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GROWTH VARIATION IN A NATURALLY ESTABLISHED POPULATION OF *PINUS SYLVESTRIS*[1]

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Abstract. We studied the variation in growth of individual trees in a population of *Pinus sylvestris* near Zürich in relation to tree age, size, and local competition. This population established naturally when the drainage pattern in a peat bog was altered after the Second World War. An unusual opportunity to study stand development was afforded when the trees were harvested in 1987 as part of a restoration program. All tree stumps were mapped, and growth since establishment was measured as cross-sectional area of wood in 5-yr intervals, using disks from the base of each tree.

The distribution of cross-sectional area was lognormal over most of the period of growth. Size at the beginning of a time interval was the primary determinant of individual growth during that interval, but age and local competition also had significant effects. Younger, smaller trees were better fitted by an exponential growth model, whereas older, larger trees were better fitted by a Gompertz (sigmoidal) model. Some of the results were very different from previous studies: (1) The spatial distribution of trees was not significantly different from random. (2) Size variability decreased during the course of stand development, even though there was no self-thinning. This was because (3) the density of natural establishment was low, and competition, although clearly detectable, was still relatively weak and symmetric after 45 yr of stand development. Thus, there was no "initial advantage" in competition, and the younger trees, which were still growing exponentially, were able to catch up with the older trees, whose relative growth rates were declining.

Key words: competition; growth rate; Pinus sylvestris; *size variation; spatial randomness; stand structure.*

INTRODUCTION

Variation among individuals is a ubiquitous and central aspect of populations of organisms. Ecologists, foresters, and agronomists have come to appreciate the importance of growth and size variation among individual plants, and researchers have begun to focus on the causes of this variation (Benjamin and Hardwick 1986, Weiner 1988). Here we use data on the growth of individual trees in a stand of *Pinus sylvestris* L. to investigate several potential causes of growth variation within a plant population: age, size, and local competition.

One starting point for the study of growth and size variation in plant populations is the analysis of size distributions during stand development. Empirical and theoretical studies have demonstrated several general trends in size structure during development of relatively even-aged crowded plant populations and have begun to provide explanations for these trends in terms of the growth of, and interactions among, individual plants. One trend that has been observed is that as the biomass of a crowded population of plants increases, the variability (inequality) in the size of individuals increases, until the onset of self-thinning (Weiner and Thomas 1986, Hara 1988). This can occur initially because of variation in intrinsic exponential growth rates (Koyama and Kira 1956), but later, asymmetric competition becomes the dominant factor in generating variation in growth rates and, thus, in increasing size variability (Weiner 1988). Here, we report on a population that shows a very different pattern of development.

To better understand the process of stand development and individual variation, we need to look at the growth, not just the size, of individuals. Plant size is a static quantity resulting from the dynamic process of growth and needs to be understood and analyzed as such. Plant growth has usually been studied at the level of the population or of the average individual, but we need to begin to study the growth of individuals within populations (Harper 1977, Huston et al. 1988, Lomnicki 1992). A major obstacle here is that reasonably good sequential measures of the sizes of all or many individuals within a plant population are difficult to obtain because the best measures of plant size are destructive. Trees in temperate climates leave a record of their growth in their annual growth rings. In the present study we use this record to reconstruct the growth histories of individuals in a population of *Pinus sylvestris.*

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What are the causes of variation in growth within populations? We address several factors that may be of primary importance.

1) The growth of a plant over a time interval is, in part, a function of the plant's size at the beginning of that interval. The quantitative analysis of plant growth (Evans 1972, Hunt 1982) has produced numerous mathematical equations to describe this relationship.

2) Age is also a potential determinant of growth. Age may act indirectly through size (since size and age are correlated), but age may also have direct effects on plant growth that are independent of size. Since most studies have looked at either size or age, the distinction between direct and indirect effects has not been made.

3) Competition among plants can cause variation in growth. Two explanations for this have been advanced. First, individual plants will vary in the degree of crowding they experience and therefore in the degree to which their growth is reduced by neighbors. Numerous models and empirical studies suggest that variation in local competition may be a major cause of variation in plant size or growth (e.g., Mack and Harper 1977, Silander and Pacala 1985, Miller and Weiner 1989, Bonan 1991). Very little is known about the relative importance of variation in local competition in generating growth variation in the field. Second, if competition is "asymmetric" or "one-sided" (Weiner 1990), i.e., if larger individuals have a disproportionate effect on smaller individuals, then differences in size will generate great variation in growth rates. On the other hand, if competition is "symmetric" (i.e., mutual negative effects among plants are size-proportional or less than size-proportional), competition will not change, or may even decrease, the variation in growth rates among competing plants.

To study growth variation in plant populations, we need general models for the growth of individual plants. Several simple models of plant growth have been advanced in the literature. The simplest and most tractable model of plant growth is the exponential model. In such a model the growth of a plant over a short time period, $t \rightarrow t + 1$ is simply its size at time t multiplied by its relative growth rate (RGR, which is often considered to be "intrinsic," i.e., genetically determined [Solbrig 1981]). The implications of an exponential model of plant growth for size variation within a population are relatively straightforward: if each plant grows exponentially, and plants vary in their RGRs (Koyama and Kira 1956) or their ages (Weiner 1988), enormous variation in plant size and absolute growth rate will be generated. In the case of RGR, size variation increases continuously over time, whereas in the case of age, size variation remains constant. The only way competition can be included in an exponential model is if it acts to change the distribution of RGRs among individuals in the population (e.g., Huston 1986), because if the RGR of an individual changes over time, that growth is, by definition, not exponential. Asymptotic (i.e., sigmoidal) growth functions, such as the classical "logistic" or the "Gompertz" equations, provide alternatives to the exponential model (Hunt 1982), and the additional parameters in these models may be better able to describe effects such as local competition or environmental heterogeneity on growth variation. Alternative formulations can reflect alternative hypotheses about the nature of growth in a given ecological context.

In the present study we used a unique data set consisting of increments in cross-sectional areas of individual trees in a natural population of *Pinus sylvestris* to investigate several potential influences on variation in plant growth. We pose the following questions about the process of stand development:

1) What was the spatial distribution of tree locations that resulted from natural colonization?

2) Did size variation increase during the course of stand development?

3) Did trees interact with each other and, if so, over what distances? Were these interactions asymmetric?

4) How did size, age, and local competition influence tree growth?

MATERIALS AND METHODS

Study site

The study site "Hagenmoos" is a degenerated raised bog 15 km south of Zürich (47°14′ N, 8°31′ E; altitude 600 m). It receives 1200 mm mean annual precipitation (Lüönd and Göttlich 1982). In areas of the bog that were never used for peat harvesting, the peat layer is >2 m deep, with a water-permeable sandy clay layer below (Lüönd and Göttlich 1982). The peat layer in the study site was ≈80 cm deep, consisting of 70 cm of sedge peat with 10 cm of *Eriophorum* peat below it. Peat soils in such raised bogs are very nutrient-poor when undisturbed, but drainage leads to an influx of oxygen in the peat layer and to a mineralization of nutrients (Grünig et al. 1986).

During the Second World War the bog was drained and used for peat cutting. After 1945 the abandoned bog was invaded by *Pinus sylvestris, Picea abies,* and *Betula pubescens* (Fig. 1). Such colonization is typical for raised bogs in central Europe that have been drained or disturbed in other ways by human activities (Briemle 1981), and *P. sylvestris* is a common pioneer in such situations. During the next 40 yr the trees grew without direct human influence. In 1987, in an attempt to restore the raised bog, the old drainage ditches were blocked and, with the exception of two areas (which appear as vertically hatched "islands" in Fig. 1), all trees were cut. About 70% of the identified trees were *P. sylvestris.* We selected a 30 × 45 m apparently homogeneous test area (Fig. 1), in which *P. sylvestris* was the dominant species, for the analyses.

Foresters and ecologists who have observed the development of this forest report that there has been very little mortality during the development of this stand

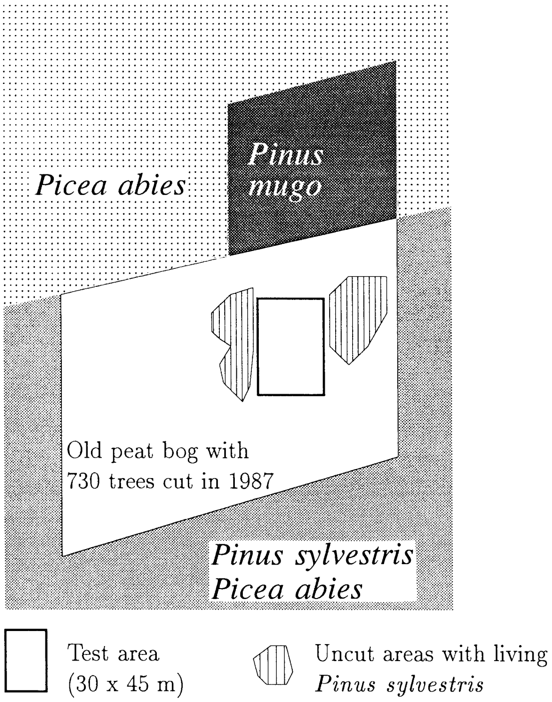

FIG. 1. Study site (adapted from Lüönd and Göttlich [1982]).

(F. Schweingruber, *personal communication*). We estimated mortality by counting all dead trees that were still standing at harvest. The mortality was $<10\%$, and we did not find any dead trees that were decaying. The extremely low mortality rate was probably not the result of density-dependent processes.

Data collection

The heights of the trees were measured from stereoscopic aerial photographs taken just before harvest. After the trees had been cut, the stumps were painted white and aerial photographs of the site were taken. Tree locations were recorded to the nearest 0.1 m from the photographs. If any two neighboring trees were so close together as to be indistinguishable from the photographs, we checked the position of the stumps on the ground to determine whether the pair consisted of separate individuals. If so, we arbitrarily set the distance between them at 0.125 m, but for the analysis of overall spatial pattern we treated them as one individual. Twenty-three stumps that could not be found on the photographs were mapped in the field by measuring the distances from stumps with known locations.

Cross-sectional disks were collected from the stem bases of all trees. In the soil of the study site, *P. sylvestris* trunks do not widen at the base (F. Schweingruber, *personal communication*). The disks were polished and photocopied and the annual growth rings were counted. To date the growth rings, we used extreme years as pointers (especially 1963, which began with an extremely cold period causing a very narrow ring in 1964; Lenz et al. 1988). Five-year growth increments, based on calendar years before the year of harvest, were cut out from the photocopies and measured with a leaf-area meter (LI-COR LI-3000-A). The use of calendar years allowed for cross-sectional analyses of the data at repeated time intervals. By repeating the procedure for some trees, we estimated that the error introduced by photocopying, cutting, and measuring the growth rings was $<2\%$. Disks of five trees that appeared on the aerial photographs were lost during the harvesting process; they are labeled as "missing" in Fig. 2.

Statistical analyses

The spatial distribution of all 211 trees, and the 188 that were *P. sylvestris* (summary statistics are given in Stoll et al. 1991), was tested for complete randomness according to methods described in Bartlett (1964) and Diggle (1983). Bartlett gives a theoretical distribution function for all $((n/2)(n - 1))$ possible interpoint distances between n points for a random spatial distribution (Poisson point process). An empirical distribution can be compared to Bartlett's distribution. We simulated 1000 random spatial distributions of the same size as our real sample and calculated for each of them the maximum differences between their cumulative distribution functions (c.d.f.'s) and Bartlett's c.d.f. The frequency distribution of these 1000 differences between the simulated c.d.f.'s and Bartlett's c.d.f. was then used to assess the significance of the actual difference between the observed c.d.f. and Bartlett's c.d.f. The percentage of the simulated distributions with a greater maximum difference from Bartlett's distribution than the maximum difference between the empirical distribution and the Bartlett's distribution was taken as the significance level (Edgington 1987). Since Bartlett presents the theoretical random distribution only for square areas, we tested the hypothesis of complete spatial randomness in the largest square possible: a 30 × 30 m square within the test area (excluding the area with y [length in Fig. 1] > 30 m). We repeated the procedure on another maximum size (and therefore partially overlapping) square (excluding the area with $y < 15$ m).

We restricted the analyses of growth and size variation among individuals to *P. sylvestris*. Of the 188 trees of this species, 19 were excluded as test individuals, either because they had died before 1987 ($n = 12$), were difficult to age from the growth rings ($n = 4$), or had colonized the site after 1952 ($n = 3$), leaving 169 trees. Individual growth curves were fitted using nonlinear regression. We chose the exponential ($A_t = A_0e^{rt}$) and the Gompertz function ($A_t = A_0{}^{e^{-ct}}$, with $A_0 = ae^{-b}$; Hunt 1982). The Gompertz function is similar to the ordinary "logistic" function except that the RGR decreases with size in a logarithmic rather than a linear fashion. Since an asymptotic model such as the Gom-

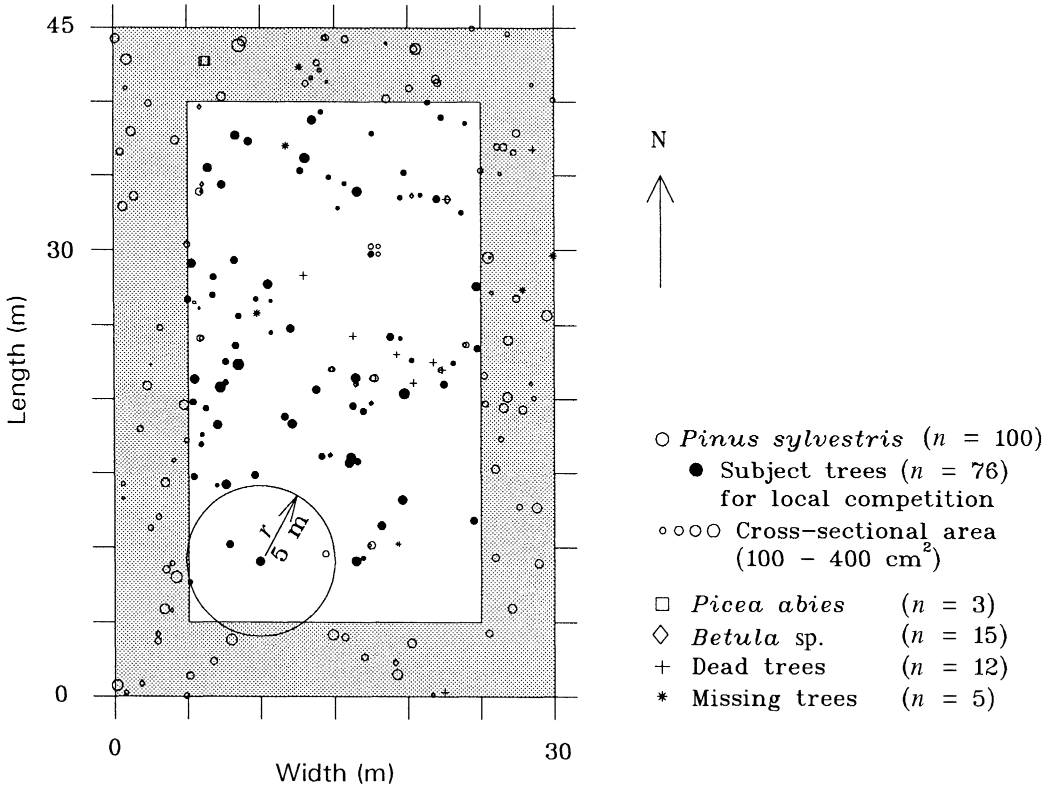

FIG. 2. Spatial distribution of all trees ($n = 211$). The sizes of symbols are proportional to the cross-sectional area of the stem at the time of harvest (1987). The 5-m border zone is shaded.

pertz model has one parameter more than the exponential model, the goodness of fit of these two alternative models was compared on the basis of Akaike's information measure (Sakamoto et al. 1986). For models with normally distributed errors, this is equivalent to using adjusted r-squares.

To investigate the influences of size, age, and local competition on variation in tree growth, we used 76 individuals from a central zone of the test area as subject trees (Fig. 2). Trees from a 5 m wide border zone or trees that grew in pairs (see *Data collection,* above) were used as "neighbors" but not as subject trees. For each subject tree an index of competition (W_r) was calculated as the sum of neighbor sizes (cross-sectional area, A) at the beginning of the growth interval in question, weighted by neighbor distances (d), taken over all neighbors within a circle of ≤ 5 m radius (r):

$$W_r = \sum_{i=1}^{n} \frac{A_i}{d_i},$$

where i represents the ith neighbor and n is the total number of neighbors within the neighborhood. This index has previously been used by Weiner (1984). The growth in stem cross-sectional area during a 5-yr time interval, e.g., 1982–1987, was then modeled by multiple regression as:

$$\begin{aligned}&\log(\text{cross-sectional area in 1987}\\&\quad - \text{cross-sectional area in 1982})\\&\quad = a \cdot \text{cross-sectional area in 1982}\\&\qquad + b \cdot \text{age} + c \cdot W_r + e,\end{aligned}$$

where e, the error term, contains all the influences that have not been measured (e.g., effects of genotype, soil, climate, herbivory) as well as random variation. The errors were tested for residual spatial autocorrelation by spectral analysis, using FORTRAN programs provided by E. Renshaw and E. D. Ford (Ford and Renshaw 1984, Renshaw and Ford 1984). We repeated this procedure for all 5-yr intervals. The use of a measure of crowding at the beginning of the growth interval as an independent variable avoids the major source of non-independence in neighborhood analysis (Thomas and Weiner 1989). We used the logarithm of the absolute growth rate (AGR) to avoid problems of heteroscedasticity and non-normal residuals. We chose to use AGR rather than relative growth rate (RGR) in our analyses, primarily because we believe that AGR is often a better reflection of the biological mechanisms of plant growth, and secondarily, because the use of RGR would have produced skewed error distributions that could not have been made normal with simple transformations. We know of no other basis on which

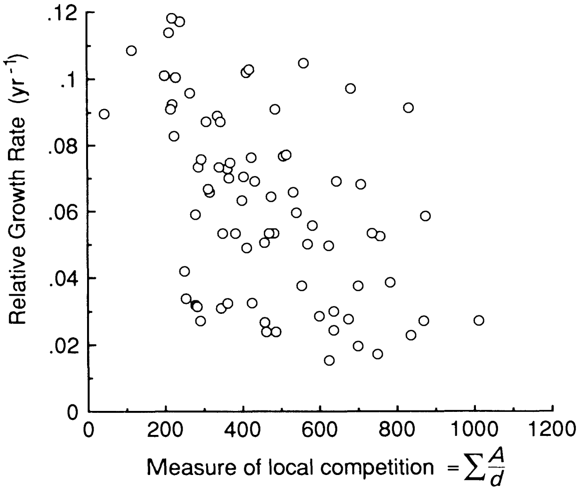

FIG. 3. Negative relationship between growth rate 1982–1987 and the index of local competition. Relative growth rate is shown here for consistency with other studies; analyses are performed on log(absolute growth rate).

to choose between these two alternative measures of growth.

For the interpretation of the relationship between the variables in the model we calculated partial correlation coefficients as measures of "effect sizes" (Cohen 1977). In addition, we constructed a path analysis model using the EQS computer program (Bentler 1989). Path analysis (Kenny 1979) is a method for testing hypothesized causal relationships with partial regression coefficients, and recently has become widely used in ecology and evolutionary biology. Effect sizes and path coefficients can be understood in the following way: if the value of a single "causal" variable were changed by one unit and all other "causal" variables were kept constant, then the "effects" variable would be changed by p units, where p is the effect size or path coefficient.

RESULTS

The spatial distribution of trees in the test area

The average density of trees within the test area was 0.16 individuals/m^2; local density within circles of 5-m radius around subject trees ranged from 0.04 to 0.29 individuals/m^2 (Fig. 2) . The hypothesis of complete spatial randomness over all scales could not be rejected. The maximum difference between the observed and the theoretical (complete spatial randomness) cumulative distance distribution function of between-tree distances was 0.03. Such a maximum difference (or larger) occurred in >176 out of 1000 simulated random spatial distributions. Thus, the probability of obtaining a maximum difference such as we observed under the null hypothesis of complete spatial randomness was >0.17. Similar results were obtained from the other quadrat. Since the test for complete spatial randomness over all scales is weak in detecting nonrandomness at any particular scale (Diggle 1983), we did not look only at the maximum differences between the c.d.f.'s. We also looked for deviation from randomness at all scales by comparing the differences between the theoretical and empirical c.d.f. to the distribution of simulated c.d.f.'s along the entire length of the c.d.f. We found no evidence for deviations from randomness at any scale within the data.

Local competition

After 1977, tree growth was significantly negatively affected by the number and size of neighbors around subject trees as measured by our competition index (e.g., 1982–1987, Fig. 3). Not only the nearest neighbors affected the growth of subject trees: a greater proportion of variance in subject tree growth could be explained if the radius of influence was increased from 2 to 5 m (Fig. 4). Early in the colonizing period, however, there was a positive correlation between the competition index and growth, i.e., early in stand development subject trees with more or larger neighbors grew faster than subject trees with fewer or smaller neighbors (Fig. 4).

Discounting the statistical weighting of neighbors that were smaller than a subject tree in the calculation of the competition coefficient (Thomas and Weiner 1989) did not increase the correlation between the competition coefficient and tree growth. On the contrary, increasing the statistical weighting of smaller neighbors improved the correlation. In a multivariate correlation with log(AGR) as dependent variable, and index of competition, age, and size as independent variables, the highest partial correlation coefficient for the index of competition occurred when the statistical weighting of neighbors smaller than the subject tree was doubled. Therefore, compared to large neighbors, small neighbors had a more than size-proportional effect on subject trees.

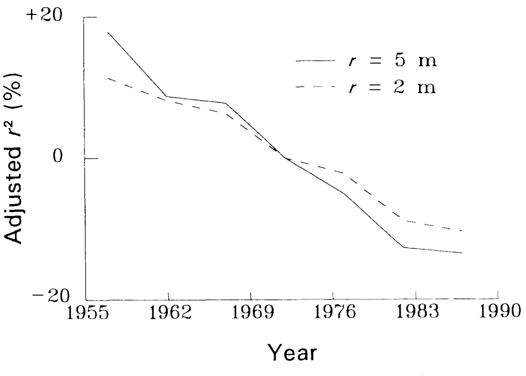

FIG. 4. Explained variance (adjusted r^2) from a univariate regression between the index of competition and absolute growth rate (AGR, log-transformed) against time. The positive and negative regions refer to positive and negative relationships respectively, between the index of competition and log AGR. The two lines show results for two different zones of influence (2 and 5 m) around subject trees.

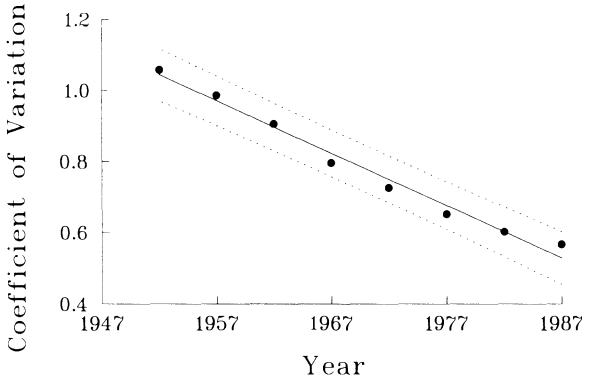

FIG. 5. Changes in the coefficient of variation in cross-sectional stem area over time (n = 76). Confidence lines of 95% (·····) were obtained from linear regression.

Individual growth curves and changes in size variation over time

Both exponential and Gompertz growth curves usually fitted the growth of individual trees in cross-sectional area very well (adjusted $r^2 > 0.90$). The difference in adjusted r^2 for Gompertz and exponential models was <0.01 for 117 trees ("intermediate"-growing trees). For 51 trees the difference in adjusted r^2 was >0.01. In 24 of these cases the exponential model provided a better fit to the observed growth, and for 27 trees the Gompertz model provided a better fit (for one tree the Gompertz model could not be fitted). The percentage of cases better fitted by each model was similar if we did not limit the comparison to those trees that had a ≥0.01 difference in adjusted r^2, but looked at all differences in the adjusted r^2; then 70 out of 168 trees were better fitted by the exponential model and 98 were better fitted by the Gompertz model. The Gompertz- and "intermediate"-growing trees were, on average, significantly older than the exponentially growing trees ($P < .01$). In 1982 both the Gompertz- and "intermediate"-growing trees were also significantly larger than exponentially growing trees ($P < .01$ and $P < .05$, respectively). However by 1987, when the trees were harvested, the exponentially growing trees had almost made up the difference in size. There was never a significant difference between the index of local competition for the exponentially vs. the Gompertz-growing trees.

The coefficient of variation of cross-sectional stem area declined monotonically from 1952 to 1987 (Fig. 5). During the early phase of colonization, the stand was composed of many small and a few large (on average older) individuals (Fig. 6).

The change in a size distribution over time can be described in terms of the relationship between size at time t and absolute growth from time t to $t + x$. Such growth–size relationships have been called "distribution-modifying functions" (Westoby 1982) or "$G(t,x)$" functions (Hara 1988). The relationship for the *P. sylvestris* population between absolute growth rate (AGR) and size (cross-sectional area) was linear on a log–log scale, with a slope <1 (e.g., Fig. 7). This means that the RGR of the larger plants is lower than that of the smaller plants. Therefore the relative difference in size between larger and smaller plants will decrease over time (see Westoby 1982).

The combined influences of size, age, and local competition on tree growth

Log AGR from 1982–1987, log size (cross-sectional area) in 1982, and height were normally distributed,

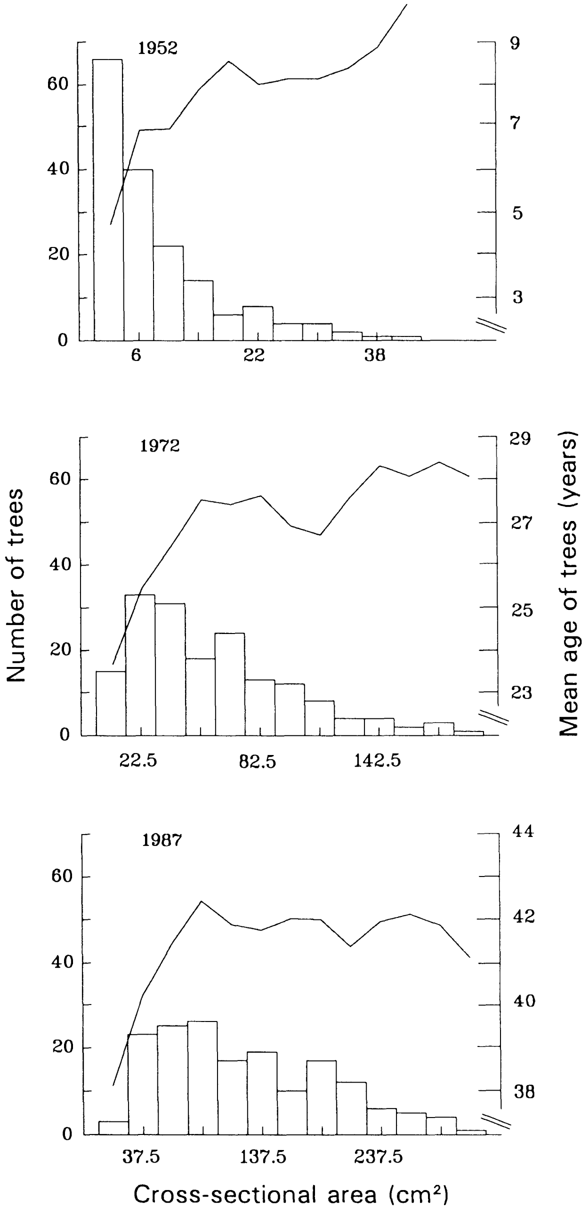

FIG. 6. Size (cross-sectional area) distributions from 1952, 1972, and 1987 (left axes). The lines give the mean ages (right axes) of the corresponding size classes. n = 169 in all cases.

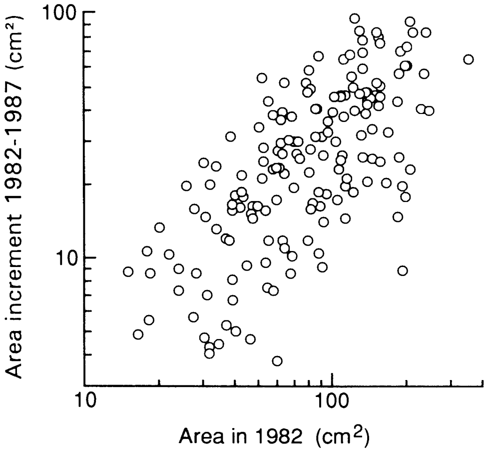

FIG. 7. "Growth-size relationship" for 1982–1987. Relationship between size (cross-sectional area) in 1982 and growth (area increment 1982–1987). Least-squares regression: log(area increment$_{1982-1987}$) = 0.8 log (area$_{1982}$) − 0.151; r^2 = 0.43). The slope is significantly greater than 0 and significantly less than 1.0 (P < .001 in both cases).

while the distribution of tree ages was negatively skewed (Fig. 8). Log AGR from 1982–1987 was positively correlated with log size in 1982, uncorrelated with age in 1982, and negatively correlated with the competition index (W_r) in 1982 (Table 1). In contrast, log size in 1982 was positively correlated with age, but not correlated with the competition index. Both log AGR from 1982–1987 and log size were not correlated with final height, which was only weakly correlated with age. Finally, age and height were positively correlated with the competition index, i.e., old trees had more or bigger neighbors than did young trees, and trees grew taller (but thinner) when they had many and/or large neighbors than when they had few and/or small neighbors.

In the multiple-regression and path models with the log AGR from 1982–1987 as dependent variable, height was not used as an independent variable because it was only measured at the end of the study and therefore could not be considered a cause. The model including the other independent variables, i.e., log size, age, and competition index (in 1982), accounted for 62% of the variation in growth. All independent variables had highly significant influences (P < .001), but based on squared partial correlation coefficients, log size had by far the greatest effect on growth ($r_{\text{part}}{}^2$ = 0.56), followed by age ($r_{\text{part}}{}^2$ = 0.16) and local competition ($r_{\text{part}}{}^2$ = 0.13). A more complete model of hypothetical causal relationships leading to variation in growth was tested by path analysis (Fig. 9). The deviation (an approximate χ^2 value) was reduced from 216.8, df = 10 for the null model to 12.3, df = 4 by fitting six parameters. All path coefficients were significantly different from zero when tested individually (P < .001). Spectral analysis yielded no evidence of spatial autocorrelation in the residuals. Log size in 1982 had the largest influence on growth from 1982–1987. Log size in 1982 was itself still positively influenced by log size in 1952, which was positively influenced by age in 1952, corresponding to the time of establishment of the population. The direct effect of age on growth was negative. Local competition increased with age and reduced growth.

DISCUSSION

The population of *P. sylvestris* described in this paper is one of the only naturally established populations of which we are aware that appears to have a random spatial distribution over many spatial scales. Most natural populations of plants show aggregated spatial distributions at one or more spatial scales (Greig-Smith 1983, Begon et al. 1990), although regular patterns have also been reported (Harper 1977, Fonteyn and Mahall 1981, Phillips and MacMahon 1981). Thus, it appears that no specific factors such as dispersal, environmental heterogeneity, etc., influenced the spatial pattern of this population of *P. sylvestris* in such a way that a regular or aggregated pattern developed at any scale within the data. These findings are remarkable because factors such as those mentioned above usually lead to nonrandomness at different spatial scales (Greig-Smith 1983). For example, dispersal from source individuals (Pielou 1977) or clustering around old stumps (Diggle 1983) can result in aggregated patterns, whereas the process of self-thinning generates a regular pattern among the survivors (Ford and Diggle 1981, Kenkel 1988). Since there were no trees in this area before establishment of the investigated population, colonization must have occurred by dispersal of propagules from the surrounding forests. Dispersal of propagules from sources outside an area may not result in an aggregated spatial pattern (as opposed to propagules coming from trees within the site). Since there was little mortality, a regular pattern could not arise from self-thinning. In the only other case of which we are aware, West (1984) presents evidence for random spatial patterns in several *Eucalyptus obliqua* plots in Tasmania.

Our results support the generalization that some aspects of plant size are often lognormally distributed (Koyama and Kira 1956). Despite strong statistical power in our study, the null hypothesis of lognormality of the distribution of cross-sectional area could not be rejected, except during the period immediately following establishment. Lognormal distributions of plant

TABLE 1. Coefficients of correlation between variables studied. A_{1982} = cross-sectional area of the stem, AGR = absolute growth rate from 1982–1987, W_r = index of competition. *P < .05; **P < .01; n = 76 (for height n = 63).

	log A_{1982}	Age	Height	W_r
log AGR	0.65**	−0.09	0.02	−0.38**
log A_{1982}		0.41**	0.12	−0.02
Age			0.27*	0.35**
Height				0.45**

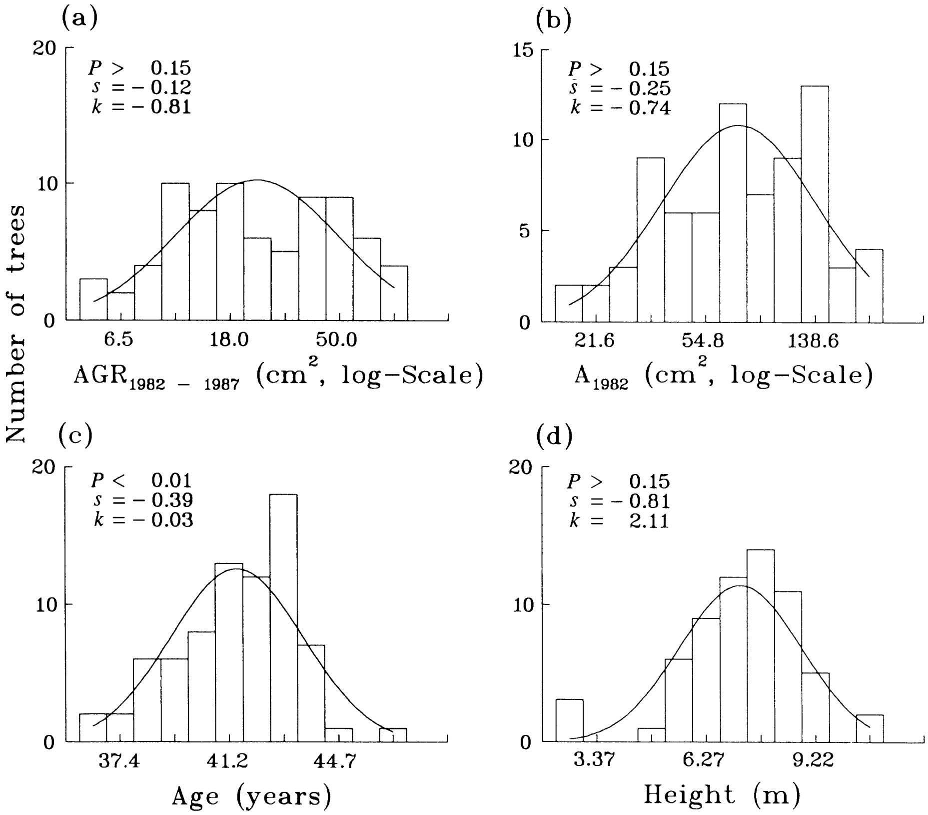

FIG. 8. Distributions of variables used in the multiple regression model. (a) absolute growth rate 1982–1987 (cm²/5 yr), (b) cross-sectional area of the stem in 1982, (c) age in 1987, and (d) height in 1987. Lines are best fit normal distributions. Summary statistics: P = error probability of rejecting normality, s = skewness, k = kurtosis. n = 76 subject trees for a–c, and n = 63 for d.

mass have been reported in several empirical studies (e.g., Ogden 1970, Harper 1977, Rees and Brown 1992), but rarely with statistical support. Most published distributions of plant mass are positively skewed on an arithmetic scale, but negatively skewed on a log scale (e.g., Cannell et al. 1984, Kohyama et al. 1990). The type of distribution depends in part on the measure of size in question, and it has been shown that simple allometric transformations are not a sound basis for inferring the distribution of one size measure from another (Weiner and Thomas 1992). The lognormal distribution of cross-sectional area in the studied population was probably not the result of exponential growth in area of individual trees.

Contrary to what has been seen in other studies and contrary to most recent models, size inequality in this population of *Pinus sylvestris* decreased during the course of stand development even though there was no self-thinning. For example, using a diffusion model to mathematically describe changes in the mass distribution of plants during stand development, Hara (1988) predicts an increasing coefficient of variation until the onset of self-thinning, and this is what has been observed in several studies (Ford 1975, Weiner and Thomas 1986, Weiner et al. 1990). Even if there were significant mortality of which we are not aware, size variability of the trees we studied (individuals alive at the end of the study period) would not be expected to decrease during self-thinning, because the decrease in size variability during self-thinning results from the removal of small individuals.

Decreasing size inequality in the early stages of population development has several important implications. First, it is evidence that not all trees grew exponentially, for if growth is exponential and there is any variation in RGRs, variability (as measured by the coefficient of variation) should increase monotonically. If growth is exponential and there is no variation in RGRs, variation in age can give rise to large size differences, but the size inequality will remain constant over time. Only if age is negatively correlated with RGR can exponential growth of all individuals result in decreasing size variability. Second, the fact that relative size difference due to differences in age *decreases* over time means either that competition was not occurring (or weak), or that competition was "symmetric," i.e., the effect of competition on older, larger trees was equal to or greater than its effect on younger, small-

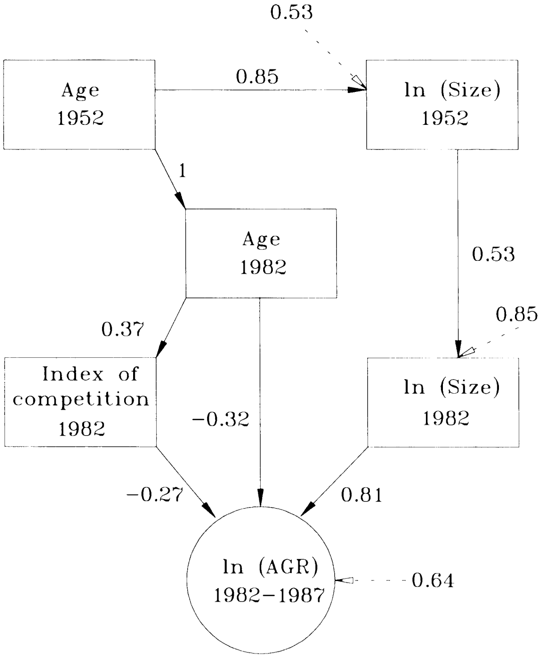

FIG. 9. Path diagram for effects of size, age, and competition on log absolute growth rate from 1982–1987. Size = cross-sectional area of the stem, AGR = absolute growth rate. The numbers give the significant ($P < .001$) path coefficients, whereas the dashed lines represent the disturbances (unknown or unmeasured causes). Total deviance of the model (approximate χ^2) = 12.3 (df = 4, $P = .015$) compared to $\approx\chi^2 = 216.8$ for the null model (df = 10, $P \ll .001$).

er trees. Since the data do provide evidence of competition, we conclude that the latter explanation must hold. Asymmetric competition will give rise to a positive correlation between size and RGR within a crowded population (Schmitt et al. 1987), thus increasing size variability. In symmetric competition, there should be no correlation, or a negative correlation, between RGR and size within a crowded population (Weiner 1990), and that is what we observe in this population. The slope of <1.0 for the log AGR–log size relationship (Fig. 7) means that the relationship between size and RGR is negative. We can say that there was no "initial advantage" (Ross and Harper 1972, Wilson 1988) in competition, and this is strong evidence that competition was symmetric. Symmetric competition seems to occur only when plants are grown for a very short period (e.g., Turner and Rabinowitz 1983), when competition occurs primarily belowground (Weiner 1986, Wilson 1988), or when plants grow taller but not wider (Ellison 1987). A review of data available on the relationship between plant density and size variability led Weiner and Thomas (1986) to conclude that initial competitive interactions in an even-aged stand are symmetric, because belowground competition can begin before shading. Competition becomes asymmetric later as competition for light becomes more important. In this population the density from natural establishment was quite low, and competition, although clearly detectable, had just begun when the RGR of the older plants was starting to decline measurably. Both the random spatial pattern and the relatively low density could be a result of dispersal-limited or safe-site-limited establishment. Our results contrast strongly with those of Knox et al. (1989), who found strong evidence of asymmetric competition in *Pinus taeda* stands before self-thinning. The differences are probably due to the intensity of competition.

In plants, density is meaningful only in relation to size. Trees grow many orders of magnitude in size during their lives; thus the density required for there to be intense competition goes down by orders of magnitude as well. The higher the density at which plants establish and/or the faster the plants grow, the sooner competitive interactions become intense. Under the conditions of relatively low density and slow growth due to the low nutrient soils in our *P. sylvestris* stand, we first see evidence of competition after three decades (Fig. 4), and initial competitive interactions appear to be symmetric, as has been observed in relatively short experiments with herbaceous plants (e.g., Turner and Rabinowitz 1983). Initial competitive interactions, when they did start, were for limiting soil nutrients, and aboveground competition had not yet become important when the stand was harvested. According to this scenario, competition would be expected to increase in intensity and asymmetry if the trees had continued to grow and the leaf area index increased.

Neighborhood analysis demonstrates the influence of competition on growth. The simple measure of local interference, together with age and size, accounted for 62% of the variation in log AGR for the subject trees from 1982–1987, and the path coefficient for the index of competition was −0.27 when variation due to age and size was removed (Fig. 9). Earlier in stand development, however, there was a positive correlation between plant growth and local crowding. Early in the colonizing period, trees may not have been large enough to compete with each other, but there may have been heterogeneity in site quality ("good" and "bad" patches) at a scale larger than an individual (Mitchell-Olds 1987). Such spatial heterogeneity would result in a positive relationship between plant growth and neighbor size. Later, the effect of environmental heterogeneity may still have existed, but competition became more important, with trees suffering more from growing with large neighbors than they gained from being in a good patch.

Discounting the effects of smaller trees (cf. Thomas and Weiner 1989) did not improve the fit of the neighborhood model. On the contrary, discounting the effects of larger trees sometimes resulted in a better fit. In other words, the effect of a neighbor on a subject plant was negatively related to the neighbor's size, i.e., larger neighbors were poorer competitors than smaller neighbors per unit size. This is especially strong evidence against competitive asymmetry.

Despite the statistical difficulties in distinguishing between alternative growth curves, especially when the number of measurements per individual is small, we can say that the growth of some trees in the study population was better described by an exponential model, whereas the growth of other trees was better described by an asymptotic (Gompertz) model. The latter group consisted mostly of older, larger trees. Thus, there was no statistical evidence in the younger trees for the decrease in RGR over time that defines an asymptotic model. If the younger trees had continued to grow longer, their relative growth rates would at some point have begun to decrease, and they might then be better fitted by an asymptotic model. Thus, it appears that younger, smaller trees, still growing exponentially, were able to catch up to the older, larger trees, whose RGRs had begun to decline before 1987. This is only possible if the younger, smaller trees are not suppressed by asymmetric competition. The decline in the RGR of older plants as they grew may have been due to internal growth constraints, because the growth of uncrowded plants is asymptotic (Hunt 1982).

Multiple-regression and path-analysis models provided insights into the role of tree size, age, and local competition in influencing plant growth rate. Not surprisingly, size was the most important factor (Fig. 9). When size was held constant in the statistical model, the tree age had a significant negative influence on growth rate (i.e., older trees grew more slowly than younger trees of the same size). This suggests the existence of an ontogenetic reduction in growth that is not mediated by size. The potential of a young tree for future growth is greater than that of an older tree of the same size.

This stand had several characteristics that were remarkable in view of recent theoretical and empirical work on stand development. They include a random spatial distribution, continuous reduction in size variability during stand development, and symmetric competition. It is certainly possible that the difference between our results and those of other studies is due to some unusual features of the abiotic environment of this forest, such as a physical restriction on the growth of the larger trees due to the clay layer, or a continually improving environment as the bog soil dried and mineralized, which for some reason benefited primarily the younger trees. It is impossible to exclude such possibilities in an intensive study on one forest; additional studies on many stands would be needed to test such hypotheses. But a more parsimonious explanation is that this population differs from others primarily in its combination of tree density, age distribution, and soil nutrient levels, not in the underlying processes that are occurring. In this view, the Hagenmoos population is just a very different "experiment," and therefore one that can provide new information about the underlying processes. In addition to insights this "experiment" may afford, it is also possible that studies on other stands might reveal that these sorts of density, age, and nutrient conditions are not so unusual in the field.

Variation among individuals within populations should be a major focus for population biologists (Harper 1977). In plants, birth and death, the demographic bases of population biology, are mediated by growth. Thus, growth variation is a central aspect of plant population biology. This study demonstrates that multivariate analysis of the growth of individuals in relatively simple "natural experiments" can provide insights into the mechanisms of stand development and variation in individual plant growth.

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