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Biomass and production of an aspen – mixed hardwood – spodosol ecosystem in northern Wisconsin[1]

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Total biomass of an aspen – mixed hardwood – spodosol ecosystem in northern Wisconsin, U.S.A., was 197 t/ha and net primary production was 11.5 t/ha per year. *Populus tremuloides* Michx. accounted for 60% of the total biomass and 56% of the annual production and *Acer saccharum* Marsh. accounted for 25% of the biomass and 28% of the annual production. For all species combined, bole wood was 63% of the total biomass and bole bark was 12%. Bole wood was 33% and bole bark was 7% of the total production. Although crowns accounted for only 15% of the total biomass, they were responsible for 49% of net annual production. Using allometric equations from the literature, root biomass and production were calculated as being approximately 10% of the total biomass and of the annual production. The average rate of total production per unit leaf tissue was 5.7 g production/g leaf tissue for *P. tremuloides* and 3.7 g/g for *A. saccharum*.

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La biomasse totale d'un peuplement de tremble, mélangé feuillu, dans un écosystème spodosol, situé dans la partie nord du Wisconsin, E.U., était de 197 t/ha et la production primaire nette était de 11.5 t/ha par an. Le *Populus tremuloides* Michx. compte pour 60% de la biomasse totale et 56% de la production annuelle et *Acer saccharum* Marsh. compte pour 25% de la biomasse et 28% de la production annuelle. Pour toutes les essences combinées le bois de la tige était 63% de la biomasse totale et l'écorce 12% alors que le bois de la tige était 33% et l'écore 7% de la production totale. Pendant que les houppiers comptaient pour seulement 15% de la biomasse totale, ils étaient responsables pour 49% de la production annuelle nette. Par les équations allométriques, la biomasse des racines et la production ont été estimées à 10% de la biomasse totale et de la production annuelle. Le rapport moyen de la production totale par unité de feuillage était de 5.7 g de production/g d'unité de feuillage pour *P. tremuloides* et 3.7 g/g pour *A. saccharum*.

[Traduit par le journal]

Introduction

Aspen (*Populus tremuloides* Michx. and *P. grandidentata* Michx.) became a major component of forests in the Great Lakes Region following logging and forest fires during the start of the 20th century and today represents one-third of Wisconsin's 1.9×10^6 ha of commercial forest (Spencer and Thorne 1972). Aspen grows on a variety of sites; the most productive stands also contain an abundance of northern hardwood species (Kitfredge 1938).

Biomass of aspen stands in the Great Lakes Region ranges from 7 to 208 t/ha (Bray and Dudkiewicz 1963; James and Smith 1977; Crow 1978; Alban *et al.* 1978) and net annual production ranges from less than 4 t/ha on poor sites to 10 t/ha on a good site (Bray and Dudkiewicz 1963; James and Smith 1977; Crow 1978). These wide ranges are probably due to differences in species composition, site quality, and age of the stands studied. The aim of this study is not only to present additional data regarding biomass and production of aspen in the Great Lakes Region, but also to explore the differences in biomass and production between trembling aspen and sugar maple (*Acer saccharum* Marsh.) in an aspen – mixed hardwood stand in northern Wisconsin, U.S.A.

Methods

Study area

A study area was selected in the Northern Highlands State Forest (45°50′ N, 89°40′ W; T40N, R7E, Sec. 19) (Fig. 1). The site is level and contains acid glacial outwash of late Wisconsin age. The overstory vegetation comprises trembling aspen with minor amounts of largetooth aspen (*Populus grandidentata* Michx.), sugar maple, red maple (*A. rubrum* L.), northern red oak (*Quercus borealis* Michx.), and white birch (*Betula papyrifera* Marsh.). The understory is predominantly sugar maple with some red maple, shrubs, and herbaceous plants. The shrub cover is mainly leatherwood (*Dirca palustris* L.) and beaked hazel (*Corylus cornuta* Marsh.). Herba-

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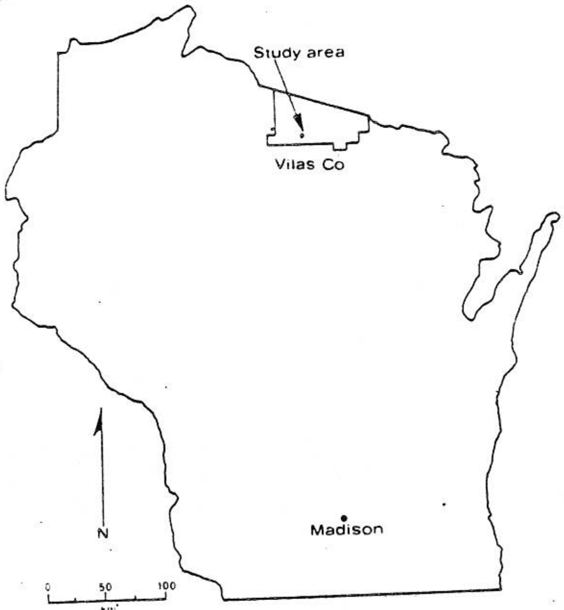

FIG. 1. Location of study area.

ceous plants include bunchberry (*Cornus canadensis* L.), Solomon's seal (*Polygonatum biflorum* Ell.), false Solomon's seal (*Smilacina racemosa* L.), Indian cucumber (*Medeola virginiana* L.), wild lily-of-the-valley (*Maianthemum canadense* Desf.), two sedges (*Carex pennsylvanica* Lam., *C. pedunculata* Muhl.), and one grass (*Oryzopsis asperifolia* Michx.). The aspen trees are 63 years old and the sugar maples are 39 to 60 years old. Site index of the aspen is 21.5 m at 50 years. The stand became established after logging and possibly fire around 1915.

The dominant soil on the site is the Pence sandy loam (Typic Fragiorthod, sandy, mixed, frigid) which is classified as an Orthic Humo-ferric Podzol in the Canadian Soil Taxonomy (Canada Soil Survey Committee 1978). A weak fragipan defines the effective rooting depth and is uniformly found between 30 and 35 cm depth. The forest floor is a mull.

The climate of the area is cool continental; mean monthly temperatures range from −11°C in January to 19°C in July, and mean annual precipitation averages 80 cm. More than half of the precipitation falls during the growing season.

Biomass and production

The diameter and species of each tree (>5 cm diameter at 1.3 m, i.e., diameter at breast height (dbh)) in three 0.04-ha permanent plots were tallied (Table 1). These data were used for selecting sample trees for dimension analysis and preparation of regression equations relating biomass and production to dbh. The diameter range of sugar maple was divided into nine size classes, each size class representing a range of 2 cm in diameter. Similarly, the diameter range of trembling aspen was divided into nine size classes, each size class representing a range of 3 cm in diameter. In late summer and before leaves had turned color, one sample tree of each species was randomly chosen from each size class with the stipulation that the sample tree be representative of other trees within that size class with regard to form, crown width, and external evidence of disease, such as conks, cankers, etc. The trembling aspen sample trees ranged in diameter from 14.7 to 39.7 cm and the sugar maple sample trees ranged in diameter from 7.5 to 23.7 cm. These diameters span the range of diameter classes. Aspen trees were chosen from different clones which were delineated on the basis of phenological characteristics (Barnes 1969).

Sample trees were submitted to dimension analysis (Whittaker and Marks 1975). Each tree was felled and the bole cut into 2 m lengths. The stump was cut at ground level and included with the lowermost section. Each section was weighed and a disk cut from the stump and the top of each section for determination of moisture content, bark:wood ratios, specific gravity, and radial growth. All samples were oven-dried at 60°C. The dry weights of the bark and wood for each section were calculated from the bark:wood ratios, the field weights, and the moisture determinations. These weights were summed for the entire tree and related to dbh in double-logarithmic regression equations:

$$[1] \quad \log_{10} y = a + b \log_{10}(\text{dbh})$$

Bole wood production was estimated by measurements of the last 5 years' radial growth along the longest, shortest, and intermediate radii on each disk. The volume of last 5 years' growth of each section was determined from the average of these measurements and the length of each section using Smalian's formula (Avery 1975). This was multiplied by wood specific gravity for the last 5 years' growth (dry weight/dry volume) to give the weight of last 5 years' growth. One-fifth of this weight (i.e., the weight of mean annual growth) was summed for all sections and related to dbh in double-logarithmic regressions. For each section, bark production was estimated using the following assumed relationship (Whittaker and Marks 1975):

$$[2] \quad \frac{\text{Annual bark production}}{\text{Bark biomass}} = \frac{\text{Annual wood production}}{\text{Wood biomass}}$$

The results were summed for the entire bole and total tree bark production was regressed against dbh (Eq. 1).

The method of branch sampling follows that recommended by Whittaker and Marks (1975). The diameter of each branch was measured, and five branches, ranging from smallest to largest and distributed throughout the crown, were sampled. All leaves and current twigs (twig growth since last terminal bud scar) were clipped from these branches and brought to the laboratory for drying. The weights of the sample branches were determined in the field and subsamples were taken for moisture determination. From the five sample branches of each tree, dry weights of leaves, twigs, and branches were related to branch diameter in double-logarithmic regressions. These equations were used to estimate branch, leaf, and twig weights for other branches on the same tree. The sum totals of estimated leaf, twig, and branch weights were regressed against dbh as above. Annual production of branch tissue was calculated using the ages of the five sample branches and the method of Whittaker (1965). The calculated production of each branch was summed for the entire tree and total estimated branch production regressed against dbh as above. Dead branch weight was also regressed against dbh in double-logarithmic regressions.

TABLE 1. Composition of the tree stratum of the aspen – mixed hardwood stand as a function of dbh class

	Basal area (m^2/ha)					Live stems/ha				
Species	5–15 cm	15.1–25 cm	25.1–35 cm	35.1–45 cm	Total	5–15 cm	15.1–25 cm	25.1–35 cm	35.1–45 cm	Total
Populus tremuloides	0.3	4.2	11.9	1.9	18.3	25	117	167	17	326
P. grandidentata	0.8	0.9	1.5	0	3.2	75	25	25	0	125
Acer saccharum	4.0	2.0	0	0	6.0	633	83	0	0	716
A. rubrum	0.4	1.1	0	0	1.5	50	42	0	0	92
Quercus borealis	0	0.2	0.7	0	0.9	0	8	8	0	16
Betula papyrifera	0.3	1.0	0.4	0	1.7	25	33	8	0	66
All species	5.8	9.4	14.5	1.9	31.6	808	308	208	17	1341

Root biomass regressions were taken from data in the literature for aspen (Young *et al.* 1964) and for maples (Whittaker *et al.* 1974). Root production for each tree was estimated using the assumed relationship (Whittaker and Marks 1975):

$$[3] \quad \frac{\text{Root production}}{\text{Root biomass}} = \frac{\text{Aboveground production}}{\text{Aboveground biomass}}$$

Estimated root production for each tree was regressed against dbh as above. Root biomass and production are less accurately estimated than biomass and production of other components because of the assumptions implicit in Eq. 3 and the assumption that regressions taken from the literature are applicable to the present site.

The regressions for trembling aspen were used to estimate the biomass and production of the minor amount of largetooth aspen on the site. Similarly, the sugar maple regressions were used to estimate biomass and production of the red maple. While the use of these regressions in this manner for largetooth aspen and red maple introduces some error into the results, this error is probably minor given the small representation of largetooth aspen and red maple in this stand (Table 1). These four species represent approximately 92% of the basal area and 94% of the stems on the site (Table 1).

A possible source of error in dimension analysis is caused by the logarithmic transformation (Beauchamp and Olson 1973). Calculation of correction factors according to the method of Beauchamp and Olson (1973) for the poorest regressions (lowest r value) did not improve estimates by more than 2 or 3%. Thus, correction factors were not used.

An additional source of error would be due to interpolation of the allometric regression equations between data points determined by subsampling. This is a limitation of dimension analysis (Whittaker and Marks 1975).

Results

Biomass and net annual production

Aboveground biomass of the trees was 177 t/ha; the aboveground production was 10.5 t/ha per year (Table 2). These figures are in the upper range of the values for upland cool temperature forests (Whittaker and Marks 1975) and show the highly productive nature of this site. The biomass figures compare favorably with those reported by Alban *et al.* (1978) for a similar site in Minnesota. The net primary production is somewhat higher than other values reported for similar stands in northern Wisconsin (Crow 1978), and is probably due to differences in soil fertility and stand age compared with the sites of Crow (1978).

Aboveground biomass of the stand and of the aspen was distributed as follows: bole wood > bole bark > live branches > dead branches > leaves > twigs. Approximately 75% of the total biomass was concentrated in the boles (wood + bark). Bole bark accounted for 12% of the total biomass, which is comparable to that of oak but greater than in most other cool temperate forests (approximately 7%; Whittaker and Marks 1975). Results reported by Alban *et al.* (1978) and Crow (1978) agree with the aboveground aspen biomass results reported here. In contrast to its distribution in aspen, biomass of the maples was distributed bole wood > live branches > bole bark > dead branches > leaves > twigs.

Aspen root biomass (both species) was estimated as 10.8 t/ha or 10% of the total aspen biomass, largely a result of the use of regressions by Young *et al.* (1964). Maple root biomass (both species) was estimated as 9.4 t/ha, or 16% of the total maple biomass, largely a result of the use of regressions by Whittaker *et al.* (1974). Total stand root biomass was therefore estimated as 20.2 t/ha, or 10.3% of total stand biomass. This is a conservative estimate compared with other values reported in the literature. Rodin and Bazilevich (1965) report two stands of *P. tremula* whose root biomasses were 16 and 20% of total stand biomass; Alban *et al.* (1978) report a root biomass of 19% of total stand biomass for a Minnesota *P. tremuloides* stand. However, despite this low root biomass estimate, estimated total stand biomass (197 t/ha) was greater than for most other deciduous forests (Art and Marks 1971) and nearly equal to the 208 t/ha reported by Alban *et al.* (1978).

Net annual aboveground production of dry matter by

TABLE 2. Aboveground biomass and net annual production, aspen – mixed hardwood stand

Species	Biomass (kg/ha)						Total aboveground biomass (t/ha)	% of aboveground biomass
	Bole wood	Bole bark	Branch	Leaf	Current twig	Dead branch		
Acer saccharum	26 000	3 700	7 900	870	43	970	39	22.0
A. rubrum	7 000	950	2 200	220	13	120	11	6.2
Populus tremuloides	78 000	17 000	11 000	1 050	230	2 040	109	61.6
P. grandidentata	13 000	2 800	1 600	220	38	370	18	10.2
Total[a]	124 000	24 000	23 000	2 360	320	3 500	177	100.0
% of aboveground biomass	70.0	13.6	13.0	1.3	0.2	2.0	100.1	
	Net annual production (kg/ha per year)						**Total aboveground production (t/ha per year)**	**% of aboveground production**
	Bole wood	Bole bark	Branch	Leaf	Current twig	Dead branch		
Acer saccharum	710	100	920	870	43	—	2.7	26.3
A. rubrum	230	31	270	220	13	—	0.76	7.4
Populus tremuloides	2 200	530	1 500	1 050	230	—	5.5	53.6
P. grandidentata	680	140	270	220	38	—	1.3	12.7
Total[a]	3 800	800	3 000	2 360	320	—	10.3	100.0
% of aboveground production	36.9	7.8	29.1	23.0	3.1	—	99.9	

[a]Due to rounding off to two significant figures, sums of individual numbers may not equal the totals shown.

the stand as a whole and by both aspen and maple was distributed bole wood > branches > leaves > bole bark > twigs. Although crowns (branches + leaves + twigs + dead branches) represented only 15% of the total biomass, their live components (branches + leaves + twigs) represented 49% of the next primary production. Production in the crowns was apportioned about equally between branches and leaves.

Net root production was estimated as 1.2 t/ha per year, or 11% of total stand net annual production. This value was within the range of 1 to 3 t/ha per year given by Bray (1963) for *Pinus sylvestris*, *Picea abies*, and *Fagus sylvatica*. However, a more recent estimate of root production in forests indicates net root production values as high as 9 t/ha per year for a *Liriodendron* forest (Harris *et al.* 1977). No studies of aspen root production were found in the literature. The figure reported here is probably a conservative estimate. However, even with this low root production estimate, total stand net annual production was 11.5 t/ha, which was greater than most other cool temperate deciduous forests (Art and Marks 1971).

Allometric regressions

All of the regression equations, except those for dead branches had r values significant at $P < 0.05$ and low errors of estimate, indicating good predictability (Table 3). The error of estimate of a logarithmic regression is the antilog of the standard error and is a value by which y should be multiplied or divided to give an expected error range (Whittaker and Marks 1975). For example, an error of estimate of 1.2 means that the standard error range for y is between $y/1.2$ and $1.2y$. Errors of estimate reported here were lowest for bole wood biomass and highest for branch production. They were also low compared with other values reported in the literature (summarized in Whittaker and Marks 1975). In addition, low r values do not always indicate greater error in the regression. For example, the regressions for aspen bole wood and bole bark production had lower r values than other production regressions, but comparable errors of estimate.

The slopes of the corresponding regressions for each species were tested for homogeneity by a t-test (Steel and Torrie 1960, p. 173). All equations were found to be significantly different ($P < 0.05$) between the two species. In general, the slopes of the maple regressions were greater than the slopes of the aspen regressions, but the intercepts of the aspen regressions were greater than those of the maple regressions (Figs. 2 and 3).

Discussion

The ratio of total production to leaf biomass (i.e., photosynthetic tissue) is 5.7 g/g for dominant and codominant trembling aspen, 4.2 g/g for codominant

TABLE 3. Allometric equations of the form $\log_{10} Y = a + b \log_{10} X$, where Y = biomass or production (kilograms) and X = dbh (centimetres). All regressions are significant at $P < 0.05$. E is the error of estimate and is the antilog of the standard error of the regression

Component	Biomass				Production			
	a	b	r	E	a	b	r	E
Bole wood								
Maple	−1.136	2.563	0.995	1.11	−3.629	3.344	0.970	1.45
Aspen	−0.766	2.199	0.993	1.10	−0.816	1.164	0.739	1.47
Bole bark								
Maple	−1.661	2.285	0.992	1.12	−4.280	3.181	0.976	1.37
Aspen	−1.360	2.146	0.977	1.19	−1.120	0.946	0.689	1.44
Crown								
Maple	−1.467	2.470	0.965	1.32	−2.179	2.456	0.973	1.29
Aspen	−1.958	2.536	0.949	1.36	−1.664	1.828	0.901	1.38
Branches								
Maple	−1.581	2.507	0.956	1.37	−2.831	2.784	0.935	1.59
Aspen	−2.420	2.768	0.947	1.41	−2.134	1.965	0.855	1.55
Leaves								
Maple	−2.222	2.224	0.935	1.41	−2.222	2.224	0.935	1.41
Aspen	−1.615	1.492	0.870	1.36	−1.615	1.492	0.870	1.36
Total aboveground								
Maple	−0.900	2.520	0.995	1.11	−2.265	2.678	0.986	1.22
Aspen	−0.685	2.249	0.994	1.09	−0.772	1.418	0.868	1.34

sugar maple, and 3.7 g/g for intermediate and overtopped sugar maple. The ratio for aspen is complicated by the photosynthetic ability of aspen bark, but photosynthesis of aspen bark constitutes only 1 to 2% of total tree photosynthesis (Foote 1975). The difference in average rate of production of the two species may be due to differences in canopy position and photosynthetic response to different light intensities. The maples in this stand are generally intermediate or overtopped and thus receive less light than the codominant aspen. Horn (1971) has suggested that early successional species such as aspen have higher rates of photosynthesis at high light intensities than late successional species such as sugar maple on the same site.

The differences between the regression equations of trembling aspen and sugar maple may be due to differences between the two species in canopy position, tolerance to shade, and successional status (i.e., early versus late successional). Differences among genera in the slopes and intercepts of allometric regressions have been noted by several authors (Bunce 1968; Whittaker and Marks 1975).

For a tree of a given dbh, maple crowns weigh more than aspen crowns (Fig. 2). The reason for this is not known, but a few hypotheses are possible. This may be due to self-pruning by aspen and retention of branches by maple, and the greater specific gravity of maple wood than aspen wood. This may also be the reason that branch biomass ranks third among all tree components for aspen but second for maple. The self-pruning of lower, shaded branches by aspen could be a consequence of its low tolerance to shade. Conversely, maples may retain branches which are shaded because of their ability to maintain positive net photosynthesis at low light intensities. Horn (1971) has suggested that greater wood specific gravity is necessary to support larger crowns in trees such as sugar maples. In addition, Wilson and Archer (1979) have suggested that increased branch diameter and formation of reaction wood are also mechanisms for supporting large crowns.

The difference between the bole wood regressions are slight and are probably due to differences in tree form and wood specific gravity. The bark of aspen trees is heavier than the bark of maples, as shown by the bark biomass regressions. This difference may be the result of greater thickness of aspen bark compared with maple bark, especially near the base of the bole. The mean thickness of aspen bark (0.61 cm) was significantly greater ($P < 0.01$) than the mean thickness of maple bark (0.35 cm). Differences between the species in bark specific gravity (not measured) may also contribute to differences in bark biomass.

Total aboveground biomass of maples is greater than total aboveground biomass of aspen for any given diameter. The difference increases with increasing diameter owing to differences in wood and crown biomass.

Differences between the two species are more apparent in the net annual production equations (Fig. 3). The maples show a wider range in production than the

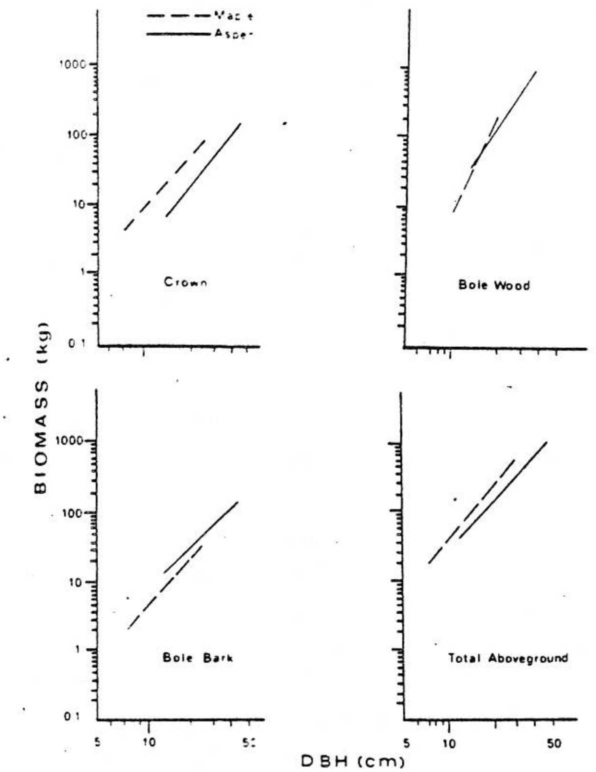

FIG. 2. Relationship between biomass and dbh for sugar maple and trembling aspen.

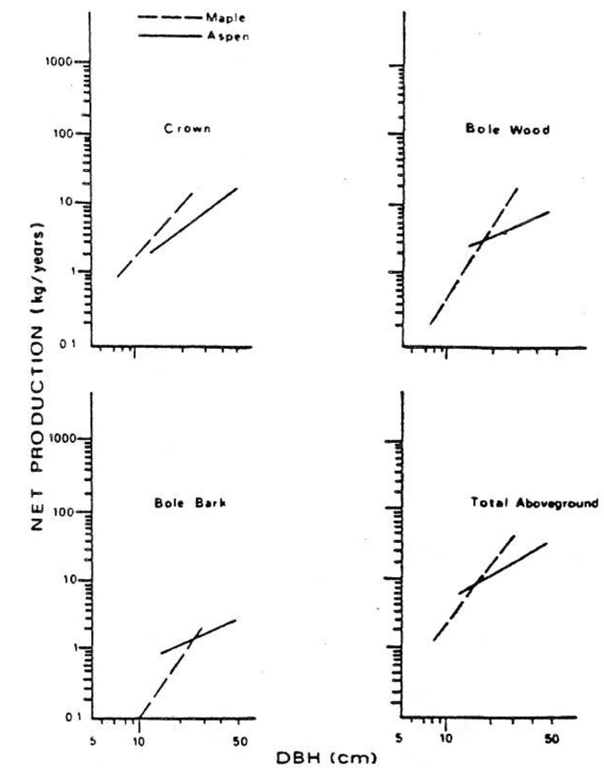

FIG. 3. Relationship between net annual production and dbh for sugar maple and trembling aspen.

aspen. This difference is due to the fact that all aspen receive roughly equal amounts of light while the maples receive various amounts of light depending on canopy position.

At smaller diameters, production of all components by aspen is greater than production by maples. However, at larger diameters, production by aspen is less than production by maples. These changes in relationship of production to dbh occur somewhere between 18 and 25 cm for wood, bark, and total aboveground production, but the change occurs at a somewhat smaller diameter for crown production. The present site is judged to be fully occupied and most of the crown production is probably expansion into gaps left in the canopy by dead or dying trees as well as annual replacement of deciduous leaves and height growth. The relationships between the leaf biomass (production) regressions, although not shown, are similar to those for the crown regressions. It is significant that the minimum diameter of codominant maples in this stand is approximately 18 cm. Thus, once the maples attain a codominant canopy possition, their rate of production is greater than the codominant aspen. These codominant aspen, being greater than 60 years old, are nearing the end of their lives and their growth is beginning to slow. More importantly, the sugar maple maintains a higher rate of production in spite of lower production per unit leaf weight because of a greater leaf biomass. Using the regression for total production, production of a 25-cm sugar maple is estimated to be 33.9 kg/year, while that of a 25-cm aspen is 17.6 kg/year. Production by the maple is 1.9 times higher than production by the aspen. However, from above, the rate of production per unit leaf weight of this codominant maple is $5.7/4.2 = 1.4$ times lower than that of the aspen. Therefore, the maple must have $1.9 \times 1.4 = 2.7$ times as much leaf biomass as the aspen. From the leaf biomass regressions, the leaf weight of the aspen would be 3.0 kg while the leaf weight of the maple would be 7.7 kg, or 2.6 times greater than that of the aspen. Thus, considerations of photosynthetic efficiency and total production closely predict the leaf biomass requirements of a tree.

The pattern of recovery after disturbance in northern hardwoods is characterized by initial establishment of both early and late successional species and rapid early production of the early successional species, such as aspen (Bormann and Likens 1979). This rapid early production suppresses the more shade tolerant late successional species, such as sugar maple, resulting in a differentiation of the canopy into dominant early successional species and overtopped late successional species. After a period of 20 to 30 years, the rapid growth of the early successional species begins to slow and they are eventually overtaken by the more shade tolerant late successional species.

This pattern of recovery after logging or other disturbance is apparently occurring on the present site. The age of the larger maples is only slightly less than that of the aspen, indicating that they became established at approximately the same time as the aspen. The diameter distribution (Table 1) indicates that the sugar maples are beginning to grow into the overstory and replace the aspen. This pattern of growth and succession in an aspen – mixed hardwood stand is apparently reflected in the relationship of production to diameter for trembling aspen and sugar maple.

Differences noted here may not be apparent in other stands composed of species more alike in silvical characteristics. In addition, such differences may not occur in more open stands in which more light penetrates the canopy. Additional work is needed to determine the effect of site quality on allometric relationships for different species.

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