The Influence of Edaphic Characteristics and Clonal Variation on Quantity and Quality of Wood Production in Populus grandidentata Michx. in the Great Lakes Region of the U.S.A.

by

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ABSTRACT

Mature (55 ± 7 years) largetooth aspen (Populus grandidentata Michx.) were harvested from three stands in northern lower Michigan, U.S.A., using dimension analysis techniques. The three harvest sites represent the range of soil quality characteristics that influence tree growth rates in the Great Lakes Region of the central U.S.A. (i.e., good, intermediate, and poor in terms of net productivity). Stem weight increment accounted for 46.4% of all abovegound tree component production at the poor site and over 52% at the good and intermediate sites. Net annual production per unit leaf weight was about 33% less for the poor site aspen as compared with the good site aspen. Total aspen tree production at the good and intermediate site was 3.7 and 2.5 times greater than production at the poor site.

Although aspens display a large difference in net productivity among the three sites and clonal groups, the wood is suprisingly uniform in density (specific gravity = 0.38 ± 0.03). Good site wood with wide rings has nearly equal wood anatomy to wood with narrow rings on the poor sites, with the difference being in the total number of cells produced. Thus, volume production in aspen is a good measure of biomass production, and good sites simply yield greater quantities of wood, of equal quality, than poor sites. A sixty-year comparison, at five-year intervals, of radial increments and bole wood production at each site indicates that good site superior clones had twice the radial growth and production of inferior clones on the good site while superior clones on the poor site had three times the growth of inferior clones at the poor site. The selection of superior aspen clones for stand regeneration could significantly increase productivity on all sites.

KEY WORDS: Populus gradidentata, clone, specific gravity, radial growth, biomass, net primary production

INTRODUCTION

Largetooth aspen (Populus grandidentata Michx.), once considered a weed tree species, has become an important source of pulpwood in the Lake States region, U.S.A., with the largest amount of pulpwood (45%) coming from this species and P. tremuloides (quaking aspen) (Leuschner, 1972; Blyth and Hahn, 1977). During the energy shortage, aspen has also been mentioned as a key species for wood conversion to energy because of its rapid growth and stand regeneration capabilities. However, little data are available on growth rates of largetooth aspen, or the effects of site conditions and genetic factors on the quantity of wood produced.

The largetooth aspen range extends from Nova Scotia west to Manitoba, Canada, and from Maryland west to Iowa, U.S.A. The rainfall regime over this range varies from a low of 51 cm on the Manitoba prairie to a high of 152 cm in the eastern Maritime Provinces of Canada. Largetooth is the most shade intolerant tree found in the deciduous forest (Fowells, 1965).

The soil factors affecting aspen growth rates are soil texture (silt and clay content) and fire history of the stand (Stoeckeler, 1948, 1960), percent clay and exchangeable bases (Einspahr and Benson, 1967) and pH (Meyer, 1956). The significance of soil texture to aspen growth rates (Kittredge, 1938; Voight et al., 1957; Strothmann, 1960; and Fralish, 1972) is indicative of the value of soil water holding capacity (i.e., presence of silt-plus-clay) to aspen productivity. The presence of silt-plus-clay content of 10 to 20% on sands or loamy sands results in site indexes of 20 m for largetooth aspen and 25 to 35% silt-plus-clay contents results in trees greater than 24 m in height at age 50 and 45 cm in diameter (Stoeckeler, 1948). Largetooth aspen is found in greater abundance on sandier soils, 6 to 42% silt-plus-clay, than quaking aspen, 18 to 81% silt-plus-clay (Stoeckeler, 1948, 1960). Largetooth's presence and survival on these drier sites has been attributed to its ability to rapidly increase leaf resistance (i.e., close stomates) at $\approx$-30 bars and avoid further water loss through transpiration. Quaking aspen is unable to increase leaf resistance at even -60 bars of leaf water potential (Tobiessen and Kana, 1974).

Thus, the presence of sufficient soil moisture and availability of exchangeable bases such as calcium and magnesium are key indicators of good site quality conditions for largetooth aspen growth. To provide representative data on growth, biomass and net production of largetooth aspen, research was conducted at three sites chosen to represent the range of soil quality characteristics found among largetooth aspen stands in the Great Lakes region of the U.S.A.

The specific objective was to develop a set of predictive models utilizing changes in radial growth (i.e., changes in diameter at breast height: dbh) to determine biomass and net primary productivity (NPP) of largetooth aspen clones on a range of glacial soils. The following questions were also addressed: (1) What are the effects of edaphic conditions and genetics (clonal variation) on quality (specific gravity) of largetooth aspen wood? (2) What are the effects of edaphic conditions and genetics (clonal variations) on the quantity of wood production? and (3) What is the growth response (biomass and NPP) of largetooth aspen on soils of varying quality over their sixty-year life-span?

The Study Sites

The research areas are located on the properties of the University of Michigan Biological Station in Cheboygan County, Michigan, U.S.A. (latitude 45° 34'north). The three sites are referred to as the good, intermediate, and poor sites on the basis of differences in site productivity suggested by comparative basal areas and stand heights. Prior to 1909, logging operations removed the conifers and northern hardwoods that had occupied these sites, and aspen seedlings invaded the disturbed soils (Barnes, 1966). Repeated fires destroyed the aboveground parts of these seedlings, but the surviving root systems were available for aspen sprout growth and clonal expansion. This led to the dominance of aspen among associated tree species (Gates, 1926). Several clones (genetically identical individuals) are the characteristic structure of aspen populations in a stand (Barnes, 1969). The measurement of one clone is equivalent only to the measurement of one tree, if several clones are present; thus, two trees from each of the clones (typically two or three clones) representing stand growth variations must be used to develop growth curves (Zahner and Crawford, 1965).

In addition to sharing a similar history of origin, the study sites are subject to nearly identical climatic and topographic influences. Each site is within 2.5 km of other sites and at about the same elevation (230 to 270 m above sea level). Slopes range from 0 to 12%, and runoff is minimal due to the sandy nature of the soils. The mean monthly temperatures at the Pellston, Michigan, Weather Station, located 11 km west of the study sites, range from -8.8°C in February to 18.4°C in July. Mean annual precipitation averaged 79.4 cm from 1942 to 1969 (Mich. Dept. Agric. 1971).

Basal areas of largetooth aspen at the sites, and average heights and mean dbh (with standard errors of the mean) for dominant and codominant largetooth aspen at the good, intermediate, and poor sites were 30.5, 27.3, 11.4 m^2/ha; 26.5, 23.1, 15.6 m; and 21.8 ± 0.5, 16.5 ± 0.2, 13.4 ± 0.3 cm. Corresponding percentages of total stems per hectare of largetooth aspen on the three sites were 48, 65 and 42. The differences in structural gradients among the three sites were not related to stand age. Trees harvested for biomass and production assessment averaged 52 ± 2 years of age at the good and intermediate sites and 60 ± 2 at the poor site. Benninghoff and Cramer (1963) and Richardson and Lund (1975) have published phytosociological and stand composition data for these sites.

Soil conditions are the primary cause of differences in tree growth and species composition among the three sites. Particle size distribution and exchangeable cation data for these soils are presented in Table 1. The poor site is an excessively drained glacial outwash plain of Rubicon sand, a member of sandy, mixed, frigid, Entic Haplorthods (Unpublished USDA-SCS Map, 1976; Grayling, Michigan). At the good and intermediate sites, larger percentages of silt and clay in Montcalm loamy sand, a member of the sandy mixed frigid Alfic Haplorthods (Unpublished USDA-SCS Map, 1976; Grayling, Michigan) effect a higher relative water-holding capacity. Horizontal stratification is complex, with upper horizons formed in a sandy material underlain by a lower horizon sequum of similar or finer textures that developed from materials deposited during previous glaciation. The B' horizon bands of finer textured material occur randomly in an A' horizon of medium sand. These bands may represent ice-rafted inclusions of unsorted till-like material trapped in the sandy outwash matrix. Where they occur in the surface meter of soils, largetooth aspen site index is significantly higher than for comparable soils without texture bands (Hannah and Zahner, 1970).

Nutrient availability data indicates differences in soil fertility among the good, intermediate, and poor sites (Table 1). Gradients corresponding to the growth differential among the sites have been reported for total nitrogen (Richardson and Lund, 1975) and exchangeable calcium, magnesium, and potassium (Adams, 1978).

TABLE 1. MEAN SOIL TEXTURE AND EXCHANGEABLE CATION CONTENTS OF SOILS AT THE GOOD, INTERMEDIATE, AND POOR ASPEN SITES IN PELLSTON, MICHIGAN

Site and Soil Series		Soil Texture[a]			Exchangeable Cations[b]			Soil Strata[c]	
		% Sand	% Silt	% Clay	Ca ppm	K ppm	Mg ppm	Horizon	Depth, cm
Good-Montcalm	A	88.2	7.4	4.4	230	26	43	A[e]	0-23
Loamy Sand	B	90.2	4.7	5.1	157	20	70	B	23-38
	B'[d]	81.1	8.8	10.1	602	196	94	A"	38-66
Intermediate-Montcalm	A	91.9	4.6	3.5	212	28	41	B"	66-84
Loamy Sand	B	93.6	3.6	2.9	54	9	69	A' & B'	84-150
	B'[d]	92.9	4.3	2.8	103	24	38	C	150+
Poor-Rubicon Sand	A	96.2	1.8	2.0	79	13	23	A	0-15
	B	96.7	1.6	1.7	26	6	34	B	15-91
	C	99.0	0.8	0.2	8	3	24	C	91+

[a] Based on a minimum of three replicates (Adams 1978).

[b] Determined by N ammonium acetate extraction of five replicates by Adams (1978).

Typical pedon descriptions by the National Cooperative Soil Survey (1976). A", B", and A' and B' horizons in Montcalm loamy sands represent soil development predating most recent glacial deposition period.

[d] Bands of reddish brown sandy loam of variable thickness randomly occurring within the A' horizon.

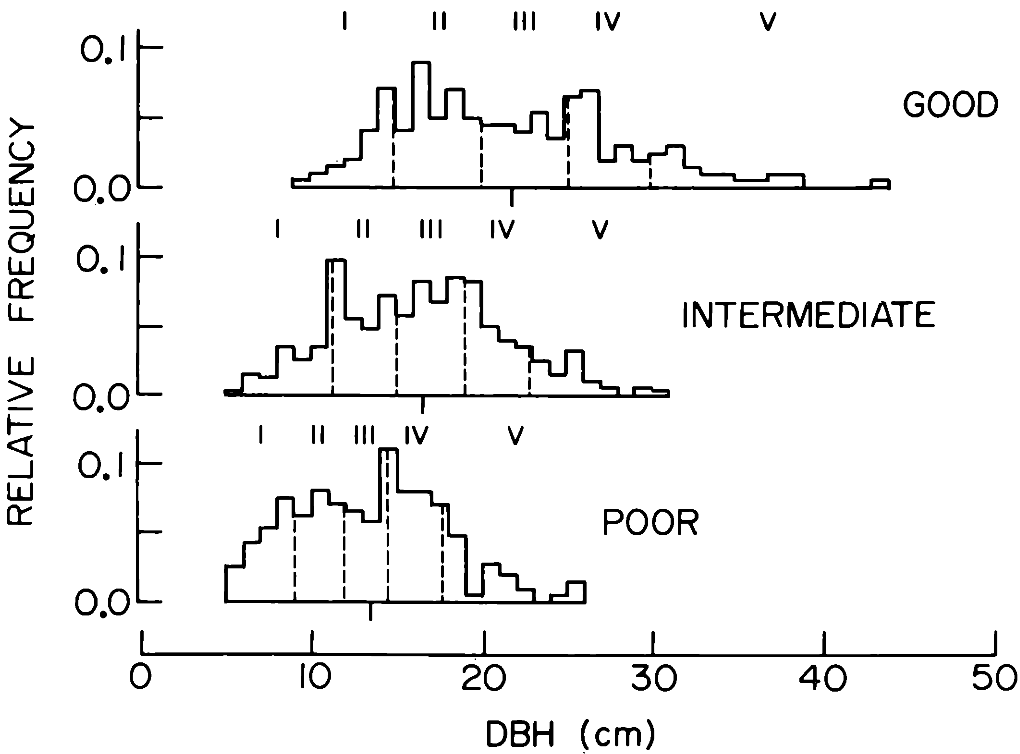
Soil horizon information for the good and intermediate soils are similiar.

METHODS

Stand Sampling

The clonal nature of aspen stands complicates attempts to measure accurately their biomass and production. Estimates based on data from one or only a few clones may be strongly biased by the influence of genetic factors on tree growth and form (Zahner and Crawford, 1965). Barnes (1966) found that the areas of clones in stands located near the study sites averaged 0.03 ha, although many were 0.04-0.08 ha in size. Procedures were designed to sample a number of clones at each site in order to distinguish the effect of both site quality and genetics on largetooth aspen growth, stand biomass, and production.

Trees selected for growth analysis and productivity determinations included both dominant and subordinate clones as well as suppressed individuals to best represent average stand conditions. In order to obtain the best precision possible for a given sample size, the trees were chosen to be well-distributed over the range of stem diameters present at each site (Demaerschalk and Kozak, 1974).



1. Relative frequencies of largetooth aspen dbh from three sites in northern lower Michigan. Dashed lines separate the dbh class intervals utilized in selection of superior, average, and inferior trees. Mean dbh at each site is indicated by a vertical line drawn below the site graph.

Dbh survey data recorded from thirty 100 m^2 quadrats systematically situated at each site provided a sample of the distribution of stem diameters. (Figure 1). The range of diameters was divided into five intervals, or dbh classes, by site. Each diameter class included 11 to 31% of the stem dbh sample. To choose the sample for a particular dbh class, the harvest area was divided into sections equal in number to the dbh class sample size. A point was randomly located within each section, and a stem within the range of the dbh class that could be easily harvested was marked for sampling. This spatial stratification was used to obtain a broader sample of the clonal genetic variability among largetooth aspen within each harvest area.

Tree Analysis Procedures

Estimates of biomass and net annual production of largetooth aspen were derived using dimension analysis techniques similar to those developed by Whittaker and Woodwell (1968, 1971). Growth rates, biomass and net production were determined for 10 to 11 trees at each site (Koerper, 1977; Koerper and Richardson, 1980).

Following dbh measurement, trees were felled at less than 1 m above the ground, and height of the tree, including its stump, was recorded. Wood growth rings on the base of the stump were counted to determine tree age.

After branch removal, the bole was cut into 1 m logs beginning at the stump, and diameter of wood at the base of each log was measured. Beginning with the first log, a 5 cm thick disc was cut from the base of every third log and at the top of the stem. These bole discs were taken to the laboratory where radial increments at five-year intervals, starting at the outer diameter of the wood, were measured to the nearest 0.1 cm. These data were analyzed along two perpendicular axes on the base. For some discs, especially those from trees of a suppressed nature, a phloroglucinol staining procedure was used (Patterson, 1959) to enhance the accuracy of measurement and counting.

A similar set of cross-sectional discs was removed from twenty-one trees at the base of every third log to determine the specific gravity of stemwood and the relationship of bark dry weight to stemwood diameter. Wood diameter along two perpendicular axes on both surfaces of each disc and disc thickness on two opposite sides were measured. The green wood volume (V) of a disc was calculated as the frustum of a right circular cone using the equation

$$V = 1/3\ pq(r_1^2 + r_2^2 + r_1 r_2)$$

where p is the value of pi, q is the mean disc thickness, r_1 is the mean radius of wood on the upper surface, and r_2 is the mean radius of wood on the lower surface of the disc. Dry weights of stemwood and stembark were measured separately for each of 130 discs. All samples were dried to a constant weight at 85°C.

The green wood volume of each log of a tree was calculated and the summed volume of the log sections of a tree was multiplied by the weighted mean of the specific gravity of stem wood from the bole disc samples of each harvested tree. The dry weight of bark of each log was calculated using a regression model of the relationship of bark weight to stem wood diameter (Koerper, 1977). Stump weights were added to bole weights to determine total aboveground stem wood and stem bark dry weights of each harvested tree.

The estimated dry wood biomass of each log five years prior to harvesting was subtracted from the estimated current stem wood biomass and the result divided by five to yield current annual wood production for each log section. Radial growth at five-year intervals was determined back to the initiation of the tree by subtracting the five-year intervals of growth (33 cm - 4 cm = 29 cm - 3 cm = 26 cm, etc.). Summing the wood production of each log and that of the stump estimated the total annual stem wood production of the tree. Current bark production was calculated by the procedure suggested by Whittaker and Woodwell (1968). For a more detailed analysis of growth procedures, see Koerper (1977) and Koerper and Richardson (1980).

Dbh measurements were taken in 1975 for all trees (stems greater than 5 cm dbh, breast height at 137 cm) in fifteen 100 m^2 (10 x 10m) quadrats systematically located at each site. The dry weights and net annual production of the components of each largetooth aspen in a quadrat were estimated using regression equations derived from combined data regression models (i.e., of two or three sites) when analysis of covariance tests indicated no significant differences among the individual site equations. Otherwise, the appropriate equation derived from data on a single site was applied (Koerper and Richardson, 1980). The means of the dry weight totals from each site (15 quadrats) were used to estimate the areal biomass and net annual production of largetooth aspen.

Data Analysis

The data for total dry weight of biomass or net annual production in g (Y) of each component were expressed as a function of stem dbh in centimeters (X). The regression equation used in the assessment of the biomass and production was $\log_e Y = a + b \log_e X$ (Draper and Smith, 1966; Dixon and Massey, 1969). The inherent bias in estimates of stand weight when converting logarithms to antilogs has been determined to be less than 2%, of minor importance when compared to variation in estimates of stand dynamics (Madgwick and Satoo, 1975) and thus a correction was not included in the final analysis. All analyses and tests were decided at the 95% confidence level. Statistical programs of the Michigan Interactive Data Analysis System (MIDAS) were utilized in these procedures (Fox and Guire, 1976).

RESULTS AND DISCUSSION

The occurrence of largetooth aspen clones on a wide range of site conditions results in large variations in site index and tree growth (Stoeckeler, 1948, 1960; Zahner and Crawford, 1965; Koerper and Richardson, 1980) and potentially in wood quality produced. Determination of the potential influence of site and genetics on wood quality (specific gravity [S.G.]) is important since pulpwood yield varies in a linear manner with S.G. (Pronin and Lassen, 1970) and a lack of variation in S.G. would mean that volume determinations are a direct measure of wood weight. If the relationship between volume and weight were essentially a constant, this would expedite field estimates of stand weight with current volume tables and aid in determining energy outputs from conversion of aspen biomass.

Specific Gravity of Stem Wood

The mean specific gravity of stem wood, weighted with respect to the wood volume of the individual disc samples, ranged from 0.357 to 0.441 at the good, intermediate and poor sites. The 95% confidence intervals of the weighted mean specific gravity of individual trees were significantly different among paired comparisons in only one instance. No significant differences ($p < 0.05$) in stemwood specific gravity were noted among the three sites. Weighted means for all disc samples taken at the good, intermediate, and poor sites were 0.383, 0.382, and 0.406, respectively. An overall weighted mean for all sites of 0.385 was used in stemwood biomass and production calculations.

Albert (1960) reported weighted mean specific gravities of 0.367, 0.379, and 0.376 for trees from good, medium, and poor site tracts near the studied stands (described by Benninghoff and Cramer, 1963) and reported no significant difference in S.G. due to site or clonal influences. Values in Albert's study based on twenty-eight trees at each site were limited to discs taken from the bottom 5.2 m of the stems, and knots were removed prior to weight and volume measurements. Inclusion of data from the upper portions of stems and the occurrence of knots in these and other samples accounted for our slightly higher values.

Few other specific gravity values have been reported for largetooth aspen. Wilde and Paul (1951) investigated two largetooth aspen stands in central Wiconsin, one 29 and the other 40 years old. The mean specific gravity at 1.52 to 1.83 m of five codominant individuals in each stand was 0.34 and 0.40, respectively. Data reported for quaking aspen (Wilde and Paul, 1951, 1959; Pronin and Lassen, 1970) showed no consistent relationship between specific gravity and stand age, nor between specific gravity and site quality. Thus, specific gravity in aspen does not vary significantly among clones or sites and can be treated as a constant.

The lack of variation in wood quality of a low density diffuse porous hardwood-like aspen was attributed by Zahner (1968) to the distribution of cell types (vessel elements, fibrous elements and wood parenchyma), and the size and thickness of cell walls to lumen. He noted that foliage production continued for most of the season on good sites and that hormone levels continued the initiation of vessels late into the season. On poor sites, summer growth was limited, few cells of any kind were produced late in the season. The uniform density of all sites (0.37 ± 0.03; Albert, 1960; 0.38 ± 0.03; Koerper, 1977) is due to a high volume of vessels occurring throughout a matrix of thin-walled fibers (2 to 4 μ) (Zahner, 1968).

The net result of these findings is that "low quality" wood is a misnomer with largetooth aspen and that volume production is a direct measure of biomass production because good sites simply produce greater quantities than poor sites.

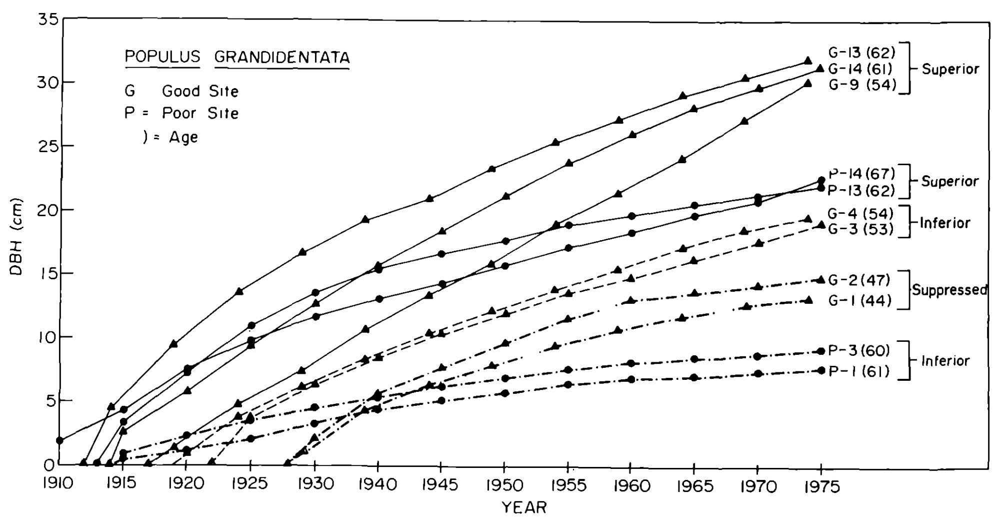
Radial Growth

The variation in height-age relationships in largetooth aspen clones was demonstrated by Zahner and Crawford (1965). They warned against the use of small measurement plots in aspen forests since the dominant trees in an area as large as one hectare might be from only one genetic group and not be representative of the growth dynamics of the entire stand.

The significant difference in radial growth reponse of superior, inferior and suppressed trees on a good site (site index of 22 m) and a poor site (site index of 14 m) is shown by the change in dbh (diameter at breast height, 1.37 m) over approximately a sixty-year period in Figure (2). Aspen are very shade intolerant (Fowells, 1965) and younger trees with slow growth often represent suppressed trees and not inferior clones. For example, the younger trees (G-1, G-2) on the good site were suppressed individuals, since other trees in the clone were of average or above size. Superior clones on the good site represented by unsuppressed trees G-13, G-14 and G-9 had double the radial increment, as indicated by the slope of the line, of inferior clones (G-4, G-3) and almost three times that of the suppressed group (G-1, G-2). Superior clones on the poor site (P-14, P-13) had more than a three-fold increase in total radial increment over the inferior clone (P-3, P-1) (Figure 2).

The rate of radial increase was highest in all trees early in their life cycle with superior clones on the good site maintaining highest radial growth rates until 1955 (40 years of age). In the first twenty years, annual radial increment averaged 0.68 cm but this decreased to 0.51 cm during the next twenty years. Superior clones on the poor site maintained their highest increment rates (0.58 cm) for the first twenty years of growth but grew less than 0.30 cm over the next twenty-year period. They averaged 0.21 cm over the 1955 to 1975 time frame. The inferior clones on the poor site did not follow the same pattern as the poor site superior clones since the growth rate from twenty to forty years increased over the first time frame (1-20 years = 0.11 cm average, 20-40 = 0.16 cm average, 40-60 = 0.09 cm average). The reason for this increase during the 20-40 year period is unclear, but may be related to the dramatic drop in stems per unit area reported for poor sites during this phase of aspen forest development (Garrett and Zahner, 1964; Fralish, 1972).

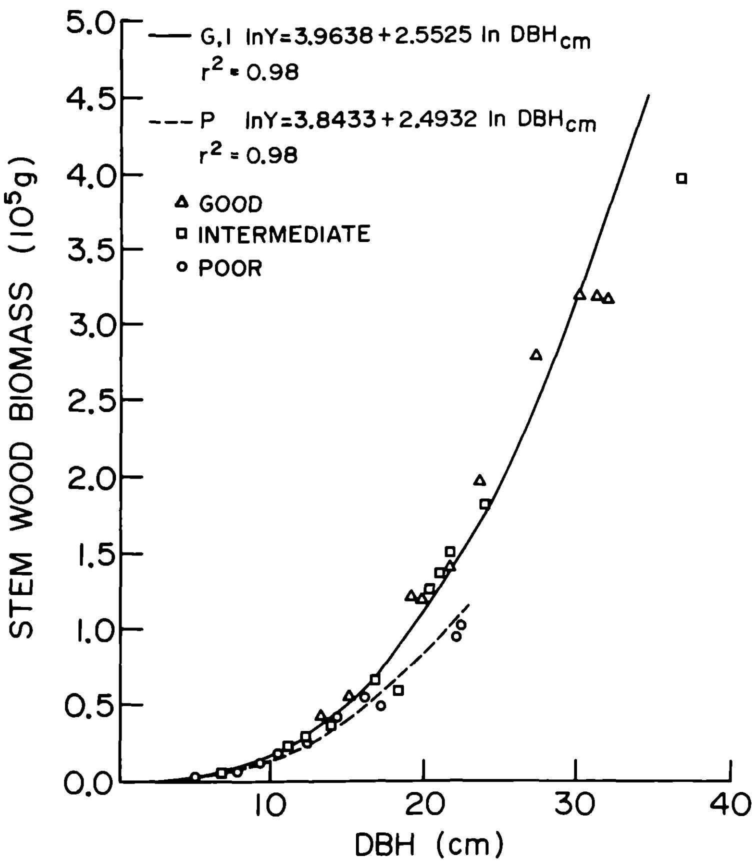
Site effects on radial growth were also significant. Superior clones on the good site had approximately 10 cm greater diameter at age 60 than superior clones on the poor site. The inferior trees on the poor site (P-3, P-1) were less than half the size of the inferior trees on the good site (G-4, G-3) (Figure 2).



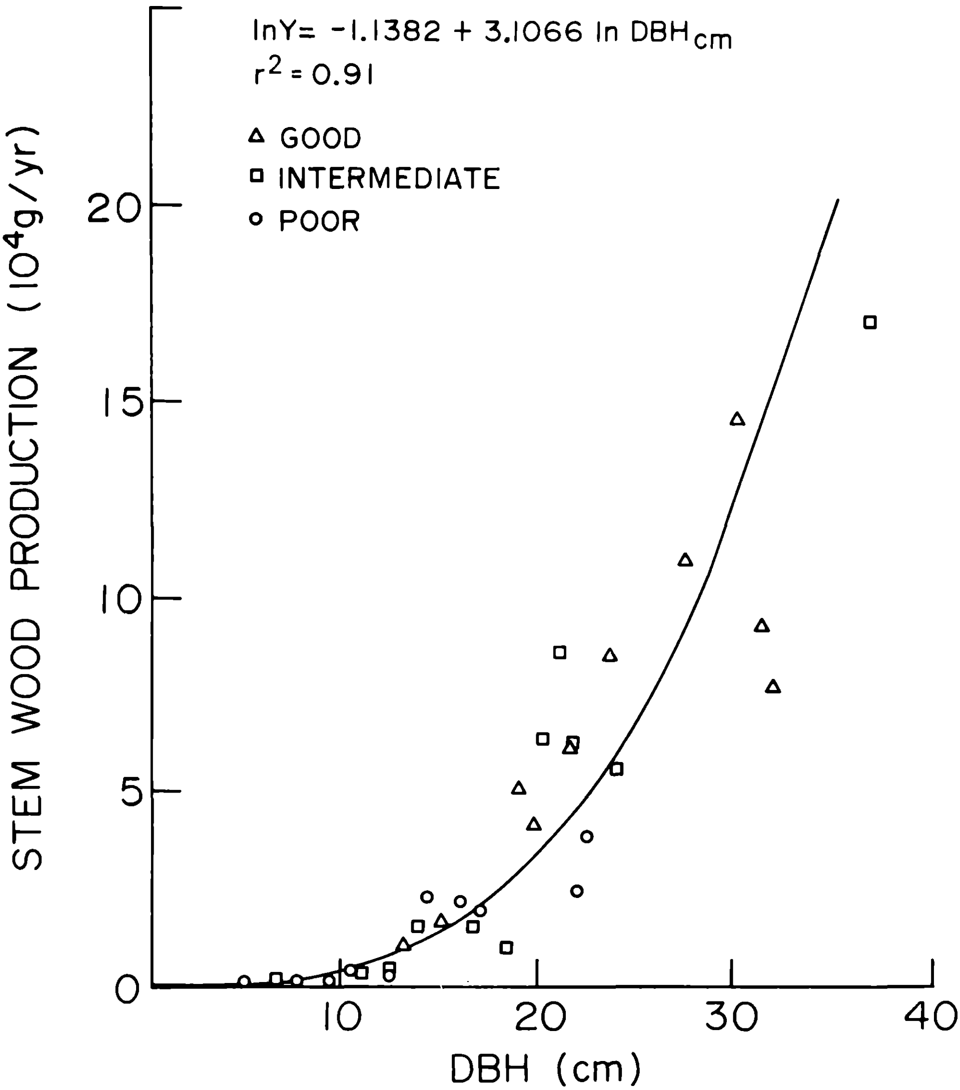
2. The change in diameter at breast height (dbh) for superior, inferior, and suppressed trees of Populus grandidentata clones on a good and poor site in northern lower Michigan over a sixty-year period.

The relationship of stemwood biomass and annual stemwood production to dbh on the three sites for all clonal groups is given by the equations for the curves shown in Figures 3 and 4. The high correlation coefficient ($r^2 = 0.98$, biomass equations; $r^2 = 0.91$, net annual production equation) and low estimate of relative error (E = 1.17, biomass, E = 1.60, production) indicates a high degree of accuracy for the fitted curves (Whittaker and Woodwell, 1971).

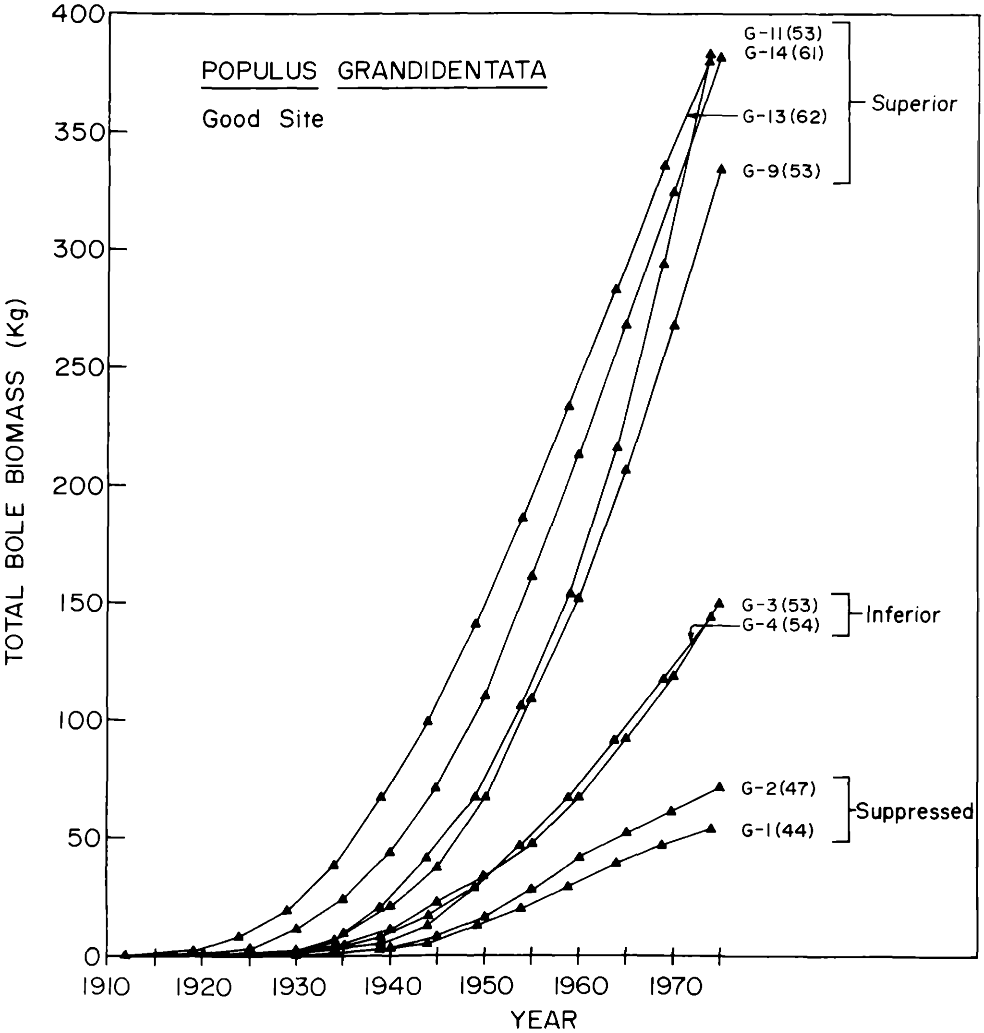
Total bole biomass for the superior clone stems on the good and poor site exceeds the inferior clones on their respective sites by a factor of 2 and 6,



3. Relation of dry weight of stemwood to dbh of largetooth aspen. Regression equations are those used for site biomass estimates (G = good; I = intermediate; and, P = poor sites).



4. Relation of annual stemwood production (dry weight) to dbh of largetooth aspen. Regression equation is for site production estimates on good, intermediate, and poor sites.

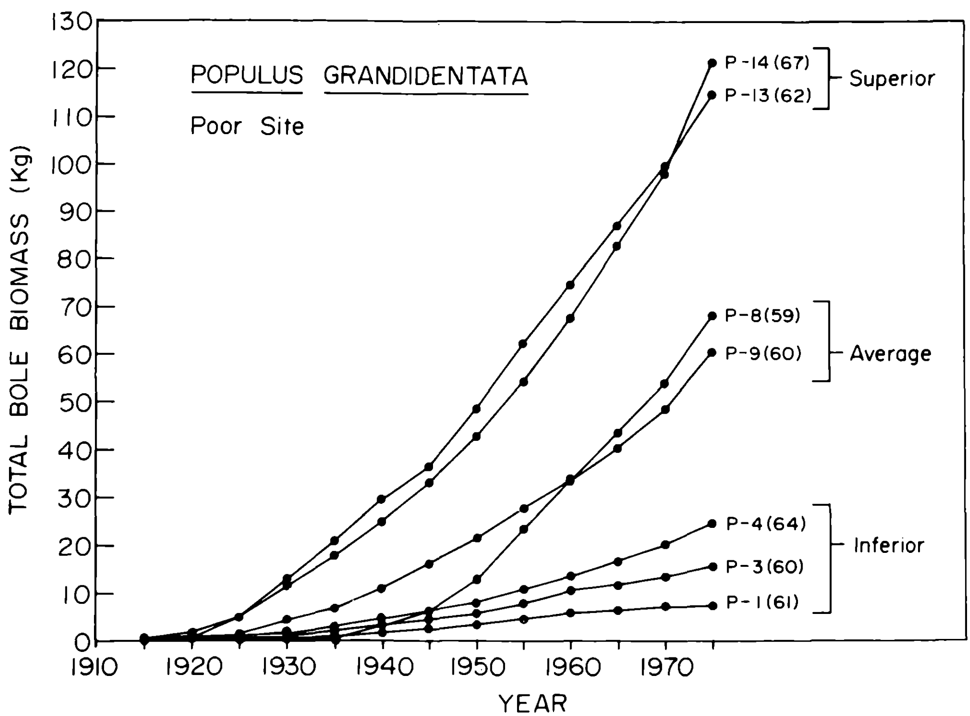


5. The amount of total bolewood biomass produced by superior, inferior and suppressed trees of largetooth aspen over a sixty-year period on a good site in northern lower Michigan.

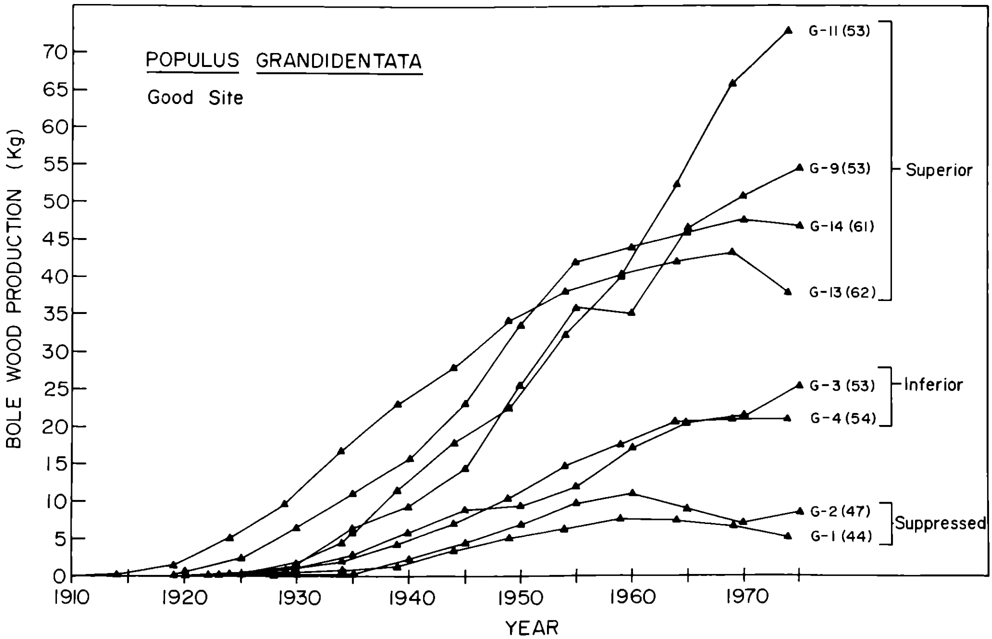
while the average clones on the poor site are three times the inferior clones of that site (Figures 5 and 6). The difference in these biomass patterns becomes significant only after twenty years of growth. This data supports the contention that the measurement of only superior clones could greatly overestimate stand production of largetooth aspen and selection of only trees from inferior clones or suppressed trees would result in an underestimate of site bole production.

The increased water holding capacity and nutrients of good site soils over poor site soils (Table 1; Roberts, unpublished data) results in 3 times and 10 times the total bole wood biomass for superior, and inferior clones on the good site versus corresponding clonal designations on the poor site (Figures 5 and 6). When the effect of edaphic conditions on total wood production is compared (Figures 2, 5, and 6), the superior clones on the poor site only out-produced the younger suppressed trees on the good site and were significantly below the inferior and superior clones on the good site when trees were compared at age 60.

The annual bole production of the superior clones on the good site over the last twenty years averaged 9 kg dry weight per tree, while the superior trees on the poor site averaged 2.4 kg/tree/year. The annual bole production for inferior and suppressed trees on the good and inferior trees on the poor site is much reduced from the good site superior trees and averaged 3.8 kg/tree/year, 1.5 kg/tree/year, and 0.4 kg/tree/year, respectively, for the last twenty years.



6. The amount of total bolewood biomass produced by superior, average, and inferior clones of largetooth aspen over a sixty-year period on a poor site in northern lower Michigan.



7. Bolewood productivity of largetooth aspen at 5-year intervals on a good site in northern lower Michigan. The individual trees harvested from clones are numbered (e.g., G-11) and their respective age at harvest given in parenthesis.

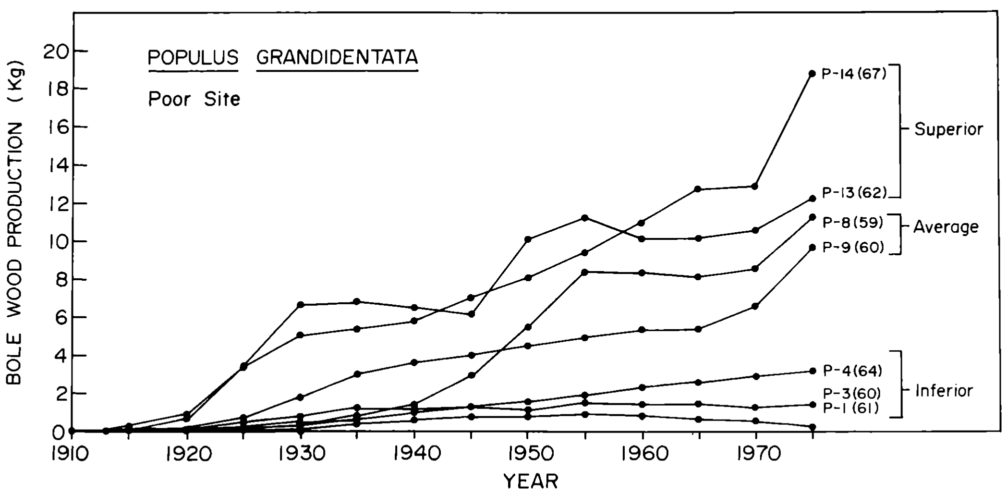
The bole wood production at the good and poor site averaged at five-year intervals over the last sixty years is given in Figures (7) and (8). The three tree groupings followed the previously demonstrated patterns (Figures 5 and 6), but individual trees of the groups displayed considerable variation in growth patterns, especially during the last 10 to 15 years. For example G-11 had the highest growth rates averaging nearly 13 kg/year over the past fifteen years. By contrast, G-13 declined in production in the last five years after reaching a growth plateau of 8 kg/year for the previous fifteen years (Figure 7). The difference in growth between the two stems (G-11 versus G-13) both from superior clones may be related to the health of individual stems, since aspen stems are susceptible to disease and often start to deteriorate after age 60 (Fowells, 1965). The inferior clones (G-3, and G-4) plateaued in growth rate by the 1970s, while the suppressed trees have declined in growth since 1960 (Figure 7). The poor site growth trends follow two basic patterns, with inferior clones reaching maximal production rates by 1940 and the better groups showing a bimodal growth increase between 1950-55 and 1970-75 (Figure 8). This corresponds to the above average rainfall reported in 1950-53 and 1970-75 (Mich. Dept. Agric., 1971, NOAA, 1971-75). Better edaphic conditions on the good site versus the poor site have resulted in a greater than three-fold increase in bole wood production rates for both superior and inferior clones at the good site over their respective counterparts at the poor sites (Figures 7 and 8).

Estimates of Aspen Tree Biomass and Net Annual Production

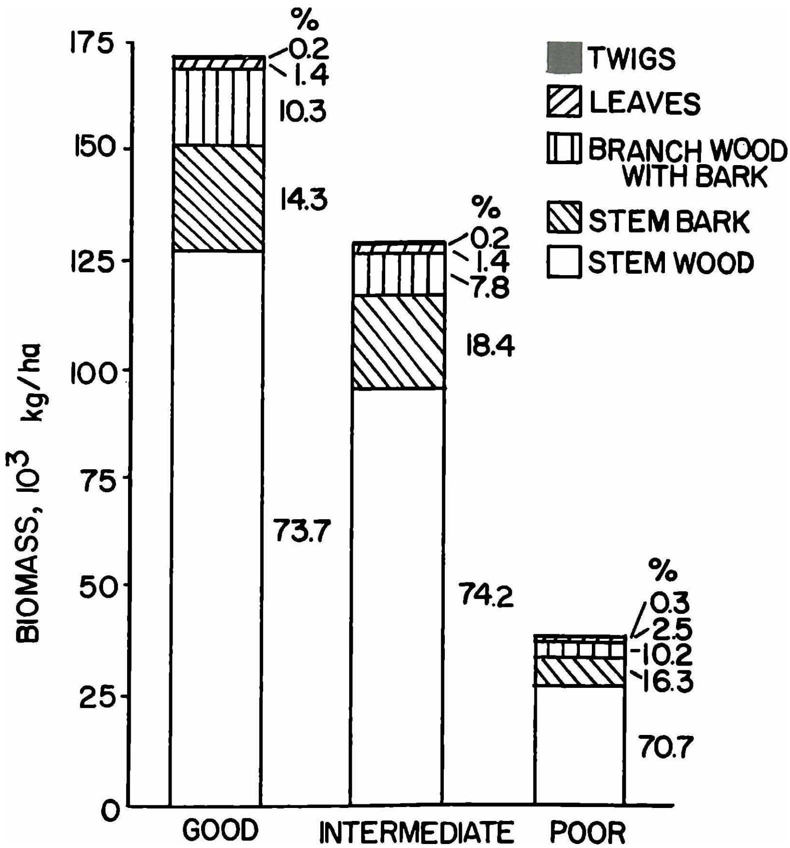
The percentage of the total aboveground biomass in each component of the trees is depicted in Figure 9. At least 87.0% of the total tree biomass was contributed by stem weight (bark + wood) at all sites. Stem wood percentages ranged from 70.7 to 74.2% and stem bark from 14.3 to 16.4%. Site differences in canopy component percentages of total aboveground biomass were slightly greater. Leaves were only 1.4% of total biomass at the good and intermediate sites, where as the poor site percentage was almost twice as large. Among the sites, percentages of total biomass in canopy components were of the order: poor (13.0%), good (11.9%), and intermediate (9.4%). Total aboveground biomass on the good site was 4.5 and 1.3 times greater than biomass at the poor and intermediate sites, respectively.

Stem weight increment accounted for 46.4% of all aboveground tree component production at the poor site and over 52.8% at the good and intermediate sites (Figure 10). Stem wood production comprised from 37.0 to 44.4% of the total production, while stem bark percentages ranged from 8.8 to 10.0%. Net annual production per unit leaf weight was about 33% less for the poor site aspen compared to the good site aspen. Total tree production at the good and intermediate sites was 3.7 and 2.5 times greater than production at the poor site.

The biomass accumulation ratios (the ratio of aboveground biomass to net annual production) among aspen stands range from 13.2 at the poor site to 17.7 at the intermediate size, with a mean of 15.5. The biomass accumulation ratio for a P. tremula forest studied by Remezov et al. (1959) was 16.8. For trembling aspen ranging in age from 6 to 41 yr (mean of 16.7 yr) in three adjacent forest types in Wisconsin (Zavitkovski, 1974), the ratio was 11.6 (Crow, 1978).



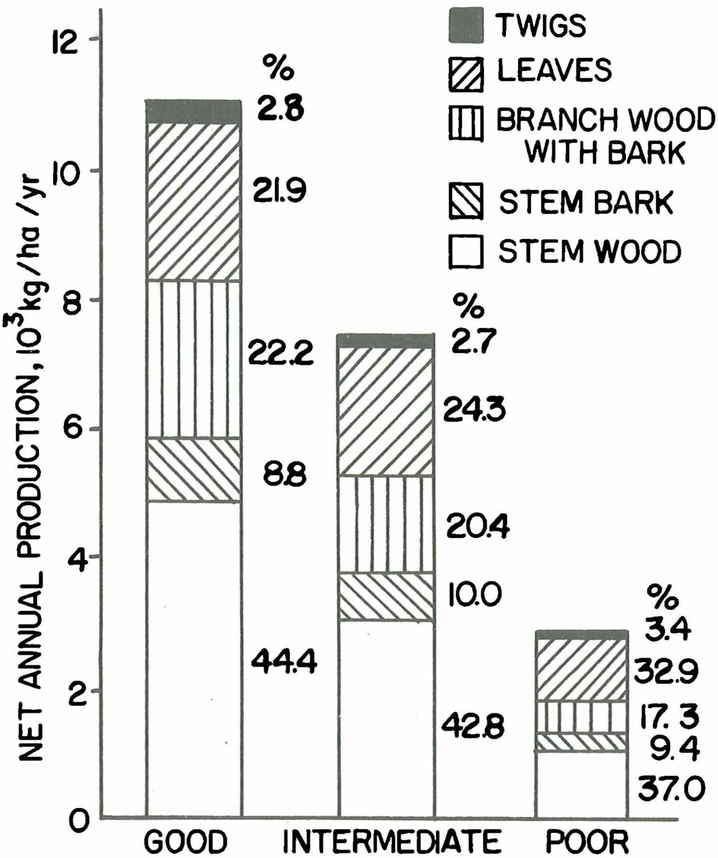
8. Bolewood productivity of largetooth aspen at 5-year intervals on a poor site in northern lower Michigan. The individual trees harvested from clones are numbered (e.g., P-13) and their respective age at harvest given in parenthesis.



9. Distribution of aboveground biomass among tree components of largetooth aspen on three soil classes in northern lower Michigan. The average total aboveground tree biomass is given in percentages. Total stand biomass is shown on the ordinate.

Estimates of areal largetooth aboveground biomass and net annual production at the good, intermediate, and poor sites are shown on the ordinate axis of Figures 9 and 10. Since aspen biomass does not represent the entire tree strata of these forests (i.e., 82, 79 and 48% of the basal area of the good, intermediate, and poor sites, respectively) interpretation and comparison of the data must be qualified in terms of their contribution to total stand dynamics.

Crow (1978) estimated the aboveground biomass of aspen with a basal area of 9.48 m^{-2} ha^{-1} (53% of the total stand basal area) on a Wisconsin site to be 45059 kg ha^{-1}; slightly higher than our 38530 kg ha^{-1} poor site value for largetooth aspen with a basal area of 11.38 m^{-2} ha^{-1} (48.3% of the total stand basal area). However, the density of aspen on loamy till soils in Wisconsin was nearly three times that of largetooth aspen at the poor site (1972 to 633 trees ha^{-1}).



10. Distribution of aboveground net annual production among tree components of largetooth aspen on three soil classes in northern lower Michigan. The average total abovegound tree production is given in percentages. Net annual production for the stand is shown on the ordinate.

The range of biomass estimates for our study sites is very similar to the 34680-175660 kg ha^{-1} range reported by Peterson et al. (1970) for trembling aspen clones in Alberta with individual stems 66 to 89 years old.

The estimated aboveground net production of largetooth aspen in the study areas was 11038, 7259, and 2925 kg ha^{-1} yr^{-1} at the good, intermediate, and poor sites, respectively. Crow (1978) reported a total net production of 8316 kg ha^{-1} yr^{-1} for a Wisconsin aspen forest type where trembling aspen made up 53% of the total basal area and 51% of the total net production. Published aboveground production values for trees in mature (41 to 52 year old) Populus forests worldwide include 9000 kg ha^{-1} yr^{-1} for a trembling aspen stand in Minnesota (Bray and Dudkiewicz, 1963), 2840 kg ha^{-1} yr^{-1} for a trembling aspen forest in Ontario (Pollard, 1972), and 15312 kg ha^{-1} for a P. tremula forest in the U.S.S.R. (Remezov et al., 1959).

CONCLUSIONS

Largetooth aspen is a low density diffuse porous hardwood which develops in clones of genotypically identical stems. The effects of site conditions and clonal variation on wood quality (specific gravity) and quantity of wood production (biomass and net production) are as follows:

1. No significant variation in specific gravity exists in largetooth aspen wood due to site conditions, effects, or clonal variation (S.G = 0.38 ± 0.03).

2. Aspen wood weight can be directly determined from wood volume measurements.

3. Superior clones have twice the radial growth of inferior clones on the good sites. Poor site superior clone stem growth exceeded inferior clone growth by a factor of three.

4. A representative sample of clonal variation on a site must be measured to estimate wood production accurately.

5. Radial growth was highest in all clones early in their life cycle, but superior clones continued high growth for nearly forty years on the good site as compared to twenty years on the poor site.

6. Bole production for superior trees on the good site and poor site averaged 9 kg/tree/year and 2.4 kg/tree/year, respectively, over the last twenty years.

7. Bole production for inferior and suppressed trees on good and inferior trees on the poor sites averaged 3.8 kg/tree/year, 1.5 kg/tree/year, and 0.4 kg/tree/year, respectively, over the last twenty years.

8. Eighty-seven percent of the total tree biomass was contributed by stem weight (bark + wood) on all sites.

9. Leaf weight was 1.4% of total biomass at the good and intermediate sites but was 2.5% at the poor site.

10. Net annual production per unit leaf weight was 33% less for the poor site aspen compared to the good site.

11. Total largetooth aspen tree production at the good and intermediate sites was 3.7 and 2.5 times greater than at the poor site.

12. The selection of superior aspen clones for stand regeneration could double productivity on all sites.

13. Predictive models were developed which can accurately predict biomass and net production from dbh over a range of site conditions and clonal variation (Koerper and Richardson, 1980).

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