

## Notes and Comments

### LEAF PRODUCTION DURING SECONDARY SUCCESSION IN NORTHERN HARDWOODS<sup>1</sup>

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Leaf biomass is an important component of forest ecosystems. It is proportional to leaf area and primary production (Bray and Gorham 1964, Baskerville 1965, Satoo 1970) and also contains a major portion of a plant's annual nutrient uptake and its contribution, through litter fall, to the forest floor (Scott 1955, Bray and Gorham 1964, Gosz et al. 1972). Thus leaf biomass reflects important developmental differences in both primary production and nutrient cycling between stands. While much information is available for changes in leaf production over time in monospecific stands (e.g., Moller, 1947, Rennie 1955, Ovington and Heitkamp 1960, Switzer et al. 1967, Weigert and Monk 1972, Marks 1974), we know of no similar published data for a mixed-species temperate forest.

#### Methods

A series of different-aged stands was selected from the United States Forest Service timber management atlases for the White Mountain National Forest, New Hampshire, from the Hubbard Brook Experimental Forest (Likens et al. 1978a) and from the Bowl Natural Area (Leak and Graber 1974). Intersite variation was minimized by selecting stands with similar slope, elevation, soil drainage, site quality (as determined by timber management atlases) and intensity of past cutting. The resulting sequence (Table 1) contained 14 stands ranging in age from 3 to 200+ yr since harvest or other serious disturbance.

Leaf biomass in older stands (7 to 200+ yr) was measured by collection of leaf litter fall (20 randomly located 0.4-m diameter traps per stand). In the two youngest stands, high stem density (15/m<sup>2</sup>) precluded the use of litter traps. Instead, foliage was sampled by a stratified clip method (Fujimori 1971; four randomly located 2 by 2 m quadrats per stand).

For both sampling schemes all leaves were sorted to species, dried (48 h at 80°C) and weighed. While discrepancies between total leaf biomass at one point in time as we have measured it and total leaf production will occur, due to herbivory (Bray 1964,

Whittaker and Woodwell 1969, Gosz et al. 1972, Reichle et al. 1973) and retranslocation (Viro 1955) these will have a relatively minor effect in most years. Leaf biomass, productivity and litter fall are therefore strongly correlated in deciduous forests.

#### Results and Discussion

Successional trends in total leaf biomass are presented in Fig. 1. Results from other studies in northern hardwoods are included for comparison. We have fit a number of different regression equations to our data (Fig. 1). Both an exponential and a quadratic equation produce results which are statistically significant and provide a standard error of the estimate near 10% of the composite sample mean (2706 kg/ha). However, the two equations suggest very different patterns of leaf production in the first 30 yr of succession which has been shown to be important in re-establishing biological control over ecosystem function after disturbance (Marks and Bormann 1972).

This early period is frequently, but not always, dominated by pin cherry (*Prunus pensylvanica*). This species has been studied in detail by Marks (1974) who notes its unique buried seed strategy and extremely high rate of net primary production which allow it to establish relatively high leaf biomass values within 3 or 4 yr after cutting. The data from our 3- and 4-yr-old stands and the exponential equation in Fig. 1 all substantiate this trend. However, there are many clear-cut stands in which pin cherry does not become dominant. Safford and Filip's (1974) control stand (4 yr old) had only 38% of its leaf biomass in pin cherry. Our 7-yr-old stand contains almost no pin cherry. The factors determining the degree of pin cherry dominance are not precisely known but this species' unique potential for high productivity may cause large differences in nutrient cycling and biomass accumulation between sites with and without pin cherry dominance, which may in turn affect long-term site fertility.

Fig. 2 presents data on total leaf biomass in pin cherry dominated sites from this study (open circles) and from Marks' study (solid circles) along with estimates of total leaf biomass for all other species in both pin cherry dominated (open squares) and non-pin cherry stands (solid squares). For stands 18 yr and older, it was impossible to determine the degree

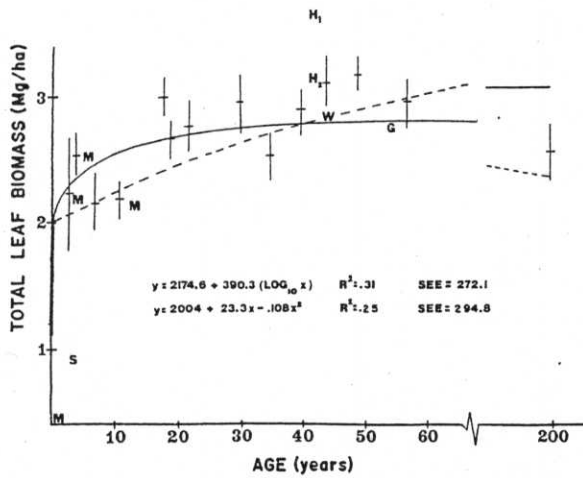


FIG. 1. Leaf biomass for a secondary succession in northern hardwoods (means and 95% confidence interval). Letters represent data of (M) Marks (1974), (S) Safford and Filip (1974), (H<sub>1</sub> and H<sub>2</sub>) Hart et al. (1962), (W) Whittaker et al. (1974), (G) Gosz et al. (1972). Lines represent two regression equations for our 14 data points. SEE is the standard error of the estimate.

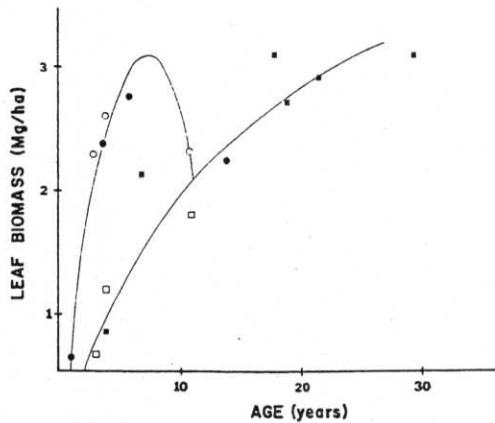


FIG. 2. Circles are total leaf biomass in pin cherry dominated stands from this study (open) and Marks (1974; solid). Squares are non-pin cherry leaf biomass in pin cherry dominated stands (open) and non-pin cherry stands (solid). Lower line is the regression for all non-pin cherry values (squares). The equation is  $Y = .344 + 2.337 \log_{10} X (R^2 = .95)$ . Upper line is sum of lower line with equation describing pin cherry biomass in stands from 1 to 14 yr of age. This equation is  $Y = .156 + .474X - .0437X^2 (R^2 = .81)$ . Upper line describes successional changes in leaf production in pin cherry stands, lower line describes non-pin cherry stands.

of initial pin cherry dominance due to that species' rapid senescence after year 6 in all but Marks' 14-yr-old stand. Total leaf production in stands from 18 to 30 yr old is used as part of the non-pin cherry biomass data set. Data for non-pin cherry biomass in Marks' stands are not included due to selection against inclusion of other species in his study areas. Three initial conclusions are suggested: (1) successional patterns in leaf production by species other than pin cherry are not greatly altered by pin cherry's presence or absence; (2) similarly, total leaf production

in pin cherry stands is apparently unaffected by the percentage of that biomass in non-pin cherry species; (3) stands with vigorous pin cherry have much higher levels of leaf production in the first 10 yr following cutting.

To obtain a quantitative estimate of the total difference in leaf production by the two types of successions, regressions were run for the non-pin cherry biomass data in Fig. 2 (lower line) and then for the

TABLE 1. Stand descriptions, total leaf biomass (kg/ha) [95% confidence interval] and distribution by species for successional sequence in northern hardwoods.

Age	3	4	7	11	18	19	22	30	35	40	44	49	57	200+	
Elevation (m)	570-630	480-540	480-510	420-450	450-510	540-600	540-570	450-510	480-540	570-600	480-540	540-580	600-690	600-630	
Total leaf biomass (kg/ha) [95% confidence interval]	2232 ±459	2565 ±171	2176 ±232	2200 ±192	3000 ±152	2648 ±168	2784 ±192	2944 ±224	2528 ±208	2896 ±160	3144 ±184	3176 ±136	2960 ±168	2544 ±216	
Percent biomass by species															
<i>Prunus pensylvanica</i>	73.0	55.6	3.6	21.8	1.9	5.7	1.9	1.3	1.2	0	0	0	0	0	
<i>Betula alleghaniensis</i> and <i>B. papyrifera</i>	6.4	4.3	23.5	19.8	3.5	18.4	8.9	10.7	16.0	15.5	23.7	19.5	9.0	10.4	
<i>Fraxinus americana</i>	0.4	0	2.2	0.3	0	3.3	0	10.6	11.2	6.2	0	23.2	0	0	
<i>Acer pennsylvanicum</i>	9.9	0.6	11.4	6.1	5.3	11.7	0.8	2.2	0.5	0	11.7	0.5	0	2.5	
<i>Acer spicatum</i> and <i>A. rubrum</i>	0	0	2.0	8.6	1.7	3.6	3.2	6.9	2.7	0	0	1.9	0	0	
<i>Acer saccharum</i>	3.8	21.5	43.9	22.1	19.2	13.7	80.5	61.0	42.6	55.4	31.2	42.5	74.0	64.1	
<i>Fagus grandifolia</i>	4.0	3.3	7.2	7.3	66.7	40.6	3.1	4.8	23.5	21.1	32.5	9.1	15.1	21.5	
Miscellaneous	3.3	14.1	6.3	14.2	1.7	3.0	1.8	2.6	2.4	1.8	0.9	3.3	1.9	1.5	

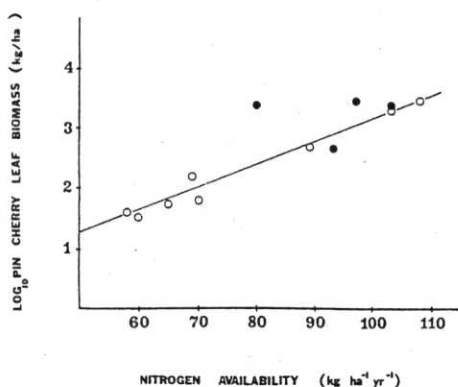


FIG. 3. Relationship between projected nitrogen availability (Aber et al. 1978) and total pin cherry leaf biomass. Solid circles are from Marks (1974), open circles are from this study. Equation is  $\log_{10}Y = -.518 + .0367X$  ( $R^2 = .79$ ).

additional leaf production due to the presence of pin cherry (region between lower and upper line in Fig. 2, see legend for equations). The upper solid line thus represents successional changes in total leaf fall in sites initially dominated by pin cherry while the lower line represents non-pin cherry succession.

In the first 11 yr, total leaf production would be 25 151 kg/ha in the pin cherry sequence versus 16 830 kg/ha in the non-pin cherry stands. This represents a significant difference in the potential for retaining nutrients on site by uptake and sequestering in biomass and, through litter fall and decomposition, in soil organic matter. Secondary effects on soil microclimate through increased light penetration in non-pin cherry stands may also cause important differences in soil temperature and water availability and hence decomposition and production.

The equations used in Fig. 2 predict a dip in total leaf production in pin cherry sites between years 6 and 11 due to a rapid decline in pin cherry. With only two data points in this region, conclusions can only be tentative, but this senescence may result from reduced nitrogen availability which has also been described for this time period (Likens et al. 1978b). Marks and Bormann (1972) and Marks (1974) have shown that pin cherry can take up large quantities of nitrogen and Safford and Filip (1974) show a strong response to fertilization in this species. These results indicate a nitrogen-demanding behavior in pin cherry. Finally, a regression obtained for total pin cherry leaf production as a function of levels of nitrogen availability as predicted by a computer model of forest floor dynamics following cutting (Aber et al. 1978) indicates a strong correlation (Fig. 3). While all of this information supports the nitrogen availability hypothesis, many other ecosystem parameters are also changing rapidly in this time period (e.g., water avail-

ability, Likens et al. 1978b; soil composition and structure, Covington 1976) and may also influence the productivity of pin cherry. More data are needed both to verify this dip in leaf production and to illuminate its cause.

Significant changes in leaf production also occur beyond year 30 (Fig. 1). These could relate to differences in site characteristics (although these have been minimized), stand history, or successional development. For example, we observed a greater than average amount of woody litter in the 35-yr-old stand suggesting that its lower leaf biomass may be due to the recent synchronous death of a number of trees. The lower value for the 200+ yr old stand may relate to a stagnation of the nutrient cycle postulated for certain northern forest types (Loucks 1970, Viro 1974), or to inherent decadence of older trees approaching their limits of longevity. The higher values for the 44- and 49-yr-old stands and the unusually large percentage in *Fraxinus* and *Betula* may be indicative of richer sites (Fowells 1965), or perhaps total leaf biomass values can increase when a significant portion of the total is in intermediate species rather than being all in tolerants. As all of the above are speculative, we suggest that the average of all the values measured for stands 30 yr and older be used as an estimate for leaf production in "mature" northern hardwood forests (2884.6 kg/ha,  $SD = 240.1$ ).

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