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GROWTH, BIOMASS YIELD, CROWN DEVELOPMENT, AND GAS EXCHANGE OF FOUR INTENSIVELY-CULTURED POPULUS CLONES IN SOUTHERN MICHIGAN

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GROWTH, BIOMASS YIELD, CROWN DEVELOPMENT, AND

GAS EXCHANGE OF FOUR INTENSIVELY-CULTURED

POPULUS CLONES IN SOUTHERN MICHIGAN

By

Kurt William Gottschalk

A DISSERTATION

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for the degree of

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ABSTRACT

GROWTH, BIOMASS YIELD, CROWN DEVELOPMENT, AND
GAS EXCHANGE OF FOUR INTENSIVELY-CULTURED
POPULUS CLONES IN SOUTHERN MICHIGAN

By

Kurt William Gottschalk

A small plot research plantation was established in 1977 using cultural practices determined at that time to best approximate the most practical and productive system for industrial users. Measurements of the growth, biomass yield, crown development, and gas exchange (stomatal conductance and photosynthesis) of these four clonal stands were taken for two years in an effort to understand the process of woody biomass production. Growth, biomass yield, and crown development were obtained from nondestructive sampling and complete measurements of all trees at the end of the season. Destructive sampling of small numbers of trees was used to develop prediction equations for the nondestructive samples. Gas exchange was measured throughout the second year using a diffusion porometer for stomatal conductance and $^{14}CO_2$-technique for photosynthesis. Measurements were taken at three crown levels. Environmental parameters were also monitored in the plots.

Biomass production for the four clones varied from 1.6 to 2.5 and 6.8 to 9.2 t ha^{-1} for the first two years. Second

year mean annual increment was 3.4 to 4.6 t ha^{-1} yr^{-1}. Maximum leaf area index ranged from 1.4 to 2.5 and 3.2 to 4.2 m^2 m^{-2} for the two years. Clone NE 353 + 308 partitioned a larger proportion of its biomass into branches, while NE 48 had higher specific leaf weights than the other clones. Gas exchange varied significantly by clone and leaf position. Upper and mid-crown leaves had higher photosynthetic rates (maximum 39 mg CO_2 dm^{-2} hr^{-1}) than lower crown leaves (maximum 28 mg CO_2 dm^{-2} hr^{-1}). NE 48 had lower photosynthetic rates than the other clones.

The major influence on all of the growth processes of the four clones was drought stress. Two minor drought periods in the first year caused only small reductions in growth, however, two major drought periods in the second year resulted in large growth reductions and reduced gas exchange rates. NE 48 appeared to be more drought tolerant than the other clones used in this study.

ACKNOWLEDGMENTS

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INTRODUCTION

An experiment was begun in the mid-1960s to produce wood fiber on very short rotations. The concept called "silage sycamore" pulled together several cultural practices similar to those utilized by agronomists in agricultural production (McAlpine et al. 1966, Herrick and Brown 1967). The silage sycamore concept was based on the use of fast-growing hardwood species, high planting densities, intensive cultural methods, including fertilization and irrigation, rotations of 5 to 10 years or less, and coppice regrowth of harvested stands. These techniques were integrated into a comprehensive silvicultural system for intensive production of wood fiber in a short time interval.

Larson and Gordon (1969a) theorized that manipulating the growth of the tree could increase wood yield. Based on these ideas, the USDA-Forest Service established a Maximum Yield Work Unit in 1971 at Rhinelander, WI to conduct research on techniques for maximizing wood fiber production (USDA-FS 1976, 1980). Supplemental funding from the Department of Energy was received beginning in 1977 (USDA-FS 1980, 1983), and in 1978 the Work Unit was expanded to a Research and Development Program. In the meantime work continued in the South on sycamore, cottonwood, and other species (Steinbeck et al. 1972, Saucier et al. 1972, Dutrow

et al. 1970, Dutrow and Saucier 1976), and in other areas of the country (Iowa State University 1975, 1976, Schreiner 1970). This system of wood fiber production has been known by several names other than "silage sycamore": intensive culture, agroforestry, short rotation forestry, and short rotation intensive culture (SRIC). The latter term is gradually becoming the accepted name. The wide interest in the area was evident by the turnout at two conferences on intensive culture of forest crops sponsored by Iowa State University in 1974 and 1975 (Iowa State University 1975, 1976) and was fueled by predictions of shortages of wood fiber and also of energy due to the energy (oil) crisis that occured in 1974-1975.

The potential use of wood to replace oil as an energy and chemical feedstock source prompted the expansion of the Forest Service program in 1976 and the involvement of the Department of Energy in 1977. The areas of research and development included in the program were: species selection and genetic improvement, stand establishment methods, fiber and energy yields in response to spacing and harvest cycles, yield response to nutrient and moisture regimes, effect of crown architecture and canopy density on yield, physiological factors influencing yield, raw material quality of intensive culture trees, diseases of intensive culture species, insect problems in intensive culture, design of mechanized equipment for intensive culture systems, and cost of producing wood for fuel and fiber (USDA-FS 1980). Summaries of the first five and twelve

years of research results from this program have been published (USDA-FS 1976, 1983).

Some of the advantages of short-rotation intensive culture are: 1) an early return on invested capital due to the short time period of the rotation; 2) high production of wood fiber on small land areas close to the mills which allows increased mechanization and lower transportation costs; 3) use of the most productive non-agricultural land, allowing less productive forest land to be maintained in forest cover for other uses; and 4) it is less objectionable to the public to grow and harvest intensively on small areas in a manner similar to agriculture and decrease clearcutting and other objectionable practices on less productive forest land (Schreiner 1970). However, there are some disadvantages to the system as well. They are: 1) a high initial cost is required to establish the plantations and acquire the necessary equipment; 2) the process is very fossil fuel intensive for both the equipment and fertilizer needs; 3) soil nutrients and organic matter can be depleted very rapidly due to the high production and whole tree utilization; 4) the wood fiber produced by the system may not be acceptable to industry for the processes they are now using. These advantages and disadvantages formed the foundation of the Forest Service research program.

Dawson and others (1978,1980) discuss the basis for managing forests for maximum biomass production. Schreiner (1970) has suggested rotations of 2 to 5 years, 6 to 15 years, and 16 to 30 years for the production of fiber,

boltwood, and sawtimber, respectively. Active programs in intensive culture of eucalypts in Brazil (Ayling and Martins 1981) and hybrid poplars in Michigan (Rose et al. 1981) are examples of how the system can be used. Economic analyses of short rotation intensive culture systems have suggested that the system is profitable only on the best sites and feasible only for large industrial owners (Dutrow and Saucier 1976, Rose et al. 1981). Rose and others (1981) showed that net energy production was feasible only if irrigation was not used. A survey of forest industries showed that they are anticipating large increases in cultural practices in the future primarily in the areas of genetics, site preparation, fertilization, and commercial thinning but little expansion of short rotation forestry was forseen (DeBell et al. 1977). Due to the economic analyses and industry projections, research emphasis on short rotation intensive culture systems in USDA-FS has waned in the last couple of years.

One major research area in the SRIC system has been the interaction of environmental factors and silvicultural practices in their effect on the morphological and physiological processes in tree crowns (Isebrands 1982, Dickmann 1979). Understanding the seasonal and perennial patterns of these processes is important to a biological approach for increasing yields of tree stands (Isebrands 1982). The objective of the Michigan State University research program is to understand the physiological and genetical bases for growth and development in

intensively-cultured, short rotation forest stands (Dickmann et al. 1979). This dissertation research project was conceived to begin to meet that objective. A small plot research plantation was established in 1977 using cultural practices (spacing, clones, fertilization, etc.) that were determined at that time to approximate the system that would be most practical and productive for an industrial user. Measurements of the growth and development of these stands were taken in conjunction with morphological, physiological, and environmental parameters in an attempt to understand the process of woody biomass production.

CHAPTER I. GROWTH AND BIOMASS YIELD

Introduction

Among the species tested for short-rotation, intensive
culture (SRIC) in the northern United States and elsewhere,
species and hybrids of the genus Populus have been used the
most. Their indeterminate growth patterns and fast juvenile
growth produce high biomass yields because of the potential
for complete utilization of the growing season (Larson et
al. 1976, Dickmann 1975). Mean annual biomass increment
(MAI) of hybrid poplars has ranged from 1.8 to 14.1 t ha^{-1}
yr^{-1} depending upon species, site, and cultural practices,
whereas native aspen stands produced MAI's of 0.6 to 5.3 t
ha^{-1} yr^{-1} (Pollard 1971, 1972a, Schlaegel 1975, Perala
1979, Heilman et al. 1972, Dawson et al. 1976, Switzer et
al. 1976, Schreiner 1970, Cannell 1980).

Biomass yield is affected by the cultural practices
used. Fertilization usually increases yield but must be
used in conjunction with other practices such as weed
control to realize its full potential (Zsuffa et al. 1977,
Harrington et al. 1979). Tree spacing affected yields but
only in combination with rotation length. The shorter the
rotation, the closer the spacing to maximize yields
(Zavitkovski et al. 1976, Bowersox and Ward 1976). With
longer rotations, spacing becomes neutral in its effect on

biomass yields, so it is better to invest less money and use wider spacings (Cannell 1980). Irrigation or naturally moist sites increased biomass yield of hybrid poplars over unirrigated or droughty sites (Cooley 1978, Zakhariev et al. 1975, Rawitz et al. 1966). The yield increases due to irrigation are because of the limiting effect water supply and drought have on poplar growth. Liphschitz and Waisel (1970a,b) showed that height and diameter growth patterns of P. euphratica were altered by the water supply available to the tree. Drought resulted in early budset, reduced cambial growth, and low biomass yields in other studies (Sucoff and Hiesey 1978, Smith and Gatherum 1974, Braun 1974).

The partitioning of biomass into plant organs changes as a stand ages. Young stands (less than 10 years) partition up to 30% of their biomass into leaves while stands older than ten years partition 1 to 5% into leaves (Person et al. 1971, Gordon and Promnitz 1976, Switzer et al. 1976). As the proportion of biomass partitioned into leaves decreases, that partitioned into woody stems and branches increases. Thus, longer rotations will increase the proportion of woody biomass formed. Genetic differences in the proportion of biomass partitioned into wood occurs, so the potential to select genetic material that favors partitioning of dry weight into woody stems can be used to increase per hectare woody biomass production (Cannell and Willett 1976, Wray and Promnitz 1976, Gordon and Promnitz 1976). Wider spacings result in higher proportions of woody biomass partitioned into branches as opposed to stem

(Heilman et al. 1972, Dawson et al. 1976). Higher proportions of branches and bark reduces the yield and quality of the biomass for some utilization processes and products; however, these factors have been shown to be unimportant or within industry standards and tolerances for many processes and products (Crist 1983).

Careful analysis of the height and diameter growth patterns in relation to climatic conditions, tree age, and cultural practices enable the forester to make decisions on how to best manage SRIC plantations to maximize biomass yield. Biomass yield and growth patterns during the first two growing seasons (1977, 1978) of a planned three-year rotation of poplar hybrids are presented here.

Materials and Methods

Experimental Design

The general plot layout was a randomized complete block design with four replications (Figure 30 Appendix). Each replication contained three plots of one poplar hybrid (Figure 1) and one plot of corn (Zea mays) (data not reported here). Three poplar plots in each replication were harvested according to the following schedule: one plot was allowed one year of growth from planting, then cut, followed by two years of coppice regrowth; one plot grew for two years before cutting, followed by one year of coppice regrowth; the third plot grew for three years before cutting. This schedule allowed the productivity of various rotations of poplar during the initial three years following establishment to be compared with corn yields. Because of

Figure 1. Plot layout of the four replications with four plots per replication.
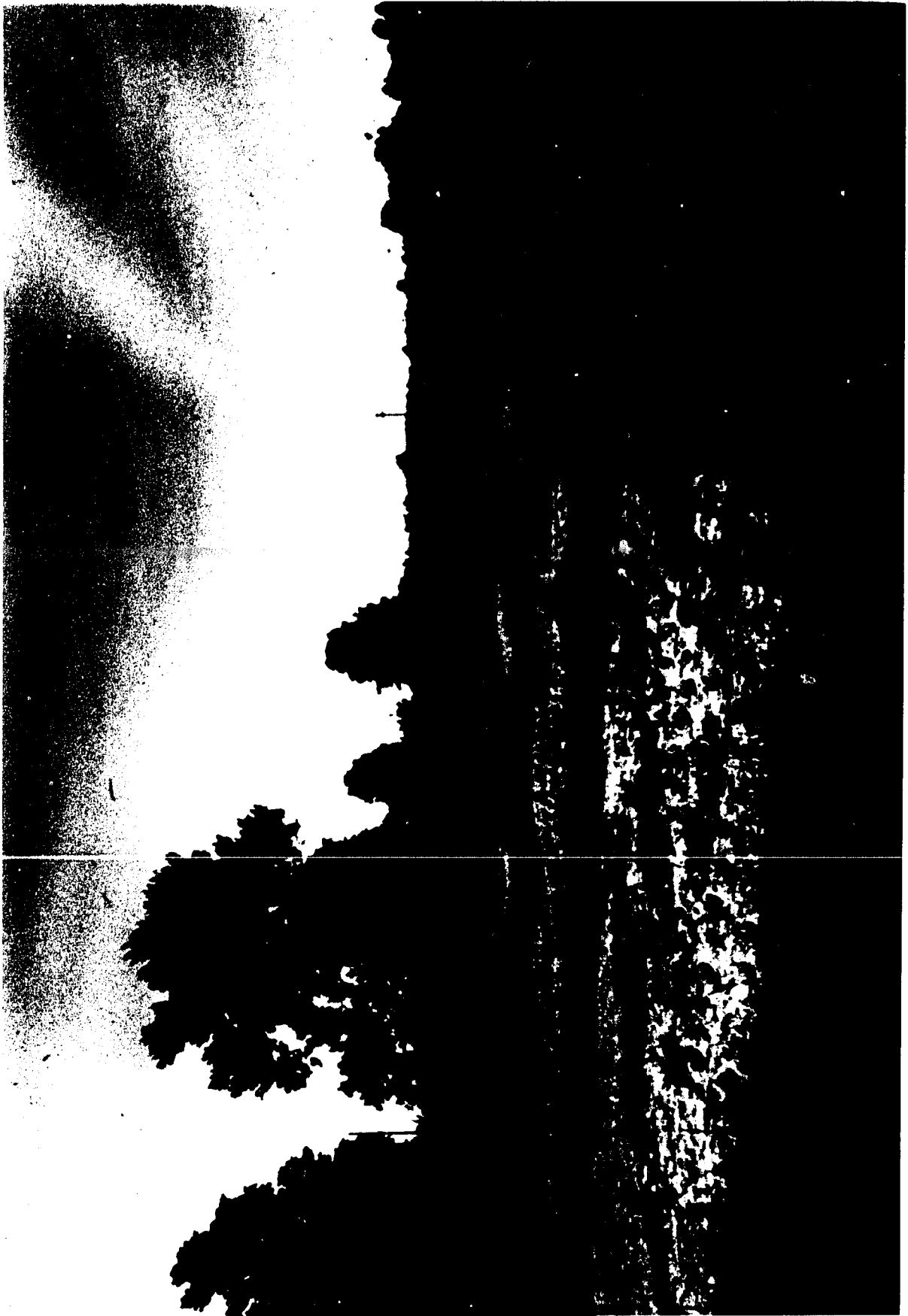
Figure 1.

this plot design objective, the yields of the individual clones reported here cannot be compared statistically, since they were not replicated.

The individual plots were 6 m wide (east-west) and 8 m long (north-south). Each plot consisted of nine east-west rows spaced 1 m apart (Figures 2 and 31 Appendix) with spacing within the rows of 0.33 m, giving a maximum plant density of 30,303 trees ha^{-1} (12,263 trees acre^{-1}). Two subplots were laid out. The growth analysis subplot consisted of rows 2 and 3 and was used for periodic growth analysis harvests. The biomass subplot consisted of rows 5 to 8 and was used for determination of height and diameter growth and biomass values. At least one border row and three border trees within a row (ca. 1 m) were located around the harvested subplots to minimize edge effects (Zavitkovski 1981a). Plots were separated by grass buffer strips of 6 m (north-south) and 5 m (east-west). The two-year initial, one-year coppice plot of clone NE 58 was suppressed by a large black cherry tree that interfered with a portion of the plot and biased that plot's data downward.

Cultural Methods

Unrooted, dormant cuttings of hybrid clones NE 353 [1] (P. deltoides x P. nigra caudina), NE 308 (P. nigra charkowiensis x P. nigra cv. Incrassata), NE 48 [P. maximowiczii x (P. x berolinensis)], NE 58 [(P. x

---

[1] USDA Forest Service, Northestern (NE) Forest Experiment Station numbers.

Figure 2. East-west row layout of a poplar plot.

Figure 2.

rasumowskyana) x <u>P. nigra</u> cv. Incrassata], and Eugenei (<u>P.</u> x

<u>euramericana</u> cv. Eugenei) were planted in early May, 1977.

Each replication contained a different clone, except that NE

353 and NE 308 were inadvertently planted together as a

random mixture in one replication.

Weed control in 1977 was accomplished by spraying 2.8

kg ha^{-1} active ingredient (ai) of simazine wettable powder

and 4.6 l ha^{-1} of amitrol-T two weeks prior to planting.

Shortly after bud break in 1978, an additional 2.8 kg ha^{-1}

ai of simazine wettable powder was sprayed on the plots.

All plots were fertilized with 224 kg ha^{-1} of 10-20-20

(N-P-K) granular fertilizer on May 17, 1977 and May 18,

1978. In addition, 75 kg ha^{-1} of ammonium nitrate (33-0-0)

was applied on August 1, 1977 and July 7, 1978. Irrigation

was not used. The soil types present were a well-drained,

slightly eroded Kalamazoo sandy loam (a fine-loamy, mixed,

mesic Hapludalf), with a 0-2% slope and a sandy clay loam to

clay loam subsoil, and a well-drained, slightly eroded

Hillsdale sandy loam (a coarse-loamy, mixed, mesic

Hapludalf), with a 2-6% slope and a sandy clay loam or loam

subsoil.

Experimental Methods

Height and Diameter Growth. At two-week intervals the

first year, stem height and diameter at 5 cm were measured

on a ten-tree permanent sample within the biomass subplot.

During the second year, trees in the biomass subplot were

divided into crown classes (dominant, codominant,

intermediate, suppressed) based on their crown light

interception and height relative to neighboring trees. Height and diameter growth patterns were determined by crown class.

Growth Analysis Harvests. A two-tree sample was selected at random within the growth analysis subplot and harvested every two weeks throughout the growing season. Stem height and diameter at 5 cm were measured prior to harvesting. Trees were partitioned into stem, branches, and leaves, oven-dried at 75 C, and weighted. Biomass partitioning was then calculated as percentage of total above-ground biomass.

Biomass Harvests. After the onset of dormancy and leaf abscission in the fall, the biomass subplots were harvested. Stem height and diameter at 5 cm were measured prior to harvesting. Each stem was then oven-dried at 75 C and weighed. Above-ground biomass yield of wood and bark and branches was obtained by totaling the weights of all the stems, converting to tonnes, and dividing by the plot area. Total above-ground biomass was then calculated by using the ratios of leaf weight to total above-ground biomass from the last growth analysis harvest prior to fall leaf abscission to estimate the leaf biomass produced.

Individual stem height (H) and diameter (D), and oven-dry weight (DW) values were used to develop a least squares regression of the mensurational variable D^2H versus dry weight for each poplar clone, for each year (Zavitkovski 1971, 1976, Zavitkovski et al. 1974, Bowersox and Murphy 1975). The allometric equation $(Y=aX^b)$ was transformed to

its logarithmic form $[\ln Y = \ln a + b(\ln X)]$ to compute the regressions. All regressions had r^2 values greater than 0.89. Bartlett's test for homogeneity of variance values was significant, so it was not possible to test for clonal differences in slope of the regressions. A correction factor for bias due to the transformation was used for each clone (Baskerville 1972). Biomass yield of wood and bark in unharvested plots was calculated via the every tree summation method (Baskerville 1965, Attiwell and Ovington 1968) using the prediction equations developed for each clone. Total above-ground biomass was then calculated in the same manner as in the harvested plots.

Results

Height Growth

First-year height growth began shortly after planting and continued until terminal bud formation occurred in late August. Clone NE 48, however, did not set bud until late September (Figure 3). Average height of the four clones ranged from 1.2 to 1.3 m (Table 1).

Second-year height growth began with bud break in early May, with clone NE 48 one week ahead of the other clones. Terminal bud formation occurred in mid-July for intermediate, suppressed, and minor stems of all clones and for dominant and codominant stems of clones NE 58 and Eugenei (Figure 4). Dominant stems of clones NE 353 + 308 set bud in late August. Dominant and codominant stems of clone NE 48 did not set bud until late September. Average second-year height of the four clones ranged from 2.0 to 2.2 m (Table 2).
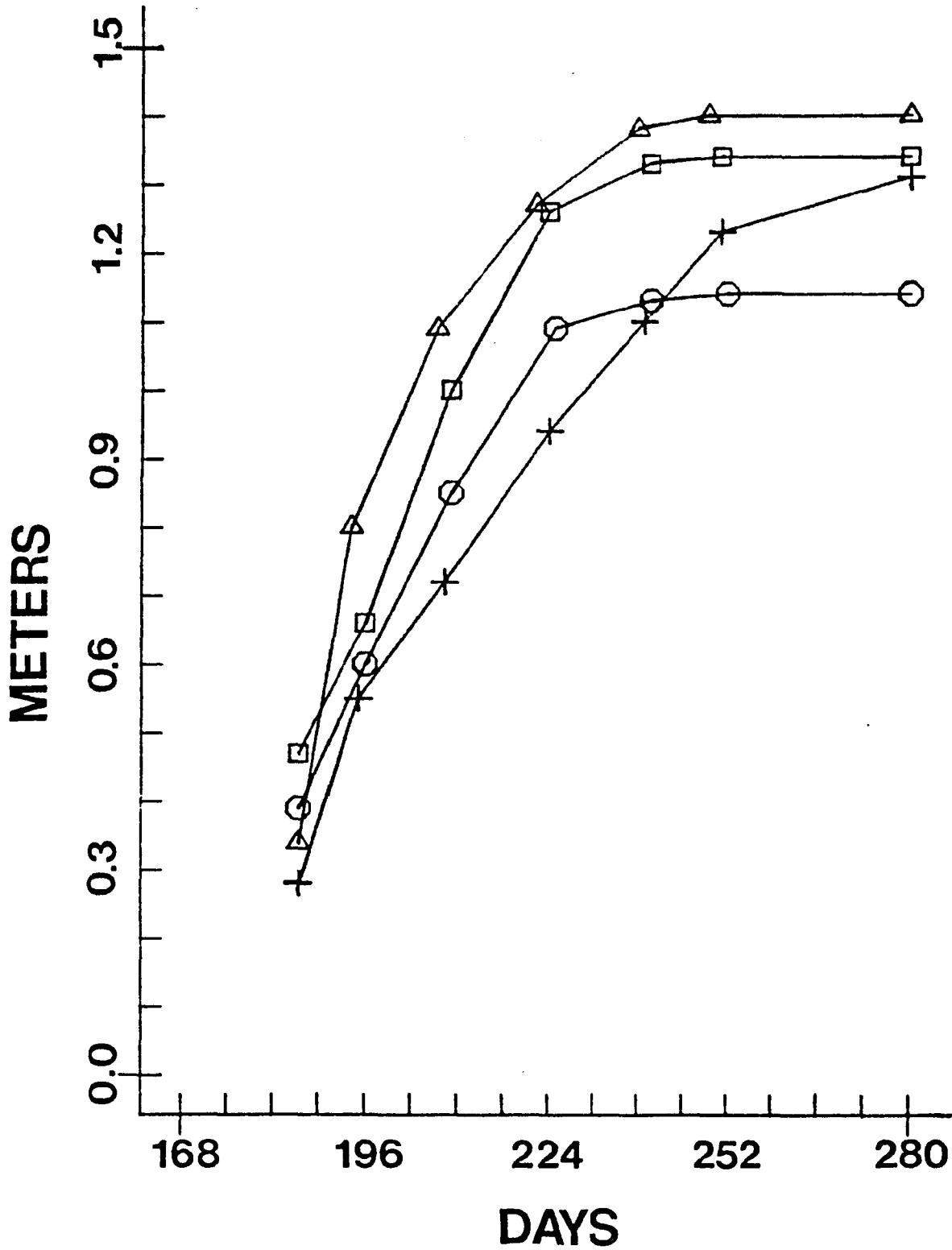
Figure 3. Seasonal height growth pattern of four hybrid
poplar clones during the first growing season (Day 161 =
June 10, NE 353+308 ▲, NE 48 +, NE 58 □ , Eugenei o).

Table 1. Height, diameter, and survival of four hybrid poplar clones after one growing season.

Clone Number	Harvested Plot			Average of all plots[a]		
	Height (m)	Diameter[b] (cm)	Survival (%)	Height (m)	Diameter (cm)	Survival (%)
NE 353+308	1.27	1.3	100	1.34	1.2	99
NE 48	1.29	1.4	98	1.18	1.2	98
NE 58	1.32	1.2	99	1.24	1.2	99
Eugenei	1.18	1.2	95	1.25	1.2	95
AVERAGE	1.26	1.3	98	1.26	1.2	98

a
 Average of one-year-old harvested plot and two one-year-old unharvested plots.

b
 Diameter was measured 5 cm above ground level or emergence from cutting.

Figure 4. Seasonal height growth pattern of dominant major
stems (Δ), codominant major stems (+), intermediate major
stems (◻), and suppressed major or any minor stems (o) of
four hybrid poplar clones during the second growing season
(Day 125 = May 5).
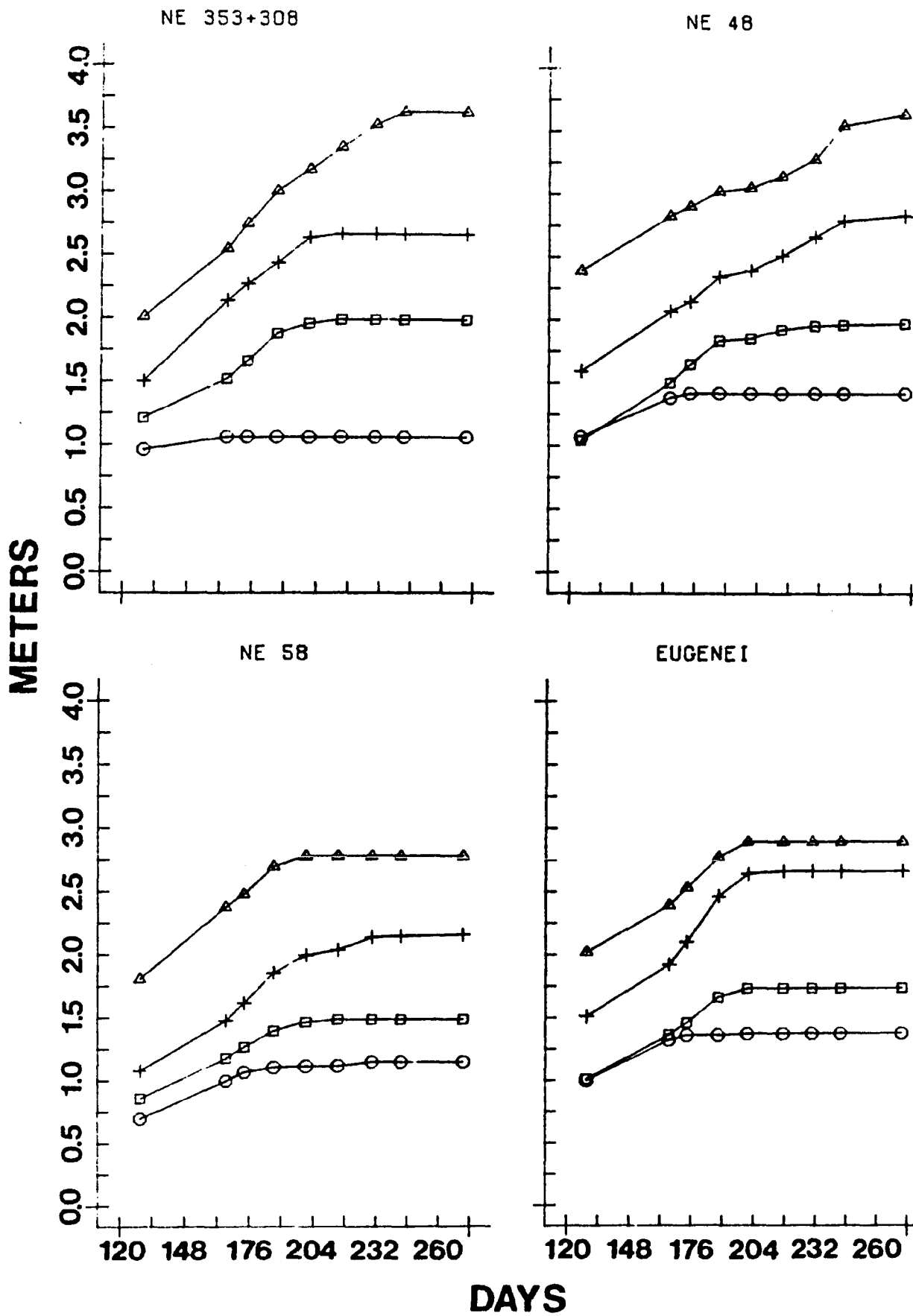
Figure 4.

Table 2. First- and second-year height, diameter, and survival of four hybrid poplar clones.

Clone Number	Harvested Plot					Average of both Plots[a]				
	First Year		Second Year			First Year		Second Year		
	Ht. (m)	Dia.[b] (cm)	Ht. (m)	Dia. (cm)	Surv. (%)	Ht. (m)	Dia. (cm)	Ht. (m)	Dia. (cm)	Surv. (%)
NE 353+308	1.33	1.2	2.07	1.7	96	1.38	1.2	2.18	1.8	95
NE 48	1.33	1.3	2.03	1.8	98	1.13	1.2	1.96	1.7	96
NE 58	1.04	1.0	1.67	1.5	100	1.20	1.2	1.98	1.6	99
Eugenei	1.24	1.1	2.10	1.8	94	1.28	1.2	2.02	1.7	96
AVERAGE	1.21	1.1	1.97	1.7	97	1.25	1.2	2.04	1.7	97

a
 Average of two-year-old harvested plot and of one two-year-old unharvested plot.

b
 Diameter was measured 5 cm above ground level or emergence from cutting.

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Diameter Growth

First-year diameter growth also began shortly after planting and continued until the beginning of September. Clone NE 48, however, continued diameter growth until late September (Figure 5). Average diameter of the four clones was 1.2 cm (Table 1). A mild drought in mid-August caused a decline in diameter growth which was most noticeable in clone NE 48 followed by NE 353 + 308 (Figure 5). Diameter growth then recovered when rainfall replenished the soil moisture (Figure 21 Chapter III).

Second-year diameter growth began shortly after bud break in early May and ceased in late June for intermediate, suppressed, and minor stems of all the clones (Figure 6). Codominant stems of all four clones ceased diameter growth in mid-July (Figure 6) when the first major drought occurred (Figure 21 Chapter III). Some of the NE 48 codominant stems recovered and grew with rains in August. Dominant stems of NE 58 and Eugenei also ceased diameter growth in mid-July; however the dominant stems of NE 353 + 308 and NE 48 maintained diameter growth until early September when a second major drought occurred. Average second-year diameter of the four clones ranged from 1.6 to 1.8 cm (Table 2).

Segregation into Crown Classes

During the first growing season, intraclonal competition within the plots began to segregate the trees into crown classes. With the onset of growth in the second growing season, segregation intensified, with some trees becoming dominants, the majority remaining codominant, some
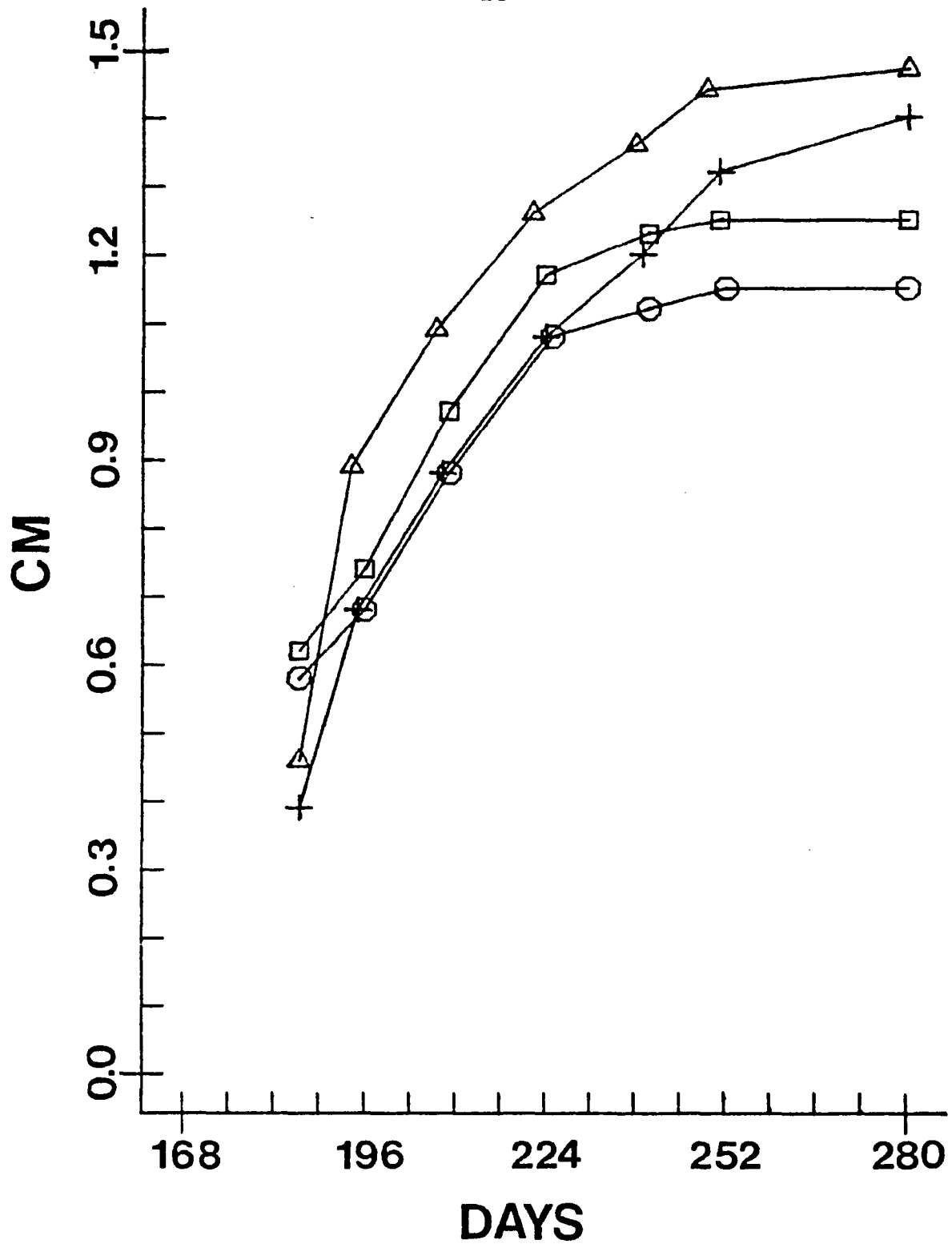
Figure 5. Seasonal diameter growth pattern of four hybrid poplar clones during the first growing season (Day 161 = June 10, NE 353+308 Δ, NE 48 +, NE 58 □, Eugenei o).

Figure 6. Seasonal diameter growth pattern of dominant
major stems (▲), codominant major stems (+), intermediate
major stems (▫), and suppressed major or any minor stems (o)
of four hybrid poplar clones during the second growing
season (Day 125 = May 5).

25
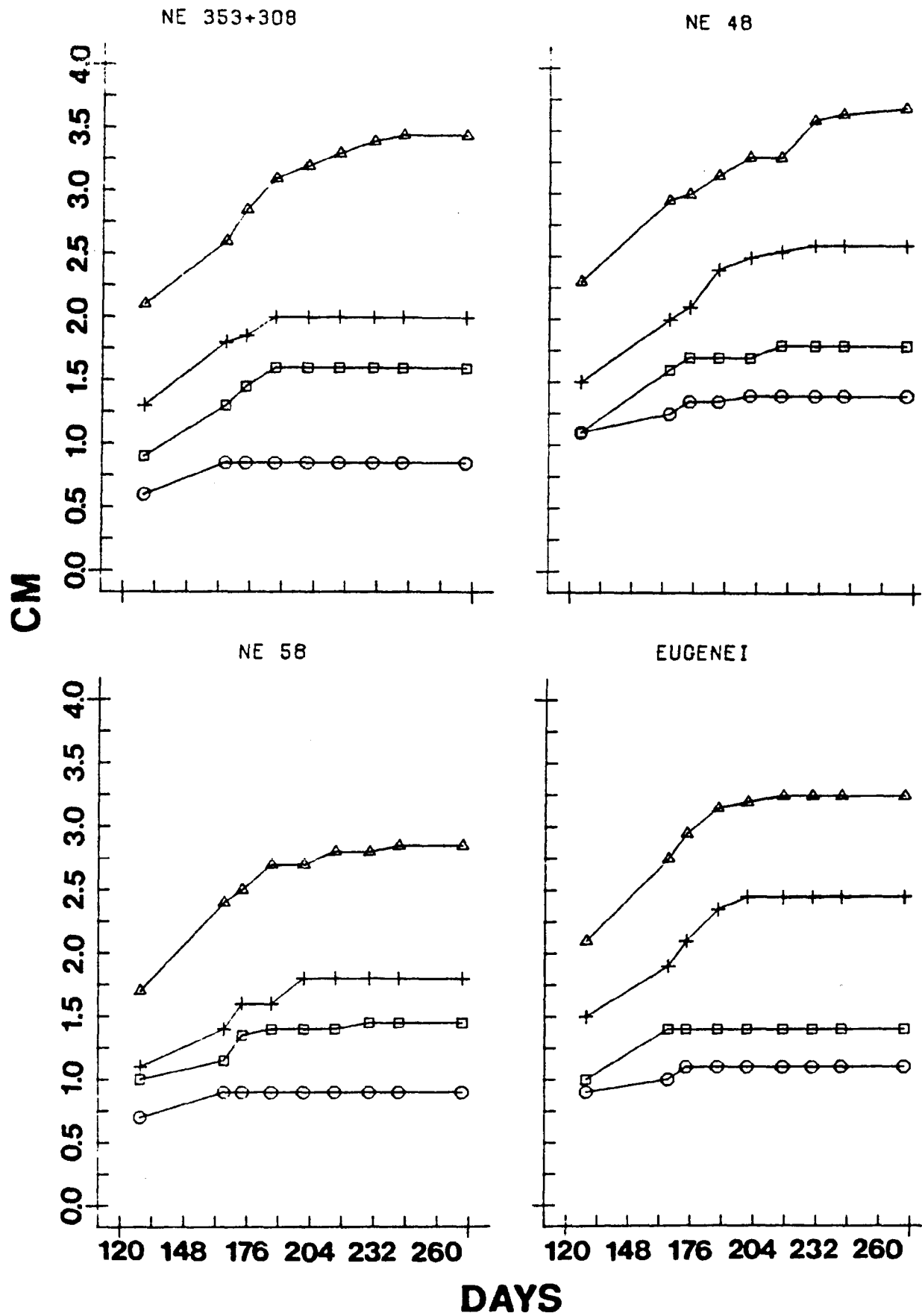
Figure 6.

becoming intermediates and a few becoming suppressed. Distribution of trees into crown classes is shown for the four clones in Table 3 and is surprisingly uniform between clones. Average height, diameter, and stem weight is given for all trees and each crown class (Table 3). As crown class moved from suppressed to dominant, height increased 2 to 3-fold, diameter 2 to 4-fold, and stem weight 10 to 20-fold depending upon clone. Clone NE 58 at the end of the first and second growing seasons is shown in Figures 7 and 8.

Biomass Yield

Stem Dry Weight Prediction Equations. Tables 4 and 5 give the regression results and prediction equations for estimating stem dry weight from the mensurational variable D^2H. All of the regressions were significant and had r^2 values greater than 0.88 for one-year-old trees and greater than 0.99 for two-year-old trees. The parameters for one-year-old trees had a larger range than the ones for two-year-old trees.

Actual and Estimated Biomass Yields. Actual biomass yield of wood and bark in the harvested plots ranged from 1.6 to 2.9 t ha^{-1} (Table 6). With the leaves added, biomass yields increased to 2.4 to 4.6 t ha^{-1}. Estimates of biomass yields using the prediction equations for one-year-old trees in unharvested plots ranged from 1.5 to 2.3 t ha^{-1} for wood and bark and 2.2 to 3.7 t ha^{-1} for total above-ground biomass.

Table 3. Average height, diameter, stem weight and number
of trees by crown class of four hybrid poplar clones after
two growing seasons.

Clone Number	Crown Class Major Stems	Number	Height (m)	Diameter[a] (cm)	Stem Weight[b] (g)
NE 353	All	50	2.74	2.3	259
+ 308	Dominant	4	3.46	3.0	452
	Codominant	33	2.92	2.5	305
	Intermediate	7	2.38	1.7	116
	Suppressed	6	1.64	1.2	48
NE 48	All	51	2.72	2.5	301
	Dominant	7	3.58	3.3	552
	Codominant	30	2.92	2.7	334
	Intermediate	9	2.16	1.9	138
	Suppressed	5	1.32	1.1	40
NE 58	All	52	2.09	1.9	155
	Dominant	5	2.73	2.5	305
	Codominant	25	2.42	2.2	204
	Intermediate	16	1.82	1.6	84
	Suppressed	6	0.90	0.8	16
Eugenei	All	49	2.54	2.3	234
	Dominant	9	3.10	3.3	465
	Codominant	26	2.68	2.4	235
	Intermediate	11	2.15	1.7	101
	Suppressed	3	1.09	0.8	19

a
 Diameter was measured 5 cm above ground level or emergence
from cutting.

b
 Stem weight includes branches and bark.

Figure 7. Clone NE 58 at the end of the first growing
season.

Figure 7.

Figure 8. Clone NE 58 at the end of the second growing
season.

Figure 8.

Table 4. Regression and prediction equation[a] parameters from D^2H versus dry weight regressions for four one-year-old hybrid poplar clones.

| Clone Number | Regression | | Coefficients | | | |
	Significance of F-ratio[b]	r^2 value	Intercept (b_0)	Variable 1 (b_1)	Significance of t value	Correction factor
NE 343+308	**	0.89	2.83	0.867	**	0.0468
NE 48	**	0.99	2.70	0.913	**	0.00297
NE 58	**	0.99	2.81	0.840	**	0.00188
Eugenei	**	0.92	2.76	0.845	**	0.0159

a
Prediction Equation: $\hat{DW} = e^{\{b_0 + b_1 (Ln\ D^2H) + CF\}}$ or $\hat{DW} = a(D^2H)^{b_1}$

Regression Equation: $Ln\ DW = b_0 + b_1 (Ln\ D^2H)$ which is the transformed form of the equation, $DW = a(D^2H)^{b_1}$

Where: DW = dry weight of wood + bark in grams.
D = diameter at 5 cm above ground level or emergence from cutting in cm.
H = height in m.
D^2H = mensurational variable, diameter squared times height in cm^2-m.
Ln = natural logarithm (base e).
e = exponential function.
CF = correction factor due to bias of transformation = $\hat{\sigma}^2 / 2$.
a = constant which equals $e^{(b_0 + CF)}$.

b
** = significant at $\alpha = 0.01$ level.

Table 5. Regression and prediction equation[a] parameters from D^2H versus dry weight regressions for four two-year-old hybrid poplar clones

Clone Number	Regression		Coefficients			
	Significance of F ratio[b]	r^2 value	Intercept (b_0)	Variable 1 (b_1)	Significance of t value[b]	Correction factor
NE 353+308	**	0.99	2.96	0.926	**	0.00968
NE 48	**	0.99	2.94	0.927	**	0.00808
NE 58	**	0.99	2.99	0.922	**	0.00788
Eugenei	**	0.99	2.98	0.893	**	0.00495

[a] Prediction Equation: $\hat{DW} = e^{\{b_0 + b_1 (Ln\ D^2H) + CF\}}$ or $\hat{DW} = a(D^2H)^{b_1}$

Regression Equation: $Ln\ DW = b_0 + b_1 (Ln\ D^2H)$ which is the transformed form of the equation, $DW = a(D^2H)^{b_1}$

Where DW = dry weight of wood + bark in grams.
   D = diameter at 5 cm above ground level or emergence from cutting in cm.
   H = height in m.
   D^2H = mensurational variable, diameter squared times height in cm^2-m.
   Ln = natural logarithm (base e).
   e = exponential function.
   CF = correction factor due to bias of transformation = $\hat{\sigma}^2/2$.
   a = constant which equals $e^{(b_0 + CF)}$.

[b] ** = significant at α = 0.01 level.

Table 6. Actual and estimated above-ground biomass yields (t ha^{-1}) of four hybrid poplar clones after one growing season

Clone Number	Harvested Plot		Average of Estimated Plots	
	Wood and bark	Wood, bark and leaves	Wood and bark	Wood, bark and leaves
NE 353+308	2.9	4.6	2.3	3.7
NE 48	2.6	3.7	1.6	2.3
NE 58	1.9	2.8	1.5	2.2
Eugenei	1.6	2.4	1.6	2.4
AVERAGE	2.2	3.4	1.8	2.6

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Actual biomass yields of wood and bark in the harvested plots at the end of the second year ranged from 5.3 to 9.8 t ha^{-1}, a 4 to 5-fold increase over the first year estimates for the same plots (Table 7). Estimates of biomass yields using the prediction equations for two-year-old trees ranged from 6.0 to 10.4 t ha^{-1}, a 3 to 7-fold increase over the first year estimates for the same plots (Table 7). The MAI (mean annual increment) of the two-year-old plots ranged from 3.4 to 4.6 t ha^{-1} yr^{-1}, with an average of 3.9 t ha^{-1} yr^{-1}.

Biomass Partitioning

Partitioning Between Organs. Early in the first year 65 to 80% of the total above-ground biomass was present as leaves and the remaining 20 to 35% as stem. The percentage in leaves dropped steadily throughout the growing season to 25 to 40% prior to leaf fall (Figure 9), whereas the percentage in stem wood increased to 60 to 75%. During the second growing season, the percentage of total above-ground biomass in leaves declined from 30 to 40% in June to 10 to 20% in September (Figure 10). The percentage in petioles declined also from 3 to 4% down to 1 to 2%. At the end of the second growing season, the woody stem comprised 65 to 75% and branches 15 to 20% of the total above-ground biomass. Table 8 gives the percentages of the total wood and bark biomass partitioned into current year stem, branches, and two-year-old stem. In the first year, 13% of the wood and bark of clone NE 353 + 308 was comprised of sylleptic branches, whereas in the other three clones,

Table 7. Actual and estimated above-ground woody biomass yields (t ha^{-1}) of four hybrid poplar clones after two growing seasons.

Clone Number	Harvested Plot		Estimated Plot		Average of Both Plots	
	Wood, bark & branches	Wood, bark & branches First year estimate	Wood, bark & branches Second year estimate	Wood, bark & branches First year estimate	Wood, bark & branches	Wood, bark & branches First year estimate
NE 353+308	8.1	2.0	10.4	2.6	9.2	2.3
NE 48	9.8	2.1	6.6	1.0	8.2	1.6
NE 58	5.3	1.2	8.2	1.8	6.8	1.5
Eugenei	7.7	1.5	6.0	1.8	6.8	1.6
AVERAGE	7.7	1.7	7.8	1.8	7.8	1.8
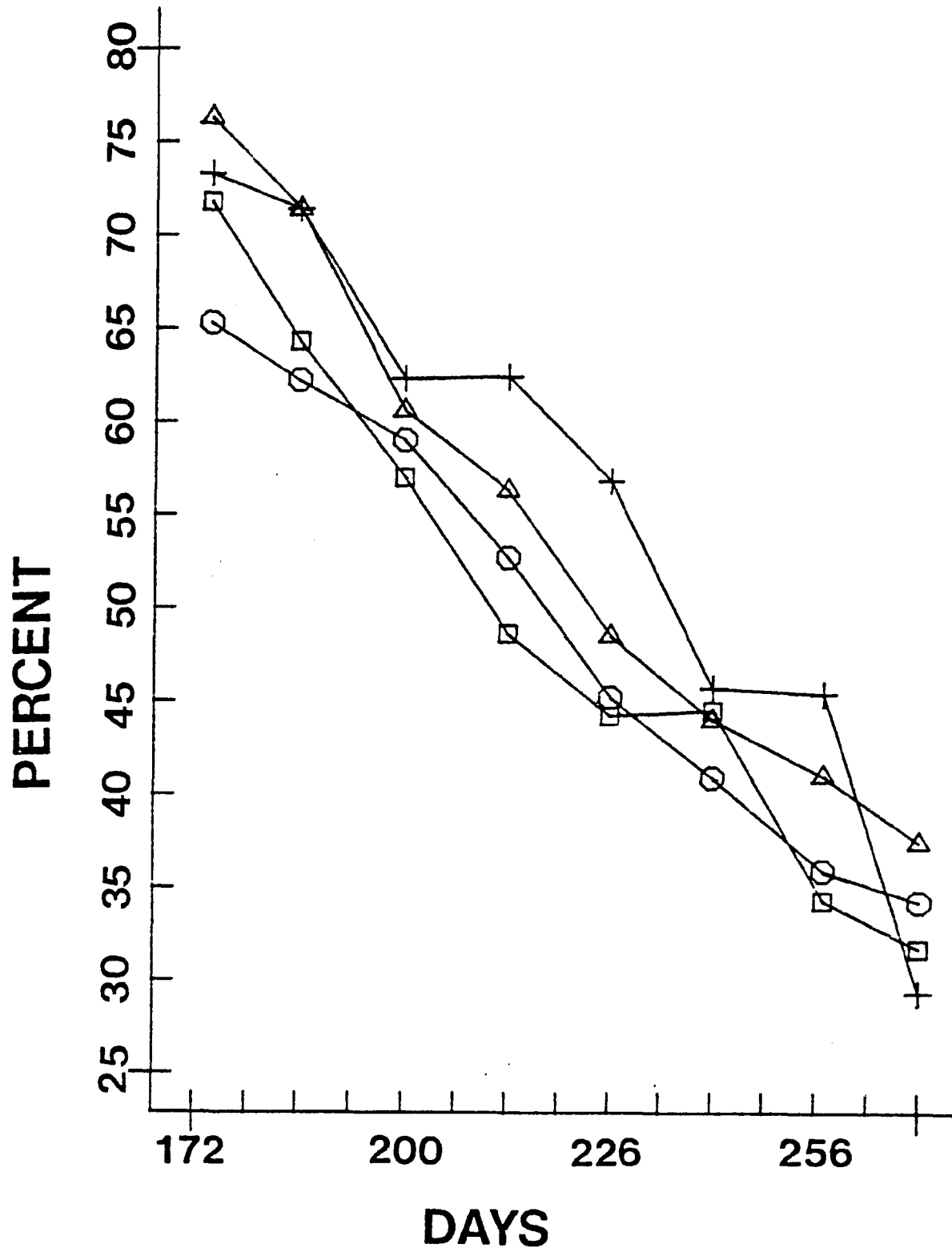
Figure 9. Seasonal change in percentage of total biomass present in leaves of four hybrid poplar clones during the first growing season (Day 172 = June 21, NE 353+308 △, NE 48 +, NE 58 □, Eugenei o).

Figure 10. Seasonal change in percentage of total biomass present in woody stem (Δ), branches (+), leaves (□), and petioles (o) of four hybrid poplar clones during the second growing season (Day 151 = May 31).
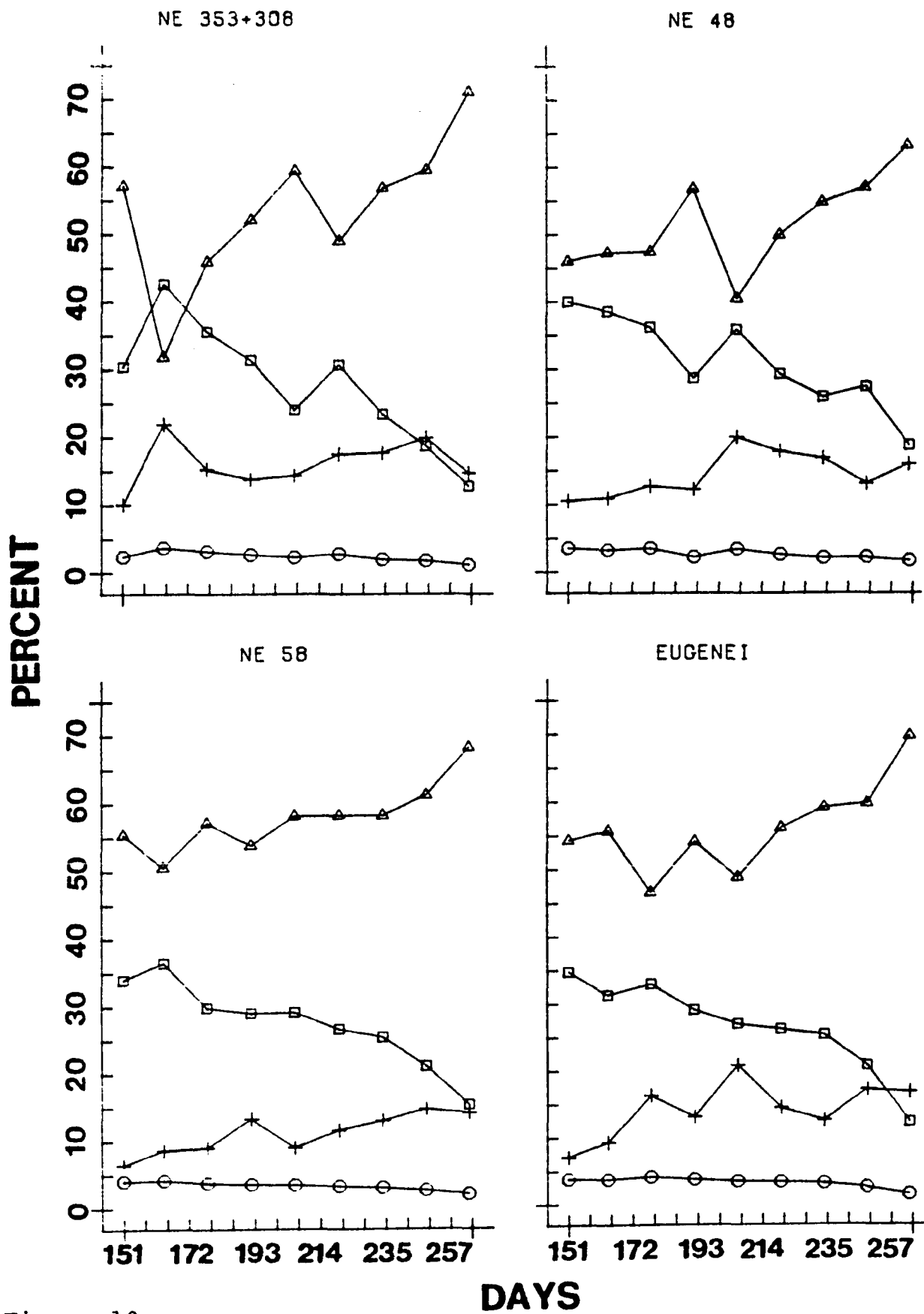
Figure 10.

Table 8. Partitioning of wood and bark biomass of four hybrid poplar clones after the first and second growing seasons.

| Clone Number | Percentage of Total Wood + Bark Biomass | | | | |
| | First Year | | Second Year | | |
	Current Stem	Current Lateral Branches	Current Stem	Two-year-old Stem	All Branches
NE 353+308	87	13	9	70	21
NE 48	98	2	9	70	21
NE 58	98	2	11	71	18
Eugenei	100	0	12	67	21
AVERAGE	96	4	10	70	20

these branches comprised only 0.3 to 2.5%. Differences in percentage of wood and bark in branches in the second growing season were not large (all approximately 20%), while current stem wood was 9 to 12% and two-year-old wood was 67 to 70% of the total wood and bark biomass.

Partitioning Between Stems. Most of the planted cuttings produced more than one shoot (Table 9). In the first year, major stems accounted for 78 to 88% of the woody biomass while minor stems accounted for 12 to 22%. During the second year, major stems became more dominant and minor stems grew little. As a result, major stems comprised 86 to 93% of the woody biomass, while only 7 to 14% was in minor stems. These minor stems are obviously on their way out of the stand.

Discussion

The high survival rates obtained in this study were due to a combination of good quality planting stock, excellent weed control, and favorable environmental conditions in the period immediately following planting. Whereas the growth potential of poplars is high, they are "prima donnas" and must be planted and cared for according to a strict silviclutural regimen (Dickmann and Stuart 1983). Anything less will produce mediocre results.

Clone NE 48 differed from the other poplar clones used in this study in timing and seasonal duration of growth; it broke bud earlier, grew faster late in the season, and set bud later. These differences in budbreak and budset are in part due to genetic differences in response to photoperiod

Table 9. Distribution of wood, bark, and branch biomass between the major and minor stems present on each cutting for four hybrid poplar clones after the first and second growing seasons.

| Clone Number | First Year | | | Second Year | | |
| | Number of stems per cutting | Percentage of woody biomass | | Number of stems per cutting | Percentage of woody biomass | |
		Major Stems	Minor Stems		Major Stems	Minor Stems
NE 353+308	1.9	88	12	1.8	93	7
NE 48	2.0	80	20	1.9	92	8
NE 58	1.8	78	22	1.7	89	11
Eugenei	1.8	78	22	1.7	86	14
AVERAGE	1.9	81	19	1.8	90	10

and temperature. Pauley and Perry (1954) demonstrated that duration of shoot growth in clones of several Populus species was sensitive to daylength and inversely correlated with the latitude of origin of each clone. In terms of tree improvement, if genotypes that can utilize the entire growing season, like NE 48, can be combined with clones having other favorable characteristics, improved growth and biomass productivity could result, although increased risk of frost damage must be considered also.

During the first growing season, a mild drought occurred that decreased diameter growth in clones NE 48 and NE 353 + 308, but more favorable conditions were created with additional rainfall. Clones NE 58 and Eugenei may have also suffered from the drought, but the lack of resumption of diameter growth with rainfall made it difficult to determine if that was the case. The severe drought periods which occurred during the second growing season reduced height and diameter growth significantly over what would have been attainable with more favorable moisture conditions.

Intraclonal competition during these drought periods was intense. Reductions in growth of the smaller stems was at least partially due to competition for light as well as water. Height growth stopped first in intermediate, suppressed, and minor stems, whereas codominant and especially dominant stems kept growing until the second major drought period occurred. The dominant stems of NE 353 + 308 and NE 48 maintained growth better than Eugenei and NE 58. Clone NE 48 again responded to early September rainfall

with a period of renewed height and diameter growth. It is
very likely that these differences in phenology among crown
classes were due to a better exploitation of the available
soil volume by the larger trees (Faulkner and Fayle 1979),
although no root distribution data were collected.
Irrigation would have increased height growth, especially
during the second growing season. Diameter growth would
have responded even more than the height growth to
irrigation since diameter growth is more sensitive to water
stress (Dickmann 1979, Bonner 1967). Blake (1981) has shown
that Tacamahaca poplars (like NE 48) have a higher water use
efficiency than Aigeiros poplars, which could explain the
greater drought tolerance of NE 48.

Unfortunately, resistance to the canker fungus Septoria
musiva is not among the genetic characteristics of clone NE
48. Incipient cankering observed during the second growing
season killed almost all of the trees during years 3 and 4.
Nonetheless, much potential apparently exists within the
species P. maximowiczii (Japanese poplar) and it should be
considered a prime candidate for poplar improvement
programs.

A review of the poplar literature showed a wide range
of height and diameter growth rates. However, growth values
very similar to those achieved by dominant and codominant
stems in this study were reported by Dawson and others
(1976), Bowersox and Ward (1976,1977), Cannell (1980), and
Merritt and Bramble (1966). Most of these studies thinned
to one stem per cutting which concentrated subsequent growth

on the major stem. In the present study, the inclusion of both major and minor stems in the average height and diameter values tended to reduce these average values below those of thinned trees. The practice of thinning to one stem per cutting is impractical for field application and consequently was not done in this study.

Cannell (1980) and Cannell and Smith (1980) discuss the possibility of a yield ceiling for biomass production of intensively-cultured temperate hardwoods of 10 to 12 t ha^{-1} yr^{-1} 4 to 5 years after planting and 10 to 30% greater yields after coppicing for 4 to 5 years. In a review of published results, Cannell and Smith (1980) show that the two major factors determining yield are age and spacing (or plant density), with species, site, and error being minor factors. The above-ground biomass yields obtained in this study agree closely with yields reported elsewhere in the literature. Larger first-year yields in the present study than those reported by Bowersox and Ward (1976) are due to their practice of thinning to one stem per cutting shortly after planting while our plots had from 1.7 to 2.0 stems per cutting. However, in the second year these minor stems became less important contributors to stand yield and eventually died. Cannell (1980) reported similar first-year yields of 2 t ha^{-1} for P. trichocarpa planted at 30,000 trees ha^{-1} as unrooted cuttings and thinned to one stem per cutting two months after planting. But second-year yields were 10 t ha^{-1}, higher than values reported here. Apparently yields in this study were decreased due to

drought in the second year and, to a smaller extent, in the first year. MAI was lower than the proposed yield ceiling due to drought and because the data represented only two years growth instead of 4 to 5 years growth.

High LWRs (leaf weight ratios) of poplar cuttings early in the season were a significant factor in their establishment and early growth. The high partitioning of weight into leaves, 50 to 80% depending upon clone, provided a large photosynthetic surface upon which further growth was based. In fact, the rapid growth of young hybrid poplars and cottonwood can be largely attributed to this large initial investment in leaves. As the season progressed and the plants became established in the soil, a larger proportion of biomass was partitioned into the stem and the proportion in leaves dropped to 10 to 40%, depending upon clone. During the second year, the initial investment in leaves was lower than in the first year (30 to 40%) and again decreased over the season (down to 10 to 20%). These results are confounded, however, by the large amount of leaf abscission which occurred due to drought during the season (see Chapter II).

The large differences in branch formation between NE 353 + 308 and the other three clones during the first season appears to be genetically related. (Branching patterns will be discussed in greater depth in Chapter II.) First-year branch biomass has also been reported for cottonwood (30%, Baker and Blackmon 1977), P. trichocarpa in Britain (28 to 30%, Cannell 1980), and for coppice growth of two hybrid

poplars in Wisconsin (7 to 23%, Crist and Dawson 1975).
Second year branch biomass was much more uniform (17.8 to
21.4%) in the present study and was similar to values reported
elsewhere for two- and three-year-old stands (10 to 35%,
Anderson and Zsuffa 1975, Heilman et al. 1972, Dawson et al.
1976, Cannell 1980). Apparently the relative branchiness of
a poplar clone during the first year cannot be used as a
predictor of branchiness in older trees.

The development of crown class segregation very early
in the life of the stands in this study has not often been
reported. Merritt and Bramble (1966) found that after five
years the individual heights of Eugenei and P. deltoides
trees in a widely-spaced plantation both followed normal
bell-shaped distributions, with a tail to the intermediate
and suppressed end. Codominant trees comprised the major
portion of their curve. Johnson and Burkhardt (1976) found
that three-year-old natural stands of P. deltoides had
already segregated into crown classes. Dominant trees were
only slightly taller than codominant trees, but had
diameters 1/3 to 1/2 larger, wider crowns, and higher live
crown length to total height ratios than codominant trees.
Although heights of live crown were not measured in the
present study, dominant trees generally had less abscission
of leaves and branches and larger crowns (see Chapter II).

The end result of segregation into crown classes will
be similar to the effects of loss of minor stems.
Suppressed and intermediate stems will gradually die
(without thinning) and their biomass will be lost. However,

the lost biomass may be more than recouped by the increased growth and quality of the surrounding trees. Wider spacings and thinnings could be utilized to prevent some of this biomass loss and to save high establishment costs for trees that will never be harvested. Very short rotations (one to two years) will prevent much biomass loss from occurring but will also decrease MAIs, while longer rotations will compound the biomass losses and necessitate intermediate thinnings to recover biomass before it is lost. Heilman and Peabody (1981) found maximum MAIs for black cottonwood at several spacings occurred at rotations of 8 years rather than 2 and 4 years. Cultural practices such as fertilization and irrigation initially decrease intraclonal competition and allow trees to survive longer. However, the increased stand growth magnifies the competition level of the stand and when shortages develop in light, water, or nutrients, use of these cultural practices hastens the loss of trees that could not successfully compete.

Another result of the segregation into crown classes is a change in the biomass distribution within trees of different classes. Dominant trees have a lower proportion of biomass in the stem and a higher proportion in leaves while the proportion in branches is about the same as in codominant trees; codominant trees show the same differences over intermediate and suppressed trees (Carter and White 1971, Zavitkovski 1971). From the standpoint of maximizing per hectare yields over longer rotations, it would be best to have a uniform stand created by frequent thinnings than

to have larger dominant trees with high branch components along with dying suppressed trees.

CHAPTER II. CROWN DEVELOPMENT

Introduction

The production of biomass by plants is dependent upon the carbohydrates available for growth. These carbohydrates are a product of net assimilation rate (NAR) and the leaf area available for light interception and photosynthesis (Watson 1952). The literature shows that dry matter yields depend more on variation in leaf area than in NAR (Larson and Isebrands 1972, Zavitkovski et al. 1974, Larson et al. 1976, Watson 1947, 1958). In this sense, leaf area duration (LAD), the integral of leaf area index (LAI, the ratio of leaf area to ground area) over time becomes the important determinant of biomass yield (Madgwick and Olson 1974, Watson 1952, 1956). Most cultural practices affect leaf area more than NAR, although the two processes can both change independently; cultural practices that increase yield do so wholly or mainly by influencing leaf growth and/or retention (Watson 1952, 1956).

The study of crown development must take into account the production of new leaves. Larson and Isebrands (1971) have shown that leaf production, growth (leaf length, area, and dry weight), and maturation of physiological function are all correlated and related to the leaf plastochron index (LPI) in cottonwood. Pieters (1974), in an indepth study of

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<u>P.</u> x <u>euramericana</u> cv. Robusta, supports these findings and
shows that under constant conditions the rate of leaf
production steadily increases with time until steady state
growth is achieved (plastochron interval decreases to a
constant value). Light intensity, temperature, moisture and
nutrient supply all affect the plastochron interval.

The annual cycle of height growth, leaf and branch
development results in a regular ordering of internodes and
branches. Isebrands and others (1977) have used the term
"height growth increment" (HGI) to represent the main-stem
growth produced in any given year. HGI's are numbered
consecutively from the base of the tree upward. Branches
which originate on an HGI segment are given the same
designation as the HGI. Branches, within an HGI, are
classified by their place of origin. Primary branches are
those which originate from lateral buds on the current
leader; secondary branches originate from lateral buds on
primary branches and increasing orders can be present up to
the age of the HGI (Maini 1966a,b, Nelson et al. 1980, 1981,
Wilson 1970). Branches can further be classified by their
growth into long and short shoots (Wilson 1970, Kozlowski
and Clausen 1966, Maini 1966a, Pollard 1970, Gregory 1980).
By the time the fourth or fifth order is reached, long
shoots usually do not bear lateral long shoots; they bear
only short shoots, many of which do not have any laterals.
So only 5 to 6 orders of branches are usually present in a
tree crown (Wilson 1970), although there is much
variabililty among species. Branch development also is

influenced by the environment and development of other
branches on the tree (Richards and Larson 1981).

Development of both leaf and branch components of
poplar crowns was measured in the same experimental plots
described in Chapter I. The purpose of this study was to
relate crown developmental patterns to biomass production in
the plots.

Materials and Methods

The experimental design and cultural methods are the
same as described in Chapter I. The growth analysis
subplots were also used for some measurements related to
crown development. Additional plots for measurement of LAI
were also used and are described below.

Leaf Area Index

First Year. LAI determinations were made on a ten-tree
permanent sample within the biomass subplot. At two-week
intervals, stem height, diameter at 5 cm, and lengths of all
leaves present on the trees were measured. A leaf marking
system was employed so that only newly matured and immature
leaves had to be measured each time. Old leaves were
accounted for by counting and recording their presence or
absence.

Second Year. Due to the large increase in tree size
and complexity in the second year, a sampling technique was
used to determine LAI. Within the biomass subplot, trees
were stratified by crown class and a stratified random
sample of ten trees was made at two-week intervals. Thus,
the structure of the sample approximated the structure of

the population. At each sampling time, a new random selection of ten trees was made (some trees were sampled more than once throughout the growing season). Height and diameter at 5 cm were measured on each tree. The ten-tree (large) sample was approximately 20% of the population.

In addition, a small sample of three trees (6% of the population), one each of the dominant, codominant, and intermediate crown classes, was selected and permanently marked for repeated measurements. These small sample trees were excluded when selections were made for the large sample. At the same sampling times as the large sample, leaf lengths were measured on all current (main) stem leaves and on branch leaves of selected sample branches on the small sample trees. Branches were divided into three classes and were of two orders. Five random samples of each branch type (order and class combination) were made and permanently marked. In some cases five or fewer branches of a type were present in which case they were all measured. The total number of branches of each type was recorded along with the height and diameter of the stem at 5 cm. A leaf marking system similar to the first year was used.

Least squares regressions of leaf length versus leaf area were developed for two-year-old leaves and were used to calculate leaf areas from the leaf length measurements. The current stem leaf area was totaled. Leaf areas of the sample branches were totaled and average leaf area calculated for each branch type. The total tree leaf area was then calculated by multiplying the total number of

branches of each type by the average area of each type and totaling all of the branch types plus the current stem.

Least squares regressions of total leaf area (TLA) per tree versus the mensurational variable D^2H were developed for each clone at each sampling time from the small sample trees [TLA = b_0 + b_1(D^2H)]. D^2H values of the large sample trees were then used to calculate total leaf area per tree using the prediction equation for that clone. Leaf areas of the ten large sample trees were totaled and divided by the ground area occupied by the ten trees to obtain LAI.

Biomass Harvests

The biomass subplots described in the first chapter were also used to determine the number and weight of branches by type. Each harvested tree was divided into its components (current leader, two-year-old stem, two-year-old branch, and each current branch type) and their dry weights determined. In addition, the number of branches of each type were counted and recorded. The June determinations of number of branches of each type were determined from counts made on the large sample trees of the first LAI sampling period.

Growth Analysis Harvests

The growth analysis subplots described in the first chapter were used to measure the leaf area on each branch type and on the current leader throughout the growing season. In addition, the number and dry weight of leaves of each type were also recorded. From this data, the leaf area ratio (LAR, the ratio of leaf area to above-ground dry

weight of the tree) an indicator of plant leafiness and specific leaf weight (SLW, the ratio of leaf weight to leaf area - the inverse of specific leaf area, SLA), a measure of the thickness or density of the leaf per unit area were calculated (Ledig 1974). The average area per leaf, distribution of leaf dry weight, numbers, and area by branch type were also determined. Leaves of all size classes and branch types were sampled for measurement of leaf length and area for use in the development of length versus area prediction equations (Larson and Isebrands 1972).

Branching Patterns

To investigate branching patterns it was necessary to have a classification system for the different types of branches. A two-division system was developed using the height growth increment (HGI) concept of Isebrands and others (1977). Orders of branching formed the first division. The orders were designated primary, secondary, tertiary, etc., with the limitation that no HGI could have more orders of branches than its age. Primary branches were branches which arose from lateral buds on the main stem. If these primary branches originated in the same year as the HGI on which they occurred (sylleptic branches) they were called current laterals. Secondary branches originated from lateral buds on primary branches, tertiary branches from lateral buds on secondary branches, etc. The highest order of branching to occur on the two-year-old trees was secondary.

The second division of branches was into three classes:
1. Short branches (true short shoots) were less than 10 cm
long and had determinate growth with little or no internode
elongation. Only preformed leaves were present in the bud
and terminal bud formation occurred several weeks after
budbreak. 2. Determinate branches had more than 10 cm of
internode elongation, displayed only early leaves that were
preformed in the buds, and set a terminal bud several weeks
after budbreak. There was not a clear distinction between
short and determinate branches, so 10 cm was arbitrarily
selected. 3. Long shoots, here called indeterminate
branches, showed indeterminate (or heterophyllous) growth
similar to the main leader and did not form a terminal bud
until later in the summer. Gregory (1980) independently
developed the same divisions of branches for sugar maple.

Each branch type was associated with a general position
in the HGI. Indeterminate branches were located in the
upper parts of the crown and graded into determinate
branches lower down. Determinate branches graded into short
branches at the bottom of the HGI. Figure 11 is a schematic
diagram of a two-year-old tree with major and minor stem and
all branch types illustrated.

<center>Results</center>

Leaf Area Index

Prediction equations for the least squares regressions
of leaf length versus leaf area of individual leaves for the
first and second year are presented in the Appendix (Tables
21 and 22). All of the regressions were highly significant,

Figure 11. Schematic diagram of a two-year-old hybrid poplar tree showing the major stem (A), minor stem (B), first-year primary branch (C), cutting (D), primary and secondary branches of indeterminate long, determinate long, and short branch types, and height growth increments (HGI) of first and second years.
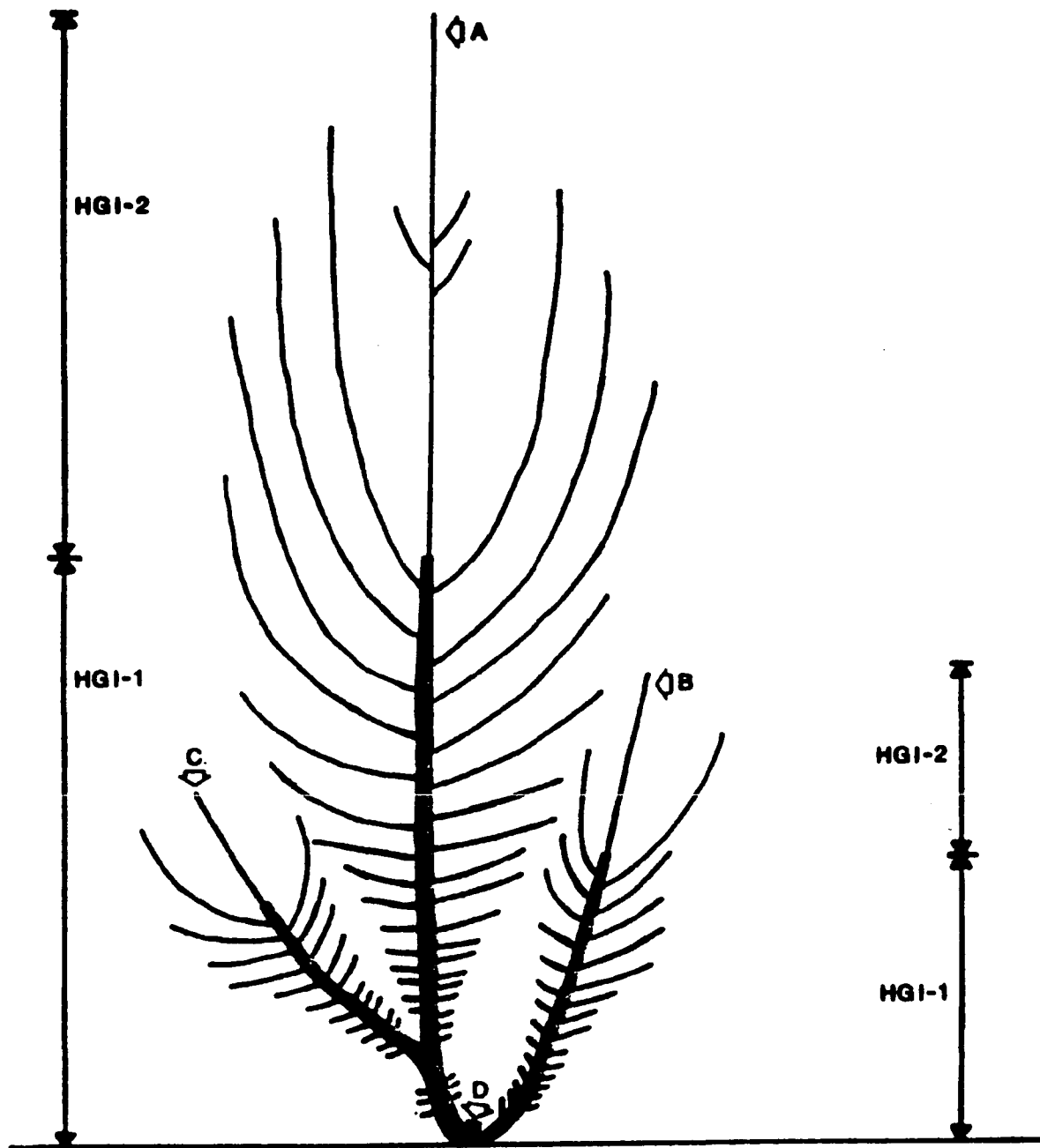
Figure 11.

having R^2 values of 0.97 to 0.99. Clone NE 48 had an elliptical leaf shape, whereas leaves of the other three clones were deltoid. NE 48's regression coefficients seemed to reflect this difference in leaf shape. Either no significant clonal differences in the coefficients was found or a lack of homogeneity of variance would not allow testing for differences. No significant differences were found between the coefficients of leaves present on different branch types, so all leaves were pooled for each clone.

The regressions of total leaf area (TLA) per tree versus D^2H that were used changed significantly from sampling period to sampling period because changes in leaf area due to abscission masked some of the increases due to growth. The r^2 values ranged from 0.93 to 0.99 for the individual sampling periods, whereas the pooled regressions for the entire season had r^2 values of 0.66 to 0.77. Thus, higher accuracy was obtained through the use of different equations for each sampling period. Had the plots been irrigated and leaf abscission minor, pooled equations for the season might have been sufficient.

Leaf area index (LAI) during the first and second years is shown in Figure 12. During the first year, LAI increased steadily as the young trees grew in size, reaching a plateau shortly after budset in late August-early September. LAI of NE 48, however, continued to increase until late September due to its later budset. LAI increased despite several periods of abscission of lower leaves following water stress (Figure 21 Chapter III), but the leaf area increase due to

Figure 12. Seasonal change in leaf area index (LAI) of four
hybrid poplar clones during the first (Day 161 = June 10)
and the second (Day 125 = May 5) growing seasons (NE 353+308
Δ, NE 48 +, NE 58 ◘ , Eugenei o).

YEAR 1

YEAR 2

M² M⁻²

DAYS

Figure 12.

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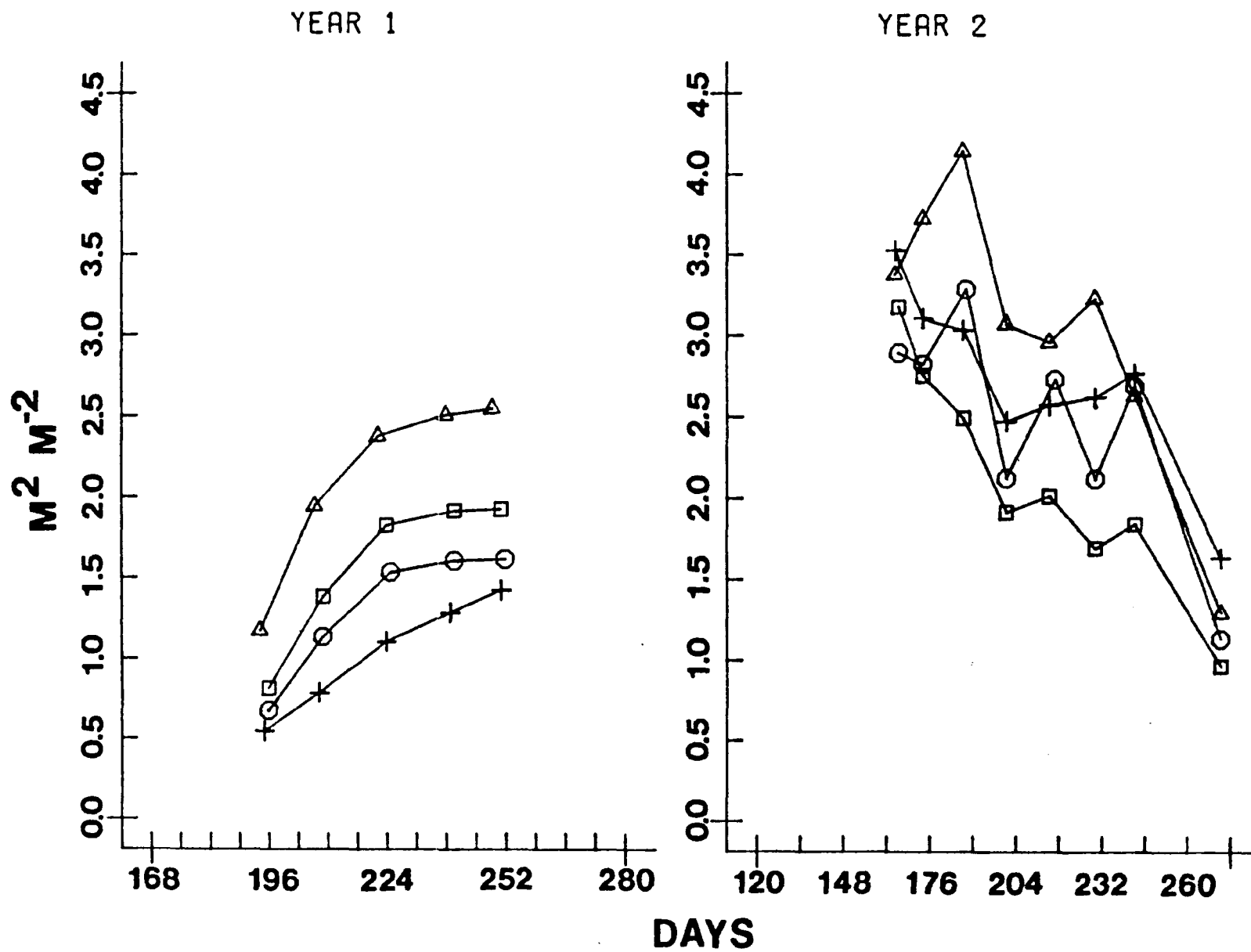
new leaves was greater than that abscised. Maximum LAI

values attained after one year were 2.5, 1.4, 1.9, and 1.6

for NE 353 + 308, NE 48, NE 58, and Eugenei, respectively.

The second year initial LAI levels were almost double

the first year maximum levels, due to growth of many primary

and some secondary branches on the first HGI. The trends of

LAI during the second year were confounded by sampling

variation from the random selection of the large sample

trees at each sampling period instead of measuring the same

trees all season. The general trend included a peak at or

shortly after the maturation of the initial budbreak flush

and then a decline throughout the season. The declines in

LAI were due to major abscission of leaves and even whole

branches in response to severe water stress (Figure 21

Chapter III). Maximum LAI levels obtained were 4.2, 3.5,

3.2, and 3.3 for NE 353 + 308, NE 48, NE 58, and Eugenei,

respectively.

A clearer picture of the trend in leaf area is shown in

Figure 13, which is a plot of the leaf area per tree of the

repeatedly sampled small sample trees over the growing

season. The clones can be divided into two groups. Clones

NE 58 and, especially, Eugenei increased in leaf area until

early July, then decreased due to water stress-induced leaf

abscission in mid-July. Leaf area then remained constant

until early September due to early terminal bud formation.

In early September, leaf abscission caused by severe water

stress again started, lowering LAI to below first-year

levels. The second group, NE 353 + 308 and NE 48, started

Figure 13. Seasonal change in total leaf area per stem of
LAI sample trees for dominant major (▲), codominant major
(+), intermediate major (▢), dominant minor (o) and
codominant minor (x) stems of four hybrid poplar clones
during the second growing season (Day 125 = May 5).
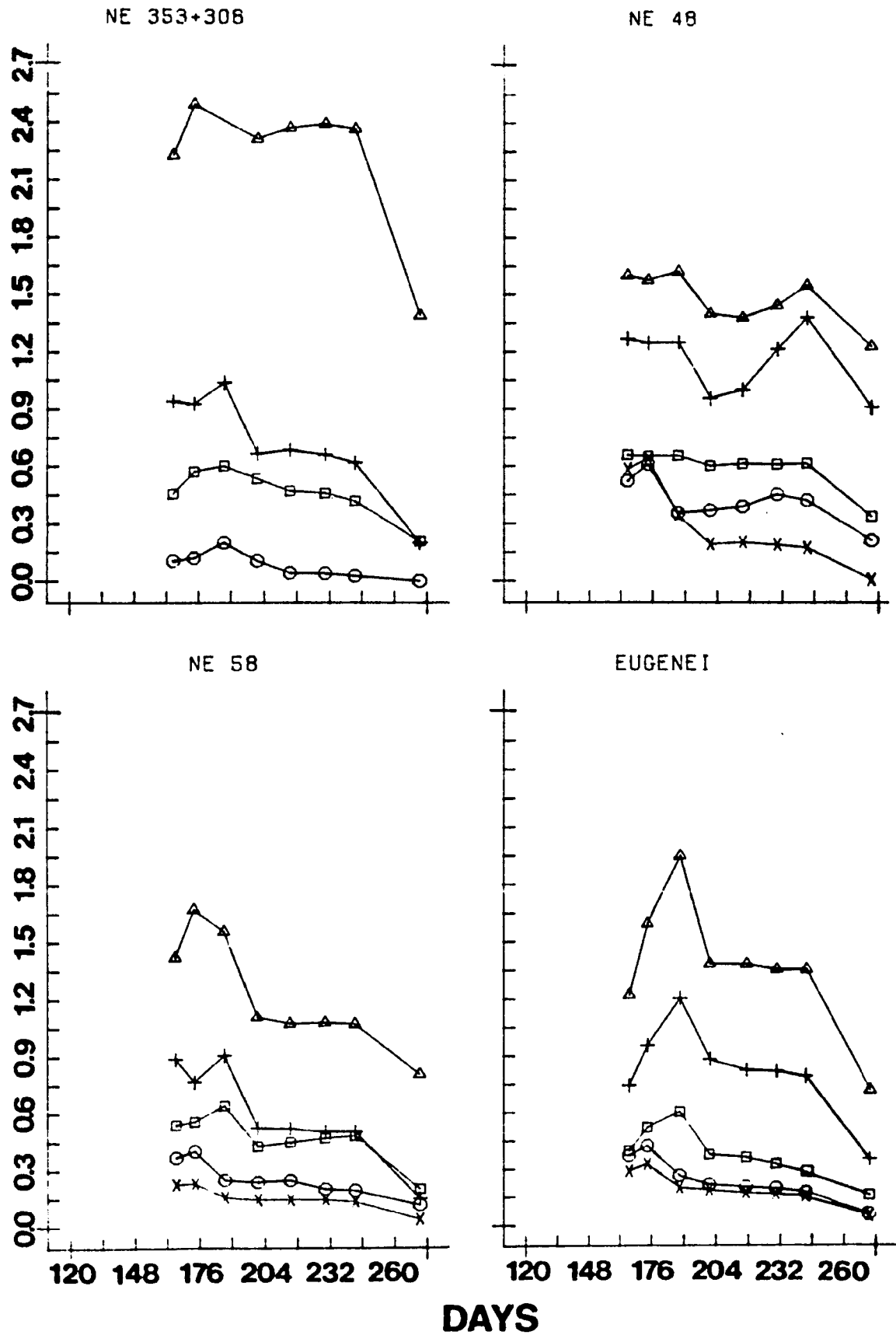
Figure 13.

out similarly to the first group, but after the first
drought period in July these clones regained some leaf area
through production of new leaves on the main stem and
indeterminate branches. When the second drought period was
at its peak in early September, terminal bud formation
occurred and leaf abscission began, resulting in lowering of
LAI to just above or below first-year levels.

Branching Patterns

During the first year, a distinct difference in
formation of current lateral branches was found. Clone NE
353 + 308 had an average of 9 branches per stem while the
other three clones averaged less than one branch per stem
(Table 10). In the second year, the two drought periods not
only resulted in leaf abscission, but also in the abscission
of entire branches after they had lost all of their leaves.
This loss of branches is shown in Table 10 by comparing the
June measurements (maximum number of branches present
several weeks after budbreak) with the late September
measurements (minimum number of branches present after two
periods of abscission). Abscission started first with the
primary and secondary short branches, then moved to the
determinate branches, whereas none of the indeterminate
branches abscissed. The reductions in total number of
branches were 35%, 54%, 69% and 61%, while reductions for
determinate and short branches were 42% and 49%, 56% and
84%, 67% and 88%, and 65% and 80%, respectively for NE 353 +
308, NE 48, NE 58, and Eugenei. Thus, loss rates varied by
clone, with NE 353 + 308 losing fewer branches than the

Table 10. Distribution of branches by branch type of four hybrid poplar clones after the first and second growing seasons.

| | First Year | Second Year | | | | | | | | | |
| | September | June | | | | | September | | | | |
Clone Number	Current[a] Laterals	Indet.	Det.	Short	Current Laterals	Total	Indet.	Det.	Short	Current Laterals	Total
NE 353+308											
Primary[b]	9.0	7.5	15.0	7.5	...	30.0	6.8	8.2	4.9	1.6	21.5
Secondary	...	0.3	2.3	10.1	...	12.7	0.3	1.9	4.0	...	6.2
Total	9.0	7.8	17.3	17.6	...	42.7	6.9	10.1	8.9	1.6	27.7
NE 48											
Primary	0.6	8.5	11.2	13.3	...	33.0	8.2	4.8	1.6	0.2	14.8
Secondary	...	0.6	1.3	1.6	...	3.5	0.6	0.7	0.8	...	2.0
Total	0.6	9.1	12.5	14.9	...	36.5	8.8	5.5	2.4	0.2	16.8
NE 58											
Primary	0.3	5.0	8.5	18.5	...	32.0	4.8	2.8	2.1	...	9.7
Secondary	...	0.1	0.2	0.7	...	1.0	0.1	0.1	0.3	...	0.5
Total	0.3	5.1	8.7	19.2	...	33.0	4.9	2.9	2.4	...	10.2
Eugenei											
Primary	0.1	7.0	10.0	16.0	...	33.0	6.6	3.4	2.8	...	12.8
Secondary	...	0.5	0.8	2.8	...	4.1	0.5	0.4	0.9	...	1.8
Total	0.1	7.5	10.8	18.8	...	37.1	7.1	3.8	3.7	...	14.6

a
Indet. = Indeterminate growth branches
Det. = Determinate growth branches with internode elongation
Short = Determinate growth branches with little or no internode elongation
Current laterals = branches originating on the current year's growth of main stem.

b
Primary branches = branches which arise from axillary bud on the main stem.
Secondary branches = branches which arise from axillary buds on the primary branches.

other three clones.

Statistical differences in numbers of branches between clones were not significant because of high variance and lack of homogeneity of variance. The high variances resulted from dominant and major stems having many branches and suppressed and minor stems few branches. However, some trends are apparent from the second-year branch data in Table 10. The number of secondary branches is directly related to the number of current laterals produced in the first year, explaining the three-fold or higher number of secondary branches produced by NE 353 + 308 as compared to the other clones. The number of primary branches produced per tree in the second year by the four clones was almost identical: 30, 33, 32, and 33, with the differences in total branches influenced by the difference in secondary branches. The production of indeterminate branches was similar for all four clones, but production of determinate and short branches was not. NE 353 + 308 produced more determinate and fewer short branches, whereas NE 58 produced fewer determinate and more short branches. The production of current laterals in the second year was zero to few for NE 48, NE 58, and Eugenei, but 1.6 branches per stem for NE 353 + 308, much smaller than its first-year production.

If the branch distribution on only the major stems by crown class is examined, a better picture of the pattern of branching is obtained. Minor stems produced few branches and all of the secondary branches were present on dominant and codominant stems. Table 11 shows branch distribution by

Table 11. Distribution of branches on major stems by crown class for four hybrid poplar clones after the second growing season.

Number	Crown Class	Number	Number of Primary Branches per Stem[a]				Number of Secondary Branches per Stem				Total
			Indet.[b]	Det.	Short	Subtotal	Indet.	Det.	Short	Subtotal	
NE 353+ 308	All	50	11.2	9.4	3.3	23.9	0.6	3.4	7.3	11.3	35.2
	Dominant	4	13.8	9.0	2.2	25.0	...	6.8	11.2	18.0	43.0
	Codominant	33	12.4	10.9	3.1	26.4	0.8	4.3	9.8	14.9	41.3
	Intermediate	7	7.4	8.1	3.6	19.1	...	...	...	....	19.1
	Suppressed	6	3.5	3.2	4.8	11.5	...	...	...	....	11.5
NE 48	All	51	12.7	6.3	0.7	19.7	1.1	1.1	1.3	3.5	23.2
	Dominant	7	18.4	6.8	...	25.2	1.3	1.8	3.6	6.7	31.9
	Codominant	30	13.6	6.4	0.2	20.2	1.6	1.4	1.4	4.4	24.6
	Intermediate	9	9.4	6.4	1.2	17.0	...	...	...	...	17.0
	Suppressed	5	5.4	4.6	2.8	12.8	...	...	...	...	12.8
NE 58	All	52	6.6	2.7	0.9	10.2	0.1	0.2	0.6	0.9	11.1
	Dominant	5	8.2	4.2	...	12.4	1.0	2.2	6.2	9.4	21.8
	Codominant	25	8.2	2.7	0.3	11.2	...	...	...	...	11.2
	Intermediate	16	5.4	2.6	1.9	9.9	...	...	...	...	9.9
	Suppressed	6	1.0	2.3	1.2	4.5	...	...	...	...	4.5
Eugenei	All	49	8.6	3.6	1.0	13.2	0.7	0.6	1.3	2.7	15.9
	Cominant	9	13.6	4.2	0.3	18.1	2.4	1.4	3.9	7.7	25.8
	Codominant	26	9.0	3.5	0.8	13.3	0.5	0.6	1.2	2.3	15.6
	Intermediate	11	5.5	3.7	1.9	11.1	...	...	...	...	11.1
	Suppressed	3	1.3	1.7	1.3	4.3	...	...	...	...	4.3

a
Primary branches = branches which arise from axillary buds on the main stem.
Secondary branches = branches which arise from axillary buds on the primary branches.

b
Indet. = Indeterminate growth branches.
Det. = Determinate growth branches with internode elongation.
Short = Determinate growth branches with little or no internode elongation.
Current laterals = branches originating on the current year's growth of main stem.

clone and crown class for the major stems at the end of the
second year. General trends included a decrease in the
number of primary branches with a decrease in crown class,
although in many cases dominant and codominant stems were
similar. Since the indeterminate branches were not affected
by abscission, their numbers reflect both initial and final
differences during the growing season. The number of
indeterminate branches decreased steadily with crown class,
with some differences between clones. The determinate and
short-branch values are final values after abscission. As
crown class decreased, the loss of branches appeared to
decrease, especially for short branches. Since lower crown
class trees had fewer branches (becasue of fewer lateral
buds) and stopped growing earlier, they retained a higher
percentage of their short and determinate branches than
higher crown class trees which sacrificed the short and
determinate branches to maintain growth on the current
leader and indeterminate branches. Again the total number
of branches per tree is highly inflenced by the number of
secondary branches and decreases with crown class.

The distribution of woody biomass into branch types is
shown in Table 12. The total amount of biomass partitioned
followed very closely the total number of branches in Table
10, while the biomass partitioned into each branch type
followed closely the numbers of branches of each type in
Table 11. Most of the branch biomass was in indeterminate
branches. One of the major differences was in two-year-old
portions of secondary branches (the first year current

Table 12. Partitioning of wood, bark, and branch biomass into various branch types for four hybrid poplar clones after the second growing season.

Clone Number	Percentage of woody biomass						
	Primary Branches[a]				Secondary Branches		
	Indet.[b]	Det.	Short	Current Laterals	Two-year-old wood[c]	One-year-old wood	Total
NE 353+308	14.8	1.7	0.3	0.8	3.2	0.6	21.4
NE 48	16.9	1.6	0.1	0.2	1.6	0.4	20.8
NE 58	15.1	1.6	0.2	...	0.7	0.2	17.8
Eugenei	17.1	1.3	0.1	...	1.9	0.5	20.9
AVERAGE	16.0	1.6	0.2	0.2	1.8	0.4	20.2

a
 Primary branches = branches which arise from axillary buds on the main stem.
 Secondary branches = branches which arise from axillary buds on the primary branches.

b
 Indet. = Indeterminate growth branches
 Det. = Determinate growth branches with internode elongation
 Short = Determinate growth branches with little or no internode elongation
 Current laterals = branches originating on the current year's growth of main stem

c
 One-year-old wood = the secondary branches which emerged from the previous season's
                      primary branches.
 Two-year-old wood = the previous season's primary branches with their second year
                      increment.

laterals that bore the buds for the secondary branches); NE

353 + 308 had approximately twice the biomass in this branch

component than the other three clones. As a result of the

flushing of lateral buds during the first year, NE 353 + 308

had a slightly smaller amount of woody biomass present in

indeterminate branches. The lower biomass and fewer number

of branches on NE 58 was partly an artifact caused by the

decreased growth of that particular plot induced by the

large black cherry tree which bordered it.

Leaf Characteristics and Distribution

Growth Analysis Parameters. The leaf area ratio

decreased steadily throughout both growing seasons (Figure

14). The first season LAR values began at 105 to 115 cm^2

g^{-1} and decreased to 30 to 50 cm^2 g^{-1}, while in the second

season, the values began at 65 to 85 cm^2 g^{-1} and decreased

to 15 to 25 cm^2 g^{-1} at the end of the season. Thus,

leafiness of the trees decreased with increasing tree size.

These decreases correspond to decreases in leaf weight

ratio (LWR) or the amount of biomass partitioned into leaves

shown in Chapter I (Figures 9 and 10).

Specific leaf weight, in general, increased throughout

both growing seasons (Figure 15). The first season SLW

values varied from 5.5 to 7.2 mg cm^{-2} early in the season to

7.5 to 8.7 mg cm^{-2} late in the season. The major exception

to the pattern was clone NE 58 in which SLW remained low and

then increased late in the season. Clone NE 48, which

maintained the highest SLW values for most of the season,

also appeared to have thicker, more leathery leaves. The

Figure 14. Seasonal change in leaf area ratio (LAR) of four
hybrid poplar clones during the first (Day 172 = June 21)
and the second (Day 151 = May 31) growing seasons (NE 353 +
308 ▲ , NE 48 +, NE 58 ◘ , Eugenei o).

Figure 14.

YEAR 1

YEAR 2

CM² G⁻¹

DAYS

73
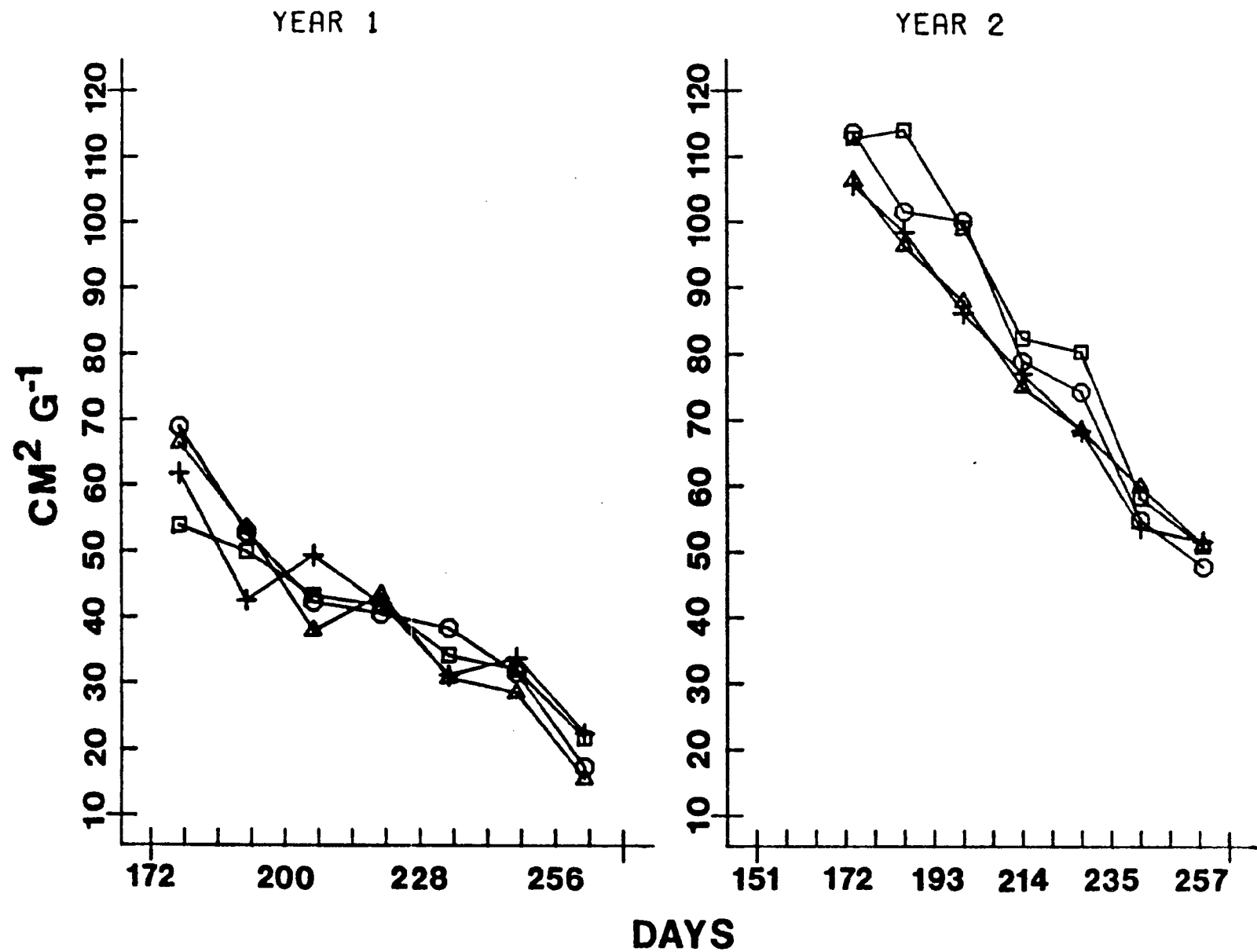
Figure 15. Seasonal change in specific leaf weight (SLW) of
four hybrid poplar clones during the first (Day 172 = June
21) and the second (Day 151 = May 31) growing seasons (NE
353+308 ▲, NE 48 +, NE 58 ◘, Eugenei o).

Figure 15.
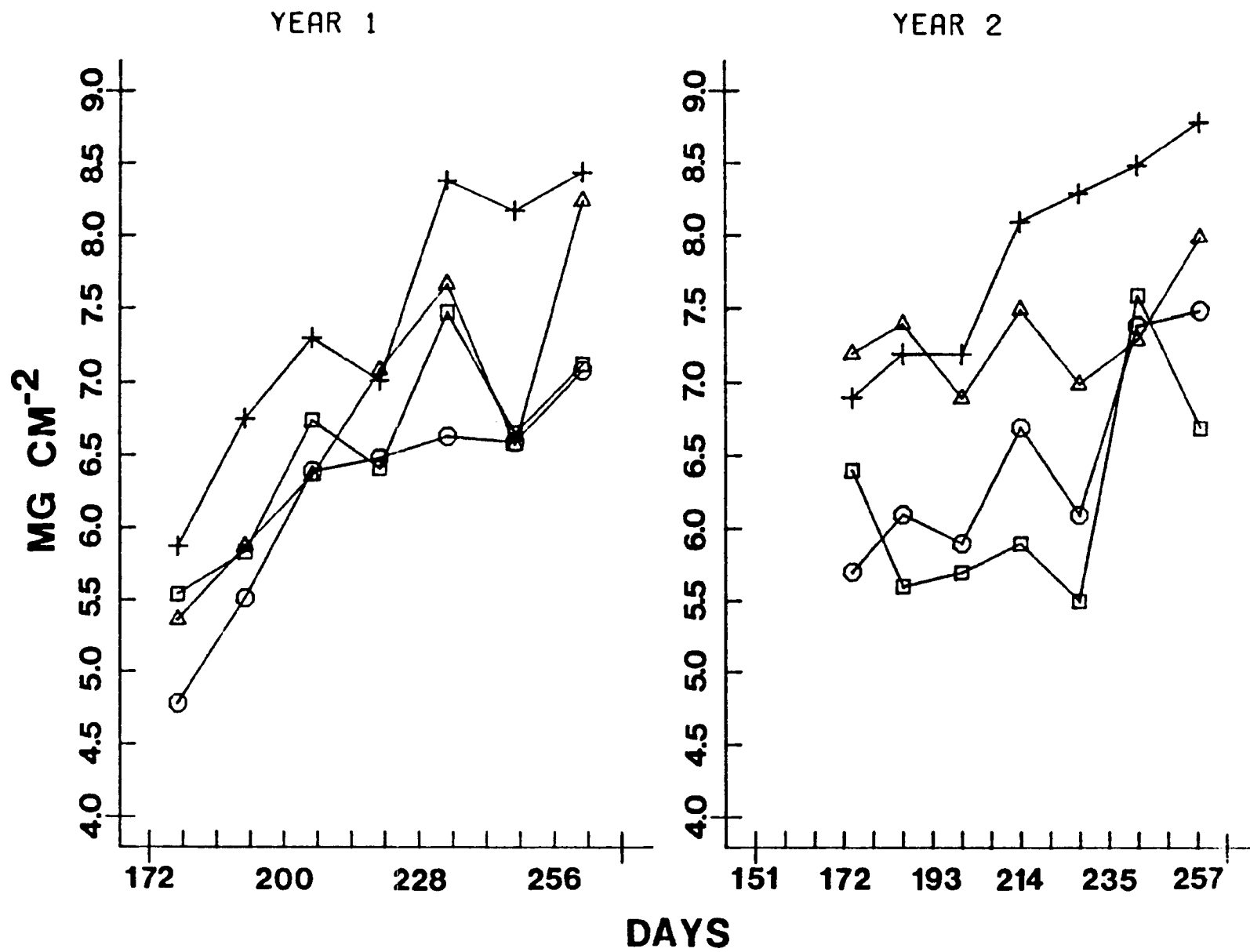
second year, SLW values were lower at the beginning of the growing season than the first year, from 4.0 to 5.3 mg cm^{-2} but ended up at similar levels of 7.0 to 8.5 mg cm^{-2}. Again NE 48 had the highest values for the entire season.

The position of leaves in the crown affected SLW (Table 13). Upper crown leaves of current leader and indeterminate branches had higher SLW values and generally had a larger increase in SLW over the season than lower crown leaves borne by determinate and short branches.

Leaf Distribution. Figure 16 shows the percentage of total tree leaf area present on branches in the first year. In accordance with the number of branches produced in the first year, the percentages are very low (5%) for all clones except NE 353 + 308, which had 40% of its leaf area present on branches. In the second year, patterns differed (Figure 17): all four clones began with 5 to 10% of total leaf area on the current leader, which increased over the season to 25 to 30% of the total leaf area. The remainder of the leaf area was distributed among the branch types, with the majority on indeterminate branches. In general, indeterminate branches carried from 45 to 70% of the leaf area throughout the season. Current leader and indeterminate branches had little loss of leaf area due to abscission. In general, both determinate, short, and any secondary branches decreased in leaf area over the season, beginning with percentages of 20 to 40 and decreasing to values less than 10 (Figure 17). These decreases were due to both abscission of leaves from these branches and

Table 13. Specific leaf weight (SLW) values by branch type for four hybrid poplar clones, early and late in the second growing season.

	Specific Leaf Weight, mg cm^{-2}							
	NE 353 + 308		NE 48		NE 58		Eugenei	
Branch Type	June 13	August 22	June 13	August 22	June 13	August 22	June 13	August 22
Current Leader [a]	5.49	8.72	7.33	9.81	6.10	8.53	5.66	7.66
Indet. Branches	5.39	7.46	6.63	9.04	5.58	7.18	5.07	6.40
Det. Branches	5.04	6.10	5.46	5.97	5.06	5.97	4.38	5.73
Short Branches	4.40	6.39	5.01	5.21	4.86	5.41	3.78	5.40

[a]
 Current Leader = current year's growth of main stem.
 Indet. = Indeterminate growth branches.
 Det. = Determinate growth branches with internode elongation.
 Short = Determinate growth branches with little or no internode elongation.
 Current laterals = branches originating on the current year's growth of main stem.
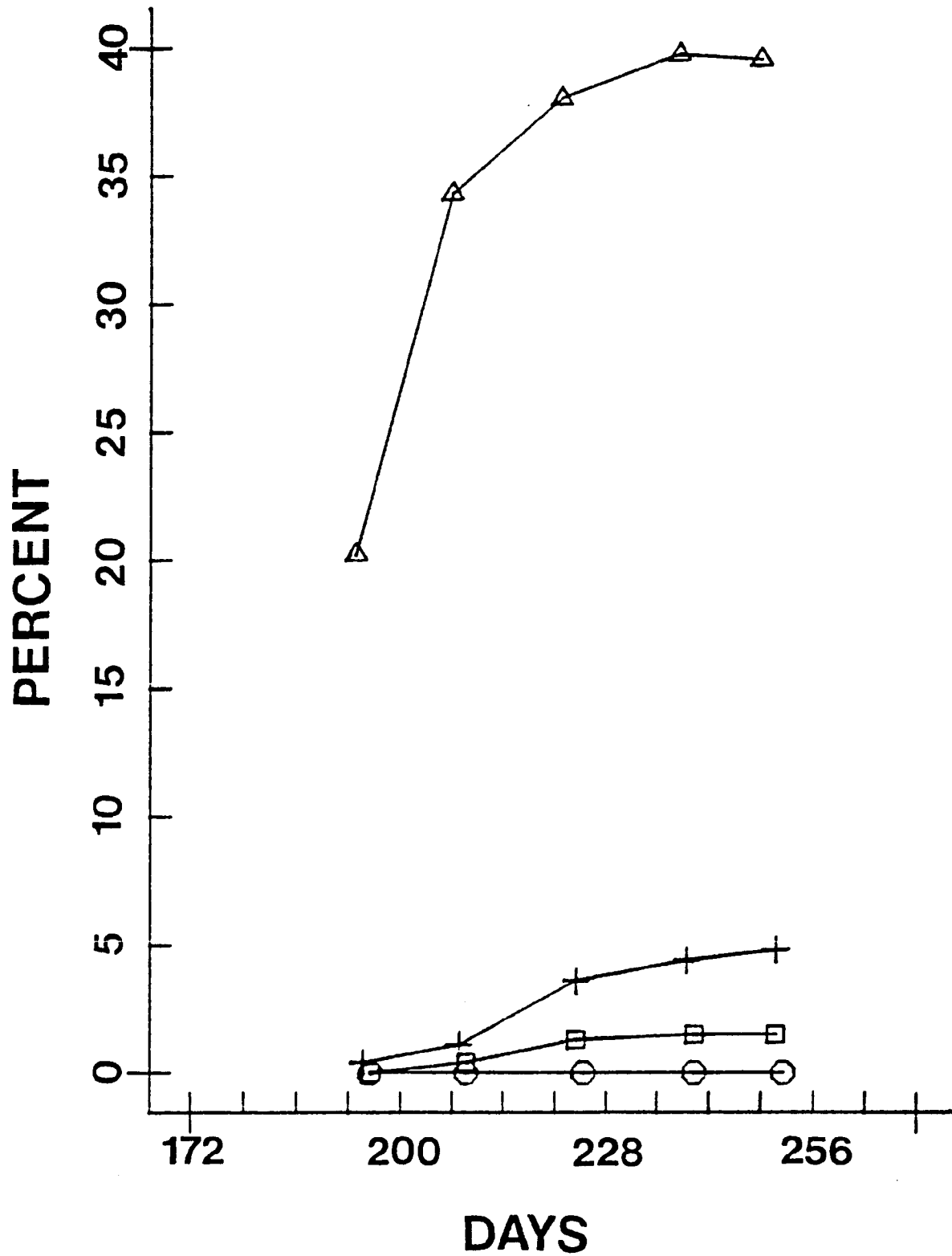
Figure 16. Seasonal change in the percentage of total tree leaf area present on branches of four hybrid poplar clones during the first growing season (Day 172 = June 21, NE 353+ 308 △ , NE 48 +, NE 58 □ , Eugenei o).

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Figure 17. Seasonal change in the percentage of total tree
leaf area present on the main stem (Δ), indeterminate long
(+), determinate long (□), and short (o) branches, and all
secondary and/or current lateral branches (x) of four hybrid
poplar clones during the second growing season (Day 151 =
May 31).
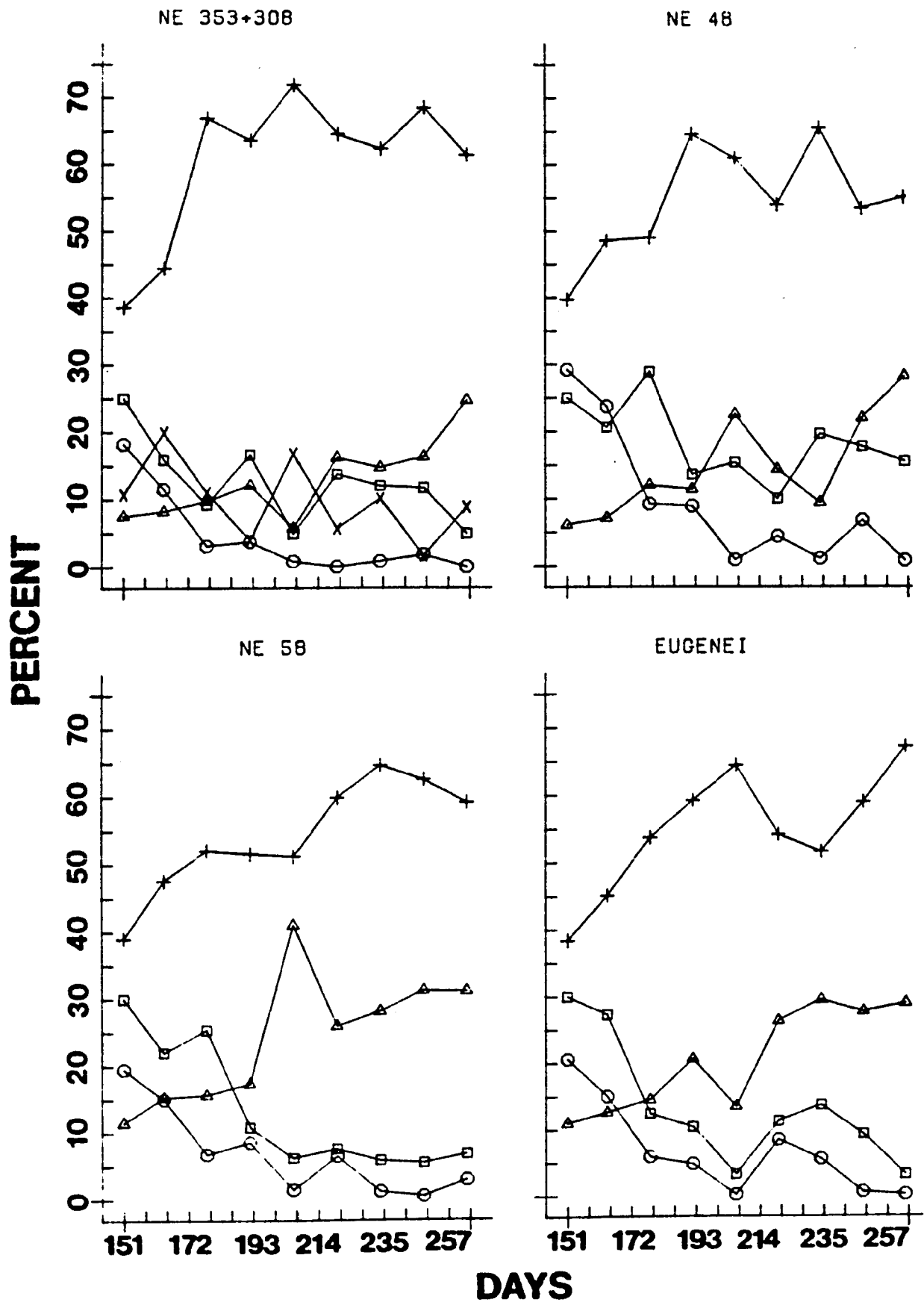
Figure 17.

increases in leaf area on the current leader and indeterminate branches.

The average leaf area and numbers present on the current leader increased throughout the second growing season before decreasing at the end of the season (Figures 18 and 19). The average leaf area and numbers present on indeterminate branches increased slightly to a plateau and remained there for most of the season. The average areas and numbers of determinate and short branches decreased slowly and steadily all season due to leaf abscission.

In general, current leader leaves were large and succulent when young, indeterminate branch leaves were smaller but still relatively large and succulent when young, whereas determinate, short, and secondary branch leaves were smallest (Table 14). Clonal differences in leaf size were present, with clones NE 58 and Eugenei   NE 48   NE 353 + 308. NE 353 + 308 had very small leaves on its short, secondary, and current lateral branches.

Discussion

Marshall (1968) discussed the various methods used to determine leaf area. One of the oldest and best nondestructive methods is the estimation of leaf area from linear measurements of leaves, a technique used since 1924 on a variety of species (Boynton and Harris 1950, Ackley et al.1958, Kubicek 1971, Fordham and Holgate 1972) including Populus (Pollard 1970, Larson and Isebrands 1972). Use of Larson and Isebrands' (1972) equation in the present study yielded even higher R^2 values than they had obtained, while

Figure 18. Seasonal change in the average leaf area present
on the main stem (Δ), indeterminate long (+), determinate
long (■), and short (o) branches, and all secondary and/or
current lateral branches (x) of four hybrid poplar clones
during the second growing season (Day 151 = May 31).
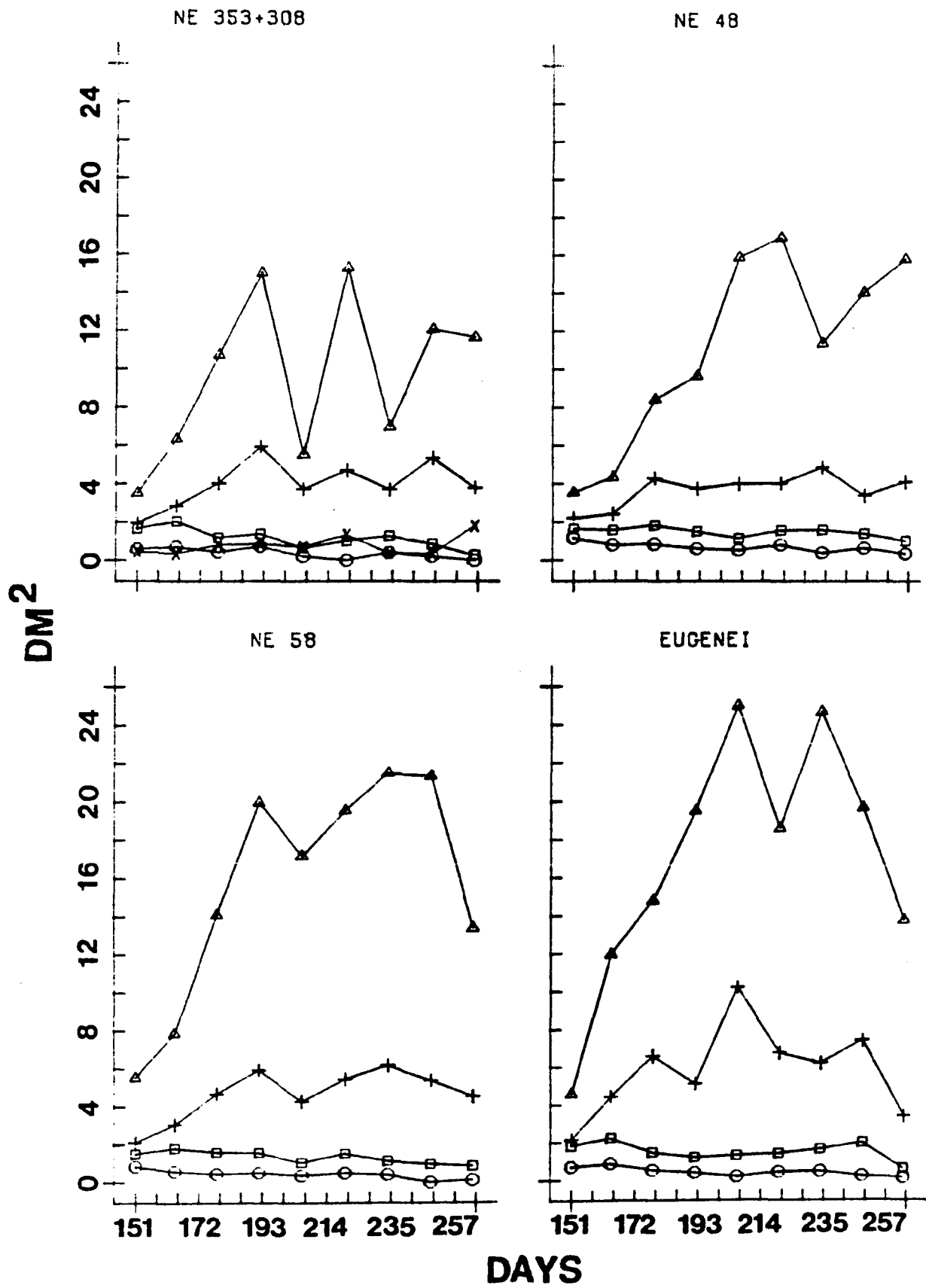
Figure 18.

Figure 19. Seasonal change in the average number of leaves present on the main stem (Δ), indeterminate long (+), determinate long (□), and short (o) branches, and all secondary and/or current lateral branches (x) of four hybrid poplar clones during the second growing season (Day 151 = May 31).
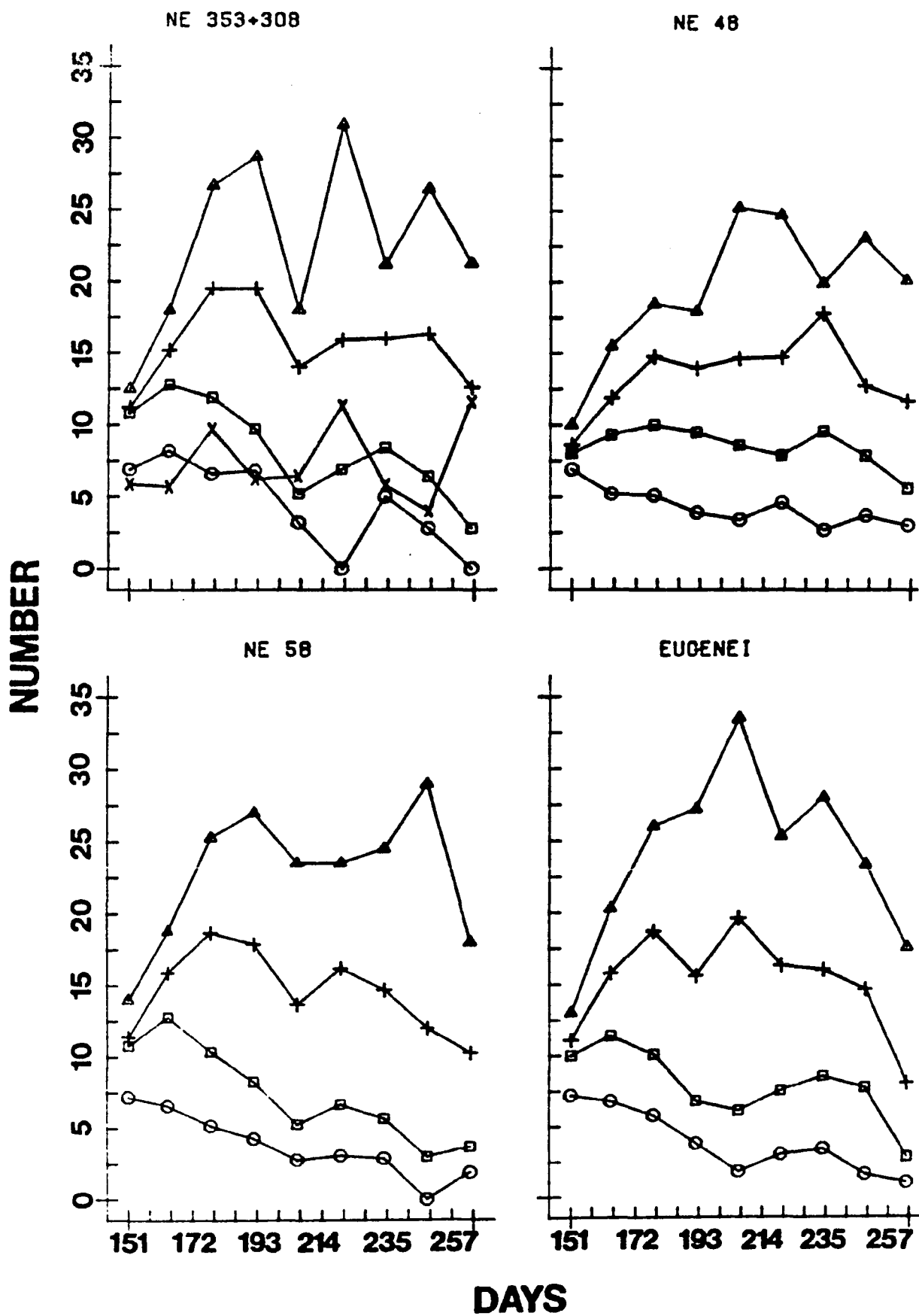
Figure 19.

Table 14. Average area per leaf by branch type for four hybrid poplar clones late in the first and second growing seasons.

| | Average Area per Leaf, cm^2 | | | | | | | |
| | NE 353 + 308 | | NE 48 | | NE 58 | | Eugenei | |
Branch Type	First Year	Second Year	First Year	Second Year	First Year	Second Year	First Year	Second Year
Current Leader [a]	66.6	45.6	64.1	60.6	87.8	92.6	67.6	84.2
Current Laterals	14.6	9.2	25.1	....	23.5	....	....	....
Indet. Branches	....	33.0	....	26.5	....	44.9	....	50.4
Det. Branches	....	13.4	....	17.6	....	32.0	....	25.6
Short Branches	....	7.5	....	15.1	....	13.2	....	12.2
All Sec. Branches	....	6.8	....	16.0	....	12.2	....	17.0

a
  Current Leader = Current year's growth of main stem.
  Indet. = Indeterminate growth branches.
  Det. = Determinate growth branches with internode elongation.
  Short = Determinate growth branches with little or no internode elongation.
  Current laterals = Branches originating on the current year's growth of main stem.

the parameter values that they calculated were very similar to the ones obtained for the four clones used in this study.

Leaf area index of natural aspen stands ranged from 0.8 to 6.6 $m^2 m^{-2}$ (Pollard 1970a, 1972a, Peterson et al. 1970, Bray and Dudkiewicz 1963). One way that intensive culture increases biomass production is by producing a closed leaf canopy earlier than natural stands. Intensively cultured research plots of poplars produced higher LAIs and leaf areas per tree than natural stands (Isebrands and Nelson 1978, 1982, Isebrands et al. 1977, Zavitkovski et al. 1974, Anderson 1979, Cannell 1980), with irrigated plots maintaining highest LAIs and leaf areas per tree (Isebrands et al. 1977, Gordon and Promnitz 1976, Schmidt 1975).

The major factor producing relatively low LAIs in this study was drought stress. Dickmann (1979) discussed the sensitivity of poplars to drought and the corresponding leaf abscission that occurs. However, not all poplars respond to drought stress in the same manner or at the same stress level. Populus tremula and P. nigra trees grown in Germany had different responses during a drought period; P. tremula retained its leaves and their function but its stomata closed preventing gas exchange, whereas P. nigra maintained gas exchange rates, but its LAI was reduced through abscission of from 50 to 80% of the original leaf volume (Neuwirth and Polster 1960). The abscission of leaves from the poplar clones in this study was primarily caused by drought stress, although Zavitkovski (1981b, 1982) presented evidence that some normal leaf fall in poplar stands may

occur in the small leaves of the lower canopy early in the
season due to low light levels.

The number of branches produced by a tree is dependent
upon cultural and biological factors such as spacing, stem
size and age, and the genetic variation inherent to the tree
(Cannell 1980, Schier 1979, Ying 1974, Koster 1976, Maini
1966a, Isebrands et al. 1977, Nelson et al. 1980, 1981).
Nelson and others (1980, 1981) reported that as spacing
increased, the number, length, and angle of origin of
branches increased, while the angle of termination generally
decreased, on nine four-year-old Populus clones. In
general, they showed that there were few clonal differences
in number and length of branches and angle of origin. More
clonal differences were evident for angle of termination.
The clones used in this study support these results as they
showed little variation in branch numbers, except for NE 353
+ 308's tendency toward production of sylleptic branches.

The purpose of a branch is to support leaves in such a
teleological manner that the leaves can absorb maximum
light, photosynthesize, and transpire water. Without these
purposes, the branch is expendable. The abscission of
branches in this study was probably an indirect effect of
water stress (Kaufmann 1982). Bohlmann (1971) and Weaver
(1978) both showed that short shoots or twigs of Populus are
quickly abscissed when all leaves and buds are removed from
them. Bohlmann (1971) also showed these shoots contained no
starch at the time of abscission. Loss of lower leaves due
to water stress is a mechanism for reducing the tree's water

use so it can maintain growth. The subsequent mobilization of all usable materials out of the short branches after they have lost their leaves is another means to provide materials for growth even at reduced gas exchange rates.

In general, the LAR and LWR decrease with increasing size of the tree or seasonal progression. The high LAR and LWR values of poplar cuttings early in the season of the first and second years is a significant factor in their establishment and early growth. The high partitioning of weight into leaves (over 70% in some clones the first year) provides a large photosynthetic surface to fuel further growth. In fact, the rapid growth of young hybrid poplars and cottonwood can be largely attributed to this large initial investment in leaves. As the season progresses and the plants become established in the soil, a greater proportion of biomass is partitioned into the stem, and the proportion in leaves drops. Wilhelm and Nelson (1978) report a similar situation in the forage crop, tall fescue, where high biomass yields were related to high initial investments in leaf area growth.

As poplar stands develop, the proportion of standing biomass represented by leaves declines as shown by the lower initial values in the two-year-old stands and values of 9.96, 5.39, and 1.71 cm^2 g^{-1} respectively for aspen stands of 5, 15, and 52 years of age (Pollard 1972a). This decline is accompanied by an increase in the proportion of biomass in stems (Switzer et al. 1976). As stands age, a lower proportion of total biomass is present in branches and more

of that biomass goes into the production of short shoots that are generally present for only a few years years (Switzer et al. 1976).

Due to genetic and environmental factors, the same quantity of dry weight partitioned into leaves may be used in different ways: either for the formation of a large leaf area with a low SLW (thin leaves) or a small leaf area with a high SLW (thick leaves) (Kallis and Tooming 1974). Pieters (1974) has shown that leaf thickness increased with leaf age in poplars and that these increases occurred after the leaves were fully grown in area. Leaf thickness was controlled by light and temperature: high light and low temperature favored thicker leaves (high SLW) and low light or shading favored thinner leaves (low SLW) (Pieters 1974, Loach 1970, Jarvis and Jarvis 1964).

Changes in SLW with crown or branch position are due primarily to shading influences. Leaves at the top of the crown, exposed to full sunlight and higher heat loads, have higher SLW's than leaves at the bottom of the crown which are in cool, deep shade (Barden 1978, Zavitkovski 1971, 1981b, Isebrands et al. 1977, Pollard 1970a, 1972a, Isebrands and Nelson 1982). The seasonal increase in SLW is partly a leaf aging response and partly due to leaf position and shading effects. SLW of the lower, older leaves does not change over time, but the newer, upper leaves have higher initial SLW values which then increase with age.

The relationship of LAI and SLW to yield is one of interaction. Thicker leaves appear to have higher

photosynthetic rates than thinner leaves (Pieters 1974).
Net photosynthesis increased with increasing SLW in apple
(Barden 1978) and several crop species (Kallis and Tooming
1974). One possible explanation for this phenomenon is that
thicker leaves have more chloroplasts per unit area (higher
leaf volume) and so have the capacity for higher
photosynthetic rates when expressed on an area basis. Thus,
for canopies with equal LAIs, the canopy with a larger SLW
will probably produce more available photosynthate for
growth than the canopy with a smaller SLW.

The distribution of leaves and leaf size both influence
the tree's ability to efficiently capture light. Young
trees in the first year had few branches and most of their
leaf area was on the current leader. In the second year,
the main stem still had a large leaf area, but the branches
displayed 75% of the total leaf area. The general pattern
is for an increasing dominance by branches, especially short
branches as trees get older (Isebrands et al. 1977,
Isebrands and Nelson 1978, 1982). Mature aspen had 98% or
more of its leaf area on short branches and only 1 to 2% on
leaders and indeterminate branches (Pollard 1970a).

As leaf area shifts to branches, especially short
branches, more light is captured and average leaf size
decreases. Pieters (1974) found that the maximum mature
leaf size within a genotype was related to light intensity
while the rate of leaf growth was dependent upon ambient
temperture. Thus, the higher the light intensity, the
larger the leaf. So as branches are shaded by leaves above

them, light intensity drops and leaf size decreases.

Clone NE 353 + 308 had the highest above-ground woody biomass production for both years of this study; it also had the highest first- and second-year LAIs and partitioned the most biomass into branches to support those leaves. NE 48 had the second highest yield, but had the lowest first-year LAI and second highest second-year LAI. However, NE 48 had the highest SLWs both years as well as horizontally oriented leaves, contributing to increased biomass production. Clones NE 58 and Eugenei had the lowest yields and very similar LAIs and SLWs both years, lower than the other two clones. So the biomass partitioned to leaf area and thickness as well as the branches to support them was directly correlated to total above-ground woody biomass yield. Differences in photosynthetic rate among the four clones and due to canopy position are presented in the next chapter.

CHAPTER III. GAS EXCHANGE

Introduction

Earlier, I mentioned that biomass production was
dependent upon sustained net photosynthetic rate and leaf
area. Leaf area and crown development were discussed in
Chapter II. Now aspects of the other determining factor --
photosynthetic rate -- will be examined.

In addition to age and developmental effects on
photosynthesis and stomatal conductance (Larson and Gordon
1969b, Ceulemans and Impens 1979, 1980, Furukawa
1972,1973a,b, Dickmann et al. 1975, Dickmann and Gordon
1975, Dickmann 1971a,b, Siwecki and Kozlowski 1973, Larson
et al. 1972, Tsel'niker and Mai 1979), many environmental
variables also influence gas exchange: light quality and
quantity, temperature, vapor pressure deficit, soil and
plant water potential, CO_2 concentration, soil fertility,
wind , and canopy position (sun or shade leaf) (Larcher
1969). A number of these influences will be discussed in
this paper, but the most significant one is the influence of
drought on gas exchange. Drought tolerance of poplars
varies between clones, species, and sites (Regehr et al.
1975, McGee et al. 1981, Tobiessen and Kana 1974, Ceulemans
et al. 1978a,b, Kelliher and Tauer 1980, Luukkanen and
Kozlowski 1972). Some of the drought tolerance mechanisms

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shown by poplars are: closure of stomata to reduce
transpiration, yellowing and abscission of older leaves,
maintenance of growth and turgor in young leaves,
exploitation of larger soil volumes by the root system, and
acclimation of enzyme functions to lower plant water
potentials (Neuwirth and Polster 1960, Furukawa 1972,
Pieters and Zima 1975, Smith and Gatherum 1974, Kelliher et
al. 1980, Domingo and Gordon 1974, Faulkner and Fayle 1979).
The recovery of function following water stress was
dependent on the duration and magnitude of the stress
(Sivakumaran and Hall 1979, Regehr et al. 1975). The loss
of leaf area is most damaging to the plant once the water
stress is removed, because leaf area cannot be quickly
replaced. However, the impact of leaf area loss is
minimized because older, shaded, less productive leaves are
abscissed rather than young, well exposed, highly productive
leaves (Neuwirth and Polster 1960, Tazaki and Ushijima 1963,
Bonner 1967).

Responses of trees to environmental variables, while
often discussed separately, are all interrelated. The
variables often change together and produce an interaction
effect which the plant then integrates into its response
(Ceulemans and Impens 1981, Pallardy and Kozlowski 1979b,
Larcher 1969). Stomatal conductance and photosynthesis are
usually directly correlated but this relationship also is
dependent on the specific factor that is limiting
photosynthesis (Ceulemans and Impens 1980, 1981, Ceulemans
et al. 1980a, Regehr et al. 1975).

Measurements of stomatal conductance, photosynthetic rate, and several of the environmental variables that influence these processes were taken in the same experimental plots as in Chapters I and II during the tree's second year of growth.

Materials and Methods

Field Sampling Procedure

In the biomass subplots described in Chapter I, weekly field measurements of photosynthesis, stomatal conductance, and environmental parameters were made on trees during their second growing season (late May to late September, 1978). Three trees each of the four clones were selected randomly from the plot interior and measured on each date. On each measurement date, leaves at three positions on the tree were sampled: upper crown – the first mature leaf below the terminal shoot apex (LPI 8 to 12); mid-crown – the first mature leaf below the the shoot apex of an indeterminate long branch located in the upper mid-crown (LPI 7 to 12); and lower crown – the first mature leaf below the shoot apex of a short or determinate long branch located in the lower portion of the crown (LPI 1 to 6) and not showing any visible signs of senescence.

Leaves were always measured in sequence from upper to lower crown on each tree before moving to the next tree. All three trees of a clone were measured in a randomized order before measurement of the next clone began. Clones were measured in randomized order between 9:30 and 14:30 (Mean Solar Time) on sunny or partly sunny days.

Notes on the condition of the trees and their growth and leaf production were reported in Chapters I and II.

Environmental Parameters

Environmental parameters were monitored during the course of the study. Maximum and minimum temperatures, relative humidity, and total solar irradiance were extracted from data published by the U.S. Weather Bureau in Lansing, Michigan and collected at a weather station on the Michigan State University campus. Precipitation was recorded from a standard rain gauge at the study site.

Undisturbed 7.6 cm diameter soil core samples of the two soil types present on the study site were collected from 0 to 30 cm and 30 to 60 cm depths. Water retention curves were developed for the two soil types and two depths (Figure 28 Appendix) using a ceramic pressure plate apparatus. Undisturbed soil cores were used for the low tension range and screened soil samples for the high tension range. Field soil moisture samples 2 cm in diameter were collected in the same manner as above 24 hours after precipitation events and periodically inbetween them. Water content was determined gravimetrically and converted to soil moisture tension using the water retention curves. Seasonal patterns of soil moisture were developed by integrating the soil moisture samples with precipitation and evaporation data.

Measurements of wet and dry bulb temperatures were taken with an aspirated pistol-type psychrometer at 20 to 30 minute intervals during the periods when photosynthesis and stomatal conductance were measured. The dry bulb

temperature was used as the air temperature. Vapor pressure deficit (VPD) was calculated by converting the wet and dry bulb temperatures to millibars of water vapor at saturation and then taking the difference of the two values and converting to kiloPascals (kPa).

Photosynthetic photon flux density (PPFD) (400 to 700 nm) was measured at the time of the photosynthetic measurements. PPFD was measured at the adaxial leaf surface in a horizontal plane at the time of $^{14}CO_2$ application using a quantum flux sensor and meter (Li-Cor, U.S.A.).

Physiological Parameters

Abaxial leaf diffusive resistance to water vapor (s cm^{-1}) was measured immediately prior to photosynthesis on the half of the leaf lamina not exposed to $^{14}CO_2$ with a diffusive resistance meter and horizontal sensor (Li-Cor, U.S.A.) that was shaded just prior to and during the measurement (Kanemasu et al. 1969, Morrow and Slatyer 1971). Leaf conductance to water vapor was obtained by taking the reciprocal of leaf diffusion resistance to water vapor. The porometer cup temperature was measured with a built-in thermistor and used as an estimate of the leaf temperature. Calibration of the porometer sensor was done at the beginning and end of the growing season.

The photosynthetic rate of individual attached leaves was measured using a labeled carbon dioxide ($^{14}CO_2$) method modified from that described by McWilliam and others (1973) and others (Incoll 1977, Strebeyko 1967, Shimshi 1969, Naylor and Teare 1975, Austin and Longden 1967). Adaxial

and abaxial surfaces of a small disc (0.5 cm^2) of the intact

leaf lamina midway between the leaf tip and base were

exposed to $^{14}CO_2$-labeled air (335 cm^3 m^{-3}) of known specific

activity (5.3 μCi l^{-1} gas mixture) for 20 seconds at a

constant flow rate of 1.33 cm^3 s^{-1} (Figure 20). After ^{14}C

treatment, the exposed leaf area was removed immediately

with a sharp cork borer. After removal, the leaf disc was

placed in 1.5 cm^3 of 0.6 N NCS solubilizer (Amersham,

U.S.A.) in a 20 cm^3 scintillation vial and digested for 24

hours in a 50 C oven. After the digestion period, the

sample was bleached with 0.5 cm^3 of 30% hydrogen peroxide

and 18 cm^3 of scintillation cocktail [60 cm^3 Spectrafluor

PPO-POPOP (Amersham, U.S.A.) and 400 cm^3 of ethylene glycol

monomethyl ether (methyl cellosolve) in 1000 cm^3 toluene]

were added to the vials. The vials were placed in a

darkened scintillation counter (Packard Tri-Carb) for

several hours to reduce the effects of chemiluminescence.

The samples were counted for 10 minutes each on wide and

narrow channels. The sample count rates were corrected for

background and counting efficiency determined from a

channels ratio/counting efficiency curve developed from

known samples (Figure 29 Appendix). Sample activities (dpm)

were calculated by dividing the the sample count rates by

the counting efficiency (expressed as a decimal).

Photosynthetic rates were calculated using the reduced

formula in Table 15. The conversion of CO_2 volume to weight

was derived from Catsky and others (1971, p. 164). The

discrimination factor to account for diffusive and

Figure 20. Photosynthetic measurement using $^{14}CO_2$ field apparatus.

Figure 20.

Table 15. Formula and constants used for calculation of photosynthetic rate.

Unreduced formula

$$P = \frac{\dfrac{3600\ sec}{hr}\quad (DF)\qquad\qquad (S)}{\dfrac{(SA)}{(-0.0026(LT)+0.65877)}\qquad (A)\qquad (T)}$$

Reduced formula

$$P = \frac{0.0717\quad (S)\quad (-0.00206\quad (LT)\quad +\quad 0.65877)}{T}$$

Where: P = photosynthetic rate, mg $CO_2 dm^{-2} hr^{-1}$

3600 sec/hr = conversion from seconds to hours.

DF = discrimination factor for $^{14}CO_2$ versus $^{12}CO_2$ = 1.1775.

S = sample activity, dpm.

SA = specific activity of $^{14}CO_2$ in gas mixture = 11.766 X 10^6 dpm/l CO_2

$(-0.00206\ mg\ CO_2\ (LT) + 0.65877\ mg\ CO_2$ = conversion factor for volume to weight for CO_2 as affected by leaf temperature (LT) C.

$\dfrac{}{l\ CO_2-C}\qquad\qquad\qquad \dfrac{}{l\ CO_2}$

A = area of sample exposed to $^{14}CO_2$ = 0.0050265 dm^2

T = time of exposure to $^{14}CO_2$, sec.

0.0717 = constant that includes time conversion, DF, SA, and A and has the units $\dfrac{sec-1\ CO_2}{hr-dm^2-dpm}$

biochemical discrimination within leaves against $^{14}CO_2$ (Van Norman and Brown 1952, Austin and Longden 1967, Incoll 1977, Yemm and Bidwell 1969, Bykov 1970, Voznesenskii et al. 1971) was calculated according to Van Norman and Brown (1952).

The use and problems encountered in the $^{14}CO_2$ method have been discussed (Austin and Longden 1967, Shimshi 1969, Strebeyko 1967, McWilliam et al. 1973, Karlsson and Sveinbjornsson 1981) and summarized (Incoll 1977). Photosynthetic rates measured with this technique are greater than net photosynthesis (Incoll 1977, Michael 1984) and may approximate gross photosynthesis in some cases. Comparisons between species utilizing this technique can be risky due to differences in $^{14}CO_2$ uptake with different genotypes (Karlsson and Sveinbjornsson 1981) but relative comparisons within a clone or crop species are very sensitive since $^{14}CO_2$ uptake characteristics are similar within the genotype.

Data Analysis

Analysis of variance for both photosynthesis and stomatal conductance was calculated using a split-split plot design with date of measurement the main plot, clone the first split plot and leaf position the second split plot. Stepwise multiple regression for both photosynthesis and stomatal conductance versus environmental and physiological parameters were calculated in an effort to partition the variation present. Transformations of the variables were performed using logarithms (base$_{10}$), reciprocals, and squares of all of the parameters in order to find the

relationship that best partitioned the variation.

The high variability of field data due to the large number of factors that can be limiting makes strict statistical tests very difficult to interpret (Incoll 1977). Webb (1972) developed a technique called boundary line analysis that can be used to analyze data from studies where interacting variables cannot be controlled or, in many cases, even identified (Hinckley et al. 1978a, Incoll 1977, Jarvis 1976, Watts 1977). The boundary line represents the limiting effect of the independent variable on the dependent variable; it is assumed that all values below this line result from independent variables or interactions of variables being limiting (Hinckley et al. 1978a, Webb 1972).

Results

Physiological Parameters

Patterns of stomatal conductance for three canopy positions are presented in Figure 22 for the second growing season. Lower crown leaves had lower stomatal conductance values (range 0.01 to 0.49 cm s^{-1}) than mid- and upper crown leaves (range 0.01 to 0.99 cm s^{-1}), which were generally similar. The major influences on the stomatal conductance patterns were the drought periods of mid-July and early September (Figure 21) which resulted in stomatal closure. The lower crown leaves reacted first and the response moved up the tree's crown. As soil moisture tensions approached -1200 to -1500 kPa, stomata were totally closed. Significant differences in stomatal conductance values were found due to date of measurement, clone, and leaf position

Figure 21. Seasonal changes in soil moisture tension for
two soil types at two depths for the first (Day 161 = June
10) and second (Day 125 = May 5) growing seasons (Kalamazoo
sandy loam, 0-30 cm Δ, 30-60 cm +, Hillsdale sandy loam,
0-30 cm □, 30-60 cm o).

Figure 21.

YEAR 1

YEAR 2

KPA x 10^{-3}

DAYS

105

Figure 22. Seasonal change in stomatal conductance to water of leaves present in the upper (▲), middle (+), and lower (o) crowns of four hybrid poplar clones during the second growing season (Day 125 = May 5).

Figure 22.

(Table 16). The significance of the interaction terms indicates that the clones and leaf positions did not react in the same manner with changes in environmental conditions.

Seasonal patterns of photosynthesis for the three canopy positions were similar to stomatal conductance patterns (Figure 23). Lower crown leaves had the lowest photosynthetic rates (range 0.6 to 28 mg CO_2 dm^{-2} hr^{-1}) while mid- and upper crown leaves were similar and usually much higher than lower leaves (range 1.7 to 39 mg CO_2 dm^{-2} hr^{-1}). The depressing influence of the two drought periods is again evident. Significant differences in photosynthetic rates were found due to date of measurement, clone, and leaf position (Table 17). Like stomatal conductance, significance of the interaction terms means differences in response of the clones and leaf positions occurred due to changes in environmental conditions.

Environmental Parameters

A wide range of values for environmental parameters were encountered during the second growing season (Table 18). These values reflect the variation in weather during a typical Michigan summer and the microclimate within the poplar stands.

For stomatal conductance, 60 to 73% of the variation within a clone could be explained by combinations of environmental parameters using stepwise multiple regression (Table 19). The first variable to enter the equation for three of the clones was PPFD in logarithmic form and VPD in logarithmic form for the remaining clone. The second

Table 16. Analysis of variance for split-split plot design of stomatal conductance to water (cm s^{-1}) date, clone, and leaf position for four hybrid poplar clones measured throughout the second growing season.

Source of Variation	Degrees of Freedom	Mean Square	Significance of F-ratio[a]
Rep.	2	0.00289	ns
Date	15	0.203	**
Error 1	30	0.0156	
Clone	3	0.0918	**
Date x Clone	45	0.0550	**
Error 2	96	0.0138	
Leaf Position	2	0.568	**
Date x Leaf Position	30	0.0805	**
Clone x Leaf Position	6	0.0203	*
Date x Clone x Leaf Position	90	0.0144	**
Residual Error	256	0.00725	
Total	575		

a
 ns not significant at α = 0.05 level.

 * significant at α = 0.05 level.

** significant at α = 0.01 level.
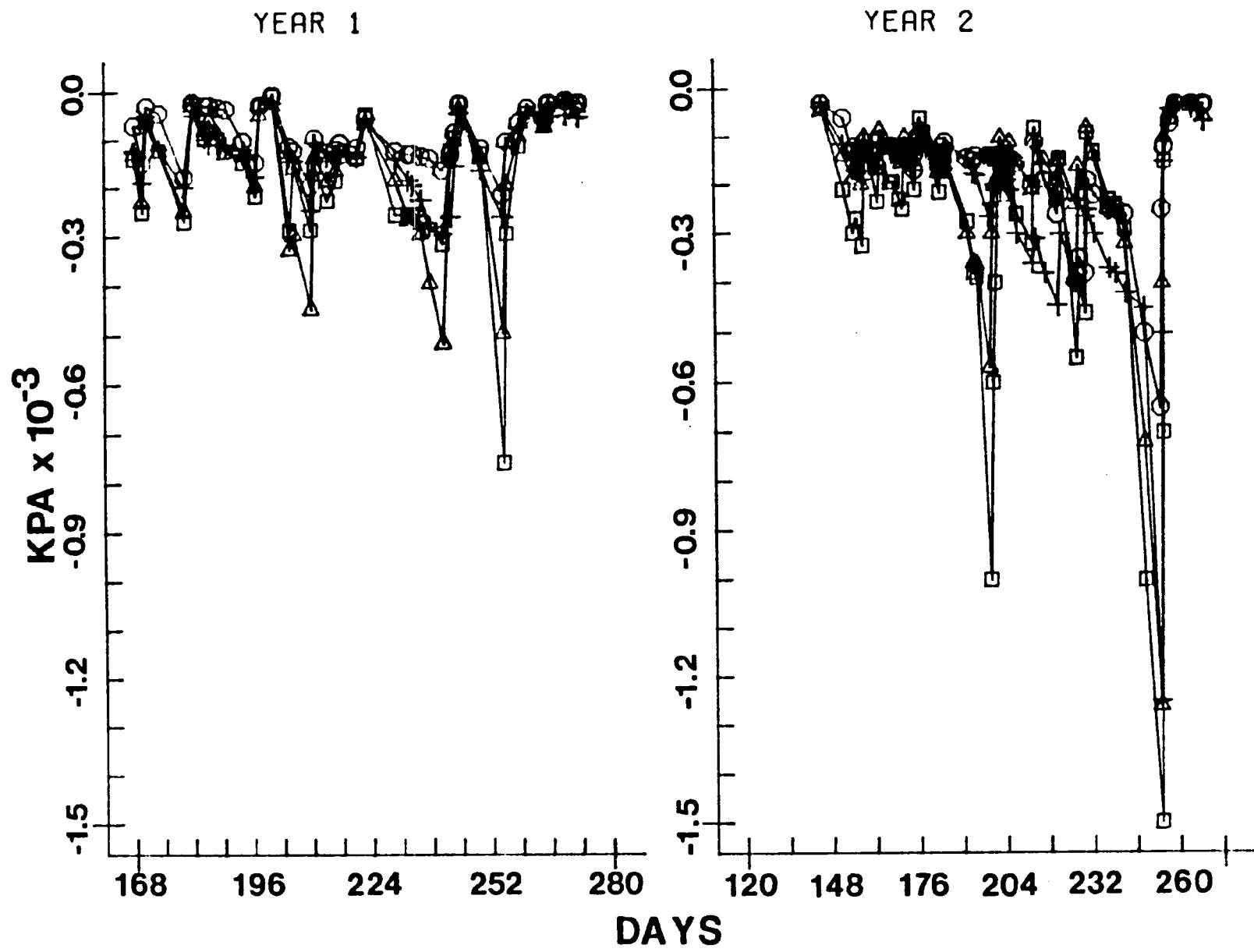
Figure 23. Seasonal change in photosynthetic rate of leaves present in the upper (Δ), middle (+), and lower (o) crowns of four hybrid poplar clones during the second growing season (Day 125 = May 5).
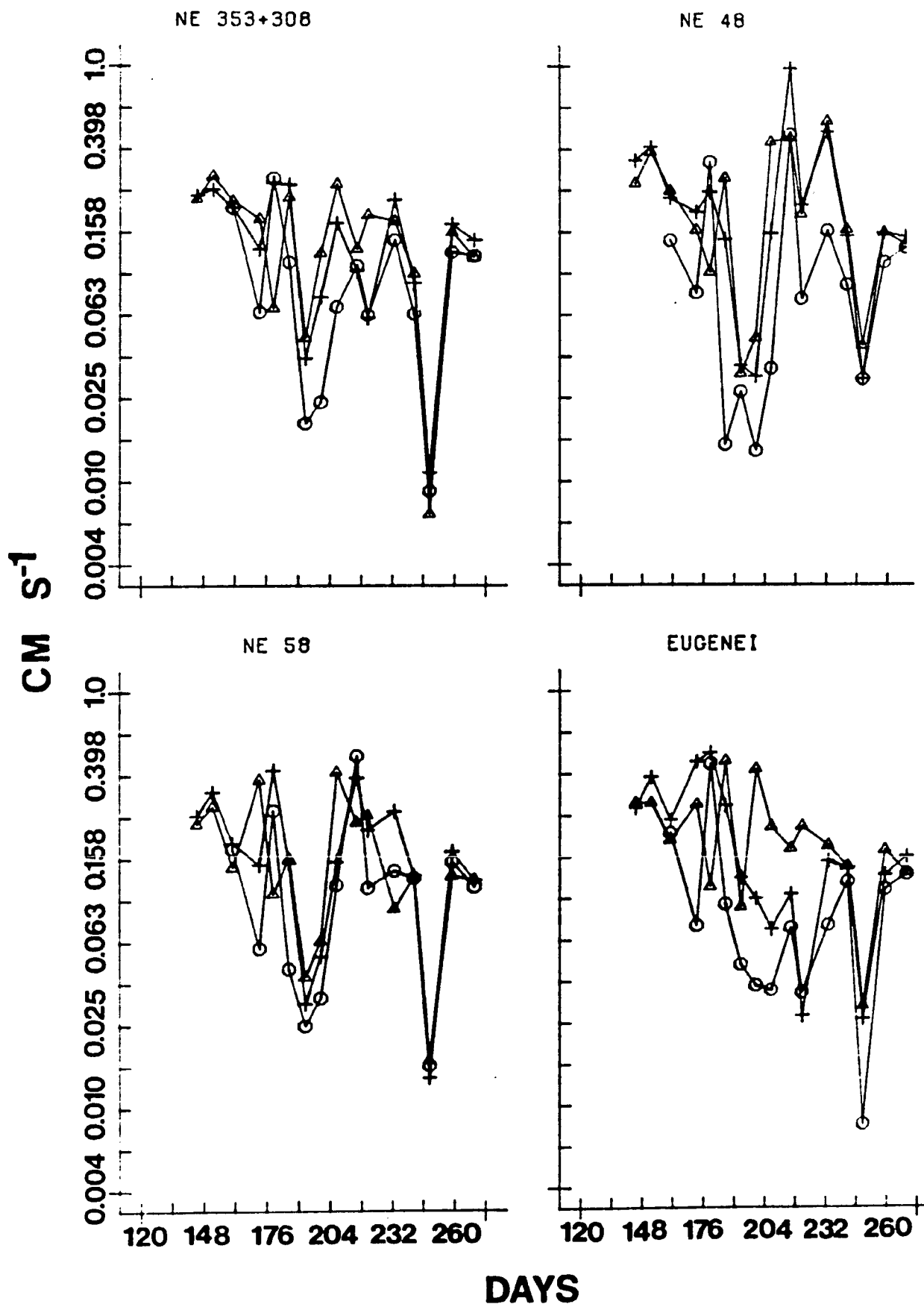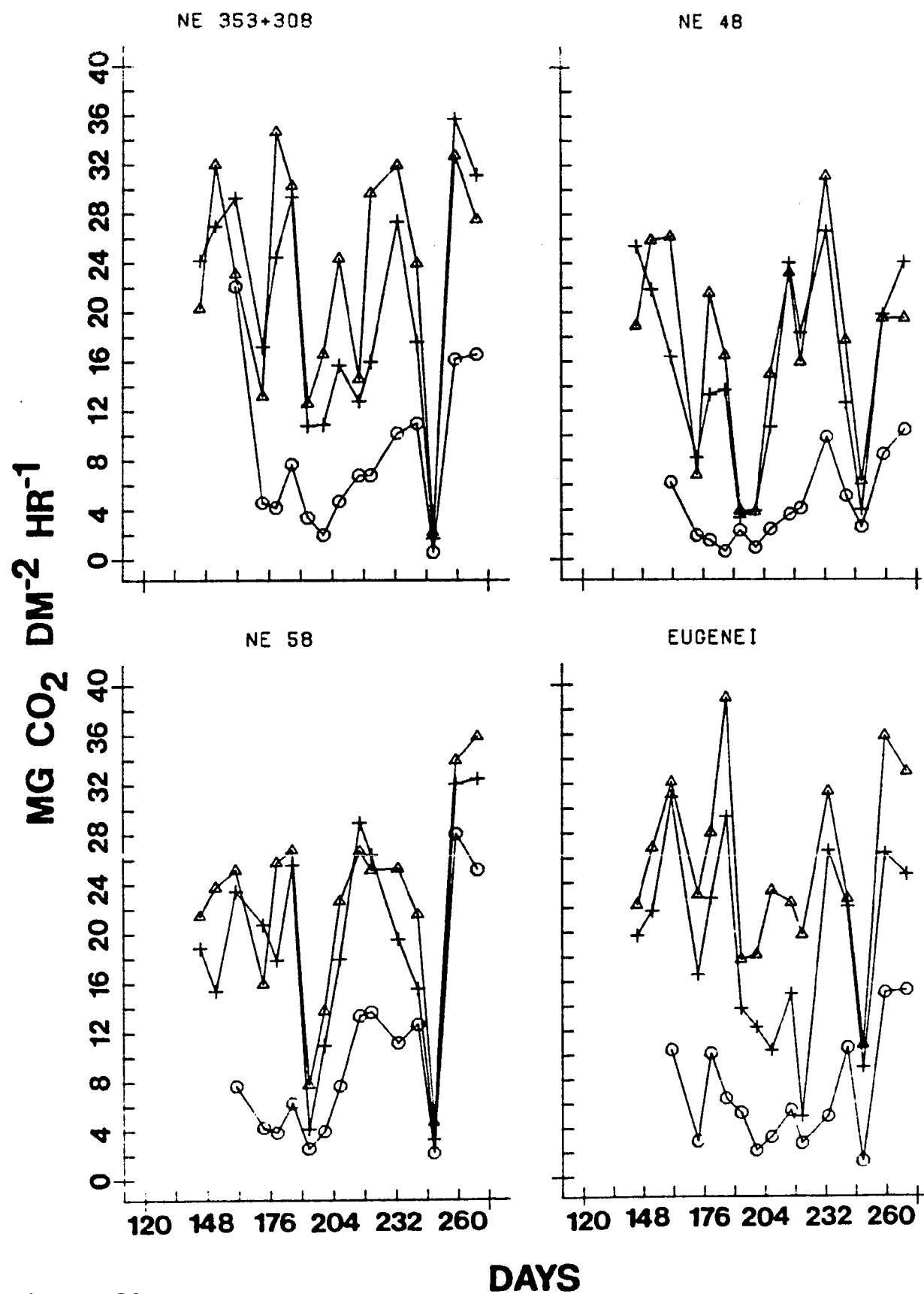
Figure 23.

Table 17. Analysis of variance for split-split plot design of photosynthetic rate $(mg\ CO_2 dm^{-2} hr^{-1})$ versus date, clone, and leaf position for four hybrid poplar clones measured throughout the second growing season.

Source of Variation	Degrees of Freedom	Mean Square	Significance of F-ratio[a]
Rep.	2	3.28	ns
Date	15	1297.79	**
Error 1	30	75.16	
Clone	3	850.05	**
Date x Clone	45	113.94	**
Error 2	96	46.07	
Leaf Position	2	12756.85	**
Date x Leaf Position	30	152.71	**
Clone x Leaf Position	6	114.12	**
Date x Clone x Leaf Position	90	29.01	ns
Residual Error	256	27.72	
Total	575		

a
ns   not significant at α = 0.05 level

*   significant at α = 0.05 level

**   significant at α = 0.01 level

Table 18. Range of environmental variables on days when gas exchange measurements were taken during the second growing season.

Environmental Variable	Range
Air temperature (AT)	18 to 32.5 C
Porometer leaf temperature (LT)	20 to 40 C
Vapor pressure deficit (VPD)	0.03 to 2.0 kPa
Photosynthetic photon flux density (PPFD)	20 to 2300 μmol m^{-2}sec^{-1}
Soil moisture tension, 0-30 cm (SMTA)	-45 to -720 kPa
Soil moisture tension, 30-60 cm (SMTB)	-35 to -450 kPa

Table 19. Stepwise multiple regression of stomatal conductance to water (cm sec^{-1}) versus environmental variables and the log$_{10}$, square, and reciprocal of these variables[a].

Clone Number	Regression		Dependent Variables		
	Significance of F-ratio[b]	r^2 value	Variables which entered regression	Coefficient	Significance of t-value[b]
NE 353+308	**	0.73	log$_{10}$VPD[c]	-0.116	**
			SMTA	2.60 x 10^{-4}	**
			PPFD	1.48 x 10^{-4}	**
			(PPFD)^2	-5.68 x 10^{-8}	*
NE 48	**	0.71	log$_{10}$PPFD	0.105	**
			SMTA	1.01 x 10^{-3}	**
			(SMTB)^2	2.23 x 10^{-6}	**
NE 58	**	0.66	log$_{10}$PPFD	8.42 x 10^{-2}	**
			SMTA	6.47 x 10^{-4}	**
			(SMTB)^2	1.04 x 10^{-6}	**
Eugenei	**	0.61	log$_{10}$PPFD	5.90 x 10^{-2}	**
			(SMTA)^2	3.36 x 10^{-7}	**
			(VPD)$^{-1}$	3.28 x 10^{-3}	*

a
 The regressions were forced through the origin and had a significance level of α = 0.05 for the partial F-ratio used for entry and deletion of variables. The regression was done independently on each of four hybrid poplar clones measured throughout the second growing season.

b
 ** significant at α = 0.01 level.
  * significant at α = 0.05 level.

c
 PPFD = photosynthetic photon flux density μmol m^{-2}s^{-1}
 VPD = vapor pressure deficit, kPa
 AT = air temperature, C
 SMTA = soil moisture tension, 0-30 cm, kPa
 SMTB = soil moisture tension, 30-60 cm, kPa

variable was soil moisture tension at 0 to 30 cm depth or
its square. Other variables entering some of the equations
were PPFD untransformed and squared, the reciprocal of VPD,
and soil moisture tension at 30 to 60 cm depth squared.
From these regressions it is apparent that the major
influences on stomatal conductance were light, soil moisture
tension, and VPD.

Boundary line plots of stomatal conductance versus
PPFD and VPD were done to further illustrate the influence
of these variables. Figure 24 shows that the relationship
between PPFD and stomatal conductance is similar for all
four clones. A light threshold occurred at approximately
100 to 150 μmol m^{-2} s^{-1}, above which light no longer limited
stomatal opening. VPD had an inverse threshold relationship
with stomatal conductance (Figure 25). Below VPD values of
1.1 to 1.3 kPa, stomatal opening was not influenced by VPD.
However, at VPD values above this threshold, stomatal
closure reduced conductance rapidly. Both of these
relationships appeared to be independent of any leaf
position effects.

Stepwise multiple regressions showed that from 84 to
90% of the variation in photosynthetic rate within a clone
could be explained by some combination of environmental
parameters and stomatal conductance (Table 20). The first
variable to enter the regression for all clones was PPFD in
logarithmic form. For three clones, the second variable was
stomatal conductance also in logarithmic form and soil
moisture tension at 0 to 30 cm depth for the remaining

Figure 24. Boundary line plot of stomatal conductance to water versus photosynthetic photon flux density for the upper (Δ), middle (+), and lower (o), crown positions of four hybrid poplar clones during the second growing season.
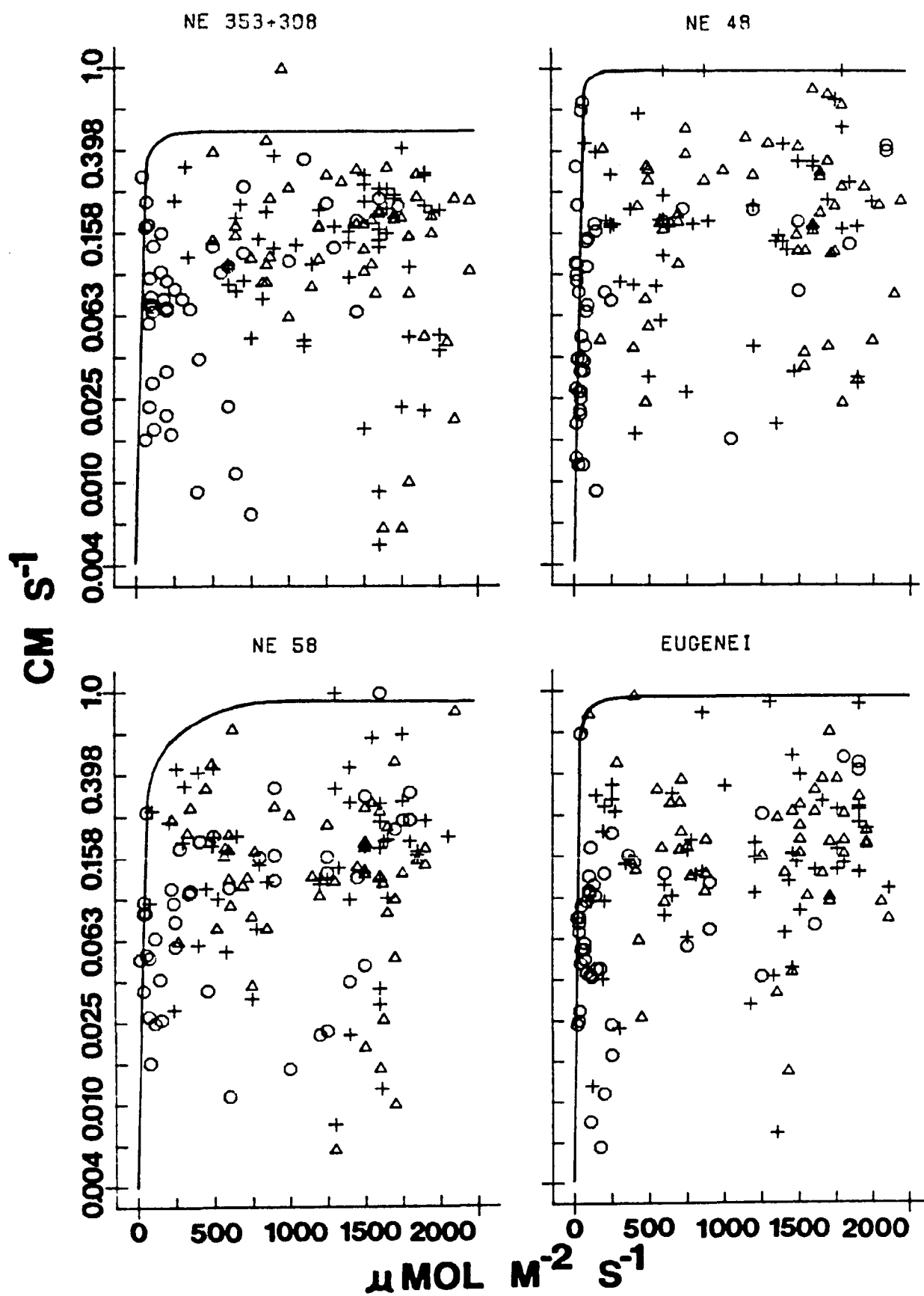
Figure 24.

Figure 25. Boundary line plot of stomatal conductance to water versus vapor pressure deficit for the upper (Δ), middle (+), and lower (o) crown positions of four hybrid poplar clones during the second growing season.
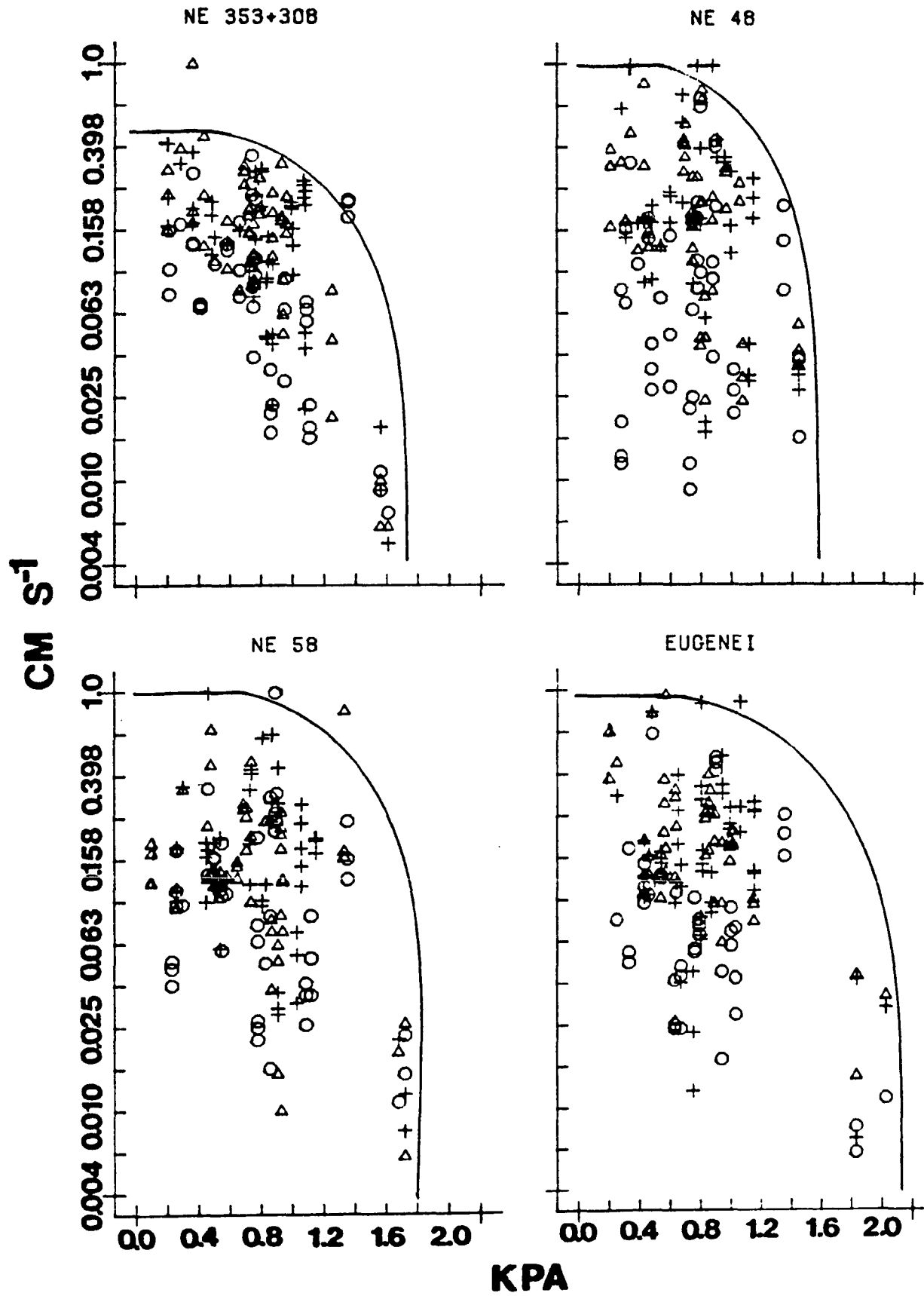
Figure 25.

Table 20. Stepwise multiple regression of photosynthetic rate (mg $CO_2 dm^{-2} hr^{-1}$) versus environmental and physiological variables and the $\log_{10}$, square, and reciprocal of those variables[a].

Clone Number	Regression		Dependent Variables		
	Significance of F-ratio[b]	R^2 value	Variables which entered regression	Coefficient	Significance of t-value[b]
NE 353+308	**	0.86	$\log_{10}$PPFD[c]	10.85	**
			$\log_{10}$St Cond	14.20	**
NE 48	**	0.84	$\log_{10}$PPFD	6.89	**
			$\log_{10}$St Cond	7.61	**
			$(SMTA)^{-1}$	309.76	**
			$(VPD)^2$	-236.29	*
NE 58	**	0.88	$\log_{10}$PPFD	11.73	**
			SMTA	4.54×10^{-2}	**
			AT	-0.447	**
			$\log_{10}$St Cond	8.72	**
			$\log_{10}$VPD	-8.64	**
			$(SMTA)^2$	4.54×10^{-5}	*
			$(St Cond)^2$	-12.13	*
Eugenei	**	0.90	$\log_{10}$PPFD	11.51	**
			$\log_{10}$St Cond	10.34	**
			VPD	-54.53	**
			$(St Cond)^2$	-10.28	*

a
  The regressions were forced through the origin and used a significance level of $\alpha=0.05$ for the partial F-ratio used for entry and deletion of variables. The regression was done independently for each of four hybrid poplar clones measured throughout the second growing season.

b
  ** significant at $\alpha= 0.01$ level
  * significant at $\alpha= 0.05$ level

c
  PPFD = photosynthetic photon flux density, $\mu mol\ m^{-2} s^{-1}$
  St Cond = stomatal conductance, $cm\ s^{-1}$
  VPD = vapor pressure deficit, kPa
  AT = air temperature, C
  SMTA = soil moisture tension, 0-30 cm, kPa
  SMTB = soil moisture tension, 30-60 cm, kPa

clone. Other variables that entered some of the equations were the reciprocal and square of soil moisture tension at 0 to 30 cm depth, VPD untransformed, squared, and in logarithmic form, stomatal conductance squared, and air temperature untransformed. From these regressions, the major influences on photosynthesis appeared to be light and stomatal conductance.

Boundary line plots of photosynthetic rate versus PPFD and stomatal conductance were used to show individual relationships. Photosynthetic rate had a hyperbolic relationship with stomatal conductance(Figure 26). Once the stomata were fully open, they had little or no further influence on photosynthetic rate. Lower crown leaves had a lower photosynthetic saturation point for stomatal conductance than upper and mid-crown leaves. The relationship between PPFD and photosynthesis also follows a rectangular hyperbola with light saturation occurring between 500 and 800 μmol m^{-2} s^{-1} (Figure 27). Lower crown leaves had lower photosynthetic rates at light saturation as well as a lower light saturation point than upper and mid-crown leaves. PPFD was the most highly correlated of any of the environmental variables with photosynthesis.

Discussion

The seasonal gas exchange patterns of the four clones were very similar, although there were small differences in their responses to individual factors. The influence of crown position was more evident for photosynthesis than for stomatal conductance. Lower crown leaves had low light

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Figure 26. Boundary line plot of photosynthetic rate versus stomatal conductance ·to water for the upper (Δ), middle (+), and lower (o) crown positions of four hybrid poplar clones during the second growing season (A = upper and middle crown, B = lower crown).
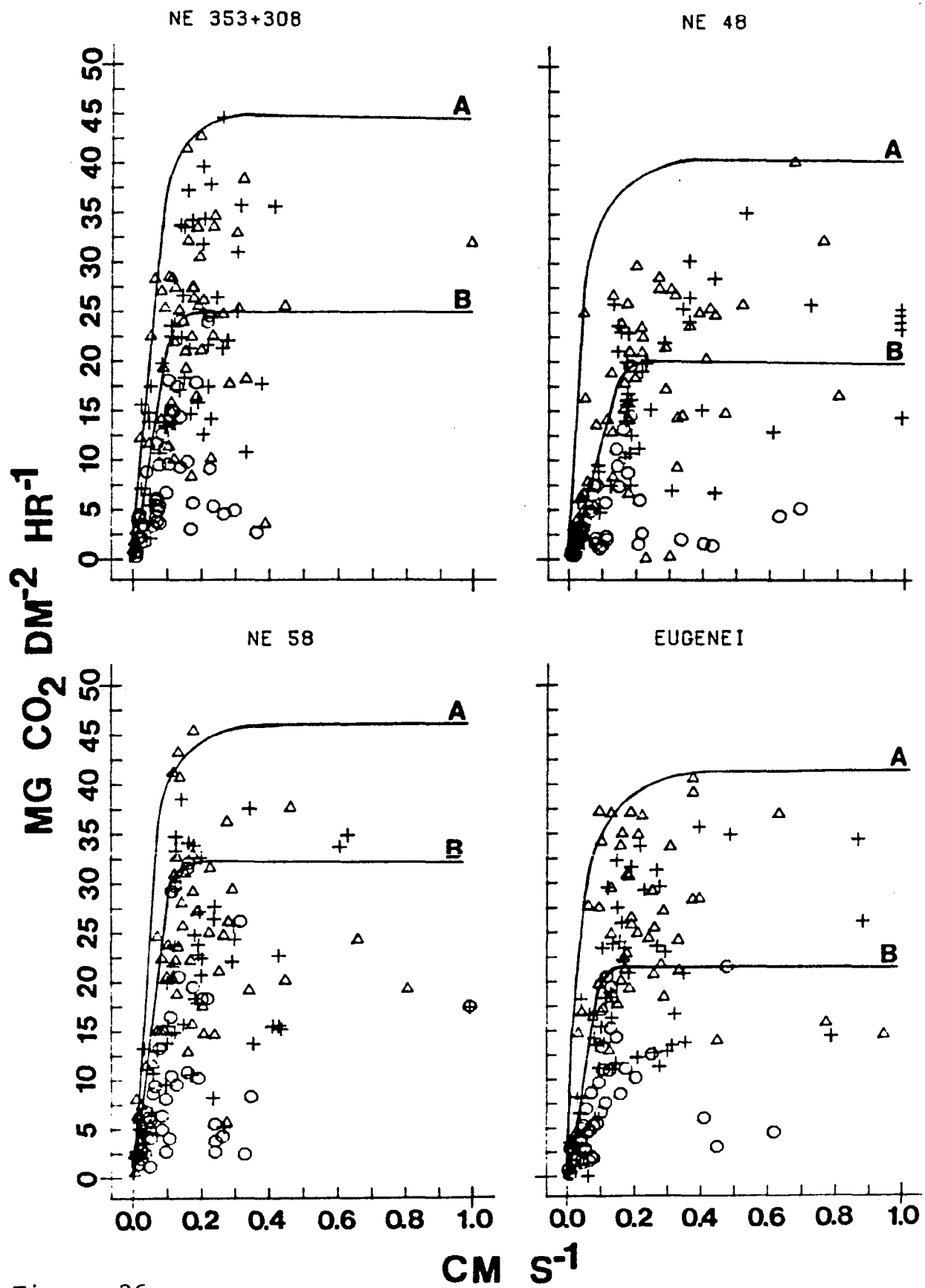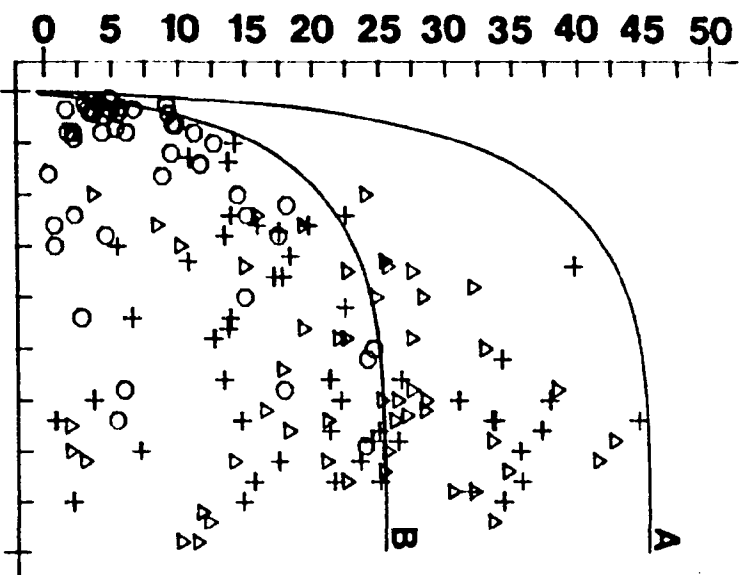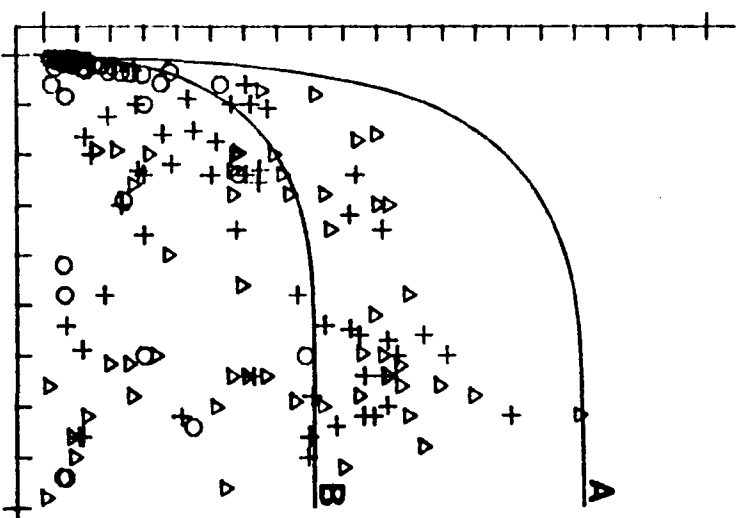
Figure 26.

Figure 27. Boundary line plot of photosynthetic rate versus photosynthetic photon flux density for the upper (Δ), middle (+), and lower (o) crown positions of four hybrid poplar clones during the second growing season (A = upper and middle crown, B = lower crown).

Figure 27.

NE 353+308

NE 58

EUGENEI

NE 48

125

MG CO$_2$ DM^{-2} HR^{-1}

μMOL M^{-2} S^{-1}
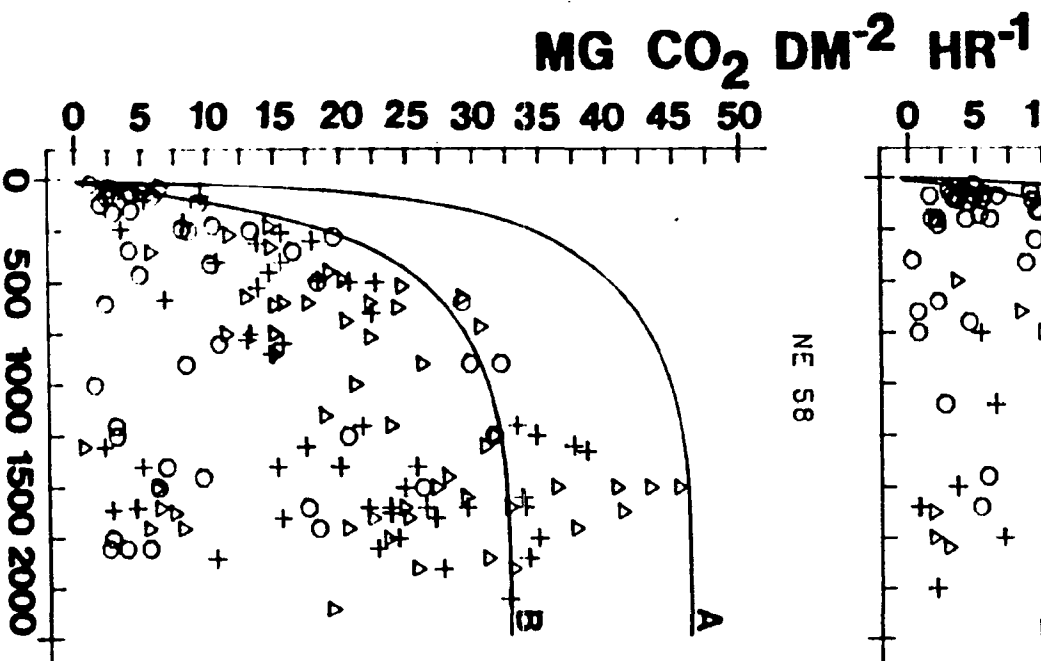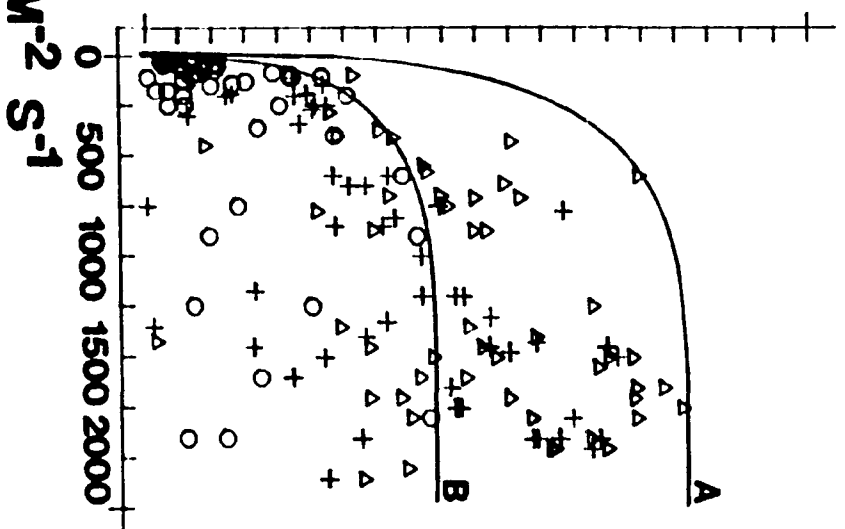
thresholds for stomatal opening, but these same light levels
were limiting to photosynthesis in these leaves (Aubuchon et
al. 1978, Lemeur and Impens 1981, Pollard 1970b, Nelson and
Michael 1982). Upper and mid-crown leaves were not limited
by light, but high leaf temperatures and mid-day stomatal
closure did limit photosynthesis (Aubuchon et al. 1978).
The lower photosynthetic rates and stomatal conductance of
NE 48 are probably related to its horizontal leaf
orientation, thick cuticle, and heavy wax deposits on the
lower leaf surface (Isebrands 1982, Nelson and Michael
1982).

The influences of PPFD, VPD, and soil moisture tension
on stomatal conductance and photosynthesis were very similar
to responses found by others. Regressions by Pallardy and
Kozlowski (1979a,b) showed PPFD to be the most important
variable followed by VPD, but there was also an interaction
between the two variables. The response to VPD was
independent of soil and plant moisture tensions. The shape
of the boundary line curves for stomatal conductance in this
study are similar to curves reported elsewhere (Pospisilova
and Solarova 1980, Jarvis 1976, Ceulemans and Impens 1980,
1981, Ceulemans et al. 1978b, McGee et al. 1981).

PPFD had a major influence on photosynthesis (Lemeur
and Impens 1981, Isebrands 1982, Michael 1984), and along,
with stomatal conductance was highly correlated with it
(Ceulemans et al. 1980a, Ceulemans and Impens 1980, 1981).
The shape of the boundary line curves for photosynthesis are
similar to curves reported elsewhere (Furakawa 1972, Larcher

1969, Pieters 1960, 1974, Fasehun 1978, Smith and Gatherum 1974, Domingo and Gordon 1974, Regehr et al. 1975, McGee et al. 1981).

NE 48 had a lower light saturation point for photosynthesis than the other three clones. In addition, NE 48 reacted to VPD declines by reducing stomatal conductance and photosynthesis sooner than the other clones. This response is one mechanism to reduce water use that helps to make NE 48 more drought tolerant than the other clones and is consistent with the higher water use efficiency and drought tolerance of Tacamahaca poplars over Aigeiros poplars shown by Blake (1981).

While soil moisture tensions were an important determining factor in both stomatal conductance and photosynthesis regressions, the influence of the two drought periods on these processes is not fully evident from the regressions. Drought stress produced major effects on the growth of the poplar clones. As mentioned in Chapters I and II, these effects included reductions in biomass yield, height and diameter growth, and premature abscission of leaves and branches. The literature discusses a number of techniques utilized by woody plants to tolerate drought stress. Stomatal control was a technique used by many trees (Hinckley et al. 1979). As drought stress developed, photosynthetic rates were depressed to near the compensation point, but upper crown photosynthetic rates were reduced much more than lower crown rates (Aubuchon et al. 1978, Hinckley et al. 1979). Both of these patterns seem to fit

the responses shown bv poplar clones in my study. Federer
(1977, 1980) and Pospisilova and Solarova (1980) showed that
the water potential at which different species and clones
reach a stress situation varies widely. One species or
clone may be undergoing severe stress while another shows no
sign of stress (Hinckley et al. 1978a). The abscission of
leaves early is one mechanism that conserves water during
drought periods so that conductance and photosynthesis in
remaining leaves can be maintained at higher levels for
longer time periods (Ginter-Whitehouse et al. 1983).
Kaufmann (1982) found increased conductance in senescing
aspen branches two months proir to any visual symptoms of
senescence. A similar phenomenon probably occurred in my
study, as many short shoots in the lower crowns, which
eventually senesced and abscised, showed higher conductance
rates than leaves in the upper canopy just as each of the
drought periods began. The loss of stomatal function due to
senescence processes is the probable cause of this increased
water loss prior to visible leaf decline.

Poplars cope with drought through stomatal closure,
leaf and branch abscission, preconditioning of processes to
stress, and exploitation of larger soil volumes.
Preconditioning is evident by comparing stomatal conductance
and photosynthesis values of the more severe second drought
period to those of the first. In both cases, reductions in
these processes were either no lower in the second drought
or did not decrease until soil moisture levels reached
higher potentials than the first drought. It is highly

likely that the precondititioning is due to increses in osmotic potential during the first drought period (osmotic adjustment) (Hinckley et al. 1978b, Parker et al. 1982).

The interactive effects of environmental variables on gas exchange measured in the field make direct correlations and interpretations difficult, especially when one or several factors may be limiting gas exchange at any given moment. This difficulty has prompted many people to use modelling approaches or more sophisticated statistical approaches such as multivariate analysis in an attempt to predict gas exchange and biomass productivity. No siginificant correlations were found between eight gas exchange variables and field productivity of eight poplar clones but some promise was shown for separating the more highly productive clones (Ceulemans et al. 1980a). Further analysis using multivariate analysis techniques showed that field productivity of poplar clones could be predicted from gas exchange parameters at their maximal values (optimal leaf age)(Ceulemans and Impens 1982). In yet another experiment, Ceulemans and Impens (1983) showed a very good correlation between gas exchange rates at their maximal values and first and second year height and biomass yield. It is only through the integration of the growth processes by the plant that the true interaction effects can be seen. Simulation models may provide one means of obtaining the same information without having to do large field experiments for many years. The data gathered in this study could be used to help formulate such a model.

SUMMARY AND CONCLUSIONS

The interrelationships of growth and biomass yield to
crown development and gas exchange of four hybrid poplar
clones has been presented in Chapters I, II, and III.
Ceulemans and Impens (1982, 1983) have shown potential for
using gas exchange parameters at maximal values (optimal
leaf age) to predict field productivity of poplar clones.
However, it is obvious that intra- and interplant
physiological relationships are necessary in order to
accurately predict productivity (Watson 1952). The results
of this study support this view as looking at only one
parameter or process would not allow you to accurately
predict biomass yield. The four clones showed differences
in growth pattern, biomass yield, LAI, branching pattern,
biomass partitioning, gas exchange, and response to drought
stress.

Increases in wood yield may be obtained by manipulating
crown shape and structure, leaf display, and photosynthetic
efficiency, the latter either through higher photosynthetic
rates or lower respiration rates (Larson and Gordon 1969a).
Photosynthetic efficiencies of short rotation
intensively-cultured poplar systems varied from 1.88 to
3.72% as spacing decreased (Lemeur and Impens 1981) which
was higher than the efficiencies of many crop plants. This

highly efficient conversion of solar energy into biomass is one of the major advantages of using short-rotation, intensive culture to grow trees.

Some of the physiologically-based management recommendations that can be made have been summarized by Isebrands (1982): 1. Clones should be selected to match the spacing and rotation length, the length of the growing season, site requirements, and desirable root characteristics. 2. Height growth is controlled by current leader leaves and factors which reduce their number, size, and growth will reduce height growth. 3. Factors that affect lateral branch leaves will not affect height growth, but will affect either lateral branch growth if prior to budset or stem diameter and root growth if after budset. The higher the branch on the tree, the greater the effect on stem diameter and root growth. 4. Pruning is not recommended until branches are older than three years. 5. Season of harvest will affect coppicing with late summer being the worst time to harvest. The results from this study provide additional support to several of these points.

The following conclusions can be drawn from this study:

1. The NE 353 + 308 clonal mixture had the highest LAI, biomass yield, and MAI; had the highest amount of biomass partitioned into branches and lowest into minor stems; and had among the highest photosynthetic rates.

2. NE 48 had the second highest LAI, biomass yield, and MAI; was intermediate in the proportion of biomass partitioned into branches and second lowest into minor stems; had the highest SLW, thickest leaves, and least amount of leaf abscission; and had the lowest photosynthetic rates.

3. NE 58 and Eugenei had the lowest LAIs, biomass yields, and MAIs; had the most biomass partitioned into minor stems and least into branches; and had among the highest photosynthetic rates.

4. Drought stress had a major impact by reducing growth and biomass yield of all the clones. Leaf and branch abscission due to this stress was less severe on NE 48 than the other clones. Gas exchange was also reduced significantly by drought stress, although NE 48 seemed to show more preconditioning to drought than the other clones.

5. NE 48 appeared to be more drought tolerant than the other three clones.

APPENDIX

Table 21. Regression and prediction equation[a] parameters from leaf length versus leaf area regressions for four one-year-old hybrid poplar clones.

Clone Number	Regression		Coefficients				
	Significance of F-ratio[b]	r^2 value	Intercept (b_0)	Variable 1 (b_1)	Significance of t value[b]	Variable 2 (b_2)	Significance of t value[b]
NE 343+308	**	0.97	-1.48	-0.0542	**	2.65	**
NE 48	**	0.98	-1.04	0.0594	**	1.87	**
NE 58	**	0.98	-1.72	-0.0291	*	2.64	**
Eugenei	**	0.99	-1.37	-0.00096	ns	2.36	**

a
Prediction Equation: $LA = e^{(b_0 + b_1(LL) + b_2(Ln\ LL) + CF)}$ or $LA = a(LL)^{b_2} e^{b_1(LL)}$

Regression Equation: $Ln\ LA = b_0 + b_1(LL) + b_2(LL)$ which is the transformed form of the equation,
$$LA = a(LL)^{b_2} e^{b_1(LL)}$$

Where: LA = leaf area in cm^2
LL = leaf length in cm
Ln = natural logarithm
e = exponential function
CF = correction factor due to bias of transformation = $\hat{\sigma}^2/2$
a = constant which equals $e^{(b_0 + CF)}$

b
ns not significant at α = 0.05 level.
* significant at α = 0.05 level.
** significant at α = 0.01 level.

Table 22. Regression and prediction equation[a] parameters from leaf length versus leaf area regressions for four two-year-old hybrid poplar clones.

Clone Number	Regression		Coefficients				
	Significance of F-ratio[b]	r^2 value	Intercept (b_0)	Variable 1 (b_1)	Significance of t value[b]	Variable 2 (b_2)	Significance of t value[b]
NE 343+308	**	0.96	-0.978	0.028	**	2.07	**
NE 48	**	0.96	-1.121	0.069	**	1.87	**
NE 58	**	0.96	-0.996	0.051	**	1.95	**
Eugenei	**	0.97	-0.986	0.066	**	1.88	**

[a]

Prediction Equation: $LA = e^{(b_0 + b_1(LL) + b_2(Ln\ LL) + CF)}$ or $LA = a(LL)^{b_2} e^{b_1(LL)}$

Regression Equation: $Ln\ LA = b_0 + b_1(LL) + b_2(Ln\ LL)$ which is the transformed form of the equation,

$$LA = a(LL)^{b_2} e^{b_1(LL)}$$

Where: LA = leaf area in cm^2
LL = leaf length in cm
Ln = natural logarithm
e = exponential function
CF = correction factor due to bias of transformation = $\hat{\sigma}^2/2$
a = constant which equals $e^{(b_0 + CF)}$

[b]
** significant at $\alpha = 0.01$ level.

Figure 28. Water retention curves for two soil types at two depths as determined with undisturbed soil cores (low tension) and screened soil (high tension) in a ceramic plate pressure apparatus (Kalamazoo sandy loam, 0-30 cm △, 30-60 cm +, Hillsdale sandy loam, 0-30 cm □, 30-60 cm o).
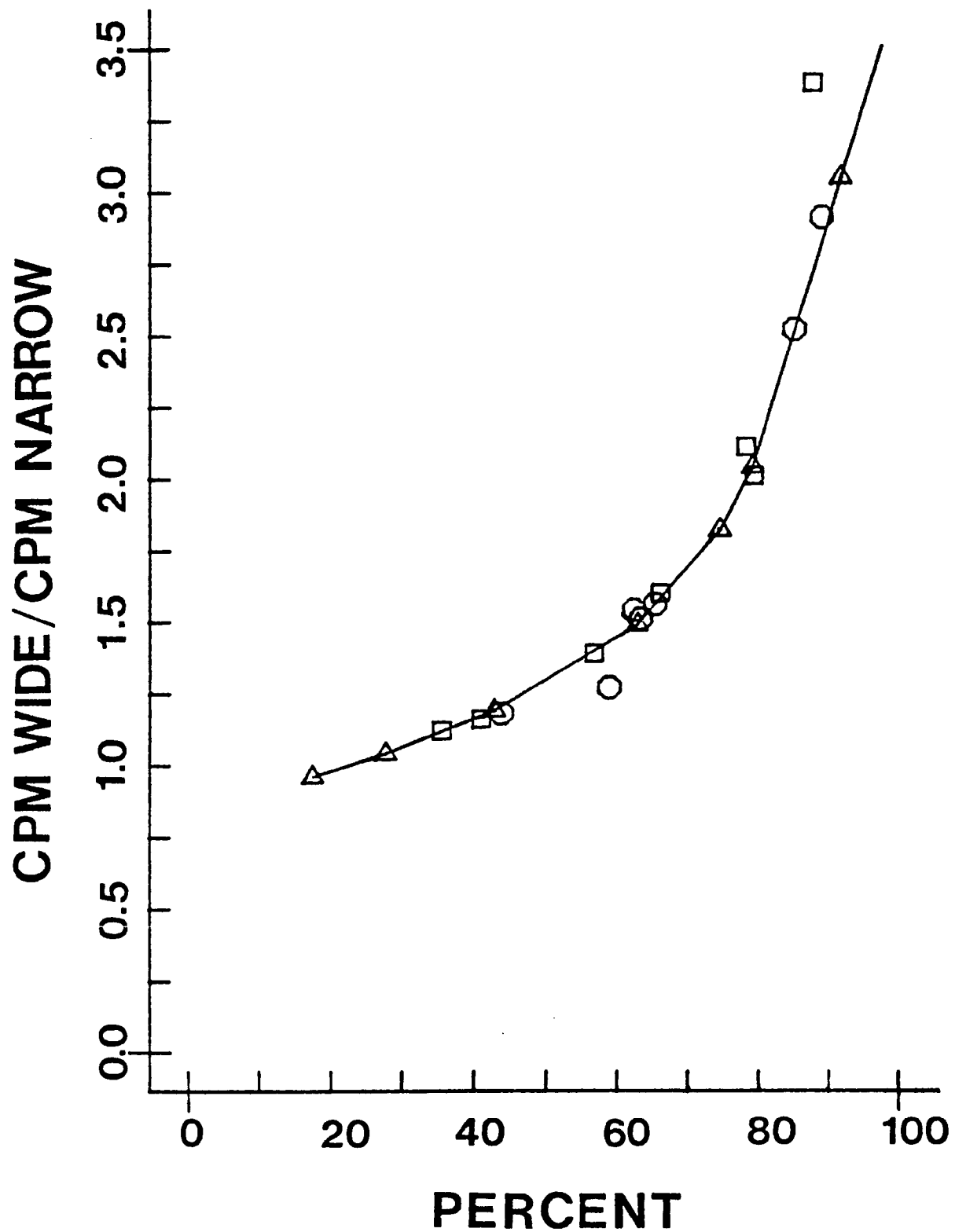
Figure 29. Channels ratio versus counting efficiency calibration curve for ^{14}C-labeled photosynthetic samples (Glass vials △ , Glass vials ▢, Plastic vials o).

Figure 30. Map of study area showing block and plot
arrangement and harvest schedule.
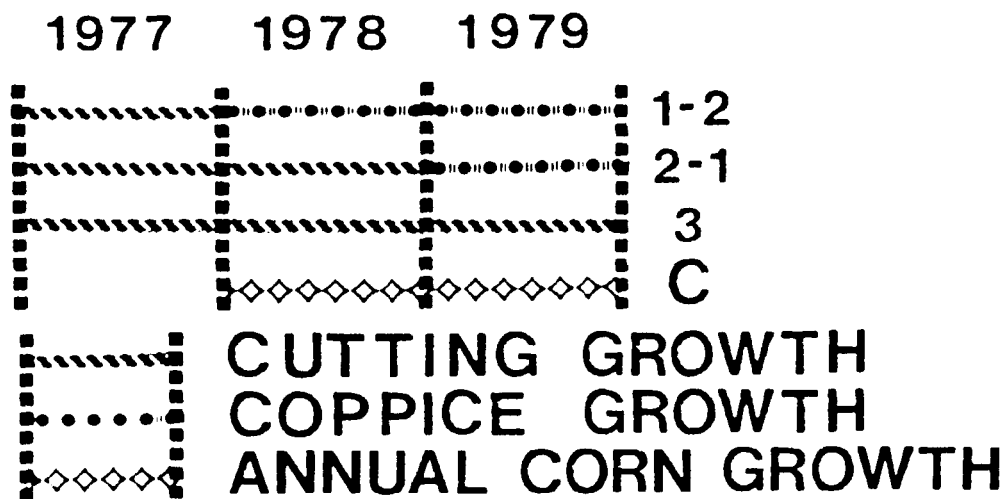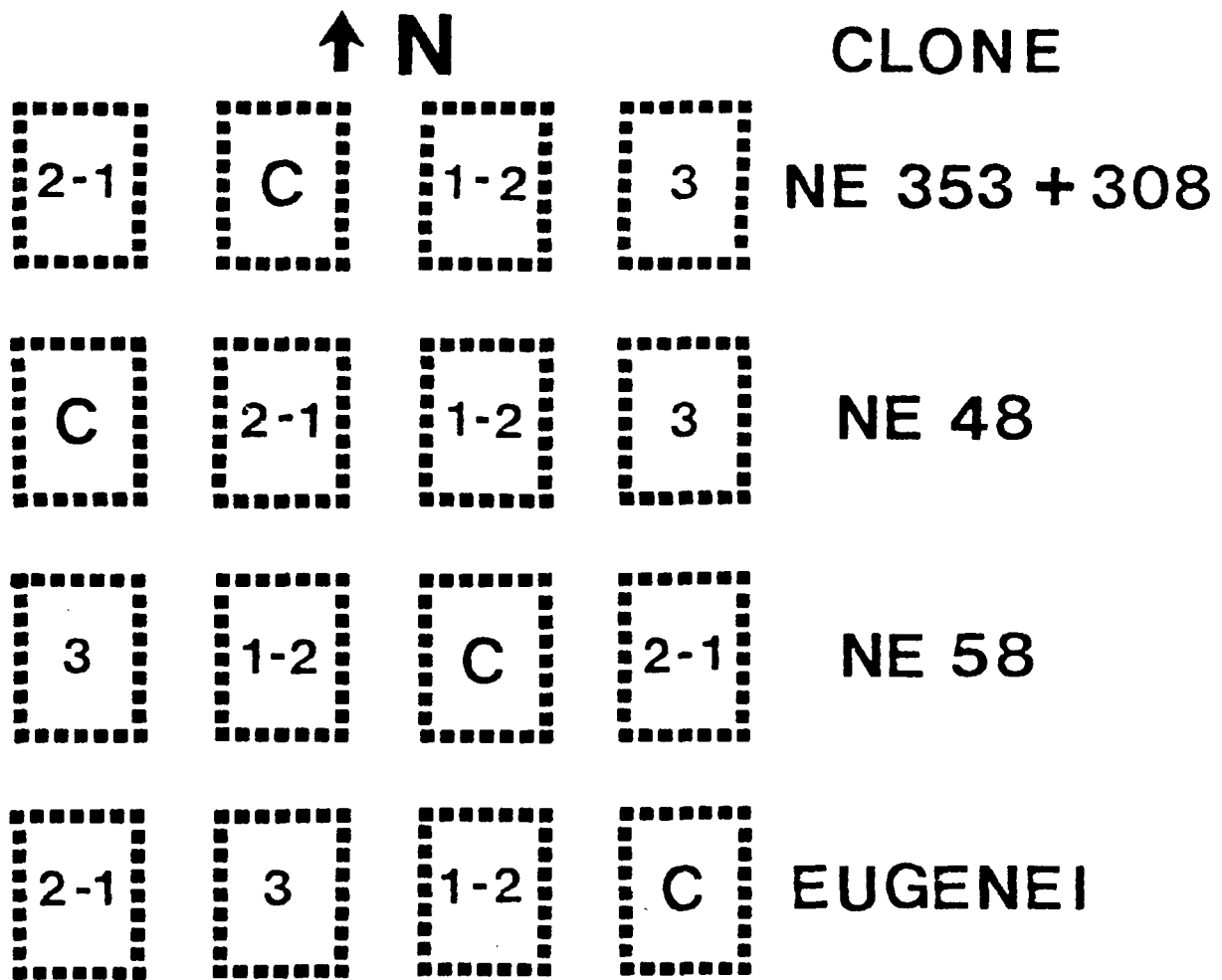
Figure 30.

Figure 31. Map of plot showing row layout, border area, large biomass and LAI subplot, and small growth analysis subplots.

↑N

GROWTH ANALYSIS SUBPLOTS

1 M

BIOMASS AND

LAI SUBPLOT
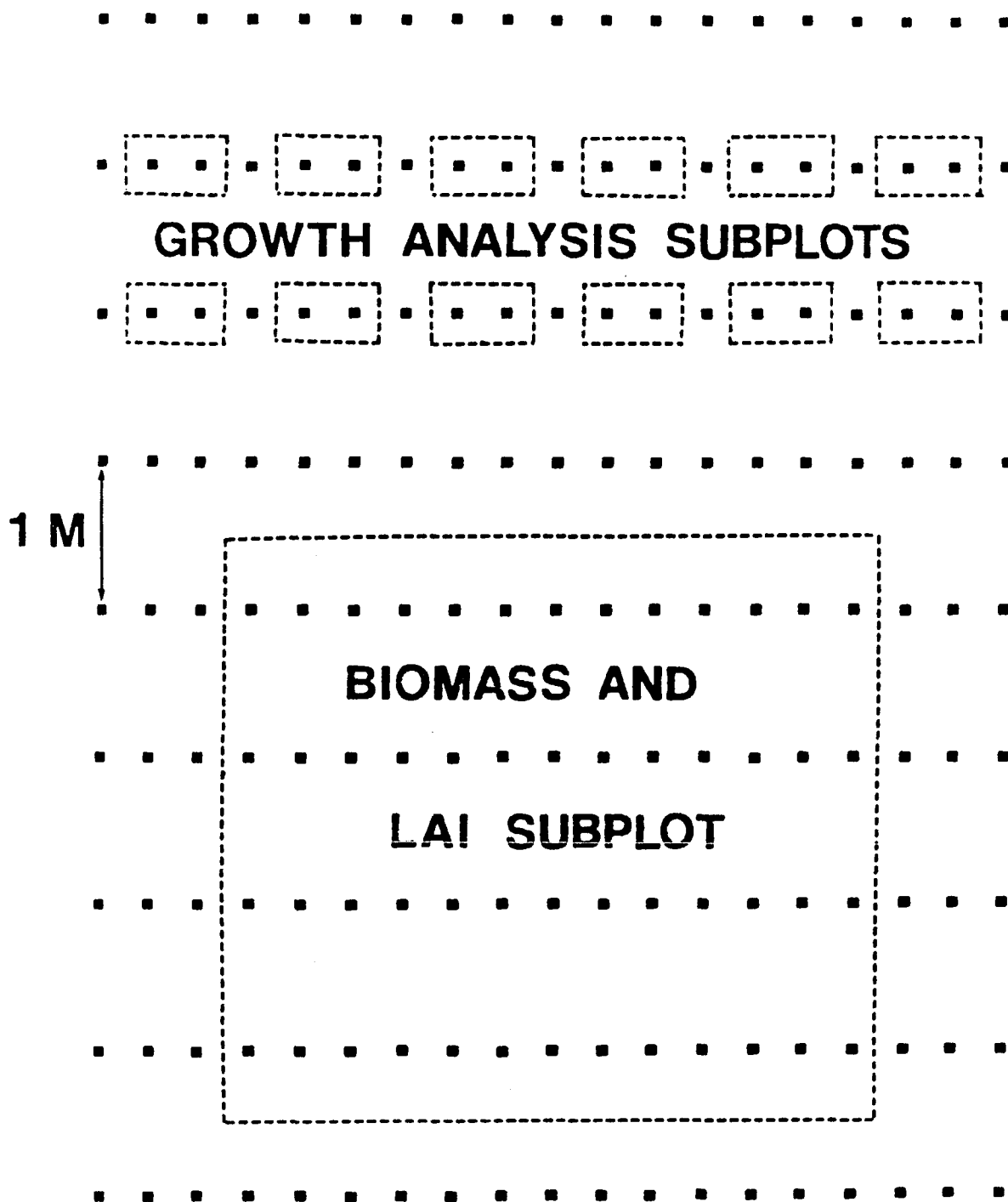
Figure 31.

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