

Effects of area on old-growth forest attributes: implications for the equilibrium landscape concept

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Abstract

To investigate applicability of the equilibrium landscape concept to various attributes of vegetation, the effects of sampling area (or grain size) on structural and compositional stand parameters were determined in an old-growth hemlock-hardwood forest. Three 1-ha plots, each gridded into 1000.01-ha subplots, were established on the Roaring Fork watershed in Great Smoky Mountains National Park, Tennessee, USA. Estimates for 10 different stand descriptors were calculated for a variety of grain sizes (subplot aggregation levels) ranging from 0.01 to 1 ha. The stand descriptors included measures of physical structure (basal area and biomass) as well as measures of species composition (relative basal area).

All stand descriptors exhibited high deviation from the corresponding 3-ha mean at grain sizes approximately observed canopy gap area (< 0.02 ha). Deviations for total tree density, basal area and biomass diminished sharply with increasing grain size, while deviations for relative basal area of four important species remained relatively high even at grain sizes > 0.5 ha.

The relationship between sample variance and grain size was inverse and approximately log-log linear for all descriptors. Biomass, basal area, and large canopy tree density had relatively steep slopes. These variables of physical structure presumably were related to canopy gap size and distribution. The remaining measures of density and relative basal area had gentler slopes, indicating a milder decrease in variation with increasing grain size. Coefficients of variation for each parameter also showed this response to grain size, with compositional parameters having relatively high variation at scales > 0.5 ha.

In general, the nature of physical structure patches (e.g. total basal area and biomass) differed from that of composition patches (e.g. relative basal area of individual species). This contrast should be considered in equilibrium landscape concepts and vegetation sampling design.

1. Introduction

The quasi-equilibrium landscape concept holds that vegetation attributes exhibit constancy when averaged over a sufficiently large area of land (Shugart 1984). This reasoning has been expressed qualita-

tively by many ecologists (Cooper 1913; Watt 1925, 1947; Whittaker 1953; Whittaker and Levin 1977; Bormann and Likens 1979; White 1979; Heinselman 1981). More recently, Shugart (1984) has expressed quasi-equilibrium landscape size as a quantitative function of disturbance patch size. He sug-

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gested that the minimum landscape area required for equilibrium is approximately 50 times the area of a typical disturbance patch. For example, a quasi-equilibrium landscape area of 1–10 ha is estimated for forests subject to small canopy gap disturbance (< 0.05 ha), while equilibrium area on a forested landscape subject to fires on the order of 10 ha in size is estimated at 500–1000 ha. Landscapes with disturbance patches larger than 1/50th of their size are “effectively nonequilibrating” (Shugart 1984).

Information on long-term dynamics of forests is difficult to obtain; the quasi-equilibrium concept, however, suggests a spatial consequence of temporal dynamics. That is, at any given point in time vegetation parameters should exhibit constancy at large enough scales. If a forested landscape is in a quasi-equilibrium state then forest stand characteristics should be stable when considered across a sufficiently large area. Which forest attributes actually exhibit constancy when averaged over an area of land is a critical issue. Biomass has often been the attribute under investigation (Bormann and Likens 1979; Shugart 1984, 1989), and it is likely to have a similar spatial pattern on the landscape as other attributes of physical stand structure such as basal area and tree density. It may not have a similar pattern to attributes of species composition, however. For this reason, a landscape size suitable for biomass equilibrium would not necessarily be in compositional equilibrium. If compositional equilibrium is found to be a viable concept, 1) what landscape size is sufficient for equilibrium, and 2) how does it differ from landscape size requirements for biomass equilibrium? Our initial hypothesis was that compositional equilibrium in a diverse forest can only be attained at larger scales than biomass equilibrium.

To address these questions we examined the response of several forest stand attributes to landscape area in an old-growth forest lacking large-scale disturbance. The forest chosen for study is dominated by hemlock and hardwoods with no history of logging or catastrophic natural disturbances including fire and large-scale wind damage (Harmon *et al.* 1983, Runkle 1985, Pyle 1988). Disturbance is predominantly in the form of small canopy

gaps (< 0.05 ha in size; Barden 1979; Runkle 1982, 1985). White and Pickett (1985) hypothesized that under a disturbance regime of small patches, vegetation may approach compositional stability. Indeed, models of compositional dynamics based on tree replacement processes suggest that these forests are near compositional equilibrium (Barden 1981). The minimum equilibrium landscape area for forests subject to this disturbance regime is hypothesized to be about 1 ha (Shugart 1984), and we considered a range of sampling areas up to this critical area in the analysis.

2. Methods

The general objectives of this study were twofold. First we determined the dependence of various stand attributes on scale of observation. The forest attributes under consideration included measures of physical stand structure such as basal area and biomass as well as those of species composition (species relative basal area). Responses of these attributes over a range of scales of observation (or sampling areas) from 0.01 to 1.0 ha were determined. In particular, we quantified the degree of variability for each parameter at several scales and determined how the variability changed with scale. Our second objective was to use these measures of variability at different scales of observation to address equilibrium landscape area requirements in these forests. Assuming that the landscape under study was near structural and compositional steady state, we estimated quasi-equilibrium landscape areas for stand parameters by noting at what land area the variability of any particular parameter became minimal.

Three 1-ha plots were established within 1.1 km of one another on the Roaring Fork watershed, Great Smoky Mountains National Park (35°41' N, 83°27' W). The permanently marked plots were located on north-facing slopes at elevations of 994 (plot 1), 960 (plot 2) and 1137 m (plot 3). Vegetation at these sites was old-growth *Tsuga*-mixed deciduous forest (Oosting and Billings 1939; Oosting and Bordeau 1955; Whittaker 1956) with no history of catastrophic fire, extensive wind damage or logging

(Harmon *et al.* 1983; Pyle 1988). The elevations of plots spanned only 177 m, and the tree stratum of all plots was dominated by *Tsuga*.

Plot dimensions were 100x 100m; each plot was divided into 100, 10x 10 m subplots. Species and DBH were recorded for all trees > 2 cm DBH within each subplot. Tree saplings (< 2 cm DBH and > 1.37 m tall) were tallied by species. Canopy structure, as well as the location and size of canopy gaps, was determined by recording canopy cover (open, average canopy, or emergent canopy) overlying the 4, 5x 5 m quadrants of each subplot.

A set of quantitative stand descriptors was generated for each subplot and for the 1-ha plots. The descriptors included: 1) tree basal area, 2) tree biomass, 3) leaf biomass, 4) sapling density (1.37 m tall to 2 cm DBH), 5) tree density (> 2 cm DBH), 6) large canopy tree (> 60 cm DBH) density, 7) *Acer saccharum* relative basal area, 8) *Fagus grandifolia* relative basal area, 9) *Halesia carolina* relative basal area, and 10) *Tsuga canadensis* relative basal area. Biomass estimates were calculated using species-specific allometric equations for the Great Smoky Mountains (Clebsch 1971). The log (mass) to log (DBH) equations were developed from measurements on a wide size range of sample trees for more than 15 species (Shanks and Clebsch 1962). Estimates of each stand descriptor, standardized to quantity per ha, were compared to the corresponding mean value across all three 1-ha plots at various sampling areas or “grain” sizes (*sensu* Wiens 1989). In order to produce a range of sampling areas (0.01, 0.04, 0.09, 0.16, 0.25, 0.36, 0.49, 0.64, 0.81 and 1.0 ha), subplots were aggregated in square blocks beginning at each corner and at the center of each 1-ha plot. Thus, five separate aggregation sets were made per plot, resulting in a total of fifteen sets for all three plots. Each set contained all the sampling areas listed above. Percent deviation of descriptor estimates for each of the 15 sets from the overall mean were plotted against area as individual points.

One way to assess spatial heterogeneity is to determine the statistical variance of attributes measured at one grain size from the mean across samples (Levin 1989). High variance indicates high spatial heterogeneity at the grain size employed. The spa-

tial pattern of vegetation on a landscape can be described by determining variance from the mean at a variety of grain sizes (Levin and Buttel 1986; Smith and Urban 1988). Because the relationship between variance and grain size is independent of the specific grain sizes chosen, it provides a basis for cross-system comparisons of spatial heterogeneity. This heterogeneity may reflect, for example, dominant patch sizes or disturbance regimes of these ecosystems.

Variance of descriptors among samples at each sampling area was calculated as the sum of squared deviations from the sample mean divided by the degrees of freedom. In order to provide a better approximation of the actual variance, degrees of freedom, rather than sample size, were used in the denominator (Sokal and Rohlf 1981). Certain aggregation blocks were deleted from the analysis to avoid spatial overlap among samples. For example, the central aggregation block was omitted from variance calculations at the 0.16 and 0.25 ha aggregation levels, while all but one corner aggregation block per plot were omitted at aggregation levels greater than 0.25 ha. The corner aggregation block included in the analysis was randomly selected.

Because the various stand parameters considered had different mean values, the variance vs. grain size relationship was not the most suitable for comparing scale dependent variability among forest attributes. To facilitate comparisons of variability among stand parameters, coefficients of variation (standard deviations expressed as a percentage of the mean) were calculated for each variable at all sampling scales using the same aggregation block design as above.

3. Results

3.1. Stand descriptor estimate vs. sampling area

All stand characteristics exhibited maximum deviation from the corresponding 3-ha mean values at the smallest grain sizes (< 0.05 ha; Fig. 1a–j). Deviations for some descriptors diminished rapidly with increasing grain size. For example, the general stand descriptors, total tree density, basal area and

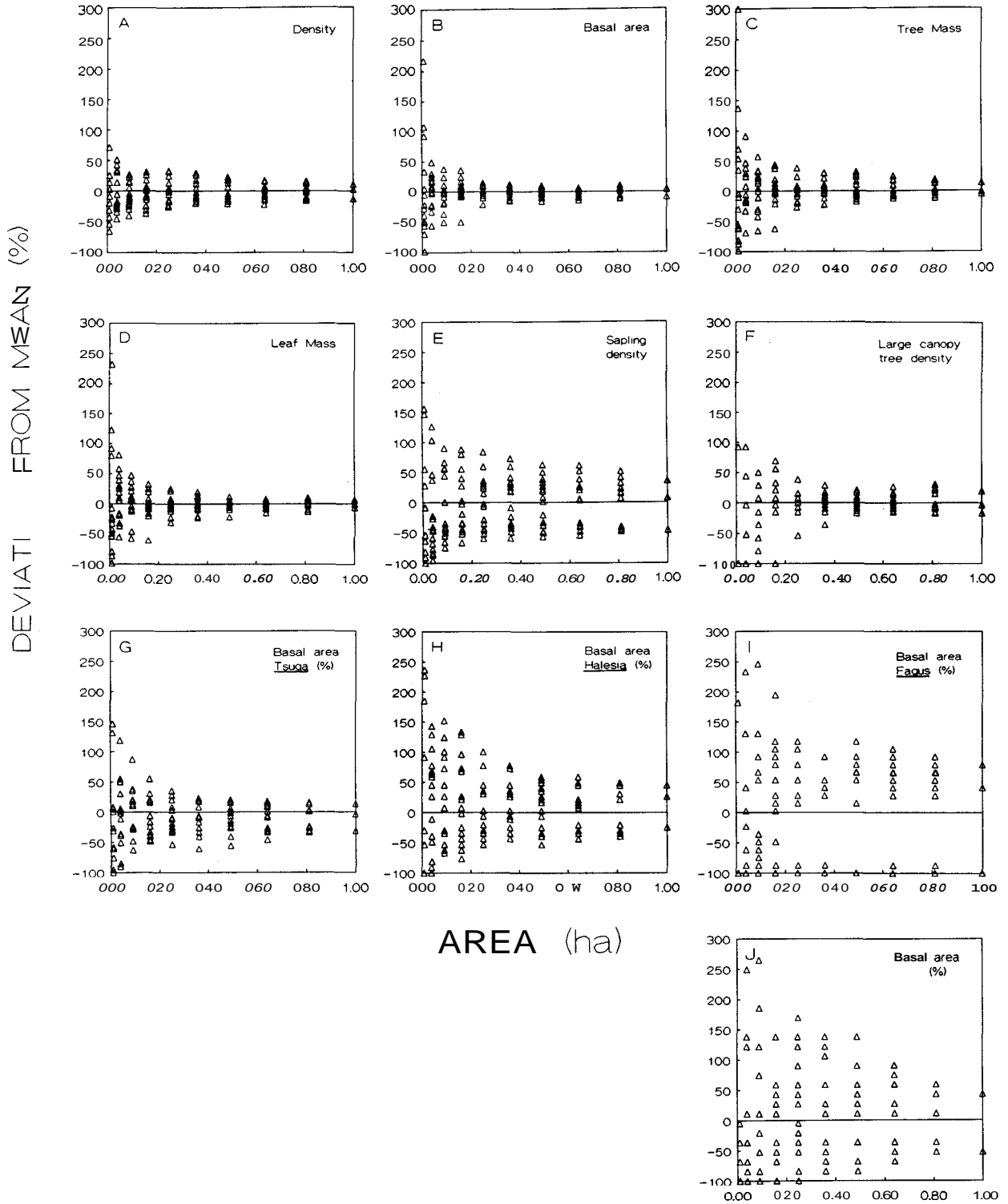


Fig. 1. Percent deviation from the 3-ha mean vs. grain size for: **A)** tree density (mean = 877 trees/ha); **B)** tree basal area (mean = 52.4 m²/ha); **C)** tree biomass (mean = 440 Mg/ha); **D)** tree leaf mass (mean = 7.3 Mg/ha); **E)** tree sapling density (mean = 1094/ha); **F)** large canopy tree density (mean = 52/ha); **G)** *Tsuga canadensis* relative basal area (mean = 41%); **H)** *Halesia carolina* relative basal area (mean = 21%); **I)** *Fagus grandifolia* relative basal area (mean = 8%); and **J)** *Acer saccharum* relative basal area (mean = 6%).

biomass, exhibited $< 50\%$ deviation from the overall mean at sampling grain sizes > 0.2 ha. (Fig. 1a–d). At a grain size of 1.0 ha, deviation was $< 15\%$ for these descriptors. Total tree density fell within 50% of the mean at grain sizes ≥ 0.09 ha (Fig. 1a). Basal area, tree biomass and leaf biomass estimates were within 50% of the mean at grain sizes ≥ 0.2 ha (1b–d).

Although deviation of total tree density estimates from the mean diminished rapidly with increasing grain size, density values for upper and lower size classes (large canopy trees and saplings) exhibited greater variation. This was particularly true for the sapling densities that deviated by as much as 50% from the mean even at grain sizes approaching 1 ha (Fig. 1e). Large canopy tree densities fell within 50% of the mean at grain sizes ≥ 0.3 ha (Fig. 1f).

In contrast to the responses of the general stand descriptors discussed above, descriptor values for individual species were highly variable across the range of grain sizes employed. In some of these, considerable variation remained even at the scale of 1 ha. Relative basal area values for *Tsuga*, the dominant species (by basal area) in all three 1-ha plots, were within 50% of the mean only at grain sizes ≥ 0.81 ha (Fig. 1g). A similar pattern was evident for *Halesia*, an abundant species in all plots (Fig. 1h). Relative basal area values for species with more sporadic distributions on the cove landscape such as *Fagus* and *Acer saccharum* deviated by more than 50% from the mean even at the scale of 1 ha (Fig. 1i–j).

3.2. Descriptor variability vs. sampling area

Coefficients of variation for each parameter (Fig. 2) generally exhibited the same trends presented above. Variation tended to diminish with increasing sampling area, but this did not hold true for the relative basal area values at scales > 0.1 ha. All of the descriptors of composition had noticeable troughs and peaks at the larger scales. Further, variation of the composition descriptors was consistently greater than that of physical structure descriptors.

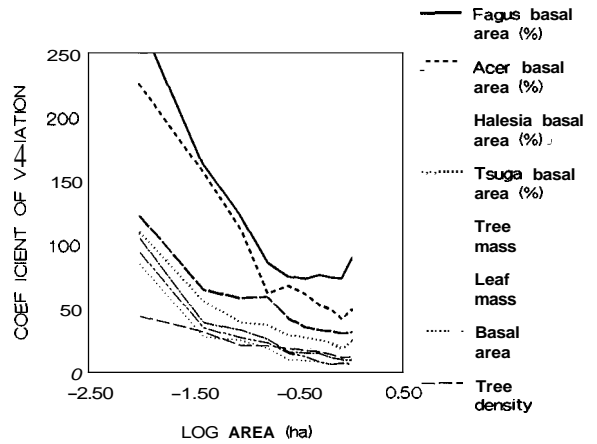


Fig. 2. Coefficients of variation vs. log grain size for several stand descriptors.

3.3. Descriptor variance vs. sampling area

An inverse relationship between variance and sampling area was common to all descriptors. On a log-log plot, the relationship was somewhat linear for all stand descriptors considered (Figs. 3a and b). Variance of all descriptors decreased steadily with increasing area up to 0.25 ha. At areas greater than 0.25 ha, descriptor variance no longer decreased steadily with increasing area as indicated by peaks and troughs in variance at the larger scales. Overall slopes of the physical structure curves (Fig. 3a) are generally steeper (except for tree and sapling density parameters) than slopes of the composition curves (Fig. 3b). This indicates a greater decrease in variance of most physical structural parameters with increasing scale, compared to compositional parameters.

3.4. Canopy gap size distribution

Canopy openings covered 13% of the area sampled. Most of the openings were 200 m² or less in size (Fig. 4). Intermediate sized gaps (250–1000 m²) were not encountered; however, one large gap (> 1000 m²) created by multiple treefalls, occurred in one plot. Because these disturbance patches were mostly < 0.02 ha in size, grain sizes larger than this area would often include gap and non-gap areas

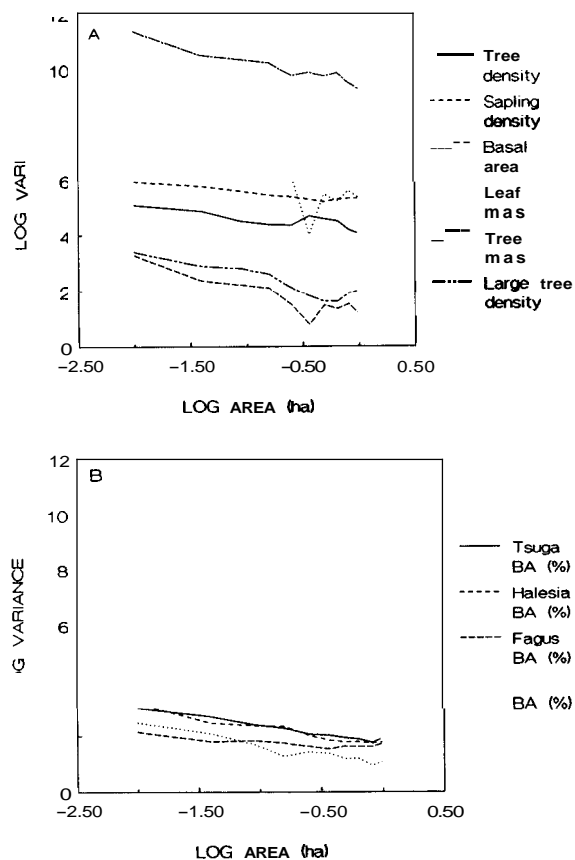


Fig. 3. Log sample variance vs. log grain size for stand descriptors: a) structural parameters, and b) compositional parameters.

and variance might be expected to diminish.

4. Discussion

Two different forms of patchiness were revealed in this study, and they were dependent on the kind of stand attributes considered. Measurements of physical structure such as biomass and total basal area reflected the size and dispersion of canopy gaps. At grain sizes less than or equal to typical gap size (0.003–0.02 ha), values of these parameters deviated strongly from the mean values over the entire 3-ha area sampled. The deviations diminished sharply with increasing sampling area for these descriptors. Spatial variation was low at scales > 0.5 ha for these parameters, suggesting that quasi-equilibrium may be attained at even smaller areas

than the estimated 1–10 ha for forests subject to a disturbance regime of small gaps. The 50:1 ratio of patch size to landscape area appears reasonable, however, when one considers the size of observed gaps. If we use a patch size of 0.01 ha, which approximates observed gap size, the equilibrium landscape area is estimated at 0.5 ha. Our findings suggest that stand biomass and basal area may require as little as 0.5–1.0 ha area for quasi-equilibrium in these forests.

Measurements of composition showed a different response to grain size. Deviation from the 3-ha mean values often remained high at grain sizes well beyond the size of the larger canopy gaps (0.02 ha). Variation in compositional parameters is substantial even at scales of 0.5–1.0 ha. Slopes of the log variance to log grain size relationship were gentler for these parameters, indicating a milder decrease in variation with increasing scale. Relative to the structural descriptors, variation remains high for all compositional descriptors at scales approaching 1 ha. Apparently, the size, intensity, and spatial distribution of compositional patches is not affected solely by gap processes. Other possible explanations include: 1) microhabitat conditions such as edaphic and climatic variation with microtopography (Kershaw and Looney 1985, Beatty and Stone 1986) 2) patterns of seed dispersal and vegetative regeneration (Grubb 1977, Hutchings 1986, Pickett and McDonnell 1989), and 3) species interactions (Kershaw 1963, Harper 1977, Kershaw and Looney 1985).

The potential for high spatial variability of compositional parameters has long been recognized (Greig-Smith 1952, Hopkins 1957, Kershaw 1957). The milder decrease in compositional parameter variation with increasing scale may result from the small sample sizes of species-specific measures relative to measures of physical structure. Consequently, the size and intensity of species patches as indicated by standard compositional descriptors are great enough that substantial spatial variation remains for many species at scales approaching 1 ha. For these forests, the 50:1 ratio of landscape area to disturbance patch area does not appear to apply to compositional parameters. A larger landscape area is required for compositional stability.

- Cooper, W.S. **1913**. The climax forest of Isle Royale, Lake Superior, and its development. *Botanical Gazette* **15**: 1–44.
- Greig-Smith, P. **1952**. The use of random and contiguous quadrats in the study of the structure of plant communities. *Annals of Botany* **16**: 293–316.
- Harper, J.L. **1977**. Population biology of plants. Academic Press, London.
- Harmon, M.E., Bratton, S.P. and White, P.S. **1983**. Disturbance and vegetation response in relation to environmental gradients in the Great Smoky Mountains. *Vegetatio* **55**: 129–139.
- Heinselman, M.L. **1981**. Fire and succession in the conifer forests of northern North America. In *Forest succession: concepts and application*. pp. 374–405. Edited by D.C. West, H.H. Shugart and D.B. Botkin. Springer-Verlag, New York.
- Hopkins, B. **1957**. Pattern in the plant community. *Journal of Ecology* **45**: 451–463.
- Hutchings, M.J. **1986**. The structure of plant populations. In *Plant Ecology*. pp. 97–136. Edited by M.J. Crawley. Blackwell Scientific Publications, London.
- Kershaw, K.A. **1957**. The use of cover and frequency in the detection of pattern in plant communities. *Ecology* **38**: 291–299.
- Kershaw, K.A. **1963**. Pattern in vegetation and its causality. *Ecology* **44**: 377–388.
- Kershaw, K.A. and Looney, J.H.H. **1985**. Quantitative and dynamic plant ecology. Edward Arnold, London.
- Levin, S.A. **1989**. Challenges in developing a theory of community and ecosystem structure and function. In *Perspectives in ecological theory*. pp. 242–250. Edited by J. Roughgarden, R.M. May and S.A. Levin. Princeton University Press, Princeton, New Jersey.
- Levin, S.A. and Buttel, L. **1986**. Measures of patchiness in ecological systems. Ecosystems Research Center Publication No. **130**, Cornell University, Ithaca, New York.
- Oosting, H.J. and Billings, W.D. **1939**. Edapho-vegetational relations in Ravenel's Woods, a virgin hemlock forest near Highlands, North Carolina. *American Midland Naturalist* **22**: 333–350.
- Oosting, H.J. and Bordeau, P.F. **1955**. Virgin hemlock forest segregates in the Joyce Kilmer Memorial Forest of western North Carolina. *Botanical Gazette* **116**: 340–359.
- Pickett, S.T.A. and McDonnell, M.J. **1989**. Seed bank dynamics in temperate deciduous forest. In *Ecology of soil seed banks*. pp. 123–147. Edited by M.A. Leck, V.T. Parker and R.L. Simpson. Academic Press, New York.
- Pyle, C. **1988**. The type and extent of anthropogenic vegetation disturbance in the Great Smoky Mountains before National Park Service acquisition. *Castanea* **53**: 183–196.
- Runkle, J.R. **1982**. Patterns of disturbance in some old-growth mesic forests in eastern North America. *Ecology* **63**: 1533–1546.
- Runkle, J.R. **1985**. Disturbance regimes in temperate forests. In *The ecology of natural disturbance and patch dynamics*. pp. 17–33. Edited by S.T.A. Pickett and P.S. White. Academic Press, New York.
- Shanks, R.E. and Clebsch, E.E.C. **1962**. Computer programs for the estimation of forest stand weight and mineral pool. *Ecology* **43**: 339–341.
- Shugart, H.H. **1984**. A theory of forest dynamics. Springer-Verlag, New York.
- Shugart, H.H. **1989**. The role of ecological models in long-term ecological studies. In *Long-term studies in ecology*. pp. 90–109. Edited by G.E. Likens. Springer-Verlag, New York.
- Smith, T.M. and Urban, D.L. **1988**. Scale and resolution of forest structural pattern. *Vegetatio* **74**: 143–150.
- Sokal, R.R. and Rohlf, F.J. **1981**. Biometry. W.H. Freeman and Company, San Francisco, California.
- Watt, A.S. **1925**. On the ecology of British beechwoods with special reference to their regeneration. II. The development and structure of beech communities on the Sussex Downs. *Journal of Ecology* **13**: 27–73.
- Watt, A.S. **1947**. Pattern and process in the plant community. *Journal of Ecology* **35**: 1–22.
- White, P.S. **1979**. Pattern, process and natural disturbance in vegetation. *Botanical Review* **45**: 229–299.
- Whittaker, R.H. **1953**. A consideration of climax theory: the climax as a population and pattern. *Ecological Monographs* **23**: 41–78.
- Whittaker, R.H. **1956**. Vegetation of the Great Smoky Mountains. *Ecological Monographs* **26**: 1–80.
- Whittaker, R.H. and Likens, G.E. **1975**. The biosphere and man. In *Primary productivity of the biosphere*. pp. 305–328. Edited by H. Lieth and R.H. Whittaker. Springer-Verlag, New York.
- Whittaker, R.H. and Levin, S.A. **1977**. The role of mosaic phenomena in natural communities. *Theoretical Population Biology* **12**: 117–139.
- Wiens, J.A. **1989**. Spatial scaling in ecology. *Functional Ecology* **3**: 385–397.