Jour. Korean For. Soc. 64:1-10. 1984

Morphological Characters of Superior Populus alba x Populus glandulosa F₁ Clones under Intensive Culture¹

Kyeong Hack Lee2 · Don Koo Lee2

密植栽培한 第一代 雜種포플러, Populus alba x Populus glandulosa Fi 優良클론의 形態學的 形質에 관한 研究

李 慶 學2・李 敦 求2

ABSTRACT

Two fast-growing clones 65-29-19 and 66-6-8 and two less fast-growing clones 66-14-29 and 66-14-99 were compared at intensively cultured plots to indentify what morphological characters are related to fast growth and high biomass yield of *Populus alba x Populus glandulosa* F₁. The plantations were established in the spring of 1982 and 1983 at the Seoul National University nursery in Suweon. Differences in dry matter production were found among two-year-old clones but not among one-year-old clones. Highly significant correlations were found between total leaf area per tree and total dry weight per tree and between total branch length per tree and total dry weight per tree for two-year-old clones. This relation was more obvious during the late growing season. Morphological characters desirable for producing high biomass identified in fast-growing clones were as follows; high shoot-root ratio, high leaf surface area per tree, long leaf retention period, and many small leaves and compact crown architecture in the upper portion of tree crown.

Key words: morphological characters; Populus alba x P. glandulosa; intensive culture; early selection.

要 約

本 研究는 biomass生産을 爲한 密植栽培에 適合한 樹種으로 우리 나라에서 開發된 第一代 雜種 포플러, Populus alba × Populus glandulosa F₁ 클론들 中 優秀한 生長을 보이는 2個의 클론과 그렇지 못한 2個의 클론, 1,2年生을 對象으로 어떠한 形態的 特性이 빠른 生長에 關聯되는가를 알아보기 爲하여 實施되었다. 本實驗은 수원에 있는 서울大學校 苗圃場에 ha當 20,000 本을 植栽한 후 試驗區를 設置하여 生長, 葉特性, 가지特性 等을 時期別로 調査, 比較하였다. 個體當 乾物質 生産量에 있어서 2年生 클론잔에는 有意差가 認定되었으나, 1年生은 認定되지 않았다. 2年生에 있어서 個體當 葉面積과 乾物質 生産量, 그리고 個體當 総 가지의 길이와 乾物質 生産量間에 高度의 相關이 나타났으며, 特히 注目할 만한 것은 이러한 相關이 生長期 後

¹ 接受 4月3日 Received April 3, 1984.

² 서울大學校 農科大學 College of Agriculture, Seoul National University, Suweon, Korea. This study was supported by grants from the Korea Science and Engineering Foundation.

半期인 8月과 9月에 더욱 뚜렷하였다. 높은 物質 生産量을 보이는 클론의 形態學的 特性은 다음과 같았다. 즉, 높은 shoot-root ratio를 보이며, 葉生長에 있어서는 光合成器官의 크기를 代表할 수 있는 個體當 葉面積이 많았고, 葉保有期間이 길어 生長을 더 오래할 수 있었다. 또한 樹冠 上部에 작은 葉이 많아서 光合成에 必要한 빛을 效率的으로 利用할 수 있었고 가지의 特性으로는 길이가 길고 가지數는 많아서 粗密한 樹冠形態를 보이는 것 들이었다.

INTRODUCTION

Breeding programs for plant yield improvement is usually based on "defect elimination" to remedy some known defects in the crop, or on "selection for high yielding traits" using advanced statistical designs and analyses. Recently, an additional valuable approach was to introduce the concept of plant ideotypes having model characteristics favorable to growth. Such plant may have leaves and branches oriented ideally for receiving the great amount of sunlight.

Poplar has been noticed as an important species in North America, Asia and Europe because of its rapid growth and high biomass production in short rotation intensive culture system.

In Korea, Populus alba x Populus glandulosa F_1 developed in 1956 at the Institute of Forest Genetics was recognized as a fast-growing species appropriate for short rotation intensive culture system. Much effort to produce superior clones has been concentrated by hybridization techniques. A research with the various clones has often been done on growth, biomass production or physiology but little on morphological characters. Accordingly, it would be meaningful to examine what morphological attributes are related to fast growth and high yield in Populus alba x Populus glandulosa F_1 under intensive culture.

The objective of this study was to find some morphological characters related to fast growth and high yield, which can be used for selecting superior Populus alba x Populus glandulosa F₁ clones at early stage. The specific objective was to compare the leaf and branch characteristics between fast- and less fast-growing clones of one- and two-year-old Populus alba x Populus glandulosa F₁ growing at a 25cm x 25cm spacing.

LITERATURE REVIEW

Selection of ideotype, or ideal plant type may be useful to plant improvement or breeding programs. Donald(1968)⁵⁾ introduced the concept of ideotype in wheat breeding. Since 1968, much effort to construct ideotypes was given to the field of crop but rarely to tree.

Brunig (1976)²⁾ established a scheme to distinguish and classify the major tree crown ideotypes; that is, tree type ideally adapted to particular conditions of solar radiation, water supply and wind. Recently, there have been several attempts to develop an ideotype for poplars. Larson and Gordon (1969)¹⁶⁾ designed an ideotype that has included some physiological characters such as 1) full utilization of the growing season by meristem, 2) compact crown and roots, and 3) high total photosynthetic production. Larson (1973)¹⁵⁾ described in detail the ideotype for cottonwood, based on selected physiological and morphological attributes. Dickmann(1975)4) suggested tree ideotypes to be used in short rotation intensive culture systems. Those ideotypes included high shoot-root ratio, upright excurrent growth habit, steep branch angle, indeterminate growth and rapid juvenile growth. The study done by Larson et al. (1976)¹⁷⁾ was more specific, but still non-quantitative, and included the production of specific wood qualities. Gordon and Promnitz(1976)¹⁰⁾ attempted to construct ideotypes from laboratory and field measurements of physiological traits using multivariate techniques and simulation models. Promnitz and Wray(1976)²⁴⁾ suggested rapid selection techniques for identifying superior clones with some physiological and morphological traits.

Leaf area, leaf size, leaf retention, and leaf display have been considered important factors influ-

encing light interception and photosynthesis, which, in turn, affect biomass production. Watson(1956)²⁵⁾ reported that two of the major limitation to plant productivity within a single growing season are the length of time required to obtain 'optimum' leaf area and the ability of the crop to maintain that area. Loomis and Williams(1963)¹⁹⁾ suggested that leaf area adjustment and manner of leaf display should be considered to improve utilization of light, indicating those affect optimum leaf area indices. The strong relations were found among leaf angle, leaf area, and canopy photosynthesis (Duncan, 1971).6) Many leaf characteristics are affected not only by most agronomic practices but also by strong genetic control (Loomis et al., 1971).20) Kramer and Kozlowski(1979)¹⁴⁾ reported that leaves with different age, position, structure, shoot type and distance from the main stem have distinctively different physiological process.

Recently, numerous studies have been done on the leaves for biomass producition under short rotation intensive culture. Gordon and Bentley (1970)9) reported that the most effective way to increase photosynthetic leaf surface under intensive culture condition was to plant tree at a close spacing and thereby to increase the total number of leaves produced in trees. In Populus, clonal variation in leaf area duration was related to the length of the active shoot growth period (Cannell and Willett, 1976)3) and to the leaf fall in autumn (Isebrands et al., 1977). The high biomass productivity of intensively cultured was closely related to the large number of leaves (Zavitkovski et al., 1977). 26) The leaf characteristics of intensively cultured Populus differed depending upon each height growth increment (Isebrands and Nelson, 1982). 11) Nelson and Michel (1982)21) found that long and short shoots of Populus 'Tristis #1' grown under intensive culture differed in the size of individual leaves, the total area and the number of leaves on their shoots. Pollard (1970)²³⁾ mentioned seasonal development of leaves and leaf area on different shoot types in young aspen and their effect upon production.

Isebrands et al. (1977)¹²⁾ explained that large leaf area came from the upper part where light is readily available during leaf area development in intensively cultured plots.

Lately, a few branch characteristics have been noticed as an important trait affecting biomass productivity. Farmer (1976)7) explained that branch characteristics such as angle from main stem. size, number, and distribution pattern play an important role in determining the crown architecture and canopy density of forest trees, both of which would be the major traits influencing forest productivity and yield. Nelson et al. (1981)²²⁾ quantified the effect of clone and spacing on several important first-order branch characteristics of 9 Populus clones under intensive culture. Thus, ideal crown architecture affected by leaf area development, leaf arrangement in shoot, and display, size or angle of branches provides well for light interception, which in turn, is closely related to high biomass production in intensive culture system.

MATERIALS AND METHODS

Plant Materials

Four clones of one- and two-year-old *Populus alba* x *Populus glandulosa* F_1 were provided as plant materials. They were selected among 13 clones planted at the Seoul National University nursery, Suweon. Among the four clones, clones 66-14-29 and 66-14-99 showed relatively low biomass production, and clones 65-29-19 and 66-6-8 did high biomass production (Kim and Lee, 1983). 13

Unrooted cuttings were individually planted on plastic pots (21 cm in diameter and 18 cm in height) in late-April. They were grown in greenhouse until early-August and then transplanted into the nursery. Two-year-old clones were provided from the plantings described by Kim and Lee (1983). Clone 66-14-29 was, however, transplanted from other plots for this study in April 17.

Methods

Three trees per each clone were randomly select-

ed to measure the growth of leaves, diameter and height. Measurement was done monthly from June through October.

Total height and diameter at 0.2 m from the soil surface were measured to the nearest 1.0 cm and 0.01 cm, respectively. Sample trees of one- and two-year-old clones were harvested in mid-September and early-October, respectively. Trees were separated into leaves, stem-branches and roots and then dried at 80°C in an oven for 72 hours. Total dry weight per tree was calculated by summing those parts. A shoot-root ratio was calculated by dividing the dry weight of leaves and stem-branches with root dry weight. A two-year-old sample tree was stratified into two height growth increments (HGI); HGI1 and HGI2 stand for the vertical growth of main stem during the previous year and that during the current year, respectively.

Leaf characteristics including the number of leaves, leaf area, and average leaf size were measured as follows. All the leaves in the terminal of main stem were counted. Every three leaves were sampled systematically to measure leaf length and width. Leaf areas were estimated by the method described by Kim and Lee(1983). Within each of the HGI's, every three long branches (greater than 50 cm in length) and every three short branches (less than 50 cm in length) were selected systematically to estimate the number of leaves and leaf area. Their estimation was the same as that adopted in the terminal. Thus, total leaf areas per tree were calculated by summing the areas from the terminal of main stem. HGII and HGI2.

Number of branches, total branch length, average branch length and angle of origin were measured for each of the HGI's and then calculated for each of the sample trees. Angle of origin, here, indicates the angle made by a branch and main stem in a connection part. All the methods used for measuring one-year-old trees were similar to those adopted for two-year-old trees. In addition, the relationships between total dry weight and the variables measured above were examined with correlation coefficient.

RESULTS

Height, Diameter Growth and Dry Weights

Clonal means of total dry weight and shoot-root ratio per tree for one-year-old Populus alba x P. glandulosa F₁ clones are shown in Tables 1 and 2, respectively. Clonal differences in total dry weight were significant at the 5 % level for two-year-old plantations but not for one-year-old plantations. The shoot-root ratio increased with increasing total dry weight. Figures 1 and 2 show seasonal changes in mean height and diameter at 0.2 m of two-yearold clones. Clone 65-29-19 showed high rate of height and diameter growth during the growing season. However, clone 66-14-29 markedly showed low rate, which may be due to late transplanting in mid-April. At one-year-old plantations, clones 66-6-8 and 65-29-19 showed relatively high growth rate (Figures 3 and 4).

Table 1. Clonal means of total dry weight per tree and shoot-root ratio per tree at two-year-old plots

					Shoot-
Clones		root			
	Stem	Leaves	Root	Total	ratio
66-14-29	97	9	48	154 a*	2.21
66-14-99	366	48	96	509 b	4.31
66-6-8	463	53	83	541 b	5.36
65-29-19	617	95	140	892 с	5.51

^{*} Figure with a column followed by the same letter indicates they are not significantly different at the 5% level.

Table 2. Clonal means of total dry weight per tree and shoot-root ratio per tree at one-year-old plots

Clones		Shoot- root ratio			
Ciones	Stem				
66-14-29	48	27	22	97	3,41
66-14-99	43	22	22	87	2.95
65-29-19	53	25	24	102	3.25
66-6-8	63	32	27	122	3,52

Leaf Growth and Area Development

Seasonal variations in the number of leaves,

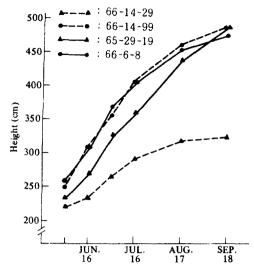


Fig. 1. Seasonal changes in mean height of twoyear-old clones.

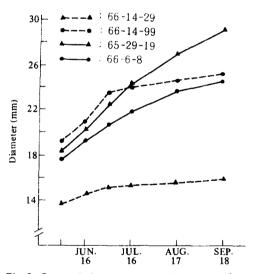


Fig. 2. Seasonal changes in mean diameter at 0.2 m from the soil surface of two-year-old clones.

total leaf area, and average leaf area per leaf of twoyear-old clones are given in Figures 5 and 6. Table 3 shows seasonal variations in the number of leaves and the leaf area of the one-year-old clones. Until mid-July, the number of leaves and the leaf area did not show significant differences among twoyear-old clones. During late growing season when most of the number of leaves and the total leaf area were occupied by current terminal and HGI2,

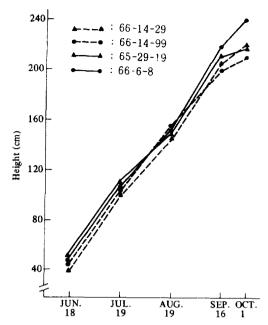


Fig. 3. Seasonal changes in mean height of one-yearold clones.

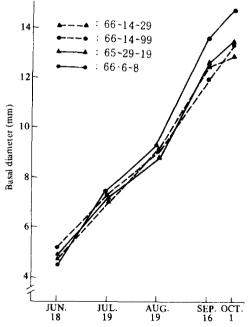


Fig. 4. Seasonal changes in basal diameter of oneyear-old clones.

clones 65-29-19 and 66-6-8 have higher leaf numbers and areas than clones 66-14-29 and 66-14-99. Fast-growing clone 65-29-19 kept them longer

even in September when those of other clones were mostly reduced (Figure 5).

The number of leaves and the total dry weight had higher correlation coefficient in August (r = 0.8205) and September (r = 0.7495) than in any other months. This close relationship was similar to that between the total leaf area and the total dry weight in August (r = 0.9304) and September (r = 0.9783).

Seasonal variations in the number of leaves and the total leaf area per tree at one-year-old clones are given in Table 4. Low correlation (r = 0.3338 to 0.5542) was observed between the number of leaves and the total dry weight. However, relatively high correlation (r = 0.7828 to 0.8622) was found between the total leaf area and the total dry weight in late growing season. The fast-growing clones 65-29-19 and 66-6-8 showed relatively high increase in the number of leaves and the total leave area from August to September.

Clonal maximum values for the number of leaves and the total leaf area were observed in mid-September for all of the one-year-old clones, whereas two-year-old clones showed their maximum

Table 3. Seasonal variation in leaf characteristics of one-year-old Populus alba x Populus glandulosa F_1 clones

C1	Number of leaves/tree				Leaf area/tree (cm)							
Clones	Jun.	Jul.	Jul.	Aug.	Sep.	Oct.	Jun.	Jul.	Jul.	Aug.	Sep.	Oct.
	16	5	16	17	18	1	16	5	16	17	18	i
66-14-29	21	28	35	51	75	74	469	1114	1679	2971	4375	4337
66-14-99	21	30	31	46	87	71	559	1419	1807	2703	4328	3693
65-29-19	20	28	35	99	160	144	479	1270	1816	2898	6319	5743
66-6-8	21	29	36	98	162	150	515	1074	2087	3446	6694	6365

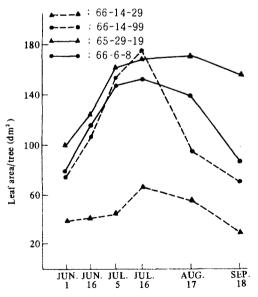


Fig. 5. Seasonal changes in total leaf area per tree of two-year-old clones.

values in July.

Branch Characteristics

Seasonal changes in the number of branches

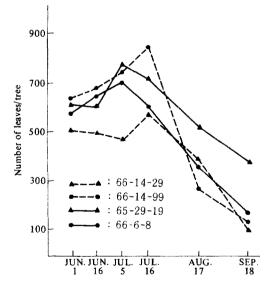


Fig. 6. Seasonal changes in the number of leaves per tree of two-year-old clones.

and total branch length of two-year-old clones are given in Figures 7 and 8. Maximum numbers of branches for clones 66-6-8 and 65-29-19 were observed in early-July whereas those of clones

Table 4. Branch angle of origin when the maximum number of branches were observed within each HGI of two-year-old clones.

Clones	HGI 1 (July 5)	HGI 2 (Aug. 17)		
66-14-29	47.32	_ *		
66-14-99	65.21	54.49		
66-6-8	65.70	58.43		
65-29-19	70.43	62.80		

^{*} no data available.

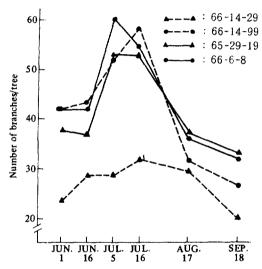


Fig. 7. Seasonal changes in average number of branches per tree of two-year-old clones.

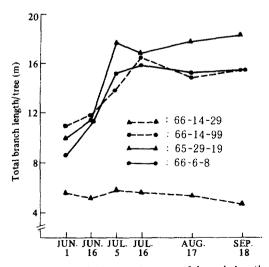


Fig. 8. Seasonal changes in sum of branch length per tree of two-year-old clones.

66-14-29 and 66-14-99 in mid-July. Since July, most of the short branches within HGII fell, which, in turn, the numbers decreased rapidly. Fast-growing clone 65-29-19 showed the continuous increase in total branch length during the growing season (Figure 8).

Total number of branches was not strongly related to the total dry weight over the whole growing season. This may be due to the fact that total branch number included the number of short branches which proportioned mostly. However, high correlation (r = 0.9024 to 0.9695) was found between the total branch length and the total dry weight in August and September when most of the short branches in HGI1 have already fallen.

Clone 65-29-19 had relatively larger branches within HGI1 than other clones in June when small young branches were found only within HGI2. It also showed many large branches within HGI2 in July, August and September when leaves on its branches were vigorously growing.

Clone 65-29-19 showed higher angle of origin than other clones. Figure 9 shows schematic diagrams of fast-growing clone 65-29-19 and less

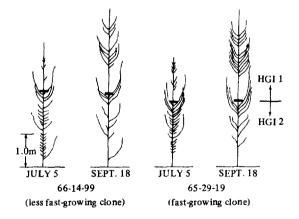


Fig. 9. Schematic diagrams showing branching geometry between fast-growing and less fast-growing clones at two-year-old plots. Diagrams were drawn to scale for clonal averages for height, height growth increment lengths, number of branches, average branch length for HGIs, and angle of branching origin. Horizontal lines indicate HGI bounderies.

fast-growing clone 66-14-99 in early-July when the branches within HGI2 began to grow and in mid-September when the growth almost stopped. Clone 65-29-19 showed earlier branching than clone 66-14-99. In September, fast-growing clone 65-29-19 produced more and larger branches than less fast-growing clone 66-14-99. Therefore, high total branch length and compact crown were exhibited by clone 65-29-19.

DISCUSSION

Height, Diameter Growth and Dry Weight

Height and diameter of a tree could be used as variables for estimating growth. As there were high correlations between dry weight and square of diameter times height for both one- and two-year-old plantations in this study, height, diameter and dry weight were considered to present actual biomass production.

The result that differences in dry matter production were significant for two-year-old clones but not for one-year-old clones was similar to that reported by Kim and Lee(1983)¹³⁾ who compared growth potential with various *Populus* hybrids. Therefore, clonal examination for biomass production in intensive culture system should be tried for more than two years.

The clones with higher biomass production also showed higher shoot-root ratio than those with less biomass (Table 1 and 2). This may be due to more effective photosynthate distribution into stems under sufficient water and nutrient conditions. Such result was suggested by Borchert(1973)¹⁾ who developed simulation model of rhythmic tree growth under constant conditions with two tropical trees, Hevea rasiliensis and Theobroma cacao.

Clone 65-29-19 showing high rate of diameter growth until late growing season produced high biomass. Therefore, it is noteworthy to examine what particular characters of clone 65-29-19 affected high diameter growth during late growing season.

Leaf Growth and Area Development

High correlation between total leaf area per tree and total dry weight per tree over most of the growing season for two-year-old clones indicates an important role of leaf in photosynthesis which directly relates to growth and wood production. Especially, remarkably high correlations between total leaf area and total dry weight per tree, and between the number of leaves and total dry weight per tree in late growing season appeared to be affected largely by photosynthesis of the late retained leaves.

High total leaf area was produced consistently by fast-growing clone 65-29-19 because of larger leaves within HGII in early growing season, and many smaller leaves within HGI2 in late growing season. Such consistent trend even in late growing season was also reported by Kim and Lee(1983)¹³⁾ who tested with same clones. Many small leaves as an ideal character of producing dry matter was suggested by Donald(1968)⁵⁾ who mentioned that a plant characterized by many small leaves scattered uniformly over the length of crown may offer advantages in dense community under high illumination. Larson (1973), 15) however, reported that medium to large leaves of cottonwood are advantageous to maximize photosynthesis per unit leaf area.

Remarkablely large number of leaves and total leaf area of fast-growing clone 65-29-19 in September may be due to the longer retention of leaves than other clones. This longer retention accelerated consistently high diameter growth and dry matter production in late growing season. Larson(1973)¹⁵⁾ also suggested long leaf retention as a character for ideotypes of cottonwood. Full utilization of the growing season could be a characteristics for ideotype of *Populus* (Larson and Gordon, 1969).¹⁶⁾ Dickmann (1975)⁴⁾ also mentioned indeterminate growth as a character of tree ideotypes to be used in short rotation intensive culture systems. This character fully utilizes the favorable conditions for growth during the frost-free growth period.

Clonal maximum values of leaf number and total leaf area at one-year-old plantations occured later than those at two-year-old plantations in this study. This fact seems to explain that young trees grow longer than old trees during the growing season (Lee, 1978). 18)

Branch Characteristics

High correlation was found between total branch length and total dry weight of two-year-old clones in August and September. It indicates that total branch length within HGI2 are more closely related to dry matter production than that within HGI1. This may be true because the branches within HGI2 have most of the total leaves in the crown and are likely to receive a great amount of light for photosynthesis (Table 4 and Figure 9). Such fact was also shown by Nelson et al. $(1981)^{22}$) who observed crown architecture according to height growth increments with various four-year-old *Populus* clones grown under intensive culture.

A fast-growing clone 65-29-19 with many long branches and high total branch length, showed compact crown in late growing season (Figure 9). Compact crown may be advantageous to growth in narrow spacings without physical interference. Similar characters in tree crowns were also stated by Dickmann (1975)⁴⁾ and by Larson and Gordon (1969)¹⁶⁾ as a tree ideotype under intensive culture system.

The angle of origin showed some differences among two-year-old clones. Fast-growing clone 65-29-19 showed larger angle than less fast-growing clones. Similar result was found in the growth study with *Populus* under intensive culture system by Hansen *et al.*²/ Dickmann (1975)⁴), however, suggested a steep angle to be more ideal for intensively cultured tree species. The relation between branch angle and dry matter production is still uncertain in *Populus*. For example, Nelson *et al.* (1981)²²) mentioned the development of a biologically meaningful variable for effective branch angle may be complex task for intensively cultured *Populus*. Therefore, the quantitative methods for analyzing entire branch systems are needed to

elucidate the relation in further studies. This kind of study was done in a tropical tree, *Terminalia* by Fisher and Honda (1979).⁸⁾

Further studies not only on morphological but physiological aspects are recommended at different spacings, in different ages and with a variety of clones in the future.

LITERATURE CITED

- Borchert, R. 1973. Simulation of rhythmic tree growth under constant conditions. Physiol. Plant. 29:173-180.
- Brunig, E. F. 1976. Tree forms in relation to environmental condition: an ecological view.
 Pages 139-156 in M. G. R. Cannell and F. T. Last, eds. Tree Physiology and Yield Improvement. Academic Press, New York, NY.
- Cannell, M. G. R. and S. C. Willett. 1976. Shoot growth phenology, dry matter distribution and root:shoot ratios of provenances of Populus trichocarpa, Picea sitchensis and Pinus contorta growing in Scotland. Silvae Genet. 25:49-59.
- Dickmann, D. I. 1975. Plant materials appropriate for intensive culture of wood-fiber in the North Central Region. Iowa State J. Res. 49(3):281-286.
- Donald, C. M. 1968. The breeding of crop ideotype. Euphytica 17:385-403.
- Duncan, W. G. 1971. Leaf angles, leaf area, and canopy photosynthesis. Crop Sci. 11: 482-485.
- Farmer, R. E., Jr. 1976. Relations between genetic difference in yield of deciduous tree species and variation in canopy size, structure and duration. Pages 119-137 in M. G. R. Cannell and F. T. Last, eds. Tree physiology and Yield Improvement. Academic Press, New York, Ny.
- Fisher, J. B. and H. Honda. 1979. Branch geometry and effective leaf area; a study of Terminalia - branching pattern. 1. Theoretical

^{*/}This was presented in research paper of Nelson et al. (1981). 22)

- trees. Amer. J. Bot. 66(6): 633-644.
- Gordon, J. C. and W. Bentley. 1970. Wood production in industrial society. Univ. Wis. For. Res. Note 150.
- Gordon, J. C. and L. C. Promnitz. 1976. A physiological approach to cottonwood yield improvement. Pages 66-88 in B. A. Thielges and S. B. Land, Jr., eds. Symposium on Eastern Cottonwood and Related Species. Greenville, MS. Sep. 28-Oct. 2, 1976.
- 11. Isebrands, J. G. and N. D. Nelson. 1982. Crown geometry of short-rotation intensively cultured *Populus*. II. Branch morphology and distribution of leaves within the crown of *Populus* 'Tristis' as related to biomass production. Can. J. For. Res. 12:853-864.
- 12. Isebrands, J. G., L. C. Promnitz and D. H. Dawson. 1977. Leaf area development in short rotation intensive cultured *Populus* plots. Pages 201-209 in Proc. of the TAPPI For. Biol. Wood Chem. Conf. Madison, WI, June 20-22, 1977.
- 13. Kim, G. T. and D. K. Lee. 1983. A technique for selecting superior *Populus alba x Populus* glandurosa F₁ clones with some physiological characters. Jour. Korean For. Soc. 59:15-30.
- Kramer, P. J. and T. T. Kozlowski. 1979.
 Physiology of Woody Plants. Academic Press,
 London. 811pp.
- 15. Larson, P. R. 1973. Physiological parameters of intensive culture; theoretical and applied. In Proc. of USDA For. Serv. In-service Workshop Intensive Culture, Rhinelander, Wisconsin, Sept. 18-19, 1973.
- Larson, P.R. and J.C. Gordon. 1969. Lead development, photosynthesis, and C¹⁴ distribution in *Populus deltoides* seedlings. Amer. J. Bot. 56(9):1058-1066.
- Larson, P. R., R. E. Dickson and J. G. Isebrands.
 Some physiological applications for

- intensive culture. USDA For. Serv., General Technical Rep. NC-21:10-17.
- 18. Lee, D. K. 1978. The influence of the geometry and distribution of root systems on coppice regeneration and growth of hybrid poplars. Unpublished Ph.D. thesis. Iowa State University, Ames, Iowa. 119pp.
- Loomis, R. S. and W. A. Williams. 1963.
 Maximum crop productivity: an estimate.
 Crop Sci. 3:67-72.
- Loomis, R. S., W. A. Williams, and A. E. Nall. 1971. Agricultural productivity. Ann. Rev. Plant Physiol. 22:431-468.
- Nelson, N. D. and D. Michel. 1982. Photosynthesis, leaf conductance, and specific leaf weight in long and short shoots of *Populus* 'Tristis #1' grown under intensive culture. Forest Sci. 28(4):737-744.
- Nelson, N. D., T. Burk and J. G. Isebrands. 1981. Crown architecture of short-rotation, intensively cultured *Populus*. I. Effects of clone and spacing on first order branch characteristics. Can. J. For. Res. 11:73-81.
- 23. Pollard, D. F. W. 1970. Leaf area development on different shoot types in a young aspen stand and its effect upon production. Can. J. Bot. 48:1801-1804.
- Promnitz, L. C. and P. H. Wray. 1976. Rapid selection techniques for identifying superior clones. USDA For. Serv., General Technical Rep. NC-21:25-31.
- Watson, D. J. 1956. Leaf growth in the relation to crop yield. Pages 178-191 in F. L. Milthorpe, ed. The Growth of Leaves. Butterworths Scientific Publication, London.
- 26. Zavitkovski, J., J. G. Isebrands and T. R. Crow. 1974. Application of growth model analysis in forest biomass studies. Pages 196-226 in Proc. the 3rd North American Forest Biology Workshop, Colorado State Univ. Fort Collins.