of spacings. Clones with a narrow crown architecture are thought to be advantageous at close spacings because they occupy less space and compete only weakly for light with their neighbors (Burk 1981, Nelson *et al.* 1981).

Branch architecture of poplar clones also differs with each height growth increment (HGI) (fig. 1) and with position within the HGI (Burk 1981; Isebrands 1982; Isebrands and Nelson 1982). The uppermost first-order branches within each HGI are usually the largest, and their length and diameter decrease basipetally (Jankiewicz and Stecki 1976). The order of branching rarely exceeds third-order in SRIC poplar plantations (Isebrands and Nelson 1982), and live branches are commonly shed (cladotopsis) in the lower crown, particularly in *Eur-americana* clones (Nelson *et al.* 1981).

**Leaf Morphology and Distribution.**--In tree crowns leaves of different age, structure, and size; on different shoot types; and at different distances from the main stem have distinctly different physiological properties (Kramer and Kozlowski 1979). These leaf characteristics have important effects on both photosynthetic rate and on the distribution of photosynthate within the tree in SRIC poplars (Isebrands and Nelson 1980; Michael *et al.* 1980; Nelson and Ehlers 1981, 1982; Nelson and Michael 1982; Isebrands 1982).

SRIC poplars aged 4 and older display their leaves in a complex crown arrangement (fig. 1) encompassing at least three orders of branching and two different shoot types (i.e., long and short shoots) (Isebrands and Nelson 1982). The distribution of leaves, leaf area, and average leaf area per leaf differ with HGI in the tree (table 1). The current terminal

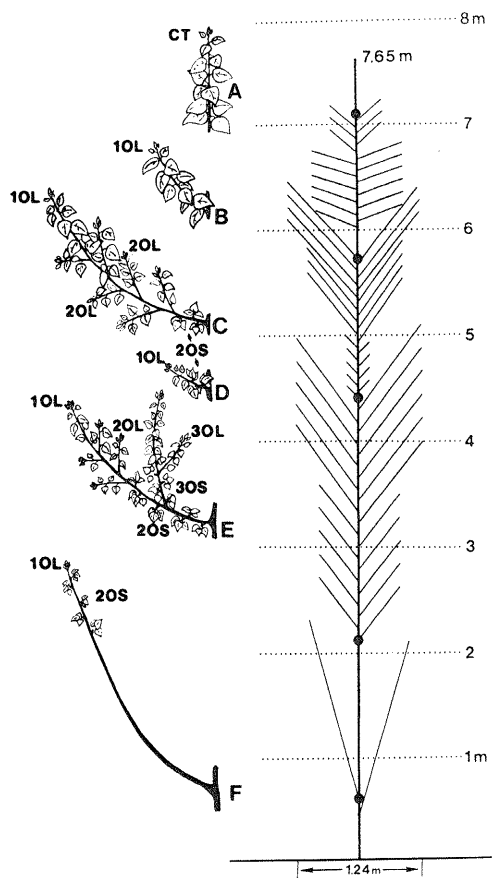


Figure 1.--Schematic of 6-yr-old *Populus* 'Tristis' grown under SRIC. Each dot on main stem delineates the beginning of an annual height growth increment (HGI). Position A is the current terminal shoot (HGI); B is a first-order long shoot (10L) on HGI 5; C is a first-order branch on HGI 4 with its terminal shoot a long shoot and with second-order long shoots (20L) and second-order short shoots (20S); D is a short first-order branch also on HGI 4 with a terminal shoot (10L) and with 20S; E is a first-order branch on HGI 3 with 10L, 20L, 20S, and third-order long shoots (30L) and third-order short shoots (30S); and F is a first-order branch on HGI 1 with a terminal shoot (10L) and 20S. Branch length and angles are drawn to scale, except that branches in the field curve upward (from Isebrands and Nelson 1982).

shoot on a 5-yr-old tree has less than 1 percent of the total number of leaves and about 1 percent of the total leaf area. However, these

Table 1.--Average number of leaves, leaf area, and leaf area per leaf within the crown of 5-yr-old SRIC *Populus* 'Tristis' trees grown at 1.2 m spacing<sup>1/</sup> (from Isebrands and Nelson 1982)

| Crown position    |                  | Leaves/position |               | Leaf area/position |               | Leaf area/leaf  |
|-------------------|------------------|-----------------|---------------|--------------------|---------------|-----------------|
| HGI <sup>2/</sup> | CT <sup>3/</sup> | No.             | Percent Total | cm <sup>2</sup>    | Percent Total | cm <sup>2</sup> |
| 5                 |                  | 29              | <1            | 1,415              | 1             | 47              |
| 4                 |                  | 414             | 6             | 11,685             | 11            | 26              |
|                   | L                | 282             |               | 8,841              |               | 31              |
|                   | S                | 132             |               | 2,844              |               | 22              |
| 3                 |                  | 1,528           | 23            | 32,728             | 31            | 16              |
|                   | L                | 1,302           |               | 28,534             |               | 21              |
|                   | S                | 226             |               | 4,194              |               | 14              |
| 2                 |                  | 2,239           | 34            | 29,645             | 29            | 12              |
|                   | L                | 1,988           |               | 26,927             |               | 13              |
|                   | S                | 251             |               | 2,718              |               | 11              |
| 1                 |                  | 2,434           | 37            | 29,136             | 28            | 11              |
| Total             |                  | 6,644           | 100           | 104,609            | 100           |                 |

<sup>1/</sup>Weighted averages for nonborder trees are based on proportional stratified sampling of the entire stand.

<sup>2/</sup>HGI=height growth increment; L=branches >0.6 cm basal diameter; and S=branches <0.6 cm basal diameter.

<sup>3/</sup>Current terminal.

leaves are the largest on the tree and are attached directly to the main stem. In subsequent HGI's the difference between the percentages of total number of leaves and total leaf area increases dramatically, reflecting a decrease in average leaf size from the upper to the lower portion of the crown.

Knowing the distribution of leaves by HGI alone does not provide a complete indication of the crown's light-intercepting ability. Leaves on a given HGI often occur in several vertical strata or light climates because of the upward growth of branches (table 2). For example, 85 percent of the total number of leaves in 6-yr-old SRIC *Tristis* occur in the three height strata from 4 to 7 m, and those leaves are on branches attached to HGI's 3, 4, and 5. Thus, leaves within a given light climate often contribute photosynthate to several different parts of the main stem. This difference has major physiological importance because lateral branches normally only contribute appreciable quantities of photosynthate to main stem below their point of attachment (Isebrands 1982). Thus, the rapid growth exhibited by some SRIC poplar clones may be related to the high percentage of their leaf area displayed in favorable light-intercepting positions within the crown.

Table 2.--Distribution of leaves within the crown of a 6-yr-old short rotation intensively cultured *Populus* 'Tristis' tree grown at 0.6 m spacing by vertical height strata and height growth increment<sup>1/</sup> (from Isebrands and Nelson 1982)

| Vertical strata | Total number of leaves | Height growth increment | Percent total |         |   |    |    |    |   |   |   |
|-----------------|------------------------|-------------------------|---------------|---------|---|----|----|----|---|---|---|
|                 |                        |                         | No.           | Percent | 6 | 5  | 4  | 3  | 2 | 1 |   |
| m               |                        |                         |               |         |   |    |    |    |   |   |   |
| 7-8             | 63                     | 4                       |               |         | 1 | 3  | -  | -  | - | - | - |
| 6-7             | 539                    | 36                      |               |         | - | 16 | 20 | -  | - | - | - |
| 5-6             | 332                    | 23                      |               |         | - | 1  | 20 | 2  | - | - | - |
| 4-5             | 393                    | 26                      |               |         | - | -  | 6  | 20 | - | - | - |
| 3-4             | 108                    | 7                       |               |         | - | -  | -  | 7  | - | - | - |
| 2-3             | 61                     | 4                       |               |         | - | -  | -  | 3  | - | 1 | - |
| <2              | -                      | -                       |               |         | - | -  | -  | -  | - | - | - |
| Total           | 1,496                  | 100                     |               |         | 1 | 20 | 46 | 32 | - | 1 | - |

<sup>1/</sup>Individual tree of average leaf area from subsample.

Although crown position and shoot type are the dominant factors determining leaf size in SRIC poplar clones (Isebrands et al. 1977, Isebrands and Nelson 1982), clonal differences in leaf size are also common (table 3). For example, at the end of 2 years in the field the leaves of NC-9922 were much larger and fewer than NE-298, but total leaf areas of the clones were not significantly different (fig. 2). Clonal differences in specific leaf weight (SLW) are also often substantial; differences in clonal averages may even exceed 20 g.m<sup>-2</sup> (Isebrands et al. 1977, Gottschalk and Dickmann 1978). SLW usually decreases from the current terminal downward toward the base of the tree (Isebrands et al. 1977, Isebrands and Nelson 1982). In addition, shoot type also has an influence on SLW; long-shoot leaves at similar positions have a higher SLW than short-shoot leaves (Isebrands and Nelson 1982).

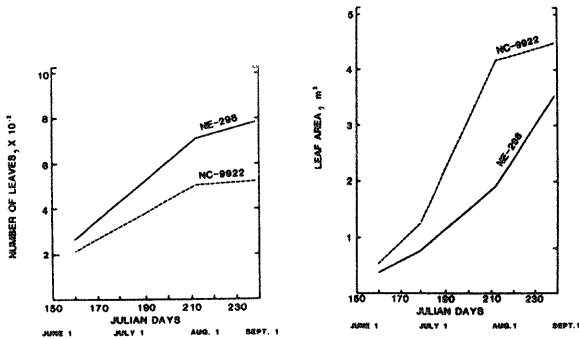


Figure 2.--Seasonal development of number of leaves and leaf area in two, 2-yr-old *Populus* clones grown under SRIC at 1.2 m spacing (NE-298, *P. nigra* cv. *betulifolia* x *P. trichocarpa*; NC-9922, probably *P. deltoides* x *P. trichocarpa*).

The crowns of hybrid poplars grown under SRIC are comprised of a higher ratio of long shoots to short shoots than other poplars (Pollard 1970). The proportion of long and short shoots also differs with clone and age; the proportion of short shoots usually increases as a tree ages (Kozlowski 1971). Five- and 6-yr-old Tristis trees grown under SRIC have 53 to 66 percent of their leaf area on long shoots, with about 95 percent of the long-shoot leaves in the upper three-eighths of the leaf-containing vertical strata. The average long-shoot leaf was 34 cm<sup>2</sup> in area, compared to 19 cm<sup>2</sup> for the average short-shoot leaf (Isebrands and Nelson 1982). The ratio of long shoots to short shoots in a poplar crown has physiological importance. For example, leaves on long shoots of Tristis have higher midseason photosynthetic rates (Nelson and

Table 3.--Seasonal patterns of growth, distribution of leaf area, leaf area per leaf, and leaf area index in two, 2-year-old poplar clones grown under intensive culture at 1.2 m spacing

| Date <sup>1/</sup><br>Clone <sup>2/</sup> | Height<br>m | Diameter<br>cm at 0.3m | Distribution of leaves |          | Distribution of leaf area |          | Leaf area per leaf |          | Leaf area index <sup>3/</sup> |         |    |                 |    |                 |     |                                 |  |                                 |  |
|---|-------------|------------------------|------------------------|----------|---------------------------|----------|--------------------|----------|-------------------------------|---------|----|-----------------|----|-----------------|-----|---------------------------------|--|---------------------------------|--|
|   |             |                        | Current terminal       | Laterals | Current terminal          | Laterals | Current terminal   | Laterals |                               |         |    |                 |    |                 |     |                                 |  |                                 |  |
| June 9                                    | 1.3         | 1.5                    | 3                      | 95       | 97                        | 8        | 5                  | 92       | 95                            | 42      | 21 | 25              | 14 | 0.4             | 0.3 |                                 |  |                                 |  |
| June 28                                   | 1.6         | 2.0                    | 4                      | 95       | 96                        | 10       | 6                  | 90       | 94                            | 74      | 32 | 38              | 23 | 0.9             | 0.7 |                                 |  |                                 |  |
| July 31                                   | 2.4         | 3.0                    | 4                      | 94       | 96                        | 12       | 8                  | 88       | 92                            | 172     | 52 | 78              | 26 | 2.8             | 1.3 |                                 |  |                                 |  |
| August 29                                 | 3.4         | 4.3                    | 5                      | 92       | 95                        | 25       | 10                 | 75       | 90                            | 288     | 87 | 70              | 43 | 3.0             | 2.4 |                                 |  |                                 |  |
| Percent                                   |             |                        |                        |          |                           |          |                    |          |                               | Percent |    | Percent         |    | Percent         |     | Percent                         |  |                                 |  |
| 9922                                      |             |                        |                        |          |                           |          |                    |          |                               | 298     |    | 9922            |    | 298             |     | 9922                            |  | 298                             |  |
| m   |             |                        |                        |          |                           |          |                    |          |                               | cm      |    | cm <sup>2</sup> |    | cm <sup>2</sup> |     | m <sup>2</sup> .m <sup>-2</sup> |  | m <sup>2</sup> .m <sup>-2</sup> |  |

<sup>1/</sup> The 1978 growing season. Each value is the mean of two replications.  
<sup>2/</sup> The clones were NC-9922, *Populus* sp., probably *P. deltoides* x *P. trichocarpa*; and NE-298, *P. nigra* x *P. trichocarpa*.  
<sup>3/</sup> Mean tree approach assuming no mortality.

Michael 1982) and contribute more photosynthate for wood production than leaves on short shoots. These observations suggest that the high biomass yields for SRIC poplars may be partially explained by the favorable long-shoot/short-shoot ratio in their crowns (Isebrands and Nelson 1982).

Leaf Areas.--SRIC poplar stands have higher leaf areas than natural stands. Leaf area index (LAI) values for 5- and 6-yr-old SRIC Tristis stands at 1.2 and 0.6-m spacings grown under less than optimum conditions were 7.6 and 8.8, respectively (Zavitkovski 1981, Isebrands and Nelson 1982). In addition, LAI's exceeded 15 in 4-yr-old SRIC Tristis grown at 0.6-m spacing, but these trees were grown in small plots and may have had somewhat inflated LAI's because of greater side light penetration (Isebrands et al. 1977).

Clones often differ greatly in LAI (Isebrands et al. 1977, Gottschalk and Dickmann 1978). Moreover, clones also differ significantly in the time required to develop maximum LAI during a growing season (fig. 2, table 3). For example, in the second year NC-9922 and NE-298 had similar leaf areas at the end of the year but most of NC-9922's leaf area was produced during July and most of NE-298's was produced during August.

The high LAI's of SRIC poplar stands result in leaves making up a large portion of the above-ground biomass. For example, in 5-yr-old Tristis grown at 1.2-m spacings, leaves accounted for 10 percent of the total biomass (Isebrands et al. 1979). Leaf biomass can approach 40 percent in young stands planted at close spacings, but that percentage decreases as stands develop and age (Gottschalk and Dickmann 1978).

Stem volume and above-ground biomass of individual trees in SRIC poplar plantations are linearly related to the total leaf area of the tree (Larson et al. 1976, Isebrands et al. 1977, Isebrands and Nelson 1982). Furthermore, stem growth at any particular height is closely related to the cumulative leaf biomass or leaf area above that point (Tadaki 1966, Larson and Isebrands 1972). Although we cannot yet define an "optimum" LAI for SRIC poplar stands, we predict that it will be at least 10. In the stands we've studied we have found no evidence of excessive LAI's that produce negative effects on growth, which is consistent with data from other crops (Watson 1952, Donald 1961). Attaining "optimum" LAI in the SRIC plantation early in the rotation and maintaining it throughout the rotation is important (Isebrands and Nelson 1982). Based on evidence from agronomic crops (Watson 1952,

Loomis and Williams 1963, Moss 1975) we suggest that the ability to rapidly attain high LAI early in the growing season and to maintain that leaf area throughout the growing season (i.e., leaf area duration) are important determinants of rapid growth in SRIC poplar stands. Extended green leaf retention in the autumn, a trait in some SRIC poplars, also contributes substantial photosynthate to late season stem and root growth (Nelson et al. 1980b,c, Isebrands 1982, Nelson et al. 1982).

Leaf Orientation.--Because photosynthesis depends on the amount of light, photosynthetic rate per unit leaf area ( $PgA$ ,  $mgCO_2m^{-2}s^{-1}$ ) is closely related to the effect that the leaf's three dimensional orientation has on light interception (Michael and Dickmann 1982). The importance of leaf orientation on light interception,  $PgA$ , and yield has been studied extensively in agronomic crops (Monteith 1965, Vidovic 1974, Austin et al. 1976), but limited information exists for trees.

As part of our study of light interception in SRIC poplars in the field, we quantified leaf orientation during the first 3 years in two clones: Tristis, which has a horizontal leaf display, and Eugenei, which has a vertical leaf display. Leaf azimuth angle, the vertical angle formed by the leaf's midrib (midrib angle), and the vertical angle formed by a line perpendicular to the midrib in the lamellar plane (lamina angle), were measured using methods developed by Max (1975). In poplar clones leaf display angles are not necessarily related to branch angles of the main tree stem, although leaf azimuth and branch azimuth are related (Burk 1981).

In the first growing season, the azimuth angle of a leaf is strongly controlled by its position along the phyllotactic spiral. Midrib angles in both clones were similar. Eugenei's observed vertical leaf orientation was a result of rotation around the midrib axis, i.e., adjustment of the lamina angle (fig. 3). By comparison, Tristis had a minimal deviation of lamina angle from  $90^\circ$  in contrast to Eugenei; this small deviation gives rise to Tristis' horizontal leaf orientation.

Zenith angle (ZA), the angle between a line perpendicular to the leaf's surface and that line's zenith (high point), provides a useful measure of leaf orientation that incorporates all rotations along a leaf's axis into one variable. When  $ZA = 0$ , for example, the leaf is horizontal; ZA values increase as leaves become more vertically oriented. During the first growing season mean ZA's were  $50^\circ$  and  $20^\circ$  for Eugenei and Tristis, respectively, and Eugenei had the widest range of ZA values. The same pattern was also observed within the crowns

of 2-yr-old trees; mean ZA's for Eugenei and Tristis were 54° and 21°, respectively.

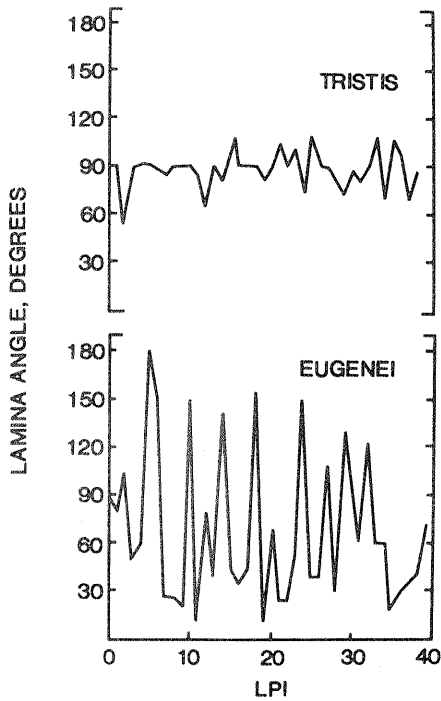


Figure 3.--Lamina angles (the angle between the vertical and a line perpendicular to the leaf midrib in the lamellar plane) for two, 1-yr-old *Populus* clones (*P. tristis* x *P. balsamifera* cv. 'Tristis #1' and *P. x euramericana* cv. 'Eugenei') by leaf position. LPI 0 (LPI, leaf plastochron index) is the first leaf below the apex attaining a lamina length of 3 cm.

Leaf orientation greatly influenced the distribution of light and photosynthetic activity within the crowns of both clones. Light interception and photosynthesis were concentrated in a few large leaves in Tristis' upper crown due to a high degree of mutual shading in the lower crown. This shading was especially evident after the first growing season. Eugenei's vertical leaf display resulted in less mutual shading and a more even distribution of light and P<sub>g</sub>A within the crown when compared to Tristis (table 4).

#### PHOTOSYNTHESIS

Photosynthetic activity varies significantly among the leaves of a poplar tree growing in the field. For example, photosynthesis varies

Table 4.--Within-crown comparison of total leaf area, light interception, and whole-leaf photosynthesis (P<sub>g</sub>L) for two, 1-yr-old *Populus* clones<sup>1/</sup>

| Clone <sup>2/</sup> | Crown level | Leaf number |        | Leaf area<br>cm <sup>2</sup> | Light interception <sup>3/</sup> |                         | P <sub>g</sub> L <sup>3/</sup><br>mg CO <sub>2</sub> s <sup>-1</sup> x 10 <sup>4</sup> |
|---------------------|-------------|-------------|--------|------------------------------|----------------------------------|-------------------------|--|
|                     |             | from base   | Leaves |                              | μ moles s <sup>-1</sup>          | μ moles s <sup>-1</sup> |  |
| Tristis             | A           | 31 - 34     | 4      | 148                          | 15 (14)                          | 80 (9)                  |  |
|                     | B           | 21 - 30     | 10     | 547                          | 60 (54)                          | 470 (55)                |  |
|                     | C           | 11 - 21     | 10     | 362                          | 26 (24)                          | 220 (26)                |  |
|                     | D           | 1 - 10      | 10     | 177                          | 9 (8)                            | 90 (10)                 |  |
|                     | TOTAL       |             | 34     | 1,234                        | 110                              | 860                     |  |
| Eugenei             | A           | 30 - 31     | 2      | 53                           | 1 (1)                            | 3 (<1)                  |  |
|                     | B           | 20 - 29     | 10     | 625                          | 37 (38)                          | 360 (43)                |  |
|                     | C           | 11 - 19     | 9      | 489                          | 34 (35)                          | 310 (37)                |  |
|                     | D           | 1 - 10      | 10     | 310                          | 26 (26)                          | 170 (20)                |  |
|                     | TOTAL       |             | 31     | 1,477                        | 98                               | 843                     |  |

<sup>1/</sup> Leaves were measured on 8-8-79.

<sup>2/</sup> Clones were Tristis - *P. tristis* x *P. balsamifera* cv. 'Tristis #1', and Eugenei - *P. x euramericana* cv. 'Eugenei'.

<sup>3/</sup> Values in parentheses are percent of total light interception or P<sub>g</sub>L.

with leaf position, leaf orientation, leaf age, and season.

Establishment Year.--The rate of photosynthesis and the quantity of photosynthate produced by a poplar tree during the first growing season in the field is largely determined by how effectively its leaves capture and utilize available light.

Field measurements within poplar crowns show that single leaf PgA varies greatly due to differences in light interception and leaf age (fig. 4). The net effect of leaf position, leaf orientation, and leaf age on whole-crown photosynthetic rates can be best assessed by measuring photosynthetic rates of leaves in their natural orientation, and then expressing photosynthesis and light interception on a whole-leaf basis for different regions of the crown. This approach allows comparisons to be made between different crown levels within a clone and among different clones.

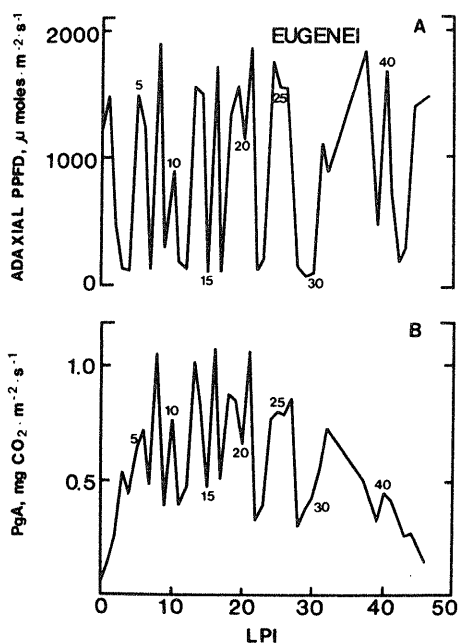


Figure 4.--Adaxial photosynthetic photon flux density (PPFD) and photosynthetic rate (PgA) for a 1-yr-old *P. euramericana* cv. 'Eugenei' tree (46 leaves) measured in the field beginning at 10:00 solar time, August 30, 1979.

During the establishment year, leaf area, light interception, and photosynthesis on a whole-leaf basis ( $Pg_L$ ,  $mgCO_2 \cdot s^{-1}$ ) in both *Tristis* and *Eugenei* reached a maximum in the upper-middle crown (level B, table 4). Light interception and  $Pg_L$  in the B level was greater in *Tristis* than in *Eugenei*, even though *Tristis* had less leaf area at that level. This difference is a direct result of clonal variation in leaf display (i.e., light interception strategies).

*Tristis*' horizontal midcrown leaves capture more light than *Eugenei*'s vertical midcrown leaves, especially when the sun's altitude is high during mid-afternoon. But *Eugenei*'s leaf display produces less mutual shading and allows more light to penetrate to the lower crown levels during mid-day. As a result, both light interception and photosynthetic rates are more evenly distributed throughout *Eugenei*'s crown than in *Tristis*' (table 4). Note that the two lower crown regions (levels C and D) accounted for 32 and 61 percent of the tree's total intercepted light and 36 and 57 percent of the total crown photosynthesis for *Tristis* and *Eugenei*, respectively.

Light interception and photosynthesis in *Tristis* are concentrated in a few young and highly productive horizontal leaves located in the upper-middle crown. Diurnally these leaves attain maximum illumination at mid-day when they are close to or above photosynthetic light saturation, and most of the intercepted light is concentrated on the upper-leaf surface. Moreover, *Tristis* leaves reach a higher  $Pg_A$  at light saturation than *Eugenei* leaves; thus, *Tristis* leaves can utilize high light intensities better than *Eugenei*. By contrast, maximum light interception occurs in *Eugenei* in late morning and late afternoon when the sun is at oblique angles to the tree. Light interception during these peak period occurs on both the upper and lower leaf surfaces. Thus, available light is efficiently utilized because a large number of leaves are illuminated. However, leaves in the lower crown of *Eugenei* must be photosynthetically responsive to illumination below light saturation in order to benefit from this pattern of light dispersal.

Another difference between the two clones in the first growing season is that the contribution of the lower crown declines rapidly in *Eugenei* late in the growing season as its leaves senesce. In *Tristis* the lower crown region remains productive throughout most of the season.

Despite the differences in patterns of light interception, *Tristis* and *Eugenei* are about equal in overall photosynthetic efficiency (PE,  $mgCO_2$  fixed/ $\mu$ mole of light photons) for the first growing season. At mid-season PE was 7.9 and  $8.3 \times 10^{-4} mgCO_2 \mu mole^{-1}$ , and in late season PE was 5.4 and  $5.7 \times 10^{-4} mgCO_2 \mu mole^{-1}$  for *Tristis* and *Eugenei*, respectively. The lower values in late season reflect leaf senescence. The similarity in *Tristis* and *Eugenei* PE's at both mid- and late season during the establishment year indicate that PE differences alone do not explain observed clonal differences in dry matter production (see Growth Analysis section).



Two-Year-Old Trees.--During the establishment year poplar clones have a simple, single-stemmed crown. However, the complexity of the crown increases in the second growing season with the development of lateral branches. As a result within-tree and between-tree competition for light increases markedly. In the second year, leaf orientation continues to have an important influence on light interception patterns, and single leaf and within-tree photosynthesis. Thus, photosynthetic patterns within the crown continue to mirror those of light interception in both clones. The horizontal leaf display in the upper crown of 2-yr-old *Tristis* trees resulted in rapid light attenuation within the crown (fig. 5). Light interception was greatest in the large, horizontal current terminal (CT) leaves that are important for height growth and stem wood production (Isebrands 1982). However, the leaves on the upper crown lateral branches of *Tristis* were still important contributors of photosynthate because they compensated for their low light interception by a large aggregate leaf area (fig. 5). The photosynthetic contribution of the lower crown region was much less than the upper because low light interception was combined with a small aggregate assimilatory area.

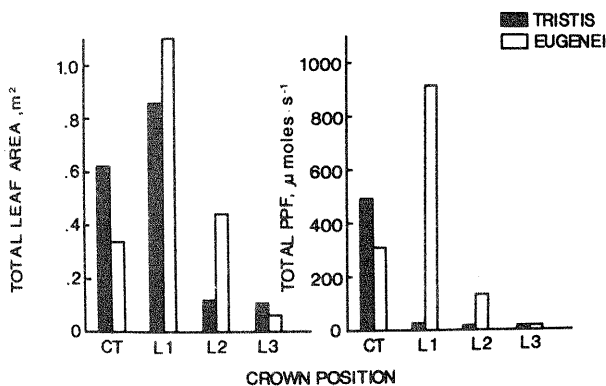


Figure 5.--Total leaf area and total photosynthetic photon flux (PPF) interception of four specific crown regions of individual 2-yr-old *P. tristis* x *balsamifera* cv. 'Tristis #1' and *P. x euramericana* cv. Eugenei trees measured on August 6, 1980. CT = current terminal; L1 = upper lateral branches; L2 = middle lateral branches; and L3 = lower lateral branches.

By contrast, light interception in Eugenei was highest in the upper and middle lateral branches because its vertical leaf display

permitted better light penetration to those positions (fig. 5). Leaves on the lower lateral branches received low levels of light and, therefore, had low PgA.

Diurnal patterns of PgL within the crown of 2-yr-old poplars differed with position and with light climate (fig. 6). PgL rates of the CT leaves were the highest in the crown, but PgL rates declined steadily with depth in the crown. *Tristis* leaves showed a typical bell-shaped curve with peaks at mid-day and that directly reflected changes in photon flux density as the day progressed (fig. 6). However, Eugenei's diurnal pattern (not shown) was more complex because of its vertical leaf display.

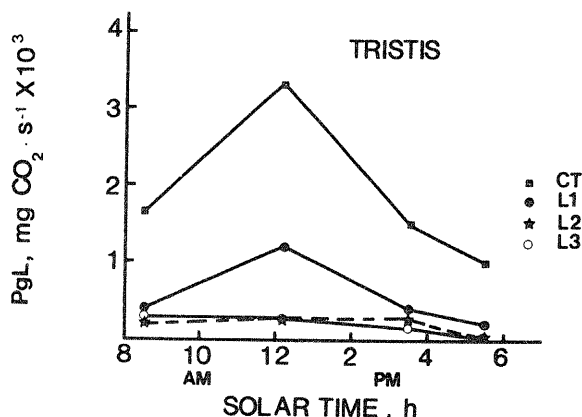


Figure 6.--Diurnal whole-leaf photosynthetic rates (PgL) of four specific crown regions of an individual 2-yr-old *P. tristis* x *balsamifera* cv. 'Tristis #1' tree measured on August 12, 1980. CT = current terminal; L1 = fifth lateral branch on height growth increment 1 (HGI 1); L2 = middle lateral branch on HGI 1; L3 = fifth lateral branch from bottom of HGI 1. Each point represents the average PgL of three leaves measured on the same lateral branch.

Three-year-old Trees.--During the third growing season second-order lateral branches develop on each first-order branch in the crown of poplars and add to the complexity of photosynthesis studies. A 3-yr-old poplar crown has four important leaf populations: (1) the current terminal leaves (i.e. HGI 3), (2) leaves on newly developed first-order lateral branches on HGI 2, (3) leaves on terminal shoots on lateral branches on HGI 1, and (4) leaves on second-order branches arising from the first-order branches on HGI 1.

The general pattern of light interception and PgA that occurs in 2-yr-old trees is also present in 3-yr-old trees. Light interception and PgA rates are highest in the CT (HGI 3) leaves of both *Tristis* and *Eugenei*. Leaves on the upper lateral branches are in a more favorable light environment and have higher PgA rates than the middle and lower branches. Young leaves on the current terminals of lower crown (HGI 1) laterals are also capable of high PgA rates if they receive adequate light. A vertical leaf display, such as in *Eugenei*, allows greater light penetration to the lower laterals resulting in greater PgA rates during midseason compared to a horizontal leaf display, such as in *Tristis*. However, *Tristis* retains its lower crown leaves much later into the growing season than *Eugenei* does. We do not presently know what effect this extended leaf area duration has on total seasonal photosynthate production.

In the third growing season *Tristis* produces both short shoots (SS) and long shoots (LS) on second-order branches in HGI 1. Photosynthetic rate of LS leaves in mid- to late season is greater than SS leaves because the mean foliage age of the LS is less than the SS; therefore, the LS are more active physiologically than the SS (Nelson and Michael 1982). Both shoot types receive low light levels after midseason and have low PgA rates when located in the lower crown, but the contribution of these shoots may be more important during the early part of the growing season when light levels in the lower crown are greater.

Late-Season Photosynthesis.--Many exotic *Populus* clones grown under SRIC in Michigan and Wisconsin retain green leaves in the autumn for 2 to 6 weeks after native aspen have lost their leaves. For example, some clones retain their leaves until November 1 or after in northern Wisconsin. Leaves on the terminal shoots of clones exhibiting significant green leaf retention have substantial photosynthetic rates during this period (Nelson et al. 1982). In two such clones PgA rates ranged from 0.16 to 0.36 mg CO<sub>2</sub> m<sup>-2</sup>s<sup>-1</sup> during the late-season period. These values reflect significant carbon fixation when compared to net photosynthetic rates for *Populus* trees growing under favorable conditions (Nelson et al. 1982) and suggest that autumnal retention of green leaves may be an important factor contributing to the rapid growth of poplars under SRIC in a cold temperate climate.

The complex network of biochemical pathways that make up the photosynthetic process converge into the processes of photosynthate production and partitioning (Wallace et al. 1976). These processes ultimately determine the components of growth and yield in trees and are amenable to study in the field with <sup>14</sup>C-tracer techniques (Isebrands 1982).

Establishment Year.--During the establishment year, growth and development of the young poplar shoot depends upon stored photosynthate until mature leaves develop and begin exporting photosynthate to the shoot. During active shoot elongation and prior to budset, upper mature leaves export photosynthate both acropetally to the newly expanding leaves and shoot and basipetally to the stem and roots (fig. 7A). At budset the direction of photosynthate export makes a dramatically basipetal shift. At this time most of the photosynthate is directed downward to the stem and roots and little if any is exported from one mature leaf to another. Lower mature leaves contribute little photosynthate upward during the establishment year (fig. 7B). After budset, export of photosynthate from lower leaves increases to the roots and decreases to the stem. Although the patterns of export are similar after budset from both upper and lower mature leaves, the total quantity of photosynthate is always greater from the upper leaves<sup>2/</sup> because their photosynthetic capacity is greater (Isebrands 1982).

Poplar clones differ distinctly in the time of budset and leaf fall (i.e., leaf duration). These differences greatly affect the quantity and distribution of photosynthate exported from leaves (fig. 7). For example, *Tristis* normally sets terminal bud from 4 to 5 weeks before the *Euramericana* clones. Therefore, the shift to basipetal export of photosynthate occurs much sooner in *Tristis*. The timing of budset in poplar during the establishment year can also be affected when herbicides are used to control weeds (Akinyemiju et al. 1982). Clones susceptible to glyphosate injury often set bud earlier than resistant clones. As a result, photosynthate distribution patterns prematurely shift downward to the stem internodes and roots.

<sup>2/</sup> Isebrands, J. G., and N. D. Nelson, unpublished data, 1983.

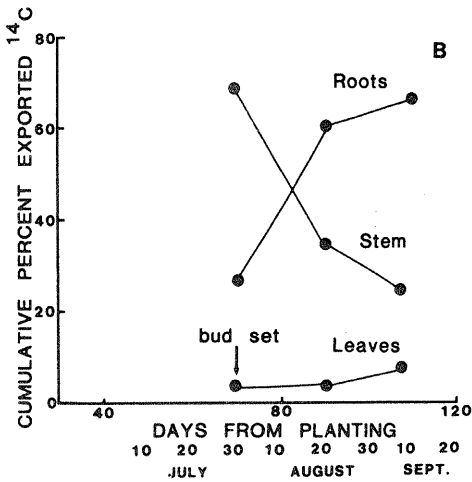
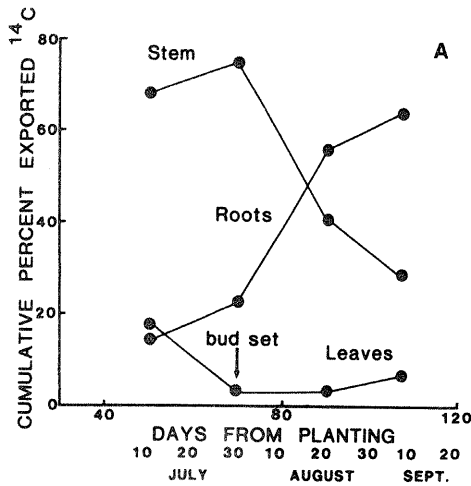


Figure 7.--Cumulative percent of exported  $^{14}\text{C}$  from mature leaves of 1-yr-old *Populus* 'Tristis' shoots grown under SRIC. A. Upper mature leaves treated with  $^{14}\text{C}$ . B. Lower mature leaves treated with  $^{14}\text{C}$ . Arrows show time at which the current terminal shoot set bud (from Isebrands 1982).

Subsequent Growing Seasons.--During the second and subsequent growing seasons the patterns of photosynthate distribution within the crown are complicated by the addition of lateral branches. The complexity of photosynthate patterns, of course, is related to

the intricate photosynthesis patterns discussed earlier. During the second year, as in the first year, shoot growth depends primarily on stored photosynthate until expanding leaves mature. Mature leaves on the current terminal are the most photosynthetically productive leaves in the crown. Carbon fixation declines from the current terminal to the lower lateral branches of the crown (Isebrands 1982).

Photosynthate distribution patterns within second year and older crowns also depends on the various budset and leaf retention times of the current terminal (CT) and lateral shoots (fig. 8). Before CT budset, photosynthate produced by the mature leaves of the CT was exported primarily to the expanding CT leaves above and the elongating CT stem itself (fig. 8A). About 20 percent of the photosynthate produced by the CT leaves was also exported to the stem and roots below. After budset, the quantity exported basipetally to the stem and roots increased, and the quantity exported to the CT itself decreased to about 20 percent. Photosynthate was rarely exported from the CT to the lateral branches.

The patterns of photosynthate distribution from mature leaves on lateral branches were similar regardless of the branch position in the crown (fig. 8B, C, and D). However, the quantity of photosynthate exported and the timing of export from the leaves showed some important differences. Before budset mature leaves of lateral branches exported both acropetally -- to the terminal shoot of the lateral and to the lateral branch itself -- and basipetally to the main stem and roots. Little photosynthate was exported from the lateral branches to the CT shoot or to the other lateral branches. After budset, the quantity of photosynthate exported to the lateral branch itself decreased and the quantity exported to the main stem below and the roots increased. Time of budset differed for various lateral branches in the crown and directly affected photosynthate distribution patterns. For example, budset in the lower and middle lateral branches often occurs 2 to 3 weeks earlier than on the upper lateral branches and 4 to 8 weeks earlier than the CT. Therefore, the basipetal shift of photosynthate export from the lateral branch itself to the main stem and to the roots occurs earlier in the lower portion of the crown than in the upper portion. However, the upper lateral branches generally contribute more photosynthate to the main stem internodes and to the roots than the lower lateral branches (Isebrands 1982).

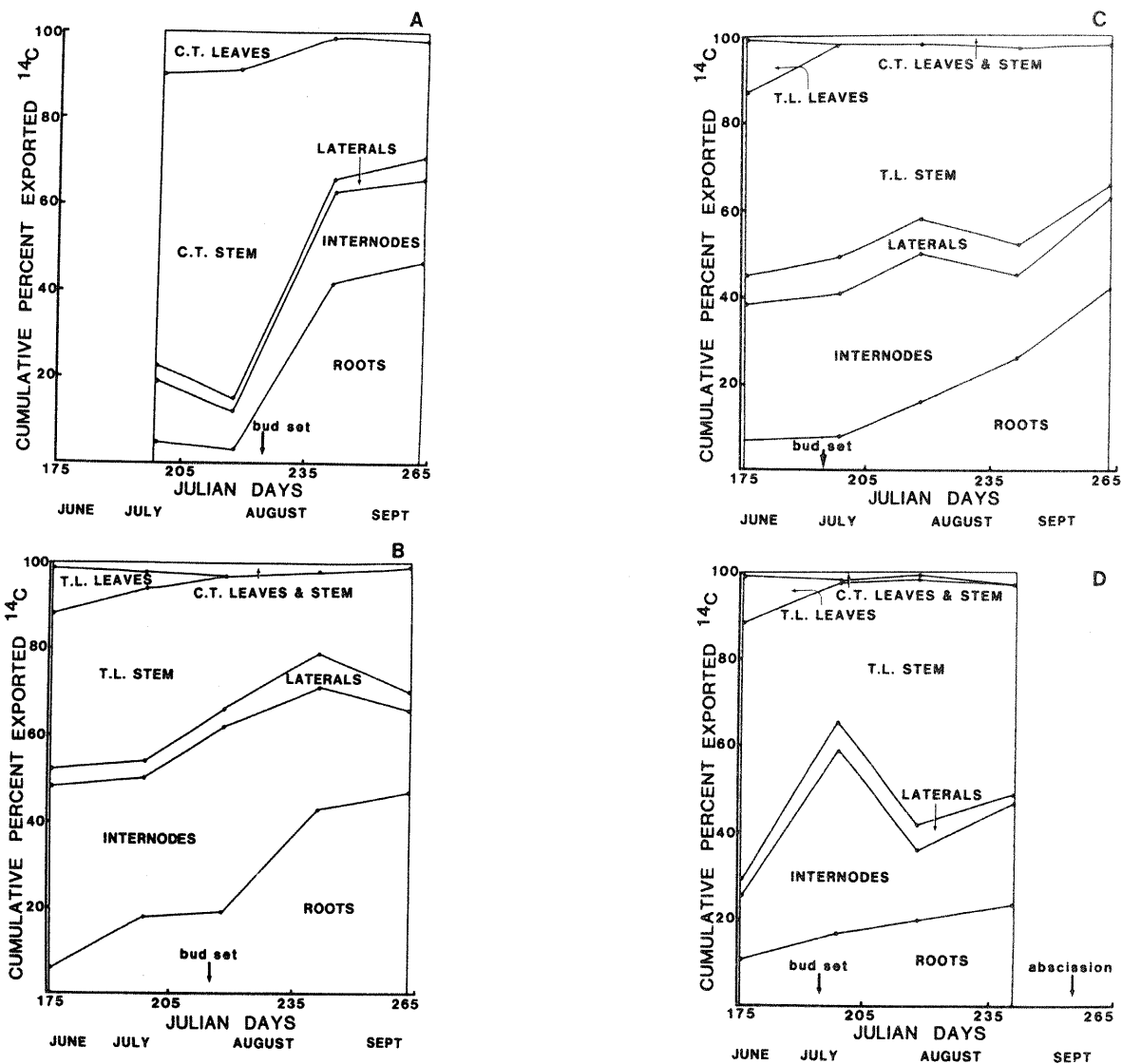


Figure 8.--Cumulative percent of exported  $^{14}\text{C}$  from mature leaves at four positions within the crown of 2-yr-old intensively cultured *P. 'Tristis'* trees treated during the course of the season. Recovery positions include current terminal (CT) leaves, CT stem, treated lateral (TL) leaves, TL stem, lateral branches other than TL, stem internodes of HGI 1, and roots. A. Mature leaves of CT shoot treated with  $^{14}\text{C}$ ; B. mature leaves of fifth first-order lateral branch from top (L1) of HGI 1 treated with  $^{14}\text{C}$ ; C. mature leaves of middle first-order branch (L2) on HGI treated with  $^{14}\text{C}$ ; and D. mature leaves of fifth first-order branch from base (L3) of HGI 1 treated with  $^{14}\text{C}$ . Area under the curves estimates the proportion of  $^{14}\text{C}$  that would be recovered in a season from a given treatment position. Arrows denote date of budset (A-D) and leaf abscission (D) at each treatment position (from Isebrands 1982).

Although lateral branches in poplar are important sources of photosynthate for wood and root production, little photosynthate from lateral branches is exported to the current terminal shoot. This suggests that lateral branches do not directly contribute to height growth in poplar. Moreover, lateral branches

do not export appreciable photosynthate to other lateral branches. Thus, the contributions of lateral branches in poplar are somewhat independent in terms of lateral branch growth. However, the main stem and roots receive localized photosynthate contributions from each of the numerous lateral branches above.

### Late Season Photosynthate Distribution.--

Poplars that exhibit substantial autumnal leaf retention and late-season photosynthesis also export considerable photosynthate from those leaves<sup>4/</sup>. For example, mature leaves of the Strathglass poplar clone (NE-1) continued to export photosynthate for at least 2 weeks after the first major frost. The photosynthate produced at this time was exported primarily to the stem and roots for storage and growth. There is also evidence that biochemical products produced by leaves in the late season are involved in the process of dormancy induction in terminal buds. These results illustrate the importance of the autumn season in poplar culture and indicate that clones that retain mature green leaves into the autumn may have an advantage over those that do not.

### GROWTH ANALYSIS

Growth analyses are quantitative expressions developed to understand biological productivity on the whole-plant level (Evans 1972, Leopold and Kriedemann 1975). They traditionally have been used to compare cultural treatments, varieties, and progenies, and to interpret factors affecting plant growth (Ledig 1974, Wallace et. al. 1976). Growth analysis techniques are also applicable to the study of photosynthate partitioning in plants (i.e., source-sink relations) (Hesketh and Jones 1980, Warren-Wilson 1981). For example, growth analyses can be used to determine whether a poplar clone achieves high yield through high photosynthetic efficiency or through efficient photosynthate partitioning.

Crop yields can be improved by cultural manipulation and/or selection and breeding. However, these methods are most efficient when the physiological processes controlling yield of the crop are understood. One of the most effective ways to achieve this understanding is through studies that integrate physiological methods with growth analyses on the same plants or in the same experiment. But studies that employ such parallel methodology to clarify the relation between physiological characteristics and yield are rare, particularly in forestry.

Growth analyses were conducted in conjunction with photosynthesis and photosynthate distribution studies of Tristis and Eugenei grown under SRIC during the establishment year. The seasonal patterns of several common growth analysis variables are shown for the two clones in fig.9.

<sup>4/</sup> Nelson, N. D., and J. G. Isebrands, unpublished data, 1983.

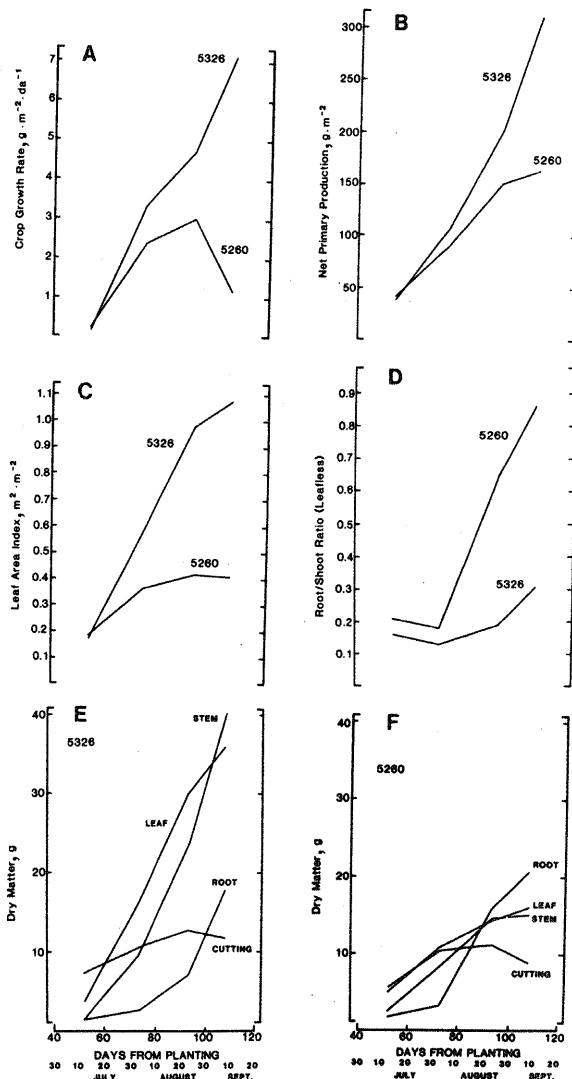


Figure 9.--A comparison during the establishment year of the seasonal patterns of several growth analysis variables for two *Populus* clones grown under SRIC (NC-5326, *P. x euramericana* cv. Eugenei; NC-5260, *P. tristis* x *P. balsamifera* cv. 'Tristis #1'). A. Crop growth rate ( $\text{g m}^{-2} \text{ day}^{-1}$ ); B. net primary production ( $\text{g m}^{-2}$ ); C. leaf area index ( $\text{m}^2 \cdot \text{m}^{-2}$ ); D. leafless root/shoot ratio; E. biomass production (g) by component for Eugenei; and F. biomass production (g) by component for Tristis. Total biomass of both above- and below-ground components are included in A and B.

Crop growth rate, the total dry matter accumulated (above and below ground) per unit land area per day, is given in Figure 9A; net primary production, the total dry matter production minus respiration losses is given in Figure 9B. Patterns of leaf area index and root dry matter to shoot dry matter are also shown (fig. 9C and D), as is seasonal accumulation of dry matter by all tree components for Eugenei (fig. 9E) and for Tristis (fig. 9F). The growth analysis variables coupled with our physiological data led to a better understanding of the growth patterns of the two clones during the establishment year. Distinct clonal similarities and differences were observed that would not have been apparent from the usual mensurational data such as height, diameter, and volume. For example, growth rate of the two clones was similar early in the season, but Eugenei maintained a high growth rate throughout the season (figs. 9A and 9B). Eugenei's growth rate was large a result of continuous leaf production (figs. 9C and 9E). The large difference in leaf area between the clones apparently was a key factor in their productivity differences. This point is further illustrated by the fact that stem dry matter production closely paralleled leaf dry matter production in both clones (figs. 9E and F). Root-shoot ratios were also distinctly different between the two clones (fig. 9D). As predicted by the photosynthate distribution data, Tristis continued root production after terminal budset and into the autumn (fig. 9D and E). In fact, root growth in Tristis continued after above-ground growth (i.e., height and diameter) had apparently stopped (fig. 9F). At the end of the season Tristis had a root/shoot ratio nearly three times greater than that of Eugenei (fig. 9D). Information on root/shoot ratios during the establishment year may be useful in selecting clones to match the sites. Clearly, both above- and below-ground growth data are needed to prevent misinterpretation when comparing clones in establishment studies.

#### SILVICULTURAL AND GENETIC IMPLICATIONS AND RECOMMENDATIONS

Knowledge gained through physiological investigations such as these can be used to modify silvicultural practices to enhance biomass productivity and in the breeding or selection of new poplar varieties adapted to SRIC systems. The importance of physiological information is evidenced by numerous gains in crop yield made by modern agronomists and horticulturists (Evans 1980). Based on the physiological data accumulated to date, the following practical applications appear evident:

1. Clonal selection and silvicultural practices should emphasize the development of maximum leaf area index for a given spacing throughout the rotation.
2. The major portion of a SRIC poplar tree's leaf area should be in the uppermost crown strata where levels of solar radiation are highest.
3. Clones with erect leaves in the upper crown will probably intercept more light after crown closure than those with horizontal leaves because erect leaves allow for maximum penetration of solar radiation into the lower crown strata.
4. Whereas poplars can usually withstand a single moderate defoliation without appreciable growth losses, massive defoliations by insects or pathogens should be prevented, especially if they are concentrated in the productive upper crown. Defoliation in autumn during the development of vegetative maturity and winter hardiness is particularly harmful.
5. Clones selected for SRIC should attain their maximum rate of leaf area production early in the growing season because such clones generally outgrow those whose maximum rate of leaf area production is not reached until late season.
6. Silvicultural practices and clonal selection should be designed to promote retention of green leaves late in the autumn after bud set, especially in the upper crown. During this time photosynthesis can still take place and much of the photosynthate produced is translocated to the stem and roots. Late-season irrigation and fertilization may promote substantial stem and root growth in clones with late leaf retention.
7. Crown photosynthetic rates are under strong genetic control in poplars and can probably be selected for. However, the cost effectiveness of such a program is currently unknown.
8. Clones with few major lateral branches should be selected for SRIC to promote a high ratio of wood to bark in harvested biomass.
9. Silviculturists and geneticists should emphasize leaf production on the current terminal shoot to increase height growth in SRIC poplars because lateral branches do not contribute photosynthate directly to height growth. However, drastically reducing the leaf area on lateral branches may indirectly affect height

growth through negative effects on carbohydrate reserves and root growth.

#### LITERATURE CITED

10. Narrow-crowned clones with steep branch angles should be used in close-spaced plantations to promote the most efficient use of growing space and maximize interception of solar radiation. Broad-crowned clones with flat branch angles should be used in wide-spaced plantations. The ranking of clones for the most important crown characteristics will not change significantly with spacing.
11. Cultural practices should promote mid-season growth of the terminal leader and uppermost lateral branches because their large, photosynthetically efficient leaves are the major suppliers of photosynthate for stem wood production.
12. A high ratio of long shoots to short shoots in the lower crown of SRIC trees should be promoted for maximum growth.
13. Determinate clones that set bud early in the growing season and thereafter translocate photosynthate to the roots should be planted on harsh, droughty sites where irrigation cannot be supplied. On mesic or irrigated sites where severe moisture deficits are uncommon, indeterminate clones that fully utilize the growing season should be planted.
14. Because the biological optimum rotation for SRIC stand occurs when the relative crown size of trees begins to diminish, stand should not be carried beyond the point where the slope of the linear regression of leaf area per tree (or crown volume) on  $D^2H$  declines.
15. To produce the most vigorous coppice stands, SRIC poplar trees should not be harvested immediately after bud set because substantial translocation of photosynthates to the root systems occurs at this time.

These recommendations collectively define our current conception of a superior "ideotype" for a SRIC poplar tree. The recommendations can be used by geneticists to select or "design" improved poplar genotypes and by silviculturists to improve their cultural practices.

#### ACKNOWLEDGMENTS

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