



ELSEVIER

Forest Ecology
and
Management

Forest Ecology and Management 70 (1994) 319–327

Productivity and growth efficiency in sugar maple forests

David D. Reed*, Kurt S. Pregitzer, Hal O. Liechty, Andrew J. Burton, Glenn D. Mroz

*School of Forestry and Wood Products, Michigan Technological University, Houghton, MI 49931, USA

Accepted 14 March 1994

Abstract

Sugar maple (*Acer saccharum* Marsh.)-dominated northern hardwood forests were examined at four locations along an acid deposition and climatic gradient in the Great Lakes region of the USA. The study sites were matched in terms of physiography, soils, stand history, and vegetative characteristics. Measurements of basal area and biomass growth were made for the 1988–1991 growing seasons. There were no significant differences in either basal area or biomass increment among the four sites over the 4 year period. There was a great deal of year-to-year variability with relative basal area growth rates ranging from as low as 0.2% to as high as 2.4% on a single site in successive years. Growth efficiency measures reflected this variability with as much as an 800% difference between successive years on a single site. When coupled with year-to-year variability of up to 34% in leaf area related to heavy seed years and defoliation, this indicates that growth efficiency and leaf area measures are not consistent indicators of aboveground productivity for tolerant deciduous species, especially if derived from short-term measurements or temporary plots.

Keywords: Productivity; Growth efficiency; *Acer saccharum*; Relative growth rate

1. Introduction

A recent report (Barnard et al., 1990) defined forests as being healthy if "... they are functioning in a manner that allows sustainable development of ecosystems with productivity at or near potential levels as determined by edaphic, climatic, and genetic factors and normal community dynamics." By defining forest health in terms of aboveground productivity, it becomes imperative to understand the normal patterns of change and variability of productivity in order to accurately assess forest health (Avery and Burkhardt, 1983; Franklin et al., 1987). It is important for one-point-in-time evaluations of for-

est health to be made with due consideration of the natural variation in productivity.

The growth and development of forests is dependent on the growth and development of individual trees (Chapman and Meyer, 1949). Vigorous growth on a tree level does not necessarily relate directly to vigorous growth on a stand level (Bickerstaff, 1946) because factors which affect growth of individual trees may not be the same factors which affect growth on the stand level (Spurr, 1952). Evaluation of factors affecting forest productivity in field settings requires an understanding of the natural variability in the measures of forest productivity as well as high quality measurement of the factors being evaluated (Schreuder and Thomas, 1991).

There has been much discussion in recent years

* Corresponding author.

concerning the usefulness of observational field data in evaluating cause and effect relationships between agents of stress and forest productivity (e.g. Schreuder and Thomas, 1991, and accompanying comments). Most attention has been placed on statistical methods to control variability in such things as climate or soil factors through study design, replication, and the use of covariates. However, there appears also to be a generally poor level of appreciation of natural temporal variability in forest productivity due to other things such as seed crop production and defoliation (Burton et al., 1991a).

This study was designed to evaluate the basal area and biomass increments and growth efficiency of sugar maple (*Acer saccharum*, Marsh.) dominated northern hardwood stands in the northern Lake States. The four study sites were selected in 1987 along a gradient of air pollution and climate. The sites are generally representative of the sugar maple-beech community of the hemlock-white pine-northern hardwoods region defined by Braun (1950). Measurements from the 1988–1991 growing seasons are summarized here to; (1) compare stand level productivity and growth efficiency as related to regional gradients of pollutant deposition and climate, and (2) evaluate the year-to-year variability of productivity and growth efficiency in these stands on a regional basis.

2. Methods

2.1. Study areas

The four northern hardwood study sites were located across the geographic range of the community from central to northern Michigan (Fig. 1); there are acid deposition and climate gradients which also extend across the region (Table 1). All sites were located on sandy, well-drained soils in second growth, sugar maple-dominated northern hardwood stands. Stands were identified following a rigorous selection process (Reed et al., 1988; Burton et al., 1991b). Selection criteria ensured that the sites were similar in terms of species composition, age, struc-

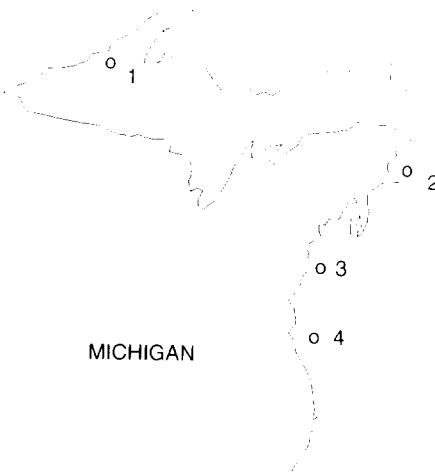


Fig. 1. Location of study sites (circled numbers).

ture, soils, physiography, and stand history (Table 1). The sandy, spodosol soils are typical of a major portion of the 5.3 million ha of northern hardwoods in the Lake States (Burton et al., 1991a). The sites have similar levels of growing season precipitation but differ in temperature and length of the growing season (Table 1).

2.2. Measurements

Each study site consisted of three $30 \times 30\text{ m}^2$ study plots surrounded on all sides by a 10 m wide buffer strip. Diameter at breast height (dbh) (1.37 m) measurements of individual trees greater than 5.0 cm [dbh] were made at permanently marked locations using diameter tapes in the fall of 1987, 1988, 1989, 1990, and 1991 after at least 50% of leaf fall had occurred. Each tree was measured by two individuals who had to agree to within $\pm 1\text{ mm}$; this resulted in a standard error (SE) of 0.3 mm or less for the individual tree measurements (based on a 10% re-measurement of sample trees). Basal area was calculated using standard mensurational formulae (Avery and Burkhart, 1983) and converted to a per hectare basis. Basal area was assigned to survivor growth (if the tree was living at the be-

Table 1
Selected characteristics of the four northern hardwood sites

	Site 1	Site 2	Site 3	Site 4
Latitude (N)	46°52'	45°33'	44°23'	43°40'
Longitude (W)	88°53'	84°51'	85°50'	86°09'
Basal area ($m^2 ha^{-1}$)	32 (0.5) ^d	30 (1.2)	30 (2.8)	30 (2.0)
Sugar maple basal area (%)	86 (7)	86 (8)	83 (5)	75 (13)
Biomass ($Mg ha^{-1}$)	261 (13)	261 (24)	274 (31)	234 (29)
Sugar maple biomass (%)	87 (6)	83 (11)	84 (5)	76 (11)
Canopy height (m)	24 (1)	27 (1)	28 (1)	24 (1)
Overstory age (years)	79 (15)	73 (6)	74 (11)	78 (5)
Mean annual precipitation ^a (mm)	870	830	810	850
SO_4^{2-} -S deposition ($kg ha^{-1} year^{-1}$) ^b	4.9	7.6	9.0	9.7
NO_3^- -N deposition ($kg ha^{-1} year^{-1}$) ^b	3.8	5.8	7.8	7.6
Mean annual temperature (°C)	4.3	5.2	5.8	7.6
Growing degree days ^c (> 5.6 °C)	1528	1736	1944	2083
Soil great group	Haplorthod	Haplorthod	Haplorthod	Haplorthod

^a 30-year means for the nearest NOAA station (NOAA, 1983).

^b Average annual (October 1987 through September 1990) wet plus dry deposition (MacDonald et al., 1992).

^c Phillips and McCulloch (1972).

^d Mean ± (Standard Deviation).

ginning and end of the year), mortality (if the tree died during the year), or ingrowth (if the tree grew to be greater than 5.0 cm [dbh] during the year).

Heights of each tree were measured in the fall of 1987 but were not remeasured each year due to the slow height growth in the stands and the low precision of height measurements. Total heights were independently measured using clinometers by two individuals until there was agreement within ± 1 m; this resulted in a SE of 0.24 m or less for individual trees (based on a 10% remeasurement of sample trees). Host et al. (1989) assembled a computer program of biomass equations for Lake States forest species. The equations in this program, along with the total heights and annual diameter measurements, were used to calculate total aboveground woody biomass (kg) for individual trees at the end of each growing season. These were assigned to survivor, ingrowth, or mortality, summed, and converted to a per hectare basis for analysis.

Expressions of growth efficiency relate stem-wood basal area or aboveground biomass production to leaf area or foliar biomass. These productivity indices are based on the assumption that stand productivity is related to leaf area

(Waring, 1983; Oren et al., 1987), and they have been related to environmental stress (Waring and Pitman, 1985; Oren et al., 1988). Growth efficiency measures used here are modeled after those described by Whittaker et al. (1974) for the Hubbard Brook ecosystem; the amount of basal area or biomass production is divided by leaf area or foliar weight. Leaf area and foliar weight for the study plots are based on individual species foliar litterfall collected on the sites as described by Burton et al. (1991a).

A one-way analysis of variance was used to examine differences in productivity and growth efficiency observed on the study sites. The three measurement plots were considered to be nested within the study sites in the analysis of variance. Annual observations were treated as repeated measurements on the same experimental units (plots). A significance level of $P=0.05$ was used for all comparisons reported here.

3. Results

Total stand basal area across the sites averaged $30-32 m^2 ha^{-1}$, 75–90% of which was sugar maple (Table 1). In two old growth northern hard-

wood stands in northern Michigan, Mroz et al. (1985) observed total basal areas of 34–43 m² ha⁻¹, 93–94% of which was sugar maple. Whittaker et al. (1974) noted basal areas of 22–26 m² ha⁻¹ in second growth northern hardwoods at Hubbard Brook with 79-year-old sugar maple. Host et al. (1988) report average total basal areas of 27.4 m² ha⁻¹ in second growth northern hardwood stands in northern lower Michigan which had significant sugar maple components.

Aboveground biomass on the four study sites ranged from 234 to 274 Mg ha⁻¹ (Table 1), below the values of 282 and 324 Mg ha⁻¹ in old growth northern hardwoods given by Mroz et al. (1985) but above the values of 145 Mg ha⁻¹ in second growth northern hardwoods in the Lake States noted by Crow et al. (1991) and 102–161 Mg ha⁻¹ observed by Whittaker et al. (1974) at Hubbard Brook. Host et al. (1988) found aboveground biomass of 172–249 Mg ha⁻¹ in stands with significant sugar maple components in northern lower Michigan; Zak et al. (1989) report that ecosystems similar to those on the study sites average 243 Mg ha⁻¹.

The following analyses are based on the sugar maple component of these stands. Similar results were found for total growth but the additional species were not the same at every site. The growth efficiency measures account for differences in initial sugar maple basal area and biomass; analyses were performed on the relative growth as well as the actual growth to account for compositional differences among the stands. Results concentrate on survivor growth to remove the variability introduced into net productivity by mortality events and ingrowth. There were no differences in basal area or biomass ingrowth among the study sites but there were differences ($P<0.005$) in mortality among the study years.

3.1. Basal area and biomass production

For sugar maple survivors, basal area production ranged from 0.23 to 0.28 m² ha⁻¹ (Table 2)

and did not differ among the four study sites. But, there were significant ($P<0.001$) differences in basal area productivity among the four study years and there was a significant ($P<0.001$) site X year interaction. Variability was greater among years than among sites. Survivor basal area growth at site four ranged from 0.05 to 0.54 m² ha⁻¹ in successive years. Similar results were found when basal area productivity was expressed on a percentage basis; the sites averaged 0.88–1.20% annual growth, but, again for site four, survivor basal area growth percent ranged from 0.22% to 2.39% in successive years. These encompass the range (1.93–2.19%) noted by Whittaker et al. (1974) at Hubbard Brook but the average productivity over the four study years is lower than what was reported for Hubbard Brook.

The four study sites were also similar in average annual aboveground sugar maple survivor biomass production. Sugar maple survivor woody biomass production ranged from 2.1 to 2.7 Mg ha⁻¹ year⁻¹ among the four sites (Table 3). There were significant ($P<0.001$) differences among years as well as a significant ($P<0.001$) site X year interaction. As was the case for basal area, year-to-year variability within sites was greater than variability among sites. On site four for example, survivor biomass productivity ranged from 0.5 to 4.6 Mg ha⁻¹ year⁻¹ in successive years. Host et al. (1988) report mean annual increments of aboveground biomass for all species to range from 2.7 to 3.6 Mg ha⁻¹ year⁻¹ in stands with significant sugar maple components in northern lower Michigan which is similar to the 3.0–3.7 Mg ha⁻¹ year⁻¹ observed for all species on the study sites (Table 1).

Similar results were found for sugar maple survivor biomass productivity expressed on a percentage basis. There were no differences among sites but there were differences among years and a significant site X year interaction. Survivor biomass increment for the sites averaged 0.89–1.28%, but survivor biomass increment ranged from 0.27 to 2.52% in successive years at site four

Table 2

Initial sugar maple basal area (Spring 1988), annual survivor sugar maple basal area increment (1988–1991), and annual relative basal area growth rate for the four study sites^a

	Site 1	Site 2	Site 3	Site 4
<i>Initial sugar maple basal area (Spring 1988) ($m^2 ha^{-1}$)</i>				
	27.4 (1.9)	25.2 (2.3)	24.8 (1.0)	22.3 (4.9)
<i>Annual survivor sugar maple basal area increment ($m^2 ha^{-1}$)</i>				
1988	0.21 (0.04)	0.20 (0.02)	0.33 (0.12)	0.23 (0.11)
1989	0.31 (0.10)	0.23 (0.07)	0.06 (0.10)	0.05 (0.07)
1990	0.35 (0.11)	0.22 (0.08)	0.46 (0.01)	0.54 (0.15)
1991	0.26 (0.08)	0.25 (0.06)	0.27 (0.06)	0.27 (0.08)
Average	0.28	0.23	0.28	0.27
<i>Relative survivor sugar maple basal area growth rates (%)^b</i>				
1988	0.77	0.79	1.33	1.03
1989	1.12	0.90	0.24	0.22
1990	1.25	0.86	1.83	2.39
1991	0.92	0.97	1.05	1.17
Average	1.02	0.88	1.11	1.20

^a Values given are the means (and Standard Deviations) from the three measurement plots at each site.

^b Relative growth rate is the annual increment expressed as a percentage of the standing crop at the beginning of the growing season.

Table 3

Initial sugar maple aboveground woody biomass (Spring 1988), annual survivor sugar maple woody biomass increment (1988–1991), and annual relative woody biomass growth rate for the four study sites^a

	Site 1	Site 2	Site 3	Site 4
<i>Initial sugar maple biomass (Spring 1988) ($Mg ha^{-1}$)</i>				
	228.4 (13.4)	226.6 (29.0)	228.3 (12.6)	179.9 (44.6)
<i>Annual survivor sugar maple woody biomass increment ($m^2 ha^{-1}$)</i>				
1988	1.8 (0.3)	1.8 (0.2)	3.2 (1.1)	2.0 (0.9)
1989	2.6 (0.7)	2.1 (0.7)	0.6 (0.9)	0.5 (0.6)
1990	2.9 (0.9)	2.0 (0.7)	4.4 (0.2)	4.6 (1.3)
1991	2.2 (0.8)	2.3 (0.7)	2.7 (0.6)	2.3 (0.7)
Average	2.4	2.1	2.7	2.4
<i>Relative survivor sugar maple woody biomass growth rates (%)^b</i>				
1988	0.79	0.79	1.40	1.11
1989	1.13	0.92	0.26	0.27
1990	1.25	0.87	1.90	2.52
1991	0.93	0.99	1.14	1.23
Average	1.03	0.89	1.18	1.28

^a Values given are the means (and Standard Deviations) from the three measurement plots at each site.

^b Relative growth rate is the annual increment expressed as a percentage of the standing crop at the beginning of the growing season.

(Table 3). The mean annual increment of biomass reported by Host et al. (1988) was between 1.4 and 1.6% for stands with significant sugar maple components.

3.2. Growth efficiency

Expressions of growth efficiency relating stemwood basal area and aboveground biomass production to leaf area and foliar biomass are given in Table 4. There were no site differences in basal area:leaf biomass or basal area:leaf area but there were significant differences among years ($P < 0.001$ for both) and significant site X year interactions ($P = 0.035$ and $P = 0.016$, respectively). Basal area:leaf biomass ranged from 0.083 to 0.124 $\text{m}^2 \text{Mg}^{-1}$ while basal area:leaf area ranged from 0.044 to 0.059 $\text{m}^2 \text{ha}^{-1}$ among the

study sites. There were greater differences between successive years for given sites than among sites for both growth efficiency measures, with both sites three and four having an eight to ten-fold increase from 1989 to 1990 (Table 4).

Similar results were found for the biomass increment growth efficiency ratios; there were no differences among sites but there were differences ($P < 0.001$ for both measures) among years and significant site X year interactions ($P < 0.001$ for both measures). Biomass increment:leaf biomass averaged 0.744–1.125 Mg Mg^{-1} among the sites but, from 1989 to 1990 had an eight-fold increase at sites three and four. Biomass increment:leaf area was less variable ranging from 0.378 to 0.508 Mg ha^{-1} among the sites but still had six to seven-fold increases from 1989 to 1990 at sites three and four.

Table 4
Survivor sugar maple growth efficiency estimates (and Standard Deviations) from the four sites

	Site 1	Site 2	Site 3	Site 4
<i>Basal area increment:litterfall foliar weight ($\text{m}^2 \text{Mg}^{-1}$)</i>				
1988	0.06 (0.01)	0.06 (0.01)	0.15 (0.05)	0.09 (0.04)
1989	0.15 (0.05)	0.08 (0.02)	0.02 (0.04)	0.02 (0.03)
1990	0.14 (0.05)	0.10 (0.04)	0.20 (0.03)	0.22 (0.08)
1991	0.09 (0.03)	0.08 (0.02)	0.10 (0.02)	0.09 (0.02)
Average	0.11	0.08	0.12	0.11
<i>Basal area increment:foliar leaf area ($\text{m}^2 \text{ha}^{-1}$)</i>				
1988	0.04 (0.01)	0.03 (0.00)	0.08 (0.02)	0.05 (0.02)
1989	0.08 (0.02)	0.04 (0.01)	0.01 (0.02)	0.01 (0.02)
1990	0.06 (0.02)	0.06 (0.02)	0.08 (0.01)	0.10 (0.03)
1991	0.04 (0.02)	0.03 (0.01)	0.04 (0.01)	0.04 (0.01)
Average	0.06	0.04	0.05	0.05
<i>Biomass increment:litterfall foliar weight (Mg Mg^{-1})</i>				
1988	0.57 (0.07)	0.59 (0.06)	1.39 (0.48)	0.80 (0.36)
1989	1.28 (0.37)	0.77 (0.20)	0.23 (0.33)	0.22 (0.24)
1990	1.17 (0.39)	0.91 (0.35)	1.94 (0.28)	1.86 (0.69)
1991	0.79 (0.29)	0.70 (0.21)	0.94 (0.22)	0.81 (0.21)
Average	0.95	0.74	1.12	0.92
<i>Biomass increment:foliar leaf area (Mg ha^{-1})</i>				
1988	0.31 (0.05)	0.30 (0.03)	0.74 (0.23)	0.41 (0.18)
1989	0.69 (0.14)	0.40 (0.11)	0.12 (0.17)	0.12 (0.13)
1990	0.49 (0.16)	0.51 (0.21)	0.78 (0.09)	0.86 (0.29)
1991	0.36 (0.15)	0.31 (0.09)	0.40 (0.10)	0.36 (0.09)
Average	0.46	0.38	0.51	0.44

* Litterfall weights (dry weight, Mg ha^{-1}) and leaf area indices ($\text{m}^2 \text{m}^{-2}$) are taken from Burton et al. (1991a).

4. Discussion

The lack of differences among the four study sites for any of the productivity or growth efficiency measurements implies that there were no detectable differences in aboveground woody production among the sites due to mean nitrate or sulfate deposition, regional climate, or site characteristics over the four study years. Burton et al. (1991a) found similar results for leaf area and biomass. Total annual precipitation, growing season (May through September) precipitation, and actual evapotranspiration were not correlated with basal area or biomass increment on the study sites. These seasonal measures may not accurately assess moisture availability during the specific times when it is physiologically important for production of aboveground woody biomass. Additional years of record will allow assessment of the importance of the seasonal pattern of precipitation and temperature on aboveground woody production.

A possible explanation of the lack of difference in productivity among the study sites is that the genotypes in the respective local sugar maple populations are adapted to the local growing season and climate conditions. Pollution sensitivity screening studies have shown no differences in susceptibility to ozone, nitrogen, or sulfur inputs in seedling material collected from these study sites (D.F. Karnosky, personal communication, 1993). There is, therefore, no evidence of genetically related differences in pollutant susceptibility of sugar maple at the study sites and no detectable effects of sulfate or nitrate deposition on the conventional productivity or growth efficiency of sugar maple. Previous studies, however, have shown very clear effects of sulfur and nitrogen deposition on sugar maple foliar stoichiometry (Pregitzer et al., 1992), canopy leaching (Liechty et al., 1990, 1992), soil chemistry (MacDonald et al., 1991), and soil solution chemistry (MacDonald et al., 1992).

Even though there is no evidence of differences in average annual aboveground woody production among the sites, there is a great amount of annual variability that is difficult to attribute to any specific cause. Burton et al.

(1991a) showed the effects of life history events on foliar production and Pregitzer and Burton (1991) demonstrated that increased seed production decreases stand leaf area and increases total nitrogen flux in litterfall. There appears to be little direct relationship between seed crop production and basal area, biomass productivity, or growth efficiency. It is possible for seed crop production to affect foliar production or growth the following year but that is difficult to evaluate given only four years of records from the study sites. Sites three and four had their lowest basal area and biomass productivity in years following heavy seed crops but sites one and two showed little change in basal area and biomass productivity in 1990 as compared with 1989, a heavy seed year.

Although not clear from the relatively short records from these sites, growth may be more dependent on the carbohydrate storage of the previous year. Spring cambial growth in hardwoods is dependent on carbohydrates stored the previous year (Kramer and Kozlowski, 1979) and somewhat less dependent on the current year's carbohydrate production. A year with high foliage production and ideal growing conditions may result in more stored carbohydrate for successive years and not necessarily more growth in the current year. Through interactions with temperature and moisture, seed crop production, and insect defoliation events, carbohydrate storage may be driving the annual variability in aboveground productivity. Lane (1991) studied the relationship between tree ring widths and the long-term climate records for these sites. He found that ring widths were positively related to weather conditions which would delay the start of the previous growing season but extend it into the previous fall, coupled with temperature conditions leading to an early start in growth in the spring of the current year. These results support the hypothesis that carbohydrate storage is the factor driving the high level of annual variability in aboveground production.

Clearly, the link between aboveground productivity and foliar biomass or leaf area is weak in these stands. Several other authors, such as Waring and Pitman (1985), Oren et al. (1988),

and Gower et al. (1992) have shown strong relationships between growth efficiency and environmental stress in conifers. One possibility is that, since conifers retain their foliage for several years, the year-to-year variability in foliar production and basal area and biomass productivity is mitigated allowing greater sensitivity in detecting environmental effects on these variables. Pines use carbohydrates produced by old needles in early spring shoot expansion (Dickmann and Kozlowski, 1968) and are not dependent on stored carbohydrates for growth initiation. The poor relationship between leaf area and productivity in sugar maple may also be due to physiological relationships; sugar maple sapwood is known to vary in its effectiveness at conducting water and in the number of annual rings involved in active conduction (Kramer, 1983). The physiological differences in sugar maple as compared with the coniferous species where better growth efficiency relationships have been identified may also play a role in the strength of the linkage between foliar production and basal area or biomass productivity.

Crown defoliation values presented by Burton et al. (1991a) for 1988–1990 show little relationship to basal area or biomass productivity for these years. Site two, for example, had 22% defoliation in late July, 1990 and only 1% defoliation in 1989, yet had roughly equal basal area and biomass increments in these 2 years. As with seed production, defoliation may affect basal area and biomass production in subsequent years but the lag effect cannot be evaluated from 4 years of measurement. There may also be an interaction between seed production and defoliation on the replacement and maintenance of stored carbohydrates that may affect production in subsequent years in a complex fashion. An implication of these results, and those of Burton et al. (1991a), is that leaf area and growth efficiency measurements made on temporary plots or measurements made every few years using a 'snapshot' approach probably have little relevance to the productive capacity of these stands. The results of this and other studies (Schreuder and Thomas, 1991; Burton et al., 1991a) indicate that detection of subtle shifts in forest productivity

due to environmental stresses against a background of extensive, natural, year-to-year variability requires multiple years of observation and careful documentation of defoliation, seed production, weather conditions, and other biotic and abiotic factors.

Acknowledgements

This study was partially funded by the Eastern Hardwoods Research Cooperative within the joint US Environmental Protection Agency/USDA Forest Service Forest Response Program. The Forest Response Program was part of the National Acid Precipitation Assessment Program. Additional funding was received from the USDA Forest Service Northern Stations Global Change Research Program. This paper has not been subject to EPA or Forest Service peer review and should not be construed to represent the policies of either agency.

References

- Avery, T.E. and Burkhart, H.E., 1983. *Forest Measurements*. Third Edition. McGraw-Hill, New York, 331 pp.
- Barnard, J.E. and Lucier, A.A. (Editors), 1990. Changes in forest health and productivity in the United States and Canada. In: Acidic Deposition: State of Science and Technology, Vol. 3. Report (16). National Acid Deposition Assessment Program. US Government Printing Office, Washington, DC, 186 pp.
- Bickerstaff, A., 1946. Balancing maximum increment per tree against maximum increment per acre. Canada Dominion Forest Service Silviculture Leaflet 22, 2 pp.
- Braun, E.L., 1950. *Deciduous Forests of Eastern North America*. Hafner Press, New York.
- Burton, A.J., Pregitzer, K.S. and Reed, D.D., 1991a. Leaf area and foliar biomass relationships in northern hardwood forests located along an 800 km acid deposition gradient. *For. Sci.*, 37: 1041–1059.
- Burton, A.J., Ramm, C.W., Pregitzer, K.S. and Reed, D.D., 1991b. Use of multivariate methods in forest research site selection. *Can. J. For. Res.*, 21: 1573–1580.
- Chapman, H.H. and Meyer, W.H., 1949. *Forest Mensuration*. McGraw-Hill, New York, 522 pp.
- Crow, T.R., Mroz, G.D. and Gale, M.R., 1991. Regrowth and nutrient accumulations following whole-tree harvesting of a maple–oak forest. *Can. J. For. Res.*, 21: 1305–1315.
- Dickmann, D.I. and Kozlowski, T.T., 1968. Mobilization by

- Pinus resinosa* cones and shoots of C¹⁴-photosynthate from needles of different ages. Am. J. Bot., 55: 900–906.
- Franklin, J.F., Shugart, H.H. and Harmon, M.F., 1987. Tree death as an ecological process: the causes, consequences, and variability of tree mortality. BioScience, 37: 550–556.
- Gower, S.T., Vogt, K.A. and Grier, C.C., 1992. Carbon dynamics of Rocky Mountain Douglas-fir: influence of water and nutrient availability. Ecol. Monogr., 62: 43–65.
- Host, G.E., Pregitzer, K.S., Ramm, C.W., Lusch, D.P. and Cleland, D.T., 1988. Variation in overstory biomass among glacial landforms and ecological land units in northwestern lower Michigan. Can. J. For. Res., 18: 659–668.
- Host, G.E., Westin, S., Cole, W. and Pregitzer, K.S., 1989. BIOMASS: an interactive program to calculate above-ground biomass of common tree species of the Lake States forests. USDA Forest Service, General Technical Report NC-127.
- Kramer, P.J., 1983. Water Relations of Plants. Academic Press, Inc. San Diego, CA.
- Kramer, P.J. and Kozlowski, T.T., 1979. Physiology of Woody Plants. Academic Press, Inc. Orlando, FL.
- Lane, C.J., 1991. Formation of sugar maple (*Acer saccharum*, Marsh.) tree rings as affected by climate. School of Forestry and Wood Products, Michigan Technological University, Houghton, MI.
- Liechty, H.O., Reed, D.D., Mroz, G.D. and Jurgensen, M.F., 1990. Comparison of cation leaching in five northern hardwood stands along an air pollution gradient using a throughfall modeling approach. In: H. Oswald (Editor), Proceedings of the 19th IUFRO World Congress, Division 1, Montreal, Canada. Forestry Canada, Hull, Que., Vol. 1, pp. 295–306.
- Liechty, H.O., Mroz, G.D. and Reed, D.D., 1993. Cation and anion fluxes in northern hardwood throughfall along an acid deposition gradient. Can. J. For. Res., 23: 457–467.
- MacDonald, N.W., Burton, A.J., Jurgensen, M.F., McLaughlin, J.W. and Mroz, G.D., 1991. Variation in forest soil properties along a Great Lakes air pollution gradient. Soil Sci. Soc. Am. J., 55: 1709–1715.
- MacDonald, N.W., Burton, A.J., Liechty, H.O., Witter, J.A., Pregitzer, K.S., Mroz, G.D. and Richter, D.D., 1992. Ion leaching in forest ecosystems along a Great Lakes air pollution gradient. J. Environ. Qual., 21: 614–623.
- Mroz, G.D., Gale, M.R., Jurgensen, M.F., Frederick, D.J. and Clarke III, A., 1985. Composition, structure, and above-ground biomass of two old-growth northern hardwood stands in Upper Michigan. Can. J. For. Res., 15: 78–82.
- NOAA, 1983. Climate Normals for the US (Base: 1951–1980), First Edition. National Climate Center, Environmental Data and Information Service, NOAA, Gale Research Company, Detroit, MI.
- Oren, R., Waring, R.H., Stafford, S.G. and Barrett, J.W., 1987. Twenty-four years of ponderosa pine growth in relation to canopy leaf area and understory competition. For. Sci., 33: 538–547.
- Oren, R., Schulze, E.-D., Werk, K.S. and Meyer, J., 1988. Performance of two *Picea abies* (L.) Karst. stands at different stages of decline. VII. nutrient relations and growth. Oecologia, 77: 163–173.
- Phillips, D.W. and McCulloch, J.A.W., 1972. The climate of the Great Lakes basin. Environmental Canada, Atmosphere Environment Climatology Studies No. 20. Toronto, Ontario.
- Pregitzer, K.S. and Burton, A.J., 1991. Sugar maple seed production and nitrogen in litterfall. Can. J. For. Res., 21: 1148–1153.
- Pregitzer, K.S., Burton, A.J., Mroz, G.D., Liechty, H.O. and MacDonald, N.W., 1992. Foliar sulfur and nitrogen along an 800 km pollution gradient. Can. J. For. Res., 22: 1761–1769.
- Reed, D.D., Mroz, G.D., Pregitzer, K.S. and Witter, J.A., 1988. Site selection procedures in the Michigan gradient study. In: J.A. Witter (Editor), Effects of an Air Pollution Gradient in Northern Hardwood Forests in the Northern Great Lakes Region. 1988 Annual Report for the Eastern Hardwoods Research Cooperative. School of Natural Resources, University of Michigan, Ann Arbor, USA, chapter II.
- Schreuder, H.T. and Thomas, C.E., 1991. Establishing cause-effect relationships using forest survey data. For. Sci., 37: 1497–1512.
- Spurr, S.H., 1952. Forest Inventory. John Wiley and Sons, New York. 476 pp.
- Waring, R.H., 1983. Estimating forest growth and efficiency in relation to canopy leaf area. Adv. Ecol. Res., 13: 327–354.
- Waring, R.H. and Pitman, G.B., 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. Ecology, 66: 889–897.
- Whittaker, R.H., Bormann, F.H., Likens, G.E. and Siccama, T.G., 1974. The Hubbard Brook ecosystem study: forest biomass and production. Ecol. Monogr., 44: 233–252.
- Zak, D.R., Host, G.E. and Pregitzer, K.S., 1989. Regional variability in nitrogen mineralization, nitrification, and overstory biomass in northern lower Michigan. Can. J. For. Res., 19: 1521–1526.