

Discordance in spatial patterns of white pine (*Pinus strobus*) size-classes in a patchy near-boreal forest

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Summary

1 White pines (*Pinus strobus*) in a c. 1 ha near-boreal aspen-red maple stand in the western Great Lakes region, USA, were allocated to five size-classes that were tested for discordance of their spatial patterns (i.e. within-size-class spatial distribution of individuals and spatial associations among different size-classes). The size-classes were 0.5–1 m tall, 1–2 m tall, 2–4 m tall, > 4 m tall but < 20 cm diameter at breast height (d.b.h.), and > 20 cm d.b.h. The size-classes also differed in age. Their spatial patterns were analysed using formulae for spatial autocorrelation with categorical data at neighbourhood (0–14 m) and stand (0–70 m) scales.

2 Size-classes clustered in neighbourhoods that differed in size ranging from 6 m in diameter (size-class 2) to 40 m (size-class 3), suggesting that the pattern of each size-class is due to a different set of environmental factors. Similar size-classes tended to be randomly or positively associated at neighbourhood scales, while the most dissimilar size-classes occupied different neighbourhoods.

3 Size-classes 1 and 2 were located farther away from seed trees than size-class 3, which was farther away than size-class 4. Thus periodic seedling invasion of a deciduous matrix may be followed by the gradual retraction of older size-classes into a refuge near the mature seed source where competition from shrubs and overstorey trees is lower. Although the lack of fine-scale clustering suggests density-dependent mortality within the refuge, few older individuals were found outside this area.

4 Two regeneration bottlenecks may structure white pine populations. First, recruitment into size-class 2 is restricted to small patches (possibly in understorey gaps) within neighbourhoods with abundant size-class 1. Relatively unrestricted recruitment to size-class 3 follows, and after that recruitment to size-class 4 is again limited, this time to refugia with sparse canopy near adult trees.

Key-words: neighbourhood effects, patch dynamics, plant demography, point pattern analysis, spatial pattern, white pine

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Introduction

During the past three decades, ecologists have devoted much attention to the importance of spatial heterogeneity at various scales. Recently, it has been shown that such heterogeneity in the distribution of individual trees within forests can scale-up to global processes, such as biosphere carbon sequestration, through its effects on such system-level and community-level properties as standing biomass and successional species turnover (Pacala & Deutschman 1995). Processes such as seed dispersal (Greene & Johnson 1989; Okubo & Levin 1989; Ribbens *et al.* 1994; Clark *et al.* 1998), seed predation

and pathogens (Janzen 1970; Connell 1971), herbivory (Cantor & Whitham 1989; Thomson *et al.* 1996), within-size-class competition (Silander & Pacala 1985; Kenkel 1988) and neighbourhood influences of overstorey trees (Frellich *et al.* 1993; Kuuluvainen *et al.* 1993; Peterson & Squiers 1995) or herbaceous plants (Maguire & Forman 1983; Burton & Bazzaz 1995) can lead to such fine-scale heterogeneity even within a homogeneous physical environment.

Within a single stand, the combination of these ecological processes with heterogeneity in the physical environment and patchy physical disturbance (Heinselman 1973; Runkle 1981) produces a variety of fine-scale neighbourhoods that differ in their suitability not only for overall forest tree regeneration but also for its different phases (seed germination, seedling growth, short- and

long-term seedling survival; Lamont *et al.* 1993; Schupp 1995). As a result, the various size-classes (seeds, germinants, seedlings, small saplings, large saplings and adults) may occupy different neighbourhoods, and therefore may have discordant spatial patterns (Augspurger 1983; Brodie *et al.* 1995; Wada & Ribbens 1997; Houle 1998). Although such differences are not yet fully understood from a multisize-class perspective, an increasing number of studies has linked differences in patterns of consecutive size-classes to environmental patchiness, distribution of parent adults, and/or within-size-class competition. For example, older size-classes are often clustered within neighbourhoods around dead trees (Stewart & Rose 1990; Moer 1993), while younger size-classes may be more strongly associated with nutrient-rich soil patches (Barot *et al.* 1999). Such shifts in location of patches of different size-classes may occur over time even within a single population, since many tree species establish abundantly on moist, nutrient-rich substrates, but recruit into more advanced stages only within high light patches, that may not correspond to the best sites for germination. Neighbourhoods suitable for different size-classes may also vary in their size, as implied by different spatial scales at which size-classes tend to cluster (Stewart & Rose 1990; Leemans 1991; Barot *et al.* 1999). The youngest seedlings may cluster at submetre scales, but saplings and adult trees may cluster at scales of many metres (e.g. Leemans 1991). Although a small patch of moss under a dense overstorey may be a very suitable environment for the youngest seedlings, a much larger canopy opening may be required for their later survival. Over time, most initially clumped, fine-scale spatial patterns become less clumped (Sternier *et al.* 1986), random (Barot *et al.* 1999) or even overdispersed (Kenkel 1988) due to density-dependent mortality. This will be affected by the scale of operation of factors such as competition, density-dependent herbivory or pathogen attacks, the initial spatial distribution of the population, and the size and spatial distribution of suitable environmental patches. Although such density-dependent mortality operates on fine spatial scales, it can explain why broader-scale distribution of older offspring is often shifted further away from parent trees than that of younger offspring size-classes (Janzen 1970; Connell 1971; Augspurger 1983; Barot *et al.* 1999).

The above studies showed that differently aged size-classes often differ in their spatial patterns due to (i) differences in the sizes of suitable neighbourhoods, (ii) differences in dispersion at the finest spatial scales, (iii) differences in the locations of suitable neighbourhoods within a stand, and (iv) differences in the locations of suitable neighbourhoods relative to seed source. However, no comprehensive comparison of the fine-scale spatial patterns of more than two or three size-classes has yet been undertaken. Moreover, the failure to incorporate fine-scale spatial distribution of trees into a forest simulation model can lead to substantial underestimation of critical stand-scale properties, such as standing tree biomass (Pacala & Deutschman 1995).

Such inaccuracies may occur due to underestimating species that show relatively low shade tolerance, fast growth in gaps and production of abundant widely dispersed seed, and consequently show a complex response to fine-scale environmental patchiness. White pine (*Pinus strobus* L.) is a good example of such a species. While we know that the current distribution of white pine saplings is more fragmented than that of seedlings and adults throughout large portions of white pine's range (Carleton *et al.* 1996), we do not know how spatial pattern may change within a single stand from size-class to size-class to cause such a discordance in distributions. A comprehensive pattern analysis using a large number of relatively narrowly-defined size-classes can help explain the role, spatial scales and temporal changes of spatial patterns in plant populations that occur in complex patchy environments.

HYPOTHESES

We will test the general hypothesis that consecutive white pine size-classes have discordant spatial patterns, by testing the following set of subhypotheses.

(a) *Increase in neighbourhood size.* Individuals can be expected to 'experience' progressively broader-scale environments as they increase in size, resulting in clustering of consecutive size-classes within progressively larger neighbourhoods.

(b) *Increase in fine-scale overdispersion.* Competition for resources from immediate neighbours of the same size-class will increase with size, causing density-dependent mortality over time at the finest scales, and thus leading to increase in average distance among closest neighbours with size-class age.

(c) *Separation of suitable neighbourhoods in space.* Although several different size-classes may be present in a stand at any point in time, they may not occupy the same stand neighbourhoods. Size-classes close in age may occur relatively close to each other in space within the same stand neighbourhood, while size-classes that differ dramatically in age may cluster in neighbourhoods located in different parts of a stand.

(d) *Increase in distance to seed trees.* While different size-classes may occur within different neighbourhoods, older offspring size-classes will be located relatively further away from adult parent trees than younger size-classes (Janzen 1970; Connell 1971).

Methods

STUDY AREA

The natural range of white pine covers an extensive area in the north-eastern USA and south-eastern Canada. Our study site is in the western Great Lakes region at *c.* 47°50' N latitude and *c.* 92°00' W longitude, just outside of the Boundary Waters Canoe Area Wilderness. The topography of the region is a mosaic of rolling hills, rock outcrops, wetlands and glaciated lakes of

varying sizes. The substrate is granitic Canadian Shield covered with shallow and rocky soils. The climate is cold-temperate continental, with mean July temperatures of 17 °C and mean January temperature of -17 °C. The ground is covered with snow from early November to late April, and the average length of a growing season is c. 100 days (Ahlgren 1969).

Patchy physical conditions and disturbance have lead to forests in this region being a mosaic of *Populus tremuloides* Michx., *P. grandidentata* Michx., *Betula papyrifera* Marshall, *Pinus strobus* L., *P. resinosa* Aiton, *P. banksiana* Lambert, *Quercus rubra* L., *Acer rubrum* L., *Picea mariana* (Miller) BSP, *P. glauca* (Moench) Voss, *Abies balsamea* (L.) Miller, *Larix laricina* (DuRoi) K. Koch. and *Thuja occidentalis* L. (Grigal & Ohmann 1975). *Pinus strobus* and *P. resinosa* stands had a complex fire regime in presettlement times with return intervals of 150–200 years for stand-killing fires and 20–40 years for surface fires (Heinselman 1973, 1981). After settlement occurred in the late 19th century, this disturbance regime was altered due to logging and, later, fire suppression policies.

STUDY SPECIES

White pine can live for 450 years and reach 46 m in height and over 100 cm diameter at breast height (d.b.h.) (Wendel & Smith 1990). In mixed forests it often assumes a dominant canopy position and, prior to its extensive logging in the late 19th century, it was the most dominant species in our study region in terms of basal area (22.3%) (Friedman *et al.* 2001). Failure to regenerate after logging resulted in very fragmented distribution of adult white pines, and this is now associated with patchy seedling and even patchier sapling distributions (Carleton *et al.* 1996). Young white pines compete poorly in gaps with fast growing shade-intolerant quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) (Reich *et al.* 1998) and survive poorly in deep shade compared with tolerant species, such as balsam fir (*Abies balsamea*) or white spruce (*Picea glauca*) (Machado 1999). Thus white pine regenerates best on sites where competition is reduced due to low soil quality (Wendel & Smith 1990) or low-intensity surface fires (Frelich & Reich 1995). Its seeds are well adapted to reach such competition-free locations as they can be dispersed by wind more than 60 m within a stand, and more than 210 m in the open. Seed dispersal occurs in August–September and good seed crops occur usually every 3–5 years (Wendel & Smith 1990).

STUDY DESIGN

At the end of summer in 1996, a 90 m × 80 m plot was randomly placed within a mature aspen stand with low-density canopy white pine c. 1 km north from Purvis Lake, north-eastern Minnesota. During 1997, a grid of 90 circular subplots, each with a radius of 1 m, spaced

10 m apart was established within the plot to characterize plot environment. In 1998, the original grid was supplemented by 72 additional subplots (each located between four previously established subplots). On all 162 subplots, percentage cover was estimated visually (to the nearest 5%) for understorey woody vegetation between 0.5 and 2.5 m tall (tall shrubs), understorey woody vegetation under 0.5 m tall (short shrubs), herbs over 0.5 m tall (tall herbs), herbs under 0.5 m tall (short herbs), moss, leaf litter, decaying wood, and bare rock. Besides the overall cover estimate for tall shrubs, percentage cover was also estimated for those woody species within this layer that comprised at least 25% of a particular subplot. Soil depth was measured at five locations near the centre of each subplot using a steel rod with engraved 0–40 cm scale. Depths over 40 cm did not occur very frequently and were recorded as 41 cm. The overstorey composition was characterized by the variable plot sampling method (Bitterlich 1984) at centres of the original 90 subplots. All the subplots and all white pine individuals above 0.5 m tall were mapped using a laser surveying station (DT-100, Topcon, Tokyo, Japan). The size of white pine individuals was measured as height for saplings under 4 m tall, and as diameter at breast height (measured at c. 1.3 m height) for individual pines above 4 m tall. To estimate the age of white pine individuals under 20 cm d.b.h., branch whorls (or obvious growth marks between successive height increments when branch whorls were missing) were counted for individuals within nine parallel transects spaced 10 m apart. The age of adult white pines (> 20 cm d.b.h.) was determined from tree ring counts from a sample of 30 trees within and around our plot taken during a related study (M. Dovčiak, unpublished data).

STUDY PLOT

Overall tree basal area was low (23 m² ha⁻¹) and the distribution of trees within the plot was patchy with a large rock outcrop at the centre and relatively dense forest at northern and southern edges (equivalent to 4 m² ha⁻¹ vs. 44 m² ha⁻¹, respectively). Aspen (mostly *Populus tremuloides* and some *P. grandidentata*) and red maple (*Acer rubrum*) were the most dominant canopy components followed by white pine (*Pinus strobus*) (Fig. 1a). Paper birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), red pine (*Pinus resinosa*) and jack pine (*Pinus banksiana*) were also present.

Surveys of the subplots indicated that approximately half of the plot was covered by 0.5–2.5 m-tall understorey woody vegetation (tall shrubs, Fig. 1b). Beaked hazel (*Corylus cornuta* Marshall) was the most abundant species in this layer, followed by red maple saplings (Fig. 1c). The mean cover per subplot was less than 5% for the remaining species – balsam fir, white spruce, green alder (*Alnus viridis* var. *crispa* Michx.) and mountain maple (*Acer spicatum* Lam.). Leaf litter, short herbs, grasses and short shrubs (< 0.5 m tall) also covered a

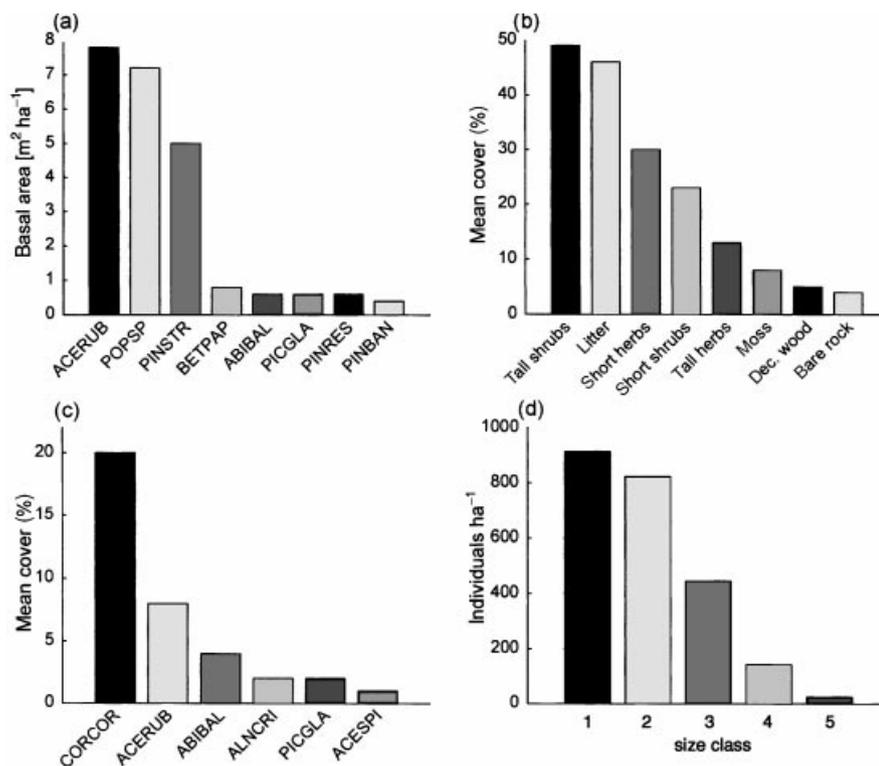


Fig. 1 (a) Overstorey composition, (b) understorey characteristics, (c) composition of tall shrubs and (d) size-class abundance. Study plot characteristics: ACERUB, *Acer rubrum*; POPSP, *Populus* sp.; PINSTR, *Pinus strobus*; BETPAP, *Betula papyrifera*; ABIBAL, *Abies balsamea*; PICGLA, *Picea glauca*; PINRES, *Pinus resinosa*; PINBAN, *Pinus banksiana*; CORCOR, *Corylus cornuta*; ALNCRI, *Alnus crispa*; ACESPI, *Acer spicatum*; tall shrubs, 0.5–2.5 m tall woody vegetation; short shrubs ≤ 0.5 m tall woody vegetation; dec. wood, decaying wood; size-class 1, saplings 0.5–1 m tall; size-class 2, saplings 1–2 m tall; size-class 3, saplings 2–4 m tall; size-class 4, saplings > 4 m tall and < 20 cm d.b.h.; size-class 5, adult trees > 20 cm d.b.h.

significant fraction of the plot while tall herbs, moss, decaying wood and bare rock occupied smaller areas (Fig. 1b). Average soil depth was 14 cm, and it was shallower on the rock outcrop in the plot centre.

DATA ANALYSES

White pine individuals were classified into five size-classes: size-class 1 (0.5–0.99 m tall), size-class 2 (1.0–1.99 m tall), size-class 3 (2.0–3.99 m tall), size-class 4 (> 3.99 m in height, but < 20 cm d.b.h.) and size-class 5 (≥ 20 cm d.b.h.). The assumption that our size-classes differ in age is corroborated by the results of Machado (1999) who worked in a similar ecosystem and found that, on average, saplings categorized into height classes (< 0.5 , 0.5–1, 1–1.5 m) indeed became older as their height increased. Further, our own analyses of branch whorl and tree ring data confirm that all size-classes differ significantly in their mean age; starting at *c.* 9 years (SE 0.3) for size-class 1, *c.* 11 years (SE 0.2) for size-class 2, *c.* 16 years (SE 0.3) for size-class 3, *c.* 23 years (1.3) for size-class 4 and *c.* 99 years (SE 5.0) for size-class 5 (adults).

Spatial relationships among individuals of each size-class, as well as among individuals of different size-classes, were analysed using formulae for spatial autocorrelation with categorical data (Sokal & Oden 1978a,b;

Cliff & Ord 1981; Frelich *et al.* 1993). Distances between all individuals were calculated, and the number of pairs of individuals that were within a prespecified distance class from each other was counted for all within-size-class as well as between-size-class pairs (observed number of pairs). Considering the existing locations of individuals as fixed and assuming their random assignment into size-classes, the expected number of within-size-class and between-size-class pairs was calculated from the total number of pairs within a specified distance class and the proportion of the pairs of interest from all possible pairs. Thus the expected number of pairs between individuals from size-classes of interest is based on the number of individuals within these size-classes, the total number of individuals and the total number of pairs within the specified distance class. The difference between the observed and expected number of pairs in the units of standard deviation, termed standard normal deviates (SND), has a standard normal distribution and the value of SND indicates how strongly the observed spatial pattern departs from randomness (Sokal & Oden 1978a,b). $\text{SND} > 1.96$ signifies more observed pairs at a particular distance class than expected if spatial patterns were random and thus indicates clumping or positive association significant at 95% level, while $\text{SND} < -1.96$ signifies less than expected number of pairs and indicates overdispersion or negative association at

this level. SND values between -1.96 and 1.96 indicate the lack of statistically significant difference between observed and expected number of pairs, or random (neutral) association. Unlike Ripley's K , the SND method does not require the specification of the initial null distribution, such as Poisson. Since SNDs compare the spatial patterns of the individual point types directly to each other, they are explicitly suited for comparisons of spatial patterns of several different point types.

To test for the increase in size-class neighbourhood size and increase in fine-scale overdispersion (subhypotheses a and b), SNDs were calculated for within-size-class pairs of individuals of each size-class for a series of distance classes. Plots of SND values against distance class were constructed for each size-class to evaluate the differences in spatial structure of individual size-classes. To test if different size-classes occupy different stand neighbourhoods relative to each other (subhypothesis c) and relative to seed trees (subhypothesis d), SNDs were calculated for pairs of individuals belonging to different size-classes for the same distance classes used to test hypotheses a and b. SND values were plotted against distance class for each size-class combination to evaluate changes in spatial association between different size-classes across space. Since SND values were calculated for seven distance classes in each analysis, spatial patterns were considered statistically significant only if at least one SND value passed Bonferroni-corrected significance level, in this case when at least one SND value was outside the -2.71 to 2.71 range, corresponding to corrected $\alpha = 0.007$ (Legendre & Fortin 1989).

The above SND analyses were performed at neighbourhood and stand spatial scales. The stand-scale analyses used 10 m distance classes (study grain or resolution), which corresponds to a neighbourhood size that was found best for predicting the influence of the overstorey on sapling growth in aspen-white pine forests (neighbourhood radius = 4–5 m; Peterson & Squires 1995). The largest distance class analysed (study extent) was set to 70 m (i.e. approximately half the distance along the plot diagonal) to exclude pairs between individuals occurring only near plot edges (Rossi *et al.* 1992). Neighbourhood-scale analyses were performed with 2 m distance classes out to a maximum distance of 14 m. This extent of neighbourhood analyses was set arbitrarily to encompass the entire 0–10 m stand-scale distance class, including its transition to the next stand-scale distance class.

Results

The density of all white pine individuals was just over 2300 individuals per ha. The individual size-classes were not equally abundant (Fig. 1d). Size-class 1 was only slightly more abundant than size-class 2, but abundance progressively decreased with age from size-class 2 to size-classes 3, 4 and 5.

STAND-SCALE SPATIAL PATTERNS WITHIN SIZE-CLASSES

The overall stand-scale spatial patterns of all individual size-classes (Fig. 2) were non-random and differed from each other (Fig. 3). The near-random pattern of size-class 1 at 0–10 m contrasted with distinctive clumping of size-class 2, while at 10–25 m size-class 1 was clumped and thus contrasted sharply with the overdispersed pattern of size-class 2 (Fig. 3a). The difference in the SND plots between these two size-classes corresponds well to the difference in their spatial patterns within the stand. Size-class 1 is nearly randomly distributed within a large triangular zone in the north-western half of the stand (hypothetical average patch size of 10–25 m) but occurs at lower density in south-eastern corner of the stand (Fig. 2a). Size-class 2 is restricted mostly to well-defined small patches (average patch size under 10 m) scattered throughout the northern two thirds of the stand (Fig. 2b).

The clustering of size-class 2 only at 0–10 m scales (Fig. 3a) also contrasts with the coarser scale clustering of size-classes 3 and 4 at 0–40 m and 0–25 m scales, respectively (Fig. 3b). The scale of clustering of size-class 3 is coarser than that of size-class 4, reflecting its wider distribution within the stand than the latter, which is concentrated within a smaller and better-defined area approximately along the stand diagonal (Fig. 2c,d). The clumping of size-class 5 (adults) at 10 m (Fig. 3b) resembles the spatial pattern of size-class 2 (Fig. 3a) more than the pattern of other size-classes. However, the spatial pattern of adults is random at scales beyond 10 m, contrasting with the overdispersed spatial pattern of size-class 2.

NEIGHBOURHOOD-SCALE SPATIAL PATTERNS WITHIN SIZE-CLASSES

All neighbourhood-scale spatial patterns of the individual size-classes were non-random and differed from each other as much as the stand-scale patterns (Fig. 4). While the neighbourhood-scale analyses confirmed and further refined descriptions of the spatial structure of the first two size-classes, new trends emerged for the two oldest size-classes. The location of the transition from randomness to clumping of size-class 1 was redefined from the broad 0–10 m stand-scale distance class down to 8–10 m neighbourhood-scale distance class, and the scale of clustering of size-class 2 was adjusted from 0 to 10 m down to 0–6 m (Fig. 4a). While size-class 3 was consistently clumped within the extent of the neighbourhood analyses (Fig. 4b), corresponding well to clumping observable at 0–10 m and 10–20 m stand-scale distance classes, size-classes 4 and 5 showed a trend toward randomness at the scales under 2 m and 7 m (Fig. 4b), that was not apparent examining only stand-scale trends (Fig. 3b). The individuals of size-class 4 were randomly associated with each other at 0–2 m scales and clustered at coarser neighbourhood

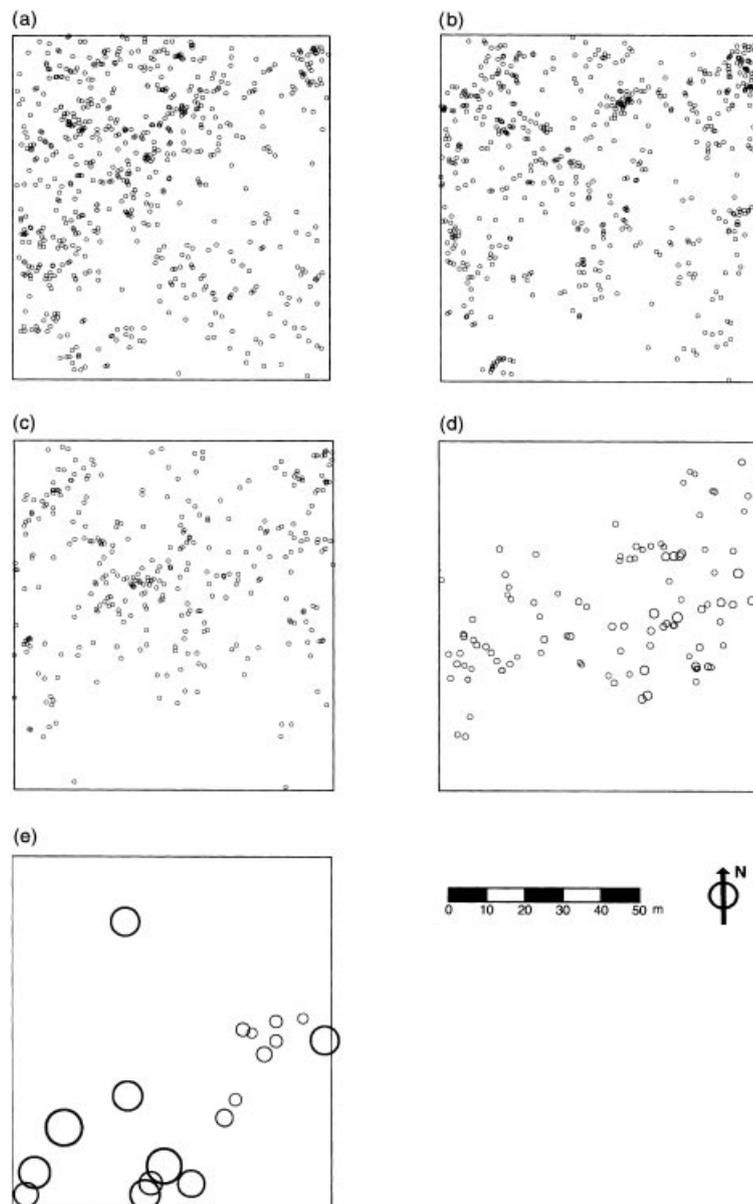


Fig. 2 Spatial distribution of the five white pine size-classes on the study plot. Size-class (a) 1, (b) 2, (c) 3, (d) 4 and (e) 5. Individuals of size-class 4 and 5 are drawn in proportion to their size (diameter at breast height).

scales, while the individuals of size-class 5 were distributed randomly at 0–7 m scales and clustered only at 7–9 m scales (Fig. 4b).

NEIGHBOURHOOD-SCALE SPATIAL PATTERNS AMONG SIZE-CLASSES

Although the within-size-class analyses showed that successive size-classes differed in the scale of clustering as well as in the degree of fine-scale overdispersion, they did not provide information on the spatial structure of size-classes relative to each other. Therefore between-size-class analyses were used to determine to what extent different size-classes tend to occupy the same neighbourhoods within a stand.

The spatial associations between size-classes 1 and 2, and between size-classes 4 and 5 were the only random

neighbourhood associations, while all the other associations were significant and more often negative at Bonferroni-corrected level. The spatial associations between size-classes became progressively more negative as the difference between their developmental stage increased (for example compare size-classes 1 and 2 in contrast to 1 and 5, and size-classes 2 and 3 in contrast to 2 and 5; Fig. 5). When comparing size-class 1 to other size-classes for example, SND values shifted first from random to negative at short-distance classes and then became progressively more negative at larger distances, indicating that this size-class is progressively less likely to occupy the same neighbourhoods with progressively older size-classes. On the other hand, size-classes similar in their developmental stage tended to have less negative (size-class 3 vs. 4), random (size-class 1 vs. 2; 4 vs. 5) and even positive (size-class 2 vs. 3) associations.

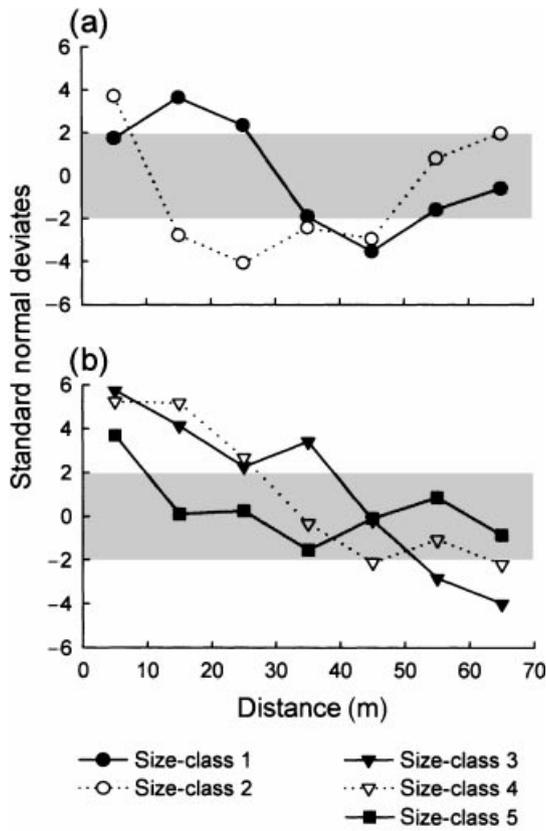


Fig. 3 Stand-scale (10 m resolution; 0–70 m study extent) within-size-class patterns: (a) size-classes 1 and 2; (b) size-classes 3, 4 and 5. The shaded band corresponds to random spatial patterns, while SND values above 1.96 indicate clumping or positive spatial association, and SND values under -1.96 indicate overdispersion or negative spatial association.

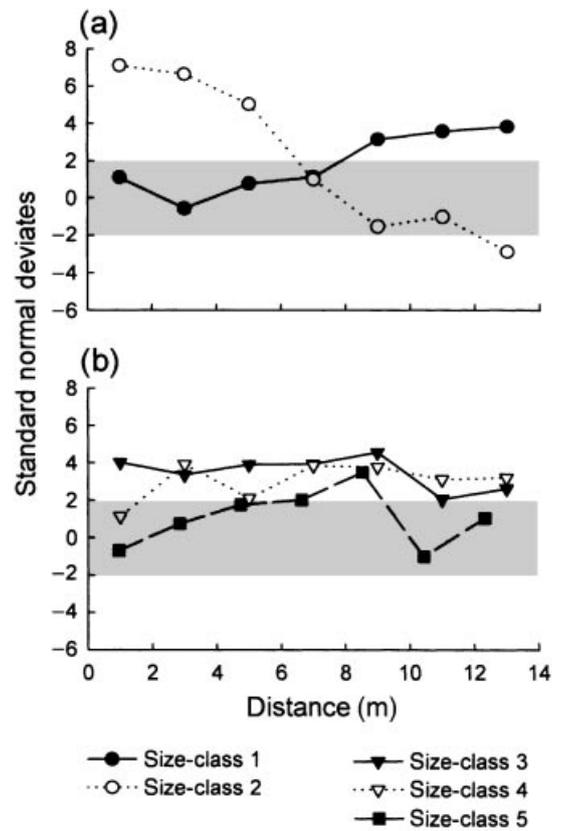


Fig. 4 Neighbourhood-scale (2 m resolution; 14 m maximum distance) within-size-class patterns. Size-classes (a) 1 and 2; (b) 3, 4 and 5. (Significance as in Fig. 3).

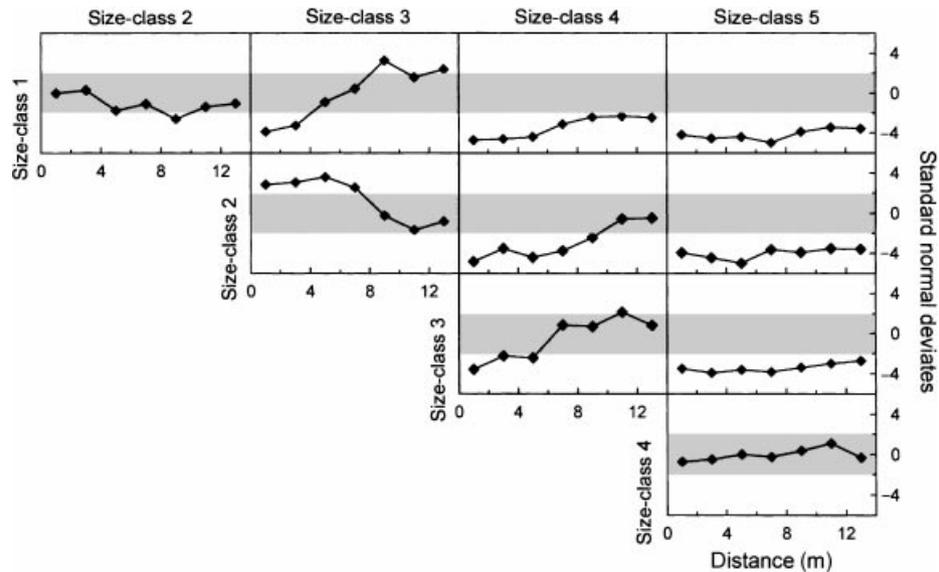


Fig. 5 Neighbourhood-scale between-size-class patterns for all size-class combinations. SND-distance plots are given for each size-class pair and are arranged next to each other in a matrix-like fashion.

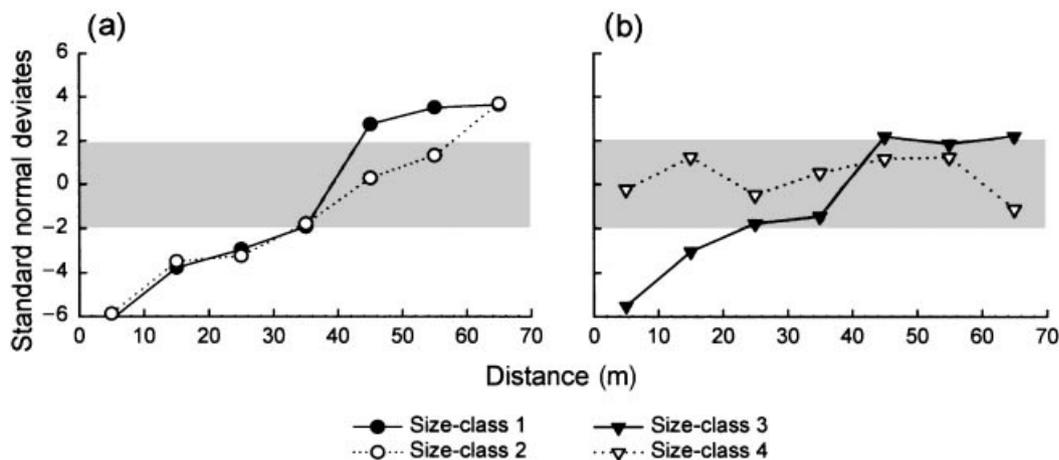


Fig. 6 Stand-scale distribution of offspring size-classes 1 and 2 (a), and 3 and 4 (b) relative to adult trees (size-class 5).

STAND-SCALE SPATIAL PATTERNS BETWEEN ADULTS AND OFFSPRING

Although the neighbourhood-scale between-size-class analyses implied that different size-classes usually do not occupy the same neighbourhoods, the stand-scale distribution of different offspring size-classes relative to seed-bearing adults (size-class 5) is of special interest for species with relatively long-distance seed dispersal, such as white pine. In spite of their quite dissimilar within-size-class spatial patterns, size-classes 1 and 2 were equally negatively associated with seed trees at distances up to 35 m, while they were positively associated with seed trees at large distances (Fig. 6a). The stand-scale association between size-class 3 and adults was negative at distances up to 25 m and near-random at large distances (Fig. 6b). In contrast, size-class 4 was randomly associated with seed trees at all distances tested (Fig. 6b). Examination of the stem maps confirmed these patterns. Size-classes 1 and 2 were most abundant in the north-western-northern portion of the stand (Fig. 2a,b), while the distribution of size-class 3 was shifted closer toward the plot centre (Fig. 2c), and the distribution of size-class 4 was restricted almost entirely to the vicinity of the plot diagonal running north-east to south-west through plot centre (Fig. 2d). At the same time, almost all seed trees occurred within the southern portion of the stand, and most of the large adult trees (i.e. those responsible for the largest part of seed production) occurred near the south-western plot edge (Fig. 2e).

Discussion

The results support our general hypothesis that size-class spatial patterns are discordant, since size-class spatial patterns differed in several aspects: (i) scale of clustering, (ii) degree of fine-scale overdispersion, (iii) lack of association of size-classes, (iv) location of suitable neighbourhoods within a stand, and (v) the distribution of offspring size-classes relative to seed trees. In the following sections we discuss our results in the context of each of our original four subhypotheses.

NEIGHBOURHOOD SIZE AND POTENTIAL LIMITING FACTORS

Although different size-classes were clustered within neighbourhoods of different sizes, the neighbourhood size did not progressively increase with increase in tree size-class, as we hypothesized. However, such neighbourhood size increase could be plausible for subsets of size-classes. Size-class 1 in our study is likely to have the smallest neighbourhoods of all size-classes (neighbourhood size < 2 m, undetectable by our analyses) that are in turn randomly arranged within the larger (10–25 m) neighbourhood. Alternatively, the spatial pattern of this size-class could mean that the conditions for seedling establishment and early survival are homogeneously suitable within the larger neighbourhood. The latter scenario is unlikely, however, since many previous studies linked the success of forest tree establishment to scales under 1 m (Leemans 1991), and to such fine-scale neighbourhood features as rootplate mounds (Stewart & Rose 1990) or decaying logs and stumps (Cornett *et al.* 1997). The larger neighbourhood within which size-class 1 is clustered coincides with thicker aspen-red maple overstorey and indeed exhibits distinct spatial variation in such fine-scale characteristics as soil depth, and the presence of moss patches, decaying stumps, forest duff, herbs and shrubs (M. Dovčiak, P. B. Reich & L. E. Frelich, unpublished data).

The clustering of size-class 2 into relatively small compact neighbourhoods embedded within the larger neighbourhood of size-class 1 indicates that recruitment into size-class 2 is spatially quite limited. In boreal forests, similar clustering of initially randomly distributed young Norway spruce seedlings was attributed mostly to drought-induced seedling mortality outside optimal microneighbourhoods (Leemans 1991). In near-boreal stands with a well-developed shrub layer, the diameter growth and survival of white pine seedlings similar in size to our size-class 1 were found to be negatively affected by competition from shrubs and other saplings (Saunders & Puettmann 1999). Since the understorey shrub layer patchily covers almost 50% of our plot, it is likely that

the recruitment into size-class 2 is limited to relatively competition-free gaps in this layer.

Large neighbourhoods of size-classes 3 and 4 indicate that these size-classes are patterned by coarser-scale phenomena than understorey gaps. Size-class 4 is clustered within a smaller neighbourhood, and it is more restricted to the rock outcrop with discontinuous canopy (unpublished data), than size-class 3. Canopy gaps have been shown to facilitate tree recruitment in many species (Runkle 1981; Leemans 1991; Kneeshaw & Bergeron 1998), and white pine saplings approximately equivalent in size to our size-classes 3 and 4 have been associated with relatively open forests (Carleton *et al.* 1996). We suggest that while the low-density overstorey in our stand allows for the recruitment into size-class 3 more-or-less freely throughout the stand, the recruitment into size-class 4 occurs predominantly on the rock outcrop where the canopy cover is sparse. The further decrease in neighbourhood size for adult trees could be interpreted as further clustering of trees into most optimal neighbourhoods, but such interpretation is not reliable since different spatial patterns of environmental conditions, such as overstorey gaps, may have existed when current adults were at the stage of current size-class 4.

FINE-SCALE OVERDISPERSION AND WITHIN-SIZE-CLASS COMPETITION

None of the size-classes were overdispersed on any of the neighbourhood scales tested (0–14 m), but there was a trend from clumping of size-classes 2 and 3 toward random distribution of size-classes 4 and 5. The individuals of size-class 5 tend to be further apart than those of size-class 4 that, in turn, are further apart than those of size-classes 3 and 2. Although we did not detect the fine-scale overdispersion that has been traditionally interpreted as the sign of within-size-class competition (e.g. Kenkel 1988), such overdispersion may often not be attainable due to initial patchy size-class distribution (Pielou 1962; Sterner *et al.* 1986). However, comparing changes in fine-scale spatial patterns of different size-classes can provide an alternative means for examining whether within-size-class competition may play a role in spatially structuring a plant population. Such an analysis can also indicate at what stage in the population development the effect of within-size-class competition may start to influence fine-scale spatial patterns of a given species through thinning. In our case, within-size-class competition may have started to manifest itself by the trend away from clumped and toward random spatial patterns at the stage of size-class 4, although it may already have been in operation at previous stages when it would be detectable through measuring physiological response or health of individual saplings.

Fine-scale, within-size-class competition interacts with the distribution and size of suitable neighbourhoods. If we assume that size-class 5 underwent similar transformations of spatial pattern to those currently represented

by our chronosequence, the fine-scale clustering at size-class 2 became completely transformed to fine-scale randomness by size-class 5. Even stronger competition-driven transformation of size-class spatial patterns was documented for a savanna palm tree where juveniles were clumped within nutrient-rich soil patches, but adults tended to randomness since they recruited mostly at patch edges where competition was lower (Barot *et al.* 1999).

SEPARATION OF SIZE-CLASSES WITHIN DIFFERENT NEIGHBOURHOODS

The hypothesis that offspring size-classes are separated in space from each other can be accepted since different size-classes did not generally occupy the same neighbourhoods (up to 10 m in diameter) within the stand. While we are not aware of any other studies of among-size-class neighbourhood relationships of offspring, studies of adult–offspring relationships are more common and usually interpret spatial associations as neighbourhood effects of adult trees upon their offspring (Turner & Franz 1985; Frelich *et al.* 1993; Moer 1993). The random association of adults and size-class 4 in our study confirms the suggestion of Frelich & Reich (1995) that white pine adults have neutral effects upon white pine recruitment into large subcanopy classes. However, our results also suggest that there may be negative effects of adults upon size-classes 1, 2 and 3. It has been suggested that white pine litter is rather unfavourable for germination and early seedling survival (Wendel & Smith 1990). It is possible that most seedlings establish away from seed trees but those surviving the unfavourable initial conditions near seed trees may contribute disproportionately more to recruitment due to lower competition from other saplings and shrubs (see Peterson & Squiers 1995; for similar effects of overstorey aspen trees).

It has been shown that canopy trees can modify the environment underneath them (Boettcher & Kalisz 1990) and influence the growth and survival of their offspring (Frelich *et al.* 1993; Kuuluvainen *et al.* 1993; Cornett *et al.* 1997), but such direct neighbourhood effects among offspring size-classes are likely to be less obvious. The negative associations between offspring size-classes occurred over distances as large as 10 m and 5 m (size-class 4 vs. 1 and 4 vs. 3, respectively), which, given the size of individuals, may not be a biologically plausible scale for either direct effects of among-size-class competition, or environmental modification caused by older size-classes. It is likely that these negative associations are due to different affinities that size-classes may have toward neighbourhoods with different underlying environments. Thus, while size-class 4 is restricted to the high light environment of the rocky ridge, size-class 1 is most abundant under relatively dense broadleaf overstorey, where substrate is likely to be moister than on the rocky ridge. Moreover, size-class 4 may have already occupied most of the favourable microneighbourhoods on the

ridge, such as soil pockets, or depressions and cracks in the rock, effectively excluding new arrivals. While radically different size-classes tend to occupy different neighbourhoods, similar size-classes are spatially close. Size-classes 1 and 2 co-occur randomly, perhaps depending on random occurrences of understorey gaps, and size-class 3 usually occurs with size-class 2, possibly reflecting the start of thinning processes within the dense patches of size-class 2. The negative association of size-class 4 with other offspring size-classes, and size-class 3 with size-class 1, describes the gradual shift of the offspring population toward the high light but dry environment of the rock outcrop.

STAND-SCALE OFFSPRING DISPERSION RELATIVE TO SEED TREES

Contrary to our hypothesis, older size-classes were distributed closer to seed trees than younger size-classes. The stand-scale population dynamics – where seedling establishment occurs mostly away from the seed source while seedling survival is promoted close to the seed source – is quite opposite from that described in tropical forests (Janzen 1970; Connell 1971; Augspurger 1983) and rather similar to the refuge dynamics described in temperate forests for trembling aspen (Cantor & Whitham 1989) and in temperate mountain meadows for glacier lily (Thomson *et al.* 1996). However, while the adult populations of aspen or glacier lily were restricted to rocky refugia due to below-ground herbivory, our offspring population gradually retracts into refugia where the competition from other vegetation is reduced. However, the random stand-scale association between adults and size-class 4 means that this retraction is not quite complete. A complete overlap of the refuges for previous and next generation of adult trees is perhaps unattainable, however, due to various changes that may have occurred in the environment within a tree's life span and the potential influence of adults upon their offspring through competition and modification of the environment. Thus consecutive generations of adult white pines may not occupy the same locations, but rather may randomly drift within certain generally suitable neighbourhoods.

SPATIOTEMPORAL DYNAMICS IN NEAR-BOREAL FORESTS

White pine population dynamics, as described in this study, could be best characterized as the process of alternating invasion and retraction. First, following years with high seed crops, white pine seedlings invade a deciduous matrix in the vicinity of seed source 'islands'. However, while these 'islands' served as refugia when current adult seed-producing white pines were at the stage of size-class 4 by limiting the amount of competition from other vegetation, they provide only a mediocre environment for seedling establishment and early survival. As a result, regeneration is more abundant within the surrounding deciduous matrix where mois-

ture and nutrient content are more favourable. Second, as a newly established size-class of pines ages and starts to compete for resources with other vegetation, its distribution retracts into neighbourhood-scale refuge habitats within the matrix due to mortality outside of favourable neighbourhoods. Third, a second retraction to larger stand-scale refugia follows as the size-class starts to experience mortality throughout the deciduous matrix due to competition with canopy trees. In the absence of more recent disturbance, these latter refuge neighbourhoods are likely to overlap partially with those occupied by the current seed trees but they are never quite the same. The lack of any particular refuge type may constitute a recruitment bottleneck and cause regeneration to fail at certain life stages. At least one such bottleneck is suggested by the results from the boreal forests of southern Canada where older saplings were low in abundance and spatially restricted to relatively open forests (Carleton *et al.* 1996).

The invasion–retraction population dynamic described earlier cannot occur in dense white pine patches that established after a fire on better sites, but it may be typical for aspen–red maple stands that contain adult white pines within patches of low-quality habitat. Since such conditions are widely present throughout large portions of the western Great Lakes region, where topography consists of a mosaic of hills, rock outcrops, wetlands and lakes, and deeper soils alternate with shallower soils, it is possible that the invasion–retraction population dynamics pertain to much of the white pine population in this region.

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