

A Technique for Selecting Superior *Populus alba* × *Populus glandulosa* F₁ Clones with Some Physiological Characters¹

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몇 生理的 特性을 利用한 第一代 雜種 포플러, *Populus*
alba × *Populus glandulosa* F₁의 優良 clone 選拔에 關한 研究¹

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ABSTRACT

To select the superior clones of *Populus alba* × *Populus glandulosa* F₁, growth and some growth-related physiological characters were examined for thirteen, one-year-old and fifteen, two-year-old clones, respectively at the Seoul National University nursery in Suweon. Clonal differences in growth (total dry weight per tree), leaf area per tree and leaf chlorophyll content per tree at two-year-old plots were highly significant at the 1% level, but not at one-year-old plots. Highly significant correlation was found between leaf area per tree and total dry weight per tree ($r=0.865$), between leaf chlorophyll content per tree and total dry weight per tree ($r=0.888$), and between photosynthetic ability per tree and total dry weight per tree ($r=0.745$). The photosynthetic ability and leaf chlorophyll content per unit leaf area of one-year-old plant increased with increasing leaf order number from top, reached maximum value in the twenty-eighth and thirty-third leaves, respectively, and then decreased gradually from those leaves to base. Clones 68-1-54, 66-26-55 and 65-22-11 showed best growth based on leaf area per tree, leaf chlorophyll content per unit leaf area and photosynthetic ability of leaf tissue per unit area. Growth yield of *Populus alba* × *P. glandulosa* F₁ clones could be estimated from either leaf area per tree or leaf chlorophyll content per tree. Therefore, measurements of leaf area and leaf chlorophyll content appear useful to select superior *Populus* clones in early growth.

Key words: *Populus alba* × *Populus glandulosa* F₁; leaf area; chlorophyll content; photosynthetic ability.

要 約

第一代 雜種 포플러 *Populus alba* × *Populus glandulosa* F₁의 優良 clone 을 選拔하기 爲해, 서울大學校 農科大學 苗圃場에서 密植栽培(20,000 本/ha)한 1, 2 年生 各各 13, 15 clones 을 對象으로 生長과 生長에 關聯된 몇 生理的 特性을 調査, 比較하였다. 個體當 乾重量, 葉面積, 單位葉面積當 葉綠素 含量에 있어서 2 年生 clone 들 間에는 高度의 有意差가 認定되었으나, 1 年生 clone 들에 있어서는 有意差가 認定되지 않았다. 個體當 乾重量과 個體當 葉面積과의 相關關係는 $r=0.865$, 個體當 乾重量과 個體當 葉綠素含量과의 相關關係는 $r=0.888$

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로 高度의 相關이 認定되었으며, 個體當 乾重量과 個體當 光合成能力과의 相關關係에서는 $r=0.745$ 로 比較의 높은 相關이 認定되었다. 1年生 clone의 葉部位別 葉單位面積當 光合成能力과 葉綠素含量은 葉順序가 增加함에 따라 增加하여 28번째와 33번째 葉에서 各各 最大值를 보였으며 그후 아래葉으로 내려올 수록 減少하는 傾向을 보였다. Clone 68-1-54, 66-26-55, 65-22-11 등은 個體當 葉面積, 單位面積當 葉綠素含量 및 光合成能力으로 보아 다른 clone들 보다 良好한 生長能力을 보였다. 第一代 雜種 포플러, *Populus alba* × *Populus glandulosa* F₁의 幼時 生長量은 個體當 葉面積이나 個體當 葉綠素含量으로 推定할 수 있었으며, 이러한 事實로 보아, 葉面積과 葉綠素含量의 測定値는 本 雜種 포플러의 優良 clone을 選拔하는 하나의 基準으로 使用될 수 있다.

INTRODUCTION

Since 1920 large increase in productivity has been achieved with agricultural crops such as corn but no comparable increase has been attained with woody plants. Thus, during the last ten years, more attention has been focused on the need for intensive silvicultural practices to increase fiber production per unit area of land.

Because of rapid growth, *Populus* has become a prominent tree species for innovative intensive culture systems designed to maximum biomass production in various parts of the world.^{6,17,20,23,35,47,48)}

The hybrid poplars, *Populus alba* × *Populus glandulosa* F₁ developed at the Institute of Forest Genetics of Korea in 1956 have shown great potentials of producing biomass. Recently, much interest have been focused on the biomass production of these *Populus* clones in Korea, because of strong coppicing ability and many root suckers.^{41,49)}

The increase in tree productivity through improved breeding technique is newly growing and interesting subject of research, particularly, on the increment of photosynthetic rates. Selection during the immature period may shorten considerable time lag and at least may eliminate undesirable genotypes early. Differences in photosynthetic rates have been observed between varieties of many crops and between clones of certain tree species.^{7,16,17,28,29,30,33,43,59)} However, the correlation between photosynthetic rates of single leaf and tree growth rate or yield has been rarely reported. Because more *Populus* species and varieties are

available than can reasonably be field-tested, a rapid technique for the selection of superior clones is desirable. The technique must be simple and fast, compared to field-growth studies that might take much time, efforts, and money.

Thus, the objective of this study was to develop a method for selecting the best clones in productivity at early stages: 1) by comparing growth of *Populus alba* × *P. glandulosa* F₁ clones and 2) by examining leaf chlorophyll content, leaf area and photosynthetic ability of leaf tissues in relation to the growth between clones.

LITERATURE REVIEW

Fast growing tree species has frequently been examined by foresters to enhance the biomass production. In particular, *Populus* was often chosen as one of the biomass producing species, and grown under intensive culture in many parts of the world to increase maximum biomass products on a unit area basis.^{6,7,17,20,23,35,41,45,48,49)}

For the yield improvement, photosynthetic activities of the plants in relation to growth have been much researched by many plant physiologists and breeders. Dickmann (1971)¹⁸⁾ investigated photosynthesis and respiration of developing leaves of cottonwood, and reported that maximum photosynthetic rate was attained just before leaf extension growth ceased. Drew and Bazzaz (1978)²²⁾ reported clonal variation in assimilate of plant parts of eastern cottonwood, and enhanced biomass products results from being allocated with more photosynthate in stem than any other parts. Such photosynthate allocation was studied in

Pinus taeda,^{13,14)} cottonwood,²¹⁾ larch and sycamore.³⁷⁾ Hodinott *et al*(1974)³¹⁾ investigated the net assimilation capacity with leaves of long and short shoots of *Ginkgo biloba*. Furukawa(1975)²⁵⁾ compared photosynthesis, postillumination CO₂ outburst, CO₂ compensation, and dark respiration in leaves of four *Populus* varieties, sunflowers and beans. Kim *et al* (1977)³³⁾ studied photosynthesis of *Populus alba* x *P. glandulosa* in relation to leaf age. Schaedle and Foote (1971)⁵⁴⁾ worked on seasonal changes in the photosynthetic capacity of *Populus tremuloides* bark. Inter- or intra-specific variation in photosynthesis under different environmental conditions were observed with poplars,^{3,20,23,27,55)} Douglas-fir^{8,9,63)} and pitch pine.³⁸⁾ Donnelly (1974)²¹⁾ reported seasonal changes in photosynthate transport within elongating shoots of *Populus grandidentata*. Clark and Lister(1975)¹⁵⁾ found interspecific variation in photosynthetic action spectra of five tree species.

Leaf chlorophyll content in relation to photosynthetic rate or productive capacity was examined with various plant species. Brougham(1960)¹⁰⁾ determined the amounts of leaf and chlorophyll per unit land area in grass species and maize. He found a highly significant correlation($r=0.912$) between the maximum growth-rate and amounts of chlorophyll above the measurement level per unit land area. Sestak(1963)⁵⁵⁾ investigated the changes in the chlorophyll content as related to the photosynthetic activity and age of *Nicotiana* leaves. He reported that the apparent photosynthesis is regardless of the leaf age in direct relation to the chlorophyll content in leaves. A marked dependence of photosynthetic rate on the amount of chlorophyll was always found at high radiation densities but not at low densities.⁵⁶⁾ The intensity of photosynthesis and the content of chlorophyll estimated in disks cut out from different areas of fodder cabbage leaves were examined, but no significant differences in photosynthesis were observed between samples removed from different parts of the leaf (Sestak 1962).⁵⁷⁾ However, Sestak and Catsky(1962)⁵⁸⁾ reported that highest photosynthetic rate and

highest chlorophyll content were found in the young but not well developed leaves of *Nicotiana sanderae*. In contrast to these facts above, Gabrielsen(1948)²⁶⁾ reported photosynthetic rate is not always dependent on the amount of chlorophyll of plant organs at any irradiation densities, but this dependence is valid only at low irradiation density. Spatial variation in leaf chlorophyll within the crown of a radiata pine sapling was reported by Wood(1974)⁶⁷⁾ who observed that the chlorophyll concentration showed different trends when expressed in relation to needle bulk and to needle surface area. Total chlorophyll amount and its seasonal change in warm-temperate evergreen oak forest at Minamata, Japan were estimated by Kirita and Hozumi(1973)³⁴⁾ who found that the chlorophyll content per unit leaf area in evergreen oak and other trees decreased and had less pronounced seasonal change toward the bottom of the forest canopy.

Photosynthetic carbon dioxide fixation with less respiration is one of the most obvious factors determining the rate of dry matter production. Natr and Spidla(1961)⁴⁶⁾ explained a modified leaf-disk method studying photosynthesis in cereals. Ishii *et al*(1977)³²⁾ suggested a method for measuring photosynthesis and respiration of leaf slices with oxygen electrode. Setlik *et al*(1960)⁶¹⁾ mentioned that leaf-disk method makes it possible to measure the average rate of photosynthesis in a representative sample of a large number of leaves.

Leaf area was usually considered a measure of the actual photosynthetic apparatus of the plants during the growing season. Strong correlation was found between leaf area index and maximum growth-rate with corn hybrids(Sprague and Curtis 1933)⁴⁸⁾ and with grasses (Brougham 1960).¹⁰⁾ Models of photosynthesis and growth incorporated with leaf area were reviewed by many researchers.^{9,36,59)}

Corley(1972)¹⁶⁾ observed the uptake rate of (¹⁴CO₂) by oil palm seedling and found heritable differences in both highly saturated and light-limited photosynthesis, and also in leaf chlorophyll

content. Such intraspecific variations in photosynthetic rate were reported by various researchers.^{29, 38,42)} Gatherum *et al* (1966)²⁹⁾ tested two hypotheses about growth characteristics of aspen poplar hybrid clones; Are there any differences in photosynthesis and respiration among clones and any differences in growth and distribution of assimilate among clones? They found clonal differences in net and gross photosynthesis, rates of photosynthesis and first-year growth. Similar results that there were clonal variation in photosynthesis and growth of hybrid poplars were reported by Bridgewater,⁷⁾ Dhir and Mohn,¹⁷⁾ Luukkanen,⁴³⁾ and Smith *et al.*⁶²⁾

There were some reports that photosynthetic efficiency of certain plants may be genetically controlled by hereditary properties. Wilkinson (1973)⁶⁶⁾ reported the efficiency of early selection in hybrid poplar clonal test was expected only to a limited range of genotypes. Hereditary properties of chloroplasts and genetic mechanisms of photosynthesis control was discussed by Nasyrov.⁴⁵⁾

Thus, clonal variations in growth-related characters may help screen the best clones in biomass production.

MATERIALS AND METHODS

1. Plant materials

Two- and one-year-old *Populus alba* × *P. glandulosa* F₁ clones were provided as plant materials. Two-year-old *Populus* plantation consisted of fifteen clones was established in mid-April of 1981. One-year-old plantation of thirteen clones were established in mid-May of 1982 at the university forest nursery in Suweon. Unrooted cuttings were planted at a density of 20,000 trees per hectare for both one- and two-year-old plantations. A randomized block design with two replicates was adopted at two-year-old plantation. Fifteen clones were allocated randomly to blocks and each clones consisted of nine trees. Similar design used at the two-year-old plot was adopted at one-year-old plantation, and thirteen clones were allocated at

random to blocks. Three hundred cuttings per clone were planted.

2. Tree measurement

In this study, three plants were selected at random to yield a sample of at least forty-five leaves for each of the fifteen, two-year-old clones, and five plants were selected to have thirty leaves for thirteen, one-year-old clones. All leaves, both juvenile and expanding, were taken from these plants and their circumferences were photocopied on paper. The leaf areas (LA) of these projections were obtained by using a planimeter which measured to the nearest 0.1cm². Various models were examined using ordinary least squares method,⁴⁰⁾ and the final model chosen was $LA = \beta_0 + \beta_1 LW$, where LW is a variable, length times width.

In this study, leaf chlorophyll content (CC) is the amount of chlorophyll (μg) per leaf area(cm²), while leaf chlorophyll content per tree is that of chlorophyll (μg) in total leaf tissue per tree.

The third to sixth leaves of lateral shoots of which tree height in 1 to 2 meters were taken for the measurement of chlorophyll content. Leaf discs (6mm in diameter) of fresh tissue were obtained by punching randomly along the leaf sides. All the pigments were extracted with 80% acetone and its absorbances were measured at wavelengths of 645 and 663nm, respectively. Chlorophyll contents were determined from Arnon's equation¹⁾: Total chlorophyll (mg l^{-1}) = $8.02A_{663} + 20.20A_{645}$

In this study, photosynthetic ability of leaf tissue (PA) means the amount of oxygen (μ mole) evolved from unit leaf area(cm²) or from unit chlorophyll content(μg) per hour under the controlled environment. Photosynthetic ability per tree was calculated from this oxygen amount times total leaf area.

Leaf tissues punched from lateral shoots were moved into distilled water promptly, and its photosynthetic ability was measured using Oxygen Electrode and Meter³²⁾ (YSI Co., Ohio, U.S.A.) in mid-August. Leaf tissues were exposed under the tungsten lamp ($300 \mu\text{E m}^{-2} \text{sec}^{-1}$) at a temperature varying between 24°C and 26°C. Four ml of 50mM

potassium-phosphate buffer(pH 7.2) solution containing 0.5mM MgCl₂, and 0.1mM CaSO₄ and 2ml of 0.625M NaHCO₃ solution were used as reaction solution.

Height and diameter at breast height of the sample trees were measured in mid-September to the nearest 1.0 and 0.01 cm, respectively. Sample trees at one-year-old plots were harvested. Dry weights (G) of all tree components including roots were measured after drying at 80°C in an oven. Total dry weights (stem and root) were regressed on the variable D²H (square of diameter at breast height times height). Then, total dry weights of two-year-old trees were estimated from the regression equation obtained with one-year-old trees.

New variables such as LC(leaf area times chlorophyll content) and LP (leaf area times photosynthetic ability) were calculated later.

RESULTS

1. Leaf area(LA)

Models of individual leaf areas predicted from

leaf length and leaf width for each clone were shown in Tables 1 and 2, and the variable, length times width(LW), appears to fit well their relationship with LA. The coefficients of determination for one-year-old plants were generally higher than those of two-year-old plants. Clonal means of the leaf area per tree at two-year-old plots were shown in Table 3, and clonal differences were highly significant at the 1% level. Clone 66-14-29 showed the largest leaf areas whereas clone 66-20-1 the smallest areas among all of the clones. Clonal peak for leaf area per tree was not consistent during the growing season(Figure 1), but clones 64-6-44, 68-1-54, 66-14-29 and 66-26-55 showed higher leaf areas than the other clones. In general, mean leaf areas for most of the clones were the highest in August except for clones 64-6-44, 66-14-29 and 66-26-55. This may be true because these *Populus* hybrids grow more vigorously in August than in July or September. Clones 64-6-44, 66-14-29 and 66-26-55 produced more leaf areas in September than in July or August. This may plants were shown in

Table 1. Relation between leaf area (LA) and length times width (LW) for each clone of *Populus alba* × *P. glandulosa* F₁ for two-year-old plants

Clone	Predicted equation	R ²	F-value	t-values for β's	
				Slope (β ₁)	Intercept (β ₀)
64- 6-44	LA=.64367 LW-.2307	.93884	660.15	25.693	.272
65-22- 4	LA=.59888 LW+1.3374	.88279	210.88	14.522	1.226
65-22-11	LA=.63712 LW-.4340	.82870	208.07	14.425	.332
65-29-19	LA=.64123 LW+.5604	.88554	332.67	18.239	.685
65-95	LA=.62154 LW+1.0087	.94224	701.57	26.487	1.625
66- 6- 8	LA=.62405 LW+.7342	.85770	259.09	16.096	.950
66-14-29	LA=.70132 LW-1.2570	.93132	583.15	24.149	.171
66-14-93	LA=.61175 LW+.1836	.84995	243.59	15.607	.258
66-14-99	LA=.66050 LW-.3235	.81137	201.00	14.177	2.229
66-15- 3	LA=.56660 LW+ 2.3345	.84850	240.88	15.520	.686
66-20- 1	LA=.58050 LW+ 1.7356	.89090	351.18	18.740	.805
66-25- 5	LA=.57651 LW+ 1.7024	.89967	385.59	19.637	2.000
66-26-55	LA=.56398 LW+ 1.7749	.84844	240.71	15.515	1.563
67- 6- 3	LA=.59160 LW+ 1.3794	.74820	127.76	11.303	.242
68- 1-54	LA=.63590 LW+.3213	.95050	845.14	29.072	.488

Critical t-values for β₁ and β₀ with d.f. 44 are 2.015 and 2.691 at 5% and 1% levels, respectively.

Table 2. Relation between leaf area (LA) and length times width (LW) for each clones of *Populus alba* × *P. glandulosa* F₁ for one year-old plants

Clone	Predicted equation	R ²	F-value	t-values for β's	
				Slope (β ₁)	Intercept (β ₀)
64- 6-44	LA=.70588 LW-1.9780	.9517	551.95	23.494	.4763
65-22- 4	LA=.64084 LW+ 0.5971	.8390	145.91	12.079	.9222
65-22-11	LA=.64410 LW-1.0822	.9838	1697.90	41.205	.5941
65-29-19	LA=.66251 LW+ 0.9691	.9867	2074.80	45.550	.6112
65-95	LA=.64959 LW- .4598	.9656	786.55	28.045	.1373
66- 6- 8	LA=.66391 LW+ 0.4082	.9812	1461.70	38.233	.8257
66-14-29	LA=.66142 LW-2.7045	.9859	1950.90	44.169	1.4206
66-14-93	LA=.62538 LW+ 1.6188	.9738	1262.80	35.536	.5644
66-14-99	LA=.66123 LW-2.6916	.9930	1963.60	29.094	1.4186
66-15- 3	LA=.62278 LW+ .7384	.9795	1335.80	36.546	.4527
66-20- 1	LA=.59668 LW+ 7.3134	.8857	216.99	14.730	1.5402
66-25- 5	LA=.65652 LW-3.4579	.9759	1134.30	33.679	1.1414
66-26-55	LA=.65696 LW+ .5132	.9568	1120.20	31.854	.7257

Critical t-values for β₁ and β₀ with d.f. 29 are 2.045 and 2.756 at 5% and 1% levels, respectively.

Table 3. Clonal means of leaf area per tree for two-year old plantation, and Duncan's new multiple range test for significant differences in leaf area per tree. Any two means not next to a common line are significantly different at 5% level

Clone	Mid-July	Mid-August	Mid-September	Leaf area (cm ²)
66-14-29	4390.0	4651.0	5039.7	4693.6
64- 6-44	3268.3	4570.3	5831.0	4556.5
66-26-55	2493.0	4137.3	4666.3	3765.5
68- 1-54	2265.3	5520.3	3247.7	3677.8
65-22-11	2059.0	4400.3	3750.3	3553.2
66-14-93	3386.3	3645.0	3309.0	3346.8
66-25- 5	2583.3	3670.0	2851.0	3034.8
65-29-19	1699.0	3823.7	3605.0	3009.2
65-15-3	2215.7	3872.3	2582.3	2890.1
65-22-4	2559.7	3031.3	2401.0	2664.0
66- 6- 8	2912.7	2918.7	1797.7	2543.0
66-14-99	2152.0	2708.0	1816.3	2225.4
65-95	1325.7	2798.7	2096.3	2073.6
67- 6- 3	2251.3	2252.3	1571.7	2025.1
66-20- 1	1609.7	2239.7	2078.0	1975.8
Mean	2501.7	3615.9	3109.2	

indicate that those clones retain leaves longer than other clones. Clonal means of LA for one-year-old

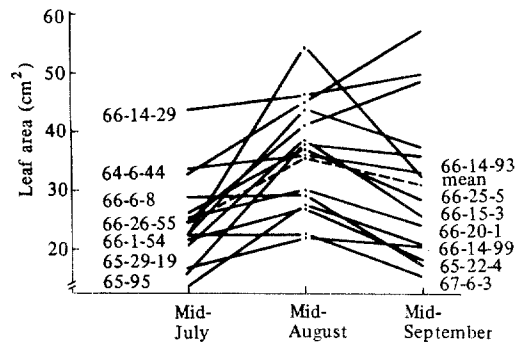


Fig. 1. Clonal variation in monthly change of leaf area per tree for two-year-old *Populus alba* × *P. glandulosa* F₁

Table 4. Clonal differences in LA were not significant at the 5% level. However, mean leaf areas of the clones 66-26-55, 65-22-4, 66-20-1, 66-6-8 and 66-15-3 were relatively higher than those of the other clones.

2. Leaf chlorophyll content per unit area (CC)

Monthly and clonal means of the leaf chlorophyll content per unit area for two-year-old plants were exhibited in Table 5, and their differences between

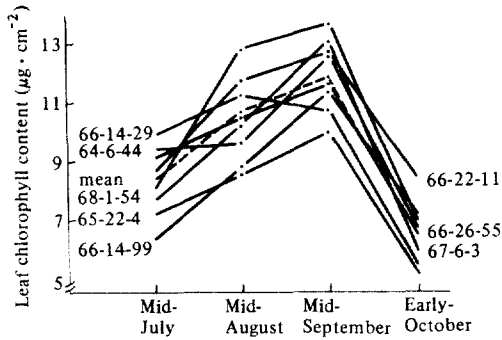


Fig. 2. Some clonal variation in monthly change of leaf chlorophyll content for two-year-old *Populus alba* × *P. glandulosa* F₁

clones were highly significant at the 1% level. The chlorophyll content of clone 68-1-54 was the highest among them whereas that of clone 65-22-4 was the lowest. Monthly variation in chlorophyll content for each clone was exhibited in Figure 2. Generally, the value of CC shows an increasing trend as trees grow larger, and maximum chlorophyll content was exhibited in September. After that, the value dropped rapidly due probably to low

physiological activities caused by decreased temperature. Clonal means of CC for one-year-old *Populus alba* × *P. glandulosa* F₁ measured in mid-

Table 4. Clonal means of total dry weight per tree, leaf area per tree leaf chlorophyll content per unit area for one-year-old *Populus alba* × *P. glandulosa* F₁

Clone	Total dry weight (g)	Leaf area (cm ²)	Leaf chlorophyll content (g · cm ⁻²)
66- 6-44	146.4	2890.0	10.16
65-22- 4	163.0	3346.9	12.04
65-22-11	131.4	3098.5	13.12
65-29-19	184.8	3047.0	12.72
65-69	139.0	2778.1	10.57
66- 6- 8	183.2	3196.3	12.05
66-14-29	94.8	2540.1	10.10
66-14-93	123.2	2856.0	11.37
66-14-99	114.8	2955.3	12.49
65-15- 3	148.6	3146.2	13.52
66-20- 1	129.4	3379.9	11.45
66-25- 5	142.4	2928.9	10.50
66-26-55	177.6	3484.0	12.04

Table 5. Clonal means of the leaf chlorophyll content, and Duncan's new multiple range test for significant differences in leaf chlorophyll content. Any two means not next to a common line are significantly different at 5% level

Clone	Mid-July	Mid-August	Mid-September	Early-October	Chlorophyll content (µg · cm ⁻²)
68- 1-54	8.04	12.85	13.73	6.96	10.40
65-22-11	8.52	11.76	12.64	8.41	10.33
65-15- 3	8.61	12.69	12.27	7.10	10.17
66-25- 5	8.06	10.41	13.31	7.00	9.70
65-29-19	8.50	11.19	12.31	6.60	9.61
65-20- 1	8.97	10.61	11.62	6.60	9.45
65-26-55	9.01	10.43	11.69	6.54	9.42
64- 6-44	9.37	9.59	11.21	7.20	9.34
66-14-29	9.83	11.23	10.71	5.42	9.30
66- 6- 8	7.56	9.88	11.82	7.61	9.21
67- 6- 3	7.51	10.20	13.09	5.91	9.41
65-95	8.82	9.93	11.91	5.41	9.01
66-14-93	8.04	11.05	10.40	6.41	8.98
66-14-99	6.25	8.75	11.38	7.04	8.36
65-22- 4	7.10	8.53	10.01	5.09	7.63
Mean	8.28	10.61	11.86	6.62	

September were shown in Table 4. and clonal differences were not significant at the 5% level. However clones 66-15-11, 65-22-11, 65-29-19 and 66-14-99 showed relatively higher values in CC than other clones.

Table 6. Clonal means of leaf area per tree, leaf chlorophyll content and photosynthetic capacity of leaf tissue per unit area for two-year-old *Populus alba* × *P. glandulosa* F₁

Clone	Leaf area (cm ²)	Chlorophyll content (μg · cm ⁻²)	Photosynthetic ability	
			(O ₂ μmole · hr ⁻¹ · cm ²)	(O ₂ μmole · hr ⁻¹ · μg ⁻¹ · chl.)
64- 6-44	4556.5	8.86	3.21	0.362
65-22- 4	2664.0	7.63	2.75	0.360
65-22-11	3553.2	10.33	2.86	0.277
65-29-19	3009.2	9.61	3.53	0.367
65-95	2073.6	9.01	3.28	0.364
66- 6- 8	2543.0	9.21	3.26	0.354
66-14-29	4693.6	9.30	3.47	0.373
66-14-93	3446.8	8.98	2.40	0.267
66-14-99	2225.4	8.36	2.19	0.262
66-15- 3	2890.1	10.17	2.74	0.269
66-20- 1	1975.8	9.70	4.19	0.432
66-25- 5	3034.8	9.70	3.44	0.355
66-26-55	3765.5	9.42	4.21	0.446
67- 6- 3	2025.1	9.14	3.04	0.333
68- 1-54	3677.8	10.40	4.37	0.420

clone 68-1-54 showed the highest value whereas the clone 66-14-29 the lowest.

4. Growth

Table 7 showed clonal means of total dry weight per tree for two-year-old plants. Clonal differences in dry weight were highly significant at the 1% level, and clone 64-6-44 was the highest and clone 66-14-29 was the lowest. Table 4. showed clonal means of total dry weight (stem and root) per tree for one-year-old plants, and clones did not differ in total dry weight at the 5% level. However clones 65-29-19, 66-6-8, 65-26-55 and 65-15-3 produced relatively high yields and clones 66-14-29, 66-14-93 and 66-14-99 did relatively low yields.

5. Variation in some physiological characters of the leaf on one-year-old plants

Table 8 and Figure 3 showed mean values of the leaf chlorophyll content, photosynthetic ability,

3. Photosynthetic ability of the leaf tissue per unit area(PA)

Table 6 shows clonal means of PA per unit area at two-year-old plots. Clonal means of PA were not significantly different at the 5% level. However,

Table 7. Clonal means of total dry weight per tree for two-year-old *Populus alba* × *P. glandulosa* F₁, and Duncan's new multiple range test for significant at the 5% level. Any two means not to a common line are significantly different at 5% level

Clone	Total dry weight (g)
66- 6-44	1147
65-22-11	979
66-14-29	949
65-29-19	825
68- 1-54	786
66-14-93	682
66-26-55	627
66-25- 5	606
66-15- 3	559
65-95	502
66-20-1	445
66- 6- 8	424
65-22- 4	388
67- 6- 3	335
66-14-99	243

Table 8. Mean values of the chlorophyll content, photosynthetic ability, leaf fresh weight and dry weight per unit area by leaf order from top for one-year-old *Populus alba* × *P. glandulosa* F₁ (measurement was done in late-August only for clones 65-22-11, 65-29-19, and 66-20-1)

Leaf order from top	Fresh weight (mg · cm ⁻²)	Dry weight (mg · cm ⁻²)	Chlorophyll content (μg · cm ⁻²)	Photosynthetic ability	
				(O ₂ μmole · cm ⁻² · hr ⁻¹)	(O ₂ μmole · hr ⁻¹ · μg ⁻¹ · chl.)
3/47	13.83	4.50	7.86	2.37	0.302
8/47	13.06	5.06	9.28	2.46	0.265
13/47	10.33	4.39	11.11	2.44	0.220
18/47	11.00	4.13	13.10	2.86	0.218
23/47	11.36	3.96	13.21	3.47	0.263
28/37	10.74	3.49	13.99	3.88	0.277
33/47	10.57	3.63	15.12	2.98	0.196
38/47	11.49	3.90	12.78	2.97	0.232
43/47	13.66	4.83	11.04	2.09	0.189

fresh and dry weight per unit area in relation to the leaf order from top for one-year-old clones 65-22-11 65-29-19 and 66-20-1. Maximum values of chlorophyll content and photosynthetic ability per unit area were observed in the thirty-third and twenty-eighth leaves, respectively(Figure 3). Maximum fresh and dry weights per unit area were observed in the third and eighth leaves, respectively (Table 8).

6. Regression and correlation analyses for dry weight, leaf area, leaf chlorophyll content per unit leaf area, photosynthetic ability, per unit leaf area, leaf chlorophyll content per tree and leaf photosynthetic ability per tree.

Table 9 shows clonal means of leaf area per tree, leaf chlorophyll content per unit area, photosynthetic ability per unit leaf area and total dry weight for two-year-old plants. Clones 68-1-54, 65-22-11, 66-26-55 and 66-25-5 showed relatively high values in leaf area, leaf chlorophyll content and photosynthetic ability whereas clones 65-22-4, 66-6-8, 66-14-59 and 67-6-3 showed relatively low values. Regression equations between means of dry weight, leaf area, leaf chlorophyll content and photosynthetic ability for two-year-old plants were shown in Table 10. Low correlations were found between dry weight and leaf chlorophyll content (r=0.400), and between dry weight and photosynthetic ability

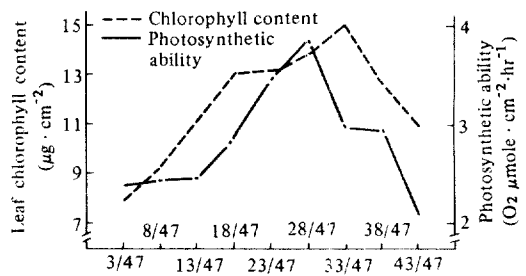


Fig. 3. Leaf chlorophyll content and photosynthetic ability in relation to leaf order from top for one-year-old *Populus alba* × *P. glandulosa* F₁

(r=0.231). High correlations were found between dry weight and leaf area (r=0.865), between dry weight and leaf area in September (r=0.883), between dry weight and leaf chlorophyll content per tree or leaf photosynthetic ability per tree (r=0.893), between dry weight and the added variables (leaf area and leaf chlorophyll content per tree (r=0.888), between dry weight and the added variables leaf area and leaf photosynthetic ability per tree (r=0.865). Relatively high correlations were found between dry weight and leaf photosynthetic ability per tree (r=0.745) and between dry weight and chlorophyll content in July (r=0.703). Scatter diagrams (Figures 4 and 5) indicate the relationship between dry weight per tree and leaf area per tree, and between dry weight per tree and leaf chlorophyll content per tree.

Table 9. Clonal means of total dry weight per tree, leaf area per tree, leaf chlorophyll content and photosynthetic ability of leaf tissue per unit area for two-year old *Populus alba* × *P. glandulosa* F₁

Clone	Total dry weight (g)	Leaf area (cm ²)	Chlorophyll content (μg · cm ⁻²)	Photosynthetic ability	
				(O ₂ μmole · dm ⁻² · hr ⁻¹)	(O ₂ μmole ; hr ⁻¹ · μg ⁻¹ · chl.)
64- 6-44	1147	4556.5	886	321	0.362
65-22- 4	388	2664.5	763	275	0.360
65-22-11	979	3553.2	1033	286	0.277
65-29-19	825	3009.2	961	353	0.367
65-95	502	2073.6	901	328	0.364
66- 6- 8	424	2543.0	921	326	0.354
66-14-29	949	4693.6	930	347	0.373
66-14-93	682	3446.8	898	240	0.267
66-14-99	243	2225.4	836	219	0.262
66-15- 3	559	2890.1	1017	274	0.269
66-20- 1	445	1975.8	970	419	0.432
66-25- 5	606	3034.8	970	344	0.355
66-26-55	627	3765.5	942	421	0.446
67- 6- 3	335	2025.1	914	304	0.333
68- 1-54	786	3677.8	1040	437	0.420

Table 10. The relations between means of dry weight (G), leaf area (LA), leaf chlorophyll content per unit leaf area (CC), photosynthetic ability per unit leaf area (PA), leaf chlorophyll content per tree (LC) and leaf photosynthetic ability per tree (LP) for two-year-old *Populus alba* × *P. glandulosa* F₁ clones

Predicted equation	R ²	F-value	t-values for β's		
			Slope (β ₂)	Slope (β ₁)	Intercept (β ₀)
PA = .42208 CC - 67.169	.2325	3.9387*		1.9850*	.3432
G = 25.931 LA - 164.69	.7484	38.6770**		6.2182**	1.2379
G = .17849 LA ₉ +79.44	.7799	46.0680**		6.7873**	1.1025
G = 1.4214 CC - 691.84	.1604	2.4826		1.5750	.8335
G = 1.9748 CC ₇ -1000.5	.5384	12.7120**		3.5653**	.9751
G = .93514 PA + 328.03	.0532	.7301		.8544	.9025
G = .02654 LC - 131.07	.7887	48.5200**		6.9656**	1.1384
G = .05076 LP + 118.67	.5553	16.2350**		4.0293**	.8726
G = 2.5620 LA + .02406 LC - 138.69	.7891	22.4560**	.1616	1.5230	1.0897
G = 26.017 LA - .00021 LP - 165.02	.7484	17.8462**	3.0344**	.0109	1.1650
G = .3179 LC + .01351 LP - 145.49	.7971	23.5690**	3.7811**	.7047	1.2180

*and **indicate significance at 5% and 1% level, respectively.

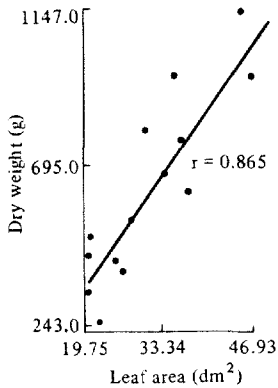


Fig. 4. Relationship between total dry weight per tree and leaf areas per tree

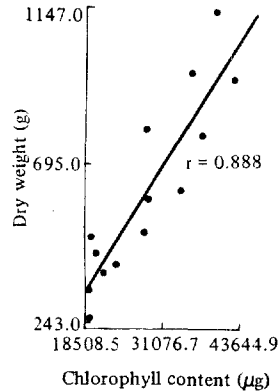


Fig. 5. Relationship between total dry weight per tree and leaf chlorophyll content per tree

DISCUSSION

1. Leaf area

The leaf as a photosynthesizing organ is important to the growth and production of woody plants. Leaf areas are usually considered a measure of the actual photosynthetic apparatus of the plant during the growing season.

Leaf length times width (LW) used in this study to estimate individual leaf area of *Populus alba* × *P. glandulosa* F₁ clones seemed to be a good independent variable (Table 1 and 2), and this result was similar to that reported by Lee and Lee (1982)⁴⁰ who examined leaf length times leaf width as independent variables for the prediction of individual leaf area of *Populus* × *euramericana* clones. In addition to LW, Gordon *et al* (1977)²⁹ added the variable, square of leaf width (W²) to the independent variables for the leaf area estimation. Sestak (1971)⁵⁹ also reported various prediction equations of estimating leaf areas of various tree species. Clonal differences in leaf area per tree existed and highly significant correlation (r=0.865) was found between total dry weight and leaf area per tree. This relation was similarly shown in the reports of Brougham (1960)¹⁰, and Sprague and Curtis (1933)⁴⁸ who found the strong correlation between the leaf area index and maximum growth rate with grasses and with corn hybrids, respectively.

2. Leaf chlorophyll content

The chlorophylls are the primary light-absorbing pigments, and the amount of chlorophyll in plants represents the magnitude of the assimilation organs. Chlorophyll contents might actually be a better measure of the photosynthetic ability per unit leaf area³⁶. Therefore, it may be correlated with the rate of dry matter production and with other growth characteristics⁵⁹. Clonal differences were present in leaf chlorophyll content per unit area and monthly mean value of chlorophyll was also significantly different. This clonal differences provided an important physiological character for selection. Clones differed in leaf chlorophyll content per tree, and significant correlation (r=0.888) was found between total dry weight per tree and leaf chlorophyll content per tree. This high relation was similar to that with corn hybrids shown by Sprague and Curtis (1933)⁶⁴ and that with *Nicotiana* by Sestak and Catsky (1962)⁵⁸. However, low correlation (r=0.482) was found between photosynthetic ability per unit leaf area and chlorophyll content. This low correlation was also shown by Gabrielsen (1948)²⁶.

3. Photosynthetic ability

Both photosynthetic carbon dioxide fixation and respiration are important factors determining the rate of dry matter production. The Oxygen Elec-

trode method used in this study to examine photosynthetic abilities of plant leaf tissues is a useful tool for a wide range of experiments in such as genetics, especially selection of certain efficient clones, because of its ease for use. Significant differences in photosynthetic ability per unit leaf area were exhibited among two-year-old *Populus alba* × *P. glandulosa* F₁ clones. Relatively high correlation ($r=0.745$) was found between total dry weight per tree and photosynthetic ability per tree. Similar results with *Populus* clones were shown by Ceulemans and Impens (1980)¹² to differ in ecophysiological gas exchange characteristics with respect to their potential field performance.

Photosynthetic ability of some clones examined in this study varied with leaf order from top to bottom; it increased with increasing leaf order up to around the thirtieth leaf which is nearly in full expansion and then decreased. Such photosynthetic variations in relation to leaf age with *P. alba* × *P. glandulosa* were reported similarly by Kim *et al* (1977)³³. Furthermore, Dickmann(1971)¹⁸ also

reported similar results, that is, photosynthesis of developing leaves of *P. deltoides* generally increased up to full leaf expansion, and then decreased. Maximum photosynthetic rate often reached before maximum area and maximum chlorophyll content in leaves were attained(Sestak 1966)⁵⁶. Another results were reported by Dickmann and Gordon (1975)¹⁹ who found the lowest photosynthetic rate in the youngest leaves, the maximum in nearly full-expanded leaves and a gradually declining rate in older leaves.

Mean photosynthetic rate of these clones varied from 219 to 431 O₂ μmole. dm⁻². hr⁻¹ (9.5-19.2 CO₂ mg. dm⁻². dm⁻². hr⁻¹) in this study, of which figures were lower than that reported by Furukawa (1975)²⁵, who examined photosynthetic rate of *Populus* clones using infra-red CO₂ analyzer.

CONCLUSION

Some growth-related physiological characters were studied during early stage to select superior

Table 11. Clonal grouping in growth potential, based on leaf area, leaf chlorophyll content and photosynthetic ability of the leaf tissue

Two-year-old plants			
Leaf area per tree	Chlorophyll content per unit area	Photosynthetic ability per unit leaf area	Clone
High	High	High	68-1,54, 66-26-55, 66-25-5
High	High	Low	65-22-11
High	Low	High	66-14-29
High	Low	Low	64-6-44, 66-14-93
Low	High	High	65-29-19, 66-20-1
Low	High	Low	66-15-3
Low	Low	High	65-95
Low	Low	Low	65-22-4, 66-6-8, 66-14-99, 67-6-3
One-year old plants			
Leaf area per tree	Leaf chlorophyll content per unit area		Clone
High	High		66-26-55, 65-22-11, 65-22-4, 66-15-3
High	Low		66-20-1
Low	High		66-14-99, 65-29-19
Low	Low		64-6-44, 65-95, 66-14-29, 66-14-93, 66-25-5

Populus alba x *P. glandulosa* F₁ clones. Clonal differences in physiological characters such as leaf area per tree, leaf chlorophyll content per unit area, and total dry weight per tree were highly significant at the 1% level for two-year-old plants, but not significant for one-year-old plants. However, variation in photosynthetic ability of the leaf tissue per unit area was not significant between clones at the 5% level.

Total dry weight per tree was highly correlated with leaf area per tree and with chlorophyll content per tree.

When each of the clones is ranked based on leaf area per tree, leaf chlorophyll content per unit area and photosynthetic ability per unit leaf area, all clones can be grouped in the following Table 11.

From the above results, the following conclusion can be obtained: 1) clones 68-1-54, 66-26-55, 65-22-11 and 65-25-5 for two-year-old plots, and clones 66-26-55, 65-22-11, 65-22-4 and 66-15-3 for one-year-old plots have better growth potential than the others and 2) particularly, clones 68-1-54, 66-26-55 and 65-22-11 can be selected as superior genotypes.

Prediction equation can be used to estimate total dry weight yields of *Populus* clones, and the equations obtained in this study were as follows;

$G = 25.931 LA - 164.69$ ($r = 0.865$) and $G = 0.0265 LC - 131.07$ ($r = 0.888$), where G, LA, LC and LP indicate total dry weight in grams, leaf area per tree in square of meter, leaf chlorophyll content per tree and photosynthetic ability of leaf tissue per tree, respectively.

LITERATURE CITED

1. Arnon, D.I. 1949. Copper enzymes in isolated chloroplasts. Polyphenol-oxidase in *Beta vulgaris*. Plant Physiol. 24:1-15.
2. Bate, G.C. and D.T. Canvin. 1971. A gas-exchange system for measuring the productivity of plant populations in controlled environments. Can. J. Bot. 49:601-608.
3. Bate, G.C. and D.T. Canvin. 1971. The effect of some environmental factors on the growth of young aspen trees (*P. tremuloides*) in controlled environments. Can. J. Bot. 49(8): 1443-1453.
4. Böhning, R.H. and C.A. Burnside. 1956. The effect of light intensity on rate of apparent photosynthesis in leaves of sun and shade plant. Amer. J. Bot. 43:557-561.
5. Botkin, D.B., G.M. Woodwell and N. Tempel. 1970. Forest productivity estimated from carbon dioxide uptake. Ecology 51:1057-1060.
6. Bowersox, T.W. and W.W. Ward. 1977. Soil fertility, growth, and yield of young hybrid poplar plantations in Central Pennsylvania. Forest Sci. 23:463-469.
7. Bridgewater, F.E., Jr. 1973. Multiple trait selection in a population of eastern cottonwood. (Abstract). Dissertation Abstracts International, B 33(12):5596.
8. Brix, H. 1971. Effects of nitrogen fertilization on photosynthesis and respiration in Douglas-fir. Forest Sci. 17(4):407-414.
9. Brix, H. and L.F. Ebell. 1969. Effects of nitrogen fertilization on growth, leaf area, and photosynthesis rate in Douglas-fir. Forest Sci. 15:189-196.
10. Brougham, R.W. 1960. The relationship between the critical leaf area, total chlorophyll content, and maximum growth rate of some pasture and crop plants. Ann. Bot. (N.S.) 24: 463-474.
11. Cannell, M.G.R. and F.T. Last. 1976. Tree Physiology and Yield Improvement. Academic Press. London. 567p.
12. Ceulemans, R. and I. Impens. 1980. Leaf gas exchange process and related characteristics of seven poplar clones under laboratory conditions. Can. J. For. Res. 10:429-435.
13. Chung, H.H. and R.L. Barnes. 1980. Photosynthate allocation in *Pinus taeda*. II. Seasonal aspects of photosynthate allocation to different biochemical fractions in shoots. Can. J. For. Res. 10:338-347.
14. Chung, H.H. and R.L. Barnes. 1980. Photosynthate allocation in *Pinus taeda*. III. Photo-

- synthate economy: its production, consumption and balance in shoots during growing season. *Can. J. For. Res.* 10:348-356.
15. Clark, J.B. and G.R. Lister. 1975. Photosynthetic action spectra of trees. I. Comparative photosynthetic action spectra of one deciduous and four coniferous tree species as related to the photorespiration and pigment complements. *Plant Physiol.* 55(2):401-406.
 16. Corley, R.H.V., J.J. Hardon and S.C. Ool. 1972. Some evidence for genetically controlled variation in photosynthetic rate of oil palm seedlings. *Euphytica* 22:48-55.
 17. Dhir, N.K. and C.A. Mohn. 1976. A comparative study of crosses between and within two geographically diverse sources of eastern cottonwood. *Can. J. For. Res.* 6(3): 400-405.
 18. Dickmann, D.I. 1971. Photosynthesis and respiration by developing leaves of cottonwood (*Populus deltoides* Bartr.). *Bot. Gaz.* 132: 253-259.
 19. Dickmann, D.I. and J.C. Gordon. 1975. Incorporation of ¹⁴C-photosynthate into protein during leaf development in young *Populus* plants. *Plant Physiol.* 56(1): 23-27.
 20. Domingo, I.L. and J.C. Gordon. 1974. Physiological responses of an aspen-poplar hybrid to air temperature and soil moisture. *Bot. Gaz.* 135(3): 184-192.
 21. Donnelly, J.R. 1974. Seasonal changes in photosynthate transport within elongation shoots of *Populus grandidentata*. *Can. J. Bot.* 52: 2547-2559.
 22. Drew, A.P. and F.A. Bazzaz. 1978. Variation in distribution of assimilate among plant parts in three populations of *Populus deltoides*. *Silvae Genet.* 27(5): 189-193.
 23. Fasehun, F.E. 1978. Effect of irradiance on growth and photosynthesis of *Populus x euramericana* clones. *Can. J. For. Res.* 8: 94-99.
 24. Foote, K.C. and M. Schaedle. 1978. The contribution of aspen bark photosynthesis to the energy balance of the stem. *Forest Sci.* 24(4): 569-573.
 25. Furukawa, A. 1975. Comparison of photosynthesis, postillumination CO₂ outburst, and CO₂ compensation in poplar varieties, sunflower, and bean. *J. Jap. For. Soc.* 57(8): 268-274.
 26. Gabrielsen, E.K. 1948. Effects of different chlorophyll concentrations on photosynthesis in foliage leaves. *Physiol. Plant.* 1:5-37.
 27. Garrett, P.W., A.L. Shigo and J. Carter. 1976. Variation in diameter central columns of discoloration in six hybrid poplar clones. *Can. J. For. Res.* 6(4):475-477.
 28. Gatherum, G.E., J.C. Gordon and B.F.S. Broerman. 1966. Effects of clone and light intensity on photosynthesis, respiration and growth of aspen poplar hybrids. *Ecology* 44: 710-716.
 29. Gordon, J.C. L.C. Pronnitz, R.R. Faltonson, H.R. Zuuring, T.C. Hennessey, P.H. Wray and D.G. Thompson. 1977. Methods of rapid, early selection of poplar clones for maximum yield potential: A manual of procedures. Final Report to North Central For. Exp. Sta., Forest Service, USDA, 123p. Iowa State Univ. Ames, Iowa.
 30. Gordon, J.C. and L.C. Promnitz. 1976. Photosynthetic and enzymatic criteria for the early selection of fast growing *Populus* clones. Pages 79-97 *In* M. Cannell and F. Last, eds. *Tree Physiology and Yield Improvement*. Academic Press. London.
 31. Hodinott, J. and E.M. van zinderen Bakker, Jr. 1974. Net assimilation in long and short shoot leaves of *Ginkgo biloba*. *Can. J. Bot.* 52(2): 329-330.
 32. Ishii, R., T. Yamagishi and Y. Murata. 1977. On a method for measuring photosynthesis and respiration of leaf slices with an oxygen electrode. *Jap. J. Crop Sci.* 46:53-57.
 33. Kim, C.S., S.K. Lee and S.W. Sun. 1977. Photosynthesis of *x Populus albaglandulosa* in relation to leaf age. *J. Kor. For. Soc.* 34: 63-71.

34. Kirita, H. and K. Hozumi. 1973. Estimation of the total chlorophyll amount and its seasonal change in a warm-temperate evergreen oak forest at Minamata, Japan. *Jap. J. Ecol.* 23(5): 195-200.
35. Larson, P.R. and J.C. Gordon, 1969. Leaf development, photosynthesis, and C^{14} distribution in *Populus deltoides* seedlings. *Amer. J. Bot.* 56(9): 1058-1066.
36. Ledig, F.T. 1974. Concepts of growth analysis. Pages 166-182. in C.P.P. Reid and G.H. Fechner, ed. Proc. of the third North American For. Biology Workshop. Colorado State Univ., Fort Collins, Colorado.
37. Ledig, F.T. and D.B. Botkin. 1974. Photosynthetic CO_2 uptake and the distribution of photosynthate as related to growth of larch and sycamore progenies. *Silvae Genet.* 23:188-192.
38. Ledig, F.T. and J.G. Clark. 1977. Photosynthesis in a half-sib family experiment in pitch pine. *Can. J. For. Res.* 7(3):510-514.
39. Ledig, F.T. and T.O. Perry. 1969. Net assimilation rate and growth in loblolly pine seedlings. *Forest Sci.* 15(4):431-438.
40. Lee, D.K. and K.H. Lee. 1982. Estimation of leaf surface area in *Populus x euramericana* clones, and contribution of leaf length and width to the area. Research paper presented at the Meeting of Korean Breeding Society, May 15, 1982.
41. Lee, D.K., S.K. Hyun and E.R. Noh. 1982. Biomass growth and production of *Populus* hybrids in Korea. A paper presented at Ad-hoc committee on Biomass Production Systems in Salicaceae. FAO International Poplar Commission. Rome, Italy, September 1982.
42. Lockhart, J.A. 1965. The analysis of interactions of physical and chemical factors on plant growth. *Ann. Rev. Plant Physiol.* 16:37-52.
43. Luukkanen, O. and T.T. Kozłowski. 1972. Gas exchange in six *Populus* clones. *Silvae Genet.* 21:220-229.
44. McCree, K.J. and T.H. Trocighton. 1965. Prediction of growth rate at different light levels from measured photosynthesis and respiration rate. *Plant Physiol.* 4:559-566.
45. Nasyrov, Y.S. 1978. Genetic control of photosynthesis and improving of crop productivity. *Plant Physiol.* 29:215-237.
46. Natr, L. and J. Spidla, 1961. Application of leaf-disk method to the determination of photosynthesis in cereals. *Biologia Plantarum* 3(3):245-251.
47. Nelson, N.D., T. Burk and J.G. Isebrands. 1980. Crown architecture of short-rotation, intensively cultured *Populus*. *Can. J. For. Res.* 11:73-81.
48. Nobel, P.S. 1974. Introduction to Biophysical Plant Physiology. W.H. Freeman and Company. San Francisco. 488p.
49. Noh, E.R. 1979. Growth performance of the hybrid poplar *Populus alba x P. glandulosa* F₁ clones on uplands in Korea. Proceedings of the Meeting concerning Poplars in France and Belgium. 17-22. Sep. 1979 IUFRO.
50. Noh, E.R., S.K. Hyun and Y.M. Kim. 1982. Biomass production of hybrid poplar, *Populus alba x P. glandulosa* F₁ grown in minirotation. in press.
51. Okafo, O.A. and J.W. Hanover. 1978. Comparative photosynthesis and respiration of trembling and bigtooth aspens in relation to growth and development. *Forest Sci.* 24:103-109.
52. Richard, J.H. and P.R. Larson. 1981. Morphology and development of *Populus deltoides* branches in different environments. *Bot. Gaz.* 142:382-393.
53. Ronald, W.G. and J.W. Steele. 1974. Biosystematics of the genus *Populus*. IV. Naturally occurring Manitoba hybrids of introduced *P. x petrowskyana* with native *P. deltoides* var. *occidentalis* and *P. balsamifera*. *Can. J. Bot.* 52(8): 1883-1887.
54. Schaedle, M. and K.C. Foote. 1971. Seasonal changes in the photosynthetic capacity of *Populus tremuloides* bark. *Forest Sci.* 17: 308-313.
55. Sestak, Z. 1963. Changes in the chlorophyll

- content as related to photosynthetic activity and age of leaves. Photochem. and Photobiol. 2:101-110.
56. Sestak, Z. 1965. Leaf aging, chlorophyll content and photosynthetic rate. Acta Univ. Carolina Biologia Supplementum 1966. 1/2: 115-118.
57. Sestak, Z. and J. Bartos. 1962. Photosynthesis and chlorophyll content in different areas of fodder cabbage leaves. Biologia Plantarum 4(1):47-53.
58. Sestak, Z. and J. Catsky. 1962. Intensity of photosynthesis and chlorophyll content as related to leaf age in *Nicotina sanderae* hort. Biologia Plantarum 4:131-140.
59. Sestak, Z., J. Catsky and P.G. Jarvis. 1971. Plant Photosynthetic Production. Manual of Methods. Dr. W. Junk N.V. Publishers. The Hague. 818p.
60. Shepard, R.D., Jr. 1975. Radial distribution of corticular photosynthate in stems of bigtooth and trembling aspen. Forest Sci. 21:370-372.
61. Setlik, I., J. Bartos and S. Kubin. 1960. Photosynthesis in leaf disks as a measure of photosynthetic capacity in crop plants. Biologia Plantarum 2(4):292-307.
62. Sörenson, F.C. and W.K. Ferrell. 1973. Photosynthesis and growth of Douglas-fir seedlings when grown in different environment. Can. J. Bot. 51(9):1689-1698.
63. Sprague, H.B. and N. Curtis. 1933. Chlorophyll content as an index of the productive capacity of selfed lines of corn and their hybrids. J. Amer. Soc. Agro. 25(11):709-724.
64. Waggoner, P.E. 1968. Predicting the effect on net photosynthesis of changes in leaf metabolism and physics. Crop Sci. 9:315-321.
65. Wilkinson, R.C. 1974. Realized and estimated efficiency of early selection in hybrid poplar clonal tests. NE. Forest Tree Improv. Conf. Proc. 21(1974):26-32.
66. Wood, G.B. 1974. Spatial variation in leaf chlorophyll within the crown of a radiata pine sapling. Aust. For. Res. 6(4):5-14.
67. Zelitch, I. 1971. Photosynthesis, Photorespiration, and Plant Productivity. Academic Press. London. 567p.