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FORUM is intended for new ideas or new ways of interpreting existing information. It provides a chance for suggesting hypotheses and for challenging current thinking on ecological issues. A lighter prose, designed to attract readers, will be permitted. Formal research reports, albeit short, will not be accepted, and all contributions should be concise with a relatively short list of references. A summary is not required.

Adult recruitment as a function of juvenile growth rate in size-structured plant populations

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Summary. The recruitment of adults in size-structured plant populations will be sensitive to changes in juvenile growth rates when: 1) mortality is high, 2) growth rates are low, 3) the difference between seedling and adult size is large and 4) self-thinning among juvenile plants is negligible. This sensitivity can be quantified by a single parameter in a simple, general expression relating recruitment to growth. The model is demonstrated for the prediction of young spruce tree densities on small plots, and the calculation of the parameter is shown for two published demographic studies. The model can also predict features of population response to an environmental gradient, such as long tails or abrupt cut-offs, even when these features are not found in the physiological response to the gradient.

The rate of escape from the vulnerability of small size is a critical factor in the life cycle of many plant species. Recruitment into the adult population may depend on many factors such as seed rain, germination rates, local environmental heterogeneity and episodic herbivory; but, in populations where the mortality rate is concentrated in the early stages of growth, adult recruitment may be highly sensitive to differences in growth rate. Some forest dynamic simulation models (Pastor and Post 1985) assume a linear relationship between growing conditions in the understory and recruitment into the adult tree population, but the form of this relationship, while plausible, is arbitrary. The purpose of this paper is to derive a simple relationship between the growth and mortality rates of juvenile plants and the rate of recruitment into the adult population. I apply the model to a field study of young spruce tree densities, and two published demographic studies of long-lived perennials.

Theory

The assumptions made in the following derivations apply to populations of long-lived perennials, and possibly to annuals with size-structured demography within the growing season. Growth and mortality are treated as continuous processes unaffected by the size or density of the surrounding members of a cohort; there is no self-thinning. This assumption may often hold for small plants and/or low sowing densities. Notice that crowding by other species or cohorts is not ruled out; only self-thinning within the cohort.

Constant mortality and growth rate

Consider the fate of a cohort of seedlings, of initial population N_0 at time $t = 0$. If the mortality rate k is constant, the remaining population at time t is:

$$N = N_0 \exp(-kt) \quad (1)$$

Each individual plant has initial size B_0 (arbitrary units) at $t = 0$, and for simple exponential growth the size of an individual at time $t > 0$ is:

$$B = B_0 \exp(rt) \quad (2)$$

where r is the rate of growth. The time taken to grow from B_0 to a 'mature' size B_x is then:

$$t_x = \frac{\ln(B_x/B_0)}{r} \quad (3)$$

Substituting (3) into (1) gives the number of seedlings surviving to size B_x.

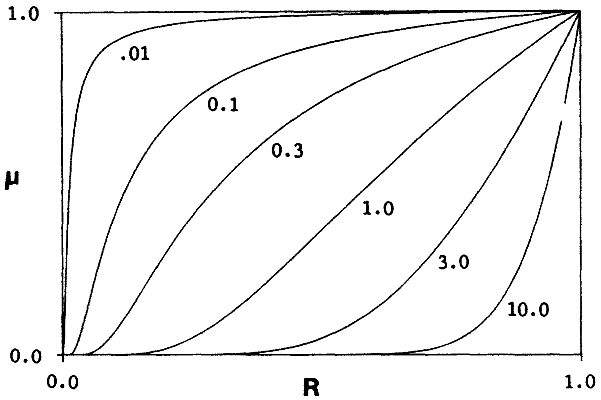

Fig. 1. Recruitment as a function of growth rate for different values of the shape parameter α. Recruitment (μ) and growth rate (R) are standardized as proportions of fixed values.

Standardizing around a particular value for r (r′) gives the following relationship, which describes the sensitivity of N to changes in r:

$$\mu = N/N' = \exp(\alpha(1-1/R)) \qquad (4)$$

where N′ is the number surviving to size B_x at $r = r'$, R is r/r', and

$$\alpha = kt_{x,r'} \qquad (5)$$

where $t_{x,r'}$ is the time to reach size B_x at $r = r'$. Fig. 1 shows the form of eq. (4) for $0 < R < 1$ at various values of α. I will show, by relaxing some of the assumptions of the preceding derivation, that eq. (4) is a rather general relationship.

Mortality varying with growth rate

The mortality rate is often higher under poor growing conditions. If k is a decreasing linear function of r between 0 and r′:

$$k = k_{max} - \frac{k_{max}-k_{min}}{r'} r \qquad (6)$$

then:

$$N' = N_o\exp\left[k_{min}\frac{\ln(B_x/B_o)}{r'}\right] \qquad (7)$$

and eq. (4) applies, with:

$$\alpha = (k_{max}\ln(B_x/B_o))/r' \qquad (8)$$

Mortality varying with size

Size-dependent mortality rates are commonly reported in the demographic literature (Harper 1977, Young 1984). Assume k is a function of size, and that between B_o and B_x this function is well approximated by a polynomial (such as a Taylor series) of degree m:

$$k = \sum_{i=0}^{m} a_i B^i \qquad (9)$$

the number of plants surviving to B_x is:

$$N = N_o\exp(-\int_0^{t_x} kdt) \qquad (10)$$

and for simple exponential growth (eq. 2):

$$\int_0^{t_x} kdt = \frac{1}{r}\left[a_o\ln(B_x/B_o) + \sum_{i=1}^{m}\frac{a_i}{i}(B_x^i - B_o^i)\right] \qquad (11)$$

Eq. (4) still applies and α is given by eq. (11) with $t_x = t_{x,r'}$, $r = r'$.

Linear growth

In some size ranges and with some measures of size, growth may be best approximated by a linear equation:

$$B = B_o + rt \qquad (12)$$

For constant k, eqs (4) and (5) both apply, with:

$$t_{x,r'} = k(B_x - B_o)/r' \qquad (13)$$

It can also be shown that eq. (4) holds if k is allowed to vary with size (as in eq. (9)), or with r (as in eq. (6)).

The interpretation of α

High values of α are associated with high juvenile mortality, low growth rate, a long period of juvenile growth, and a large difference between the initial and adult sizes. When $R = 1$, $d\mu/dR = \alpha$, so α is also a measure of the sensitivity of N to changes in the growth rate near r′. When $\alpha >> 1$, it may be possible to explain much of the variance in adult recruitment rates by differences in growth rates alone. For small values of α, factors related to differences in initial population size (N_o) are likely to be more important.

Spruce tree recruitment

In most forest studies, trees begin to be counted as adults when they reach breast height (1.3 m). This is also the size at which trees in forest simulation models

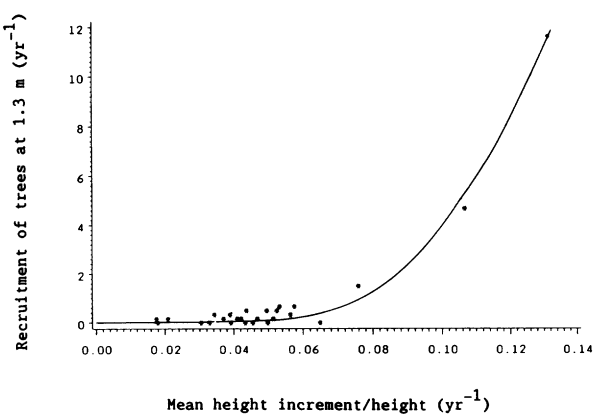

Fig. 2. Recruitment rate (yr^{-1}) of spruce trees to a height of 1.3 m as a function of mean height increment/height for the twenty-six study plots. Curve is eq. (4) fitted by non-linear least squares regression.

of the 'gap model' type (Shugart 1984) are normally introduced. Most or all of the conditions for expecting high α values are likely to be met by recruitment of adult trees at breast height. The mortality of small trees is typically high (Harper 1977, Oliver and Larson 1990), and seedlings may take years or even decades to reach a height of 1.3 m. Based on these considerations, the relationship between recruitment of trees at breast height and growth rate should be curved upward (as in Fig. 1 for $\alpha > 1$), and differences in growth rate should account for a large amount of variance of recruitment rates.

This conjecture was tested for spruce tree regeneration in a southern boreal forest. The study area is an environmental monitoring site in the eastern part of Tiveden National Park in S. Central Sweden. Twenty six circular study plots (10 m radius) were visited, covering a wide range of canopy densities and soil conditions. For each plot, the number of small trees (between 0.5 and 2.25 m height) was recorded. The height increments of the previous four growing seasons were recorded for each small tree to the nearest 0.5 cm. The maximum height increment possible appeared to be linearly correlated with height, so the growth rate of each tree was calculated as the ratio of mean annual height increment to the mean height of the previous four growing seasons. The average growth rate was then calculated for each plot. Recruitment was the number of trees reaching 1.3 m height in the previous four years of growth plus the next two years (based on extrapolated mean growth rates for each tree), averaged to a mean rate per year for each plot. The recruitment and average growth rate of one plot with a high density of small trees were based on a subsample from a 1.8 m wide strip running N-S through the middle of the plot.

The relationship between the number of small trees and the mean height increment/height is curved upward as predicted (Fig. 2). Eq. (4) was fit to the data by non-linear least squares estimation, giving a value of 3.51 for α, when $r' = 0.1315$ yr^{-1} and $N' = 11.6$ trees yr^{-1}. The fitted equation accounts for 98.5% of the variance in N.

Demographic studies of long-lived perennials

Some demographic studies of long-lived perennials include the information necessary to calculate α values without a direct measurement of the relationship between growth rate and recruitment. I demonstrate this for two published studies.

Weller (1985) recorded demographic and growth data for *Lithospermum caroliniense* on the sand dunes of Lake Michigan, U.S.A. For one of the sites (Dune 2), the mean age at first flowering was ~3.5 yr. The age at first flowering was generally >4 yr at a poorer site, implying that maturity is probably at least partly controlled by the accumulation of biomass. The mean annual survival rate was ~73%, giving $k = 0.31$. By eq. (5), $\alpha = 1.1$. This level implies that some variation in adult recruitment (adult = flowering) may be accounted for by growing condition variations, but controls on N_O may be equally or more important. In fact, Weller (1985) reports that the burial depth of seeds is a strong predictor of seedling emergence and subsequent population density.

Young (1984) reported growth and demographic data for rosette shrubs on Mt. Kenya. For individual rosettes of *Lobelia keniensis*, the overall size is well represented by the length of the largest leaf. Rosettes under 2 cm in size had a growth rate of 0.16 cm yr^{-1}. By eq. (12) ($B_x = 2$ cm, $B_o = 0$ cm), t_x was ~12.5 years. The mortality rate was ~23% yr^{-1}, giving $k = 0.26$ yr^{-1} and $\alpha = 3.27$. The recruitment rate of individuals >2 cm should therefore be fairly sensitive to growing conditions.

Discussion

I pointed out earlier how the model derivation depends on the assumption that self-thinning within the cohort is negligible. Self-thinning sets an upper limit on the density of plants at a particular size, making the recruitment rate insensitive to changes in the growth rate. A flat relationship between adult recruitment and growth rate therefore does not distinguish between a population with a low α and a population with juvenile self-thinning.

Eq. (4) is one explanation for the difference between the physiological and population response of a species to an environmental gradient. Physiological responses to environmental factors may be almost parabolic (e.g.

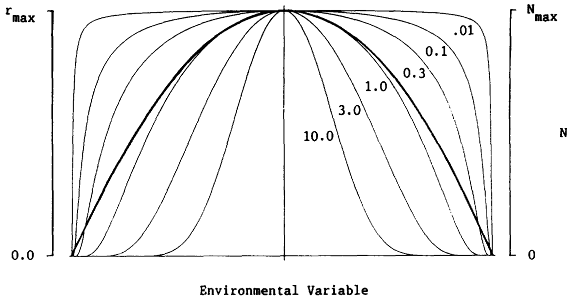

Fig. 3. Growth response (dark curve) and population responses (by eq. 4) for different α values plotted against a hypothetical environmental variable.

net photosynthetis vs temperature: Larcher 1980), but species abundances on environmental gradients often have extended tails (e.g. Austin 1987). Fig. 3 shows a parabolic growth response curve to an environmental gradient and the corresponding values of μ for various values of α; for $\alpha > 1$ the μ curves are close to a classic 'bell' shape. A species with a low α value could be abundant right up to the limits of its environmental tolerance; this pattern was reported for *Lactuca serriola* in Great Britain by Prince et al. (1985). Differences between physiological and population responses can arise without density-dependent effects or interspecific competition.

The relationship described in this paper is a fairly general consequence of size-structured as opposed to age-structured demography. One practical application of the theory is to provide a rational basis for modeling tree recruitment in forest dynamic simulation models. More generally, the model suggests further linkages between demographic patterns and the ecosystem processes that control individual growth rates.

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