

GROUP SELECTION IS IMPLICATED IN SELF-THINNING

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ABSTRACT: The frequency of mortality was studied in 18 full-sib families of Douglas-fir grown at a high density. Variation in the frequency of mortality among these families was interpreted as a genetic response of the families to density stress, and thus a form of density dependent selection or self-thinning. The intensity of selection and change of fitness due to selection were 0.0664 and 0.0044 respectively. It was concluded that the rate of self-thinning in natural populations may have a genetic component; self-thinning represents a major form of biological (viability or zygotic) selection, and it is analogous to Wright's inter-demic or group selection.

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Introduction

The self-thinning rule (Harper, 1977; Westoby, 1984) describes the ratio of relative growth and density dependent mortality rate of competing individuals in even-aged single species plant populations. At high densities, individuals with superior competitive abilities suppress and gradually eliminate the less competitive individuals from the population (Harper, *op. cit.*; Westoby, *op. cit.*). Differential biomass accumulation of taller and suppressed individuals precedes a number of changes in biomass components and determines mortality rates in self-thinning populations. Thus, the self-thinning rule predicts the demographic (natural selection) consequences of the various phases of biomass accumulation within populations (Westoby, 1984). The frequency of mortalities may vary among self-thinning populations just as individuals do within populations. The probabilities of the survival of individuals and populations under environmental stresses may be a function of their relative fitnesses (Bradshaw, 1984). Survival probabilities of individuals are quantified in terms of fitness (Fisher, 1930), or as a property of their genetic composition in relation to the environment (Christiansen, 1984), or both. Furthermore, it has been argued that differential mortality among populations may indicate inter-population selection (Lewontin, 1961). Similarly, Antonovics and Levin (1980), and Westoby (1984) have suggested that the differential mortality of individuals within and among self-thinning populations may be a form of density-dependent self-regulating mechanism and thus an important selective force in plant populations.

The density-dependent mortality rate among competing individuals could be monitored demographically in experimental populations by exposing a known number of individuals from genetically well defined populations to a constant density. This would facilitate the measurement of the relative fitness of populations, in response to density stress, in terms of Malthusian parameters such as age specific birth and death rates. Demographic approaches towards measuring selection intensities in plant populations have been suggested (Solbrig, 1980; Bradshaw, 1984). The objectives of this study were to examine the relative changes in biomass accumulation and the frequency of mortality, and also to estimate some quantitative parameters of selection in several self-thinning families of coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco. var. *menziesii*) seedlings. Seedlings were used as a model system, because evolutionary changes at the juvenile stages can be used as predictive indices of adult life-histories (Prout and McChesney, 1985; Strauss and Ledig, 1985).

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Materials and methods

The experimental material consisted of 18 full-sib families derived from pair-wise controlled crosses among open-pollinated trees. Twelve-day old germinating seeds from each of these crosses were transplanted providing equal spacing in a 50:50 peat vermiculite mixture placed in 6 cm wide circular styrofoam seedling containers at a density of six seedlings per container ($2124/m^2$) with 10 replications (containers). The density was maintained until the cotyledons completely covered the surface of the container, which took approximately two weeks from the day of transplantation. The seedlings then were grown under green house conditions for 170 days (5.6 months). Plant protection and irrigation were provided to the seedlings; hence, there was no incidence of pests or drought during their growth. In jack pine, although both hierarchical growth and mortalities were observed at higher densities (10 seedlings per pot = $3540/m^2$), virtually no mortality was observed at the lowest density (1 seedling per pot = $354/m^2$) (Govindaraju, 1984 and unpublished observations). Therefore, it was inferred that mortality among seedlings in the present study was largely due to density-dependent factors. Seedlings were harvested at the end of the study ignoring the edge effects, and measurements were immediately made on the height and fresh weight (biomass) of individual seedlings. Mortalities were recorded for each replication and for each family. Plants from each of the families were grouped as either dominant or suppressed, based on mean height (West and Borough, 1983; Govindaraju, 1984). Competition influences the morphology of competing individuals and leads to asymmetric distribution of plant sizes, which has been termed "size hierarchy." The differences in size (dominant vs suppressed) among competing individuals has been suggested to reflect self-thinning (Harper, 1977). Accordingly, variation in both height and mortality at the end of the study were taken as indices of self-thinning (Harper, Loc. cit; Gorham, 1979). The following assumptions were made: a) families and populations are synonymous (Falconer, 1981; Slatkin, 1981), and hence, all the 18 families represent a metapopulation (Wilson, 1973) of populations (self-thinning systems), and b) self-thinning is a form of density-dependent regulation of populations (Antonovics and Levin, 1980; Anderson and Arnold, 1983); thus, various families used in this study approach the self-thinning rule at different rates, largely as a function of genetic differences in density responses among respective families.

The mortality (q_i), was defined as $(1_x - 1_{x+1}) / 1_x$; where, 1_x and 1_{x+1} are the initial and final densities. Following Lewontin (1961; 1979), the proportion of individuals survived ($r_i = 1 - q_i$) of a given family was used as an index of fitness (w_i) of that family. The ratio between the total number of survivors and the original number in the metapopulation was used as an index of mean fitness. Because selection at the population level is defined as the genetic change brought about by differential extinction (Christiansen, 1984), the "change of mean relative fitness due to selection," during self-thinning was calculated using the following formula, $CFS = (\bar{w} - \bar{w}_0) / \bar{w}_0$ (O'Donald, 1970); where, CFS is the change of fitness due to selection (mortality during self-thinning), $\bar{w} = (w_i n_i) / n_i$, and n_i is the survival at 170 days. The frequencies of mortalities of families were used to calculate the selection intensity according to the formula $I = (w_0 - \bar{w}) / w_0$ (Van Valen, 1965); where w_0 (highest w_i value) is the optimum fitness, and \bar{w} is the mean fitness for all the families combined. The relationship between average biomass production per individual and the rate of mortality among the sibships was analyzed using the Spearman rank correlation (r_s).

Results and discussion

The dominant and the suppressed groups differed significantly for height and weight (biomass) indicating that in self-thinning populations dominants assimilate relatively greater biomass than suppressed individuals (Table 1). The

Table 1. Descriptive statistics for various parameters among self-thinning families of Douglas-fir.

Family	Total No. of Individuals $N_i=1 \times$	Biomass components				Mortality (q_i)	Proportion of individuals survived $r_i=1-q_i$
		Suppressed		Dominants			
		(N') Height (cm)	Weight (g)	(N'') Height (cm)	Weight (g)		
1	60	19 11.95 \pm 3.19	1.03 \pm 0.56	35 17.91 \pm 1.55	2.18 \pm 0.44	.100	.9000
2	60	28 10.11 \pm 1.86	1.10 \pm 1.86	31 15.02 \pm 1.40	1.78 \pm 0.45	.016	.9833
3	60	24 12.08 \pm 2.89	1.27 \pm 0.63	33 17.35 \pm 1.75	2.00 \pm 0.49	.050	.9500
4	60	29 10.27 \pm 2.04	1.08 \pm 0.37	30 14.07 \pm 1.38	1.77 \pm 0.35	.016	.9833
5	60	25 13.28 \pm 1.88	1.32 \pm 0.41	23 18.41 \pm 2.22	2.47 \pm 0.82	.200	.8000
6	60	26 10.67 \pm 2.50	0.92 \pm 0.36	33 16.31 \pm 1.30	1.91 \pm 0.54	.016	.9833
7	60	26 10.43 \pm 1.72	0.93 \pm 0.27	27 16.92 \pm 2.08	2.08 \pm 0.54	.116	.8833
8	60	28 7.63 \pm 1.42	0.80 \pm 0.30	29 11.59 \pm 1.58	1.59 \pm 0.43	.050	.9500
9	60	25 11.38 \pm 2.23	1.14 \pm 0.48	30 16.43 \pm 1.47	2.15 \pm 0.43	.083	.9166
10	60	29 12.58 \pm 2.22	1.33 \pm 0.46	25 19.22 \pm 2.15	2.55 \pm 0.88	.100	.9000
11	60	27 11.77 \pm 2.74	1.88 \pm 0.42	31 17.72 \pm 1.50	2.35 \pm 0.54	.033	.9666
12	60	27 11.68 \pm 2.18	1.33 \pm 0.66	29 16.62 \pm 1.22	2.34 \pm 0.61	.066	.9333
13	60	23 13.72 \pm 3.22	1.45 \pm 0.69	33 19.41 \pm 1.27	2.54 \pm 0.59	.066	.9333
14	60	22 9.37 \pm 2.78	0.91 \pm 0.49	30 15.98 \pm 2.63	2.20 \pm 0.73	.133	.8666
15	60	22 14.79 \pm 2.08	1.43 \pm 0.51	25 19.73 \pm 1.48	2.36 \pm 0.79	.216	.7833
16	60	26 13.42 \pm 1.87	1.31 \pm 0.49	32 18.85 \pm 1.53	2.14 \pm 0.41	.033	.9666
17	60	21 13.01 \pm 2.52	1.42 \pm 0.50	36 18.02 \pm 1.21	2.35 \pm 0.53	.050	.9500
18	60	23 10.74 \pm 3.84	0.82 \pm 0.66	29 19.47 \pm 2.42	2.13 \pm 0.80	.133	.8666
Mean	25.00	11.54 ¹	1.15 ³	30.00	17.18 ²	.082	.9180
S.D.	2.87	2.93	0.53	3.47	2.58	0.63	

¹ 2Significance ($p \leq 0.001$)³ 4Significance ($p \leq 0.001$)

differential accumulation of biomass subsequently brings about numerical changes through mortality, in agreement with previous reports (Harper, 1977; Westoby, 1984). The numerical variations (demographic response) of each population to density stress is shown in the frequency of mortality (q_1) at a constant density. Mortality varied significantly among families ($\chi^2 = 42.65$, $p \leq .01$), ranging from 0.016 to 0.216. The variation in the monthly mortalities among families indicates that the rate of self-thinning varies among families. The variation in biomass production between the dominants and the suppressed groups, and the associated mortalities demonstrate the links that exist between developmental processes and demographic responses in relation to self-thinning. The relationship between average biomass production per individual, and the rate of mortality among families was positive ($r_s = 0.4094$; Fig. 1), and approached significance ($p \leq 0.0916$). Because the self-thinning rule also predicts a positive relationship between total biomass and mortality, the results support the predictions of the self-thinning rule (Westoby, 1984).

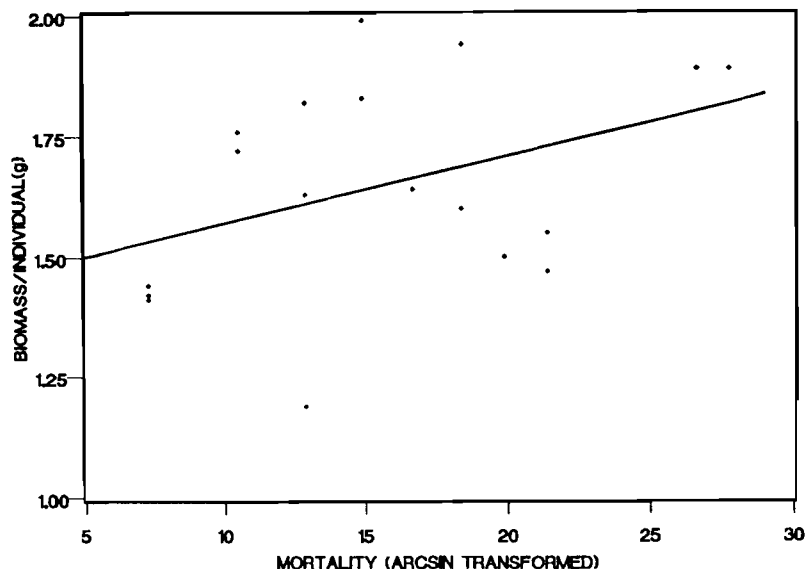


Fig. 1. Association between biomass per individual and mortality ($Y=1.43+0.014x$).

The capacity for survival, or fitness (w_1), of each population ranged from 0.7833 to 0.9833. In density-dependent populations, groups of individuals survive as a function of their genetic variation, and increase at the expense of those not possessing it (Bradshaw, 1984). The genetic variation is perhaps reflected in the variation for height growth, biomass production, and variation of frequency of mortality among individuals of self-thinning populations. Mortality is a threshold trait, and governed by polygenic inheritance, and the expression of polygenic characters are affected by the environmental factors (Falconer, 1981). Therefore, the frequency of mortality among an array of interacting genotypes in these families may be determined by an interaction between genetic and environmental factors. Thus, mortality of individuals within each family could be interpreted as intrademic selection (Wright, 1963) in relation to genetic variation of the competing individuals. The intensity of selection (I), and the change of fitness due to selection or mortality (CFS), in the metapopulation of families, were 0.0664 and 0.0044 respectively. Although the I , and the CFS values

are small, they clearly demonstrate that the intensity of selection due to density stress can be measured, and that self-thinning could bring about evolutionary changes in plant populations.

Families are equivalent to populations, and from an evolutionary view point they are analogous to groups (Falconer, 1981; Slatkin, 1981). Hence, the differential selection among self-thinning populations due to mortality may correspond to interdemic (group) selection (Wright, 1956). The term group selection is used in the sense of Wright's inter-group selection (Wright, 1963); where, natural selection acts on the small random allele frequency differences among demes, or on whole sets of genotypes (Wright, 1931). Similarly, "selection at the population level or group selection is defined as genetic change that is brought about or maintained by the differential extinction and/or proliferation of populations," Wade (1978). Slatkin and Wade (1978) indicated that many quantitative characters, such as viability, respond to group selection. Indeed, Goodnight (1985) demonstrated group (inter-demic) selection in Arabidopsis thaliana. More recently, Slatkin (1987) has stressed the importance of interdemic or group selection in differentiation and evolution of natural populations. Accordingly, because viability may be a normally distributed (Gaussian) quantitative trait among natural populations of organisms (Haldane, 1930; Slatkin and Wade, 1978; Turelli, 1986), I maintain that differential mortality among an array of self-thinning populations of Douglas-fir in this study is analogous to interdemic (group) selection in the Wrightian sense.

Families of interacting genotypes may occur as complete or partial groups in natural populations of Douglas-fir, and selection among populations can be caused by differential extinction, founding of new populations, or expansion of existing populations (Wright, 1978). Differential extinction of genotypes due to self-thinning, particularly during colonization, may lead to substantial genetic changes both within and among groups of individuals throughout the life cycle of these populations. Biological fitness includes both viability and reproductive fitnesses. Thus, mortality in self-thinning populations may represent an important component of selection (viability or zygotic) in Douglas-fir. Whether variation among these populations in the probability of mortality or viability fitness reflects reproductive fitness needs to be established. Both viability and size-dependent fertilities are well known in plants (Harper, 1977). In forest trees, survival ability is generally used as a substitute to estimate reproductive fitness (Ledig, 1986). Recently, Nagylaki (1987) has investigated the relationship between viability and fertility in evolution. He found that the mean fitness in monoecious species (e.g. Douglas-fir) is the product of mean viability and mean fertility. The present study demonstrated that self-thinning may be a tripartite process involving genetic, developmental and demographic factors, which show a simultaneous response to density stress. Self-thinning in natural populations of plants represents both intra- and inter-demic selection processes, and thus plays an unifying role between genetics and ecology (Westoby, 1984; Bradshaw, 1984); this is consistent with the notion that competition and self-thinning may be an integral part of selection and evolution (Mather, 1969; Bazzaz et. al., 1982).

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