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FINE-SCALE SPATIAL AND TEMPORAL VARIATION IN THE DEMOGRAPHY OF A PERENNIAL BUNCHGRASS¹

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Abstract. Most life history studies assume that demographic transition rates within a population are temporally and spatially invariant. A violation of these assumptions may have important consequences in the analysis of long-term processes such as population growth and stability. To examine the potential problems, I studied the demography of a size-classified population of *Danthonia sericea*, a long-lived grass species, using standard matrix analysis techniques. The study was conducted for two June-to-June transition periods at five locations along a well defined soil/vegetation gradient in a field located in Durham, North Carolina. Demographic transition rates, and predictions of long-term population growth, differed markedly between transition periods and among locations, with the biggest differences being attributable to location. Elasticity analysis indicates that, in all cases studied, a large proportion of long-term population growth can be ascribed to demographic processes associated with individuals in the largest size classes. However, this aspect of the demography of *Danthonia sericea* does not differ appreciably among locations or between years and, consequently, does not explain the observed demographic variability. I argue that some of the variability arises from differences in the rate of recruitment of smaller individuals into the larger size classes. Although elasticity analysis indicates that the raw rate of recruitment through reproduction is of little importance to population growth, germination and early establishment success may play a significant role in determining long-term population growth rates, particularly if good recruitment years are infrequent. This can be shown if more than one transition period is considered explicitly in the demographic analysis. It is suggested that future demographic studies account for year-to-year variation in transition rates by incorporating stochastic matrix theory in the analysis of long-term population processes.

Key words: *Danthonia sericea*; demography; elasticity; life history; spatial variation; temporal variation; transition matrices.

INTRODUCTION

The demographic structure of a plant population can vary dramatically over a very small spatial scale (Sarukhán and Harper 1973, Sarukhán 1974). These variations may be induced by small-scale variation in the environment (Aston and Bradshaw 1966, Jain and Bradshaw 1966, Fowler and Antonovics 1981*b*, Louda 1982, Thompson 1983, Fowler 1984). There can also be substantial temporal variation in demographic parameters due to year-to-year heterogeneity in environmental conditions (Bierzychudek 1982, Mack and Pike 1983, Kuryshes and Khvorostyanskaya 1984). Unfortunately, an underlying assumption of many demographic analyses is that demographic parameters are time and space invariant. Demographic heterogeneity may average out for a population sampled at a large spatial scale (Sprugel 1976, Hughes and Jackson 1985) or over a long time scale (M. Slatkin, *personal communication*) and give the impression of demographic uniformity. However, ignoring local spatial and year-

to-year variation in the analysis of demographic processes can lead to mistaken conclusions about the factors influencing the demography of a species and prohibit an understanding of the potential for population growth and stability (Cohen 1979*b*, Tuljapurkar 1986, Moloney 1986*c*).

For many organisms, such as long-lived perennial plants, there is a strong correlation between size and demographic success. For these species, a demographic analysis focusing on size or stage structure, rather than age, is most appropriate for understanding population dynamics (Lefkovitch 1965, Vandermeer 1978, Caswell 1982, Kirkpatrick 1984, Sarukhán et al. 1984). Several recent studies have used the Lefkovitch matrix model, an extension of the Leslie matrix model that classifies a population according to its size structure, to investigate the demography of plant populations (Hartshorn 1972, Caswell and Werner 1978, Bierzychudek 1982, Meagher 1982). However, few have investigated the impact of fine-scale spatial and temporal variation on the development of meaningful demographic models. In this paper I will present a demographic analysis of a perennial grass species, *Danthonia sericea* Nutt. (Radford et al. 1968), that compares demographic parameters over a 2-yr period among five

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locations along an environmental gradient. The objective was to identify the critical demographic stages underlying changes in population structure among these locations, and, by comparing year-to-year variation, to assess the problems introduced by the assumption of time invariance.

NATURAL HISTORY OF *DANTHONIA SERICEA*

Danthonia sericea, downy oatgrass, is a long-lived, perennial grass species, which grows primarily on well drained, sandy soils at the edges of pine-oak forests on the coastal plain and piedmont of eastern North America. (*Danthonia sericea* will hereafter be referred to as *Danthonia*.) Its distribution within the United States ranges from Massachusetts south to northern Florida and then westward to Louisiana (Hitchcock 1971, Lindauer and Quinn 1972). *Danthonia* is a cool-season grass growing primarily during the spring and fall. Vegetative spread occurs through basal tillering, with little lateral extension; individual genets form relatively discrete clusters of tillers. Most germination occurs in early spring after overwintering of dormant seed in the soil. Whether a significant seed bank exists is not known. However, air-dried seed can remain viable for at least 10 yr (K. Clay, *personal communication*). This suggests that, in the absence of significant seed predation, a seed bank could play an important role in the recruitment of new individuals into *Danthonia* populations. Exact reproductive phenology varies according to local environmental conditions (Lindauer and Quinn 1972). At the study site discussed in this paper, culm formation begins in early spring, pollination occurs in mid-May, and seed is dropped in early June. Reproduction is primarily through open pollination of chasmogamous flowers, although 5% of the seed production may be attributable to selfing within cleistogamous flowers (Clay 1982).

METHODS

Study site

The *Danthonia* population under study was located in a mown field at the edge of an oak-pine woodland on the campus of Duke University in Durham, North Carolina (see Fowler and Antonovics 1981a, Moloney, *in press* for a detailed description of the study area). Sampling was confined to a 12 × 28 m region, which was characterized by a well-defined soil/vegetation gradient changing monotonically along the length of the field (Moloney 1986a, *in press*). Five subsets of the *Danthonia* population, which will be referred to as locations A, B, C, D, and E, were located by placing 0.5 × 11 m band transects perpendicular to the primary soil/vegetation gradient. The locations of the transects were chosen to characterize distinct demographic regions within the *Danthonia* population. Five 0.5 × 0.5 m quadrats were located at random within each transect (see Moloney 1986a and *in press* for more detail).

Moloney (1986a and *in press*) provides a more detailed discussion of the distribution of *Danthonia* and other plant species within the study area.

Sampling methodology

All *Danthonia* individuals were permanently tagged in each quadrat during June of 1983. Censuses of all plants were conducted during June 1983, June 1984, and June 1985, with an additional census of new seedlings during June 1986. Seeds germinating during 1984 and 1985 were tagged upon first observation as seedlings. Flowering culms produced by each individual were first noted during April and counted during June of each year. Individuals were classified into six size categories according to the number of leaves present. The size categories, determined by the methodology outlined in Moloney (1986b), were (1) size class one, 1–2 leaves; (2) size class two, 3–6 leaves; (3) size class three, 7–13 leaves; (4) size class four, 14–27 leaves; (5) size class five, 28–56 leaves; and, (6) size class six, > 56 leaves. The category of 1–2 leaves was chosen a priori as representing newly germinated individuals. Each size category was also constrained to consist of no fewer than 5% of the total observations.

An individual *Danthonia* plant was defined to be any group of tillers in which no two tillers were separated at the base by > 1.5 cm. Two exceptions to this definition were allowed: (1) any tiller separated from an individual by > 1.5 cm, but exhibiting evidence of a prior physical connection, was considered a member of the individual; and (2) tillers found within 1.5 cm of each other, but known to have arisen from different seed, were considered distinct individuals. In most cases, individuals were easily identified as closely packed clusters of daughter tillers. However, in dense swards it was sometimes difficult to identify discrete boundaries, as tillering occurs primarily underground. Because of this, it is best to view members of the two largest size classes of *Danthonia* as ecological individuals, not genetic individuals. In most cases these two categories are identical, but in some instances they might diverge.

Transition matrices

I used techniques developed for the analysis of Lefkovich matrices to study demographic differences among the five study locations for two different census intervals (see Lefkovich 1965, Vandermeer 1975, Caswell 1978, 1982, 1986 for an introduction to the theory of life history analysis using size-classified data). The number of individuals in size class i at location k during census t will be represented by the value x_{ikt} . The column vector \mathbf{x}_{kt} will be used to represent the distribution of individuals among size classes for location k at census t . The probability of an individual in size class j at census t being in size class i at census $t + 1$ will be represented as p_{ijkt} . The transition probabilities p_{ijkt} were determined by dividing the frequency of transitions

from size class j to size class i over the census period t to $t + 1$ by x_{ijk} . These parameters represent maximum-likelihood estimates of the transition probabilities.

Let c_{ikt} represent the number of culms produced by individuals in size class i at location k at census t , and let $g_{k(t+1)}$ represent the number of seeds at location k germinating after census t and surviving to census $t + 1$. An estimate of the number of living germinants at census $t + 1$ attributable to each individual within size class i at location k at census t will be represented as r_{ikt} . Given the previous definitions,

$$r_{ikt} = [g_{k(t+1)} \cdot c_{ikt}] / [x_{ikt} \cdot \sum_i c_{ikt}] \quad (1)$$

This definition of r_{ikt} , a predictor of reproductive success at census $t + 1$ for individuals of size i at census t at location k , assumes that the population at location k is closed, with all germinating seed being produced locally, and that seed carry-over beyond the first overwintering period can be ignored. Eq. 1 is also valid under seed migration, if movement of seed into quadrats is balanced by movement out.

A direct estimate of culm production at location D could not be made in 1983; individuals were marked after the other locations had been censused and some culms had already abscised. Indirect estimates of r_{iDt} for the 1983–1984 transition period were made using the protocol outlined in the Appendix.

Transition matrices, M_{kt} , describing the demographic change at location k from census t to census $t + 1$ can be defined as follows:

$$M_{kt} = ((a_{ij}))_{kt}, \quad (2)$$

where

$$\begin{cases} a_{ij} = p_{ijk} + r_{ikt} & \text{for } i = 1 \\ a_{ij} = p_{ijk} & \text{for } i \neq 1. \end{cases}$$

Confining the entry of the r_{ikt} terms to the first row of the matrix is legitimate if census periods of 1 yr are considered; all new germinants surviving to a June census were found within the smallest size class. Change in the population from census t to census $t + 1$ can be easily represented by the matrix equation

$$x_{k(t+1)} = M_{kt} \cdot x_{kt}. \quad (3)$$

Transition matrices were determined for each location over the 1983–1984 and 1984–1985 June-to-June transition periods.

The death rate of individuals within size class j , d_{jkt} , can be determined by the equality

$$d_{jkt} = 1 - \sum_i p_{ijk}. \quad (4)$$

Log-linear analysis

I used log-linear contingency table analysis, an analog of analysis of variance, to study the effects of

location (L) and year-to-year variation (Y) on the demographic fate (F) of individuals. (See Fienberg 1977, Caswell 1986 for a complete discussion of the analysis and its interpretation.) The six size categories were analyzed separately. Transitions from an initial size at the beginning of a census period were placed into three categories representing demographic fate at the end of the census period: (1) number of individuals declining in size or dying; (2) number of individuals not changing in size; and, (3) number of individuals decreasing in size. Transition classes were pooled into three categories to insure that sample sizes were adequate for the analysis. For individuals starting in the largest size class, only categories (1) and (2) were included. The resulting contingency tables were partitioned by location and transition period.

Two forms of analysis are presented in the results. ‘‘Marginal association’’ tests the significance of an interaction effect in the absence of other effects of the same order, whereas ‘‘partial association’’ tests the significance of an effect with all other effects of the same order present in the model (Caswell 1986). Analysis by partial association is more conservative.

A parallel log-linear analysis was conducted to study the effects of location (L) and year-to-year variation (Y) on culm production. The third effect in this analysis was demographic fate (F), which was the number of culms produced by all individuals of a given size class in a particular location and year. Demographic fate therefore represents the distribution of culms among size classes at the time of flowering and is an indirect measure of the proportional contribution of the different size classes to reproductive output. Only five size classes were included in the analysis, as no individuals in the smallest size class produced culms during the study.

Asymptotic properties

Predictions of long-term, asymptotic growth rates and stable population structures were made for each of the transition matrices using the power method to obtain the leading eigenvalue (λ_1) and associated left-hand (v) and right-hand (w) eigenvectors (Anton 1977). The leading eigenvalue, when M_{kt} is a time invariant matrix, is the asymptotic value of the growth rate at location k based on demographic parameters determined at census t (Charlesworth 1980, Caswell 1986). The relative magnitudes of the elements of w represent the relative abundances of individuals in the corresponding size classes of the population after reaching a stable distribution (Caswell 1978).

Elasticity analysis

Let s_{ij} represent the sensitivity of λ_1 to a change in the value of a_{ij} . As shown by Caswell (1978),

$$s_{ij} = \frac{\partial \lambda_1}{\partial (a_{ij})} = \frac{v_i \cdot w_j}{\langle v, w \rangle}. \quad (5)$$

TABLE 1. Values within locations for selected demographic parameters. Estimates are based on number within an area of 0.25 m², i.e., the size of sample quadrats within locations. *N* = 5 quadrats in all cases.

Location		Number of individuals			Number of culms			Number of recruits		
		1983	1984	1985	1983	1984	1985	1984	1985	1986
A	\bar{X}	31.0	114.6	64.4	17.8	26.0	27.8	102.8	4.0	5.4
	(SD)	(14.3)	(38.6)	(17.4)	(6.8)	(15.2)	(11.4)	(48.6)	(2.1)	(3.8)
B	\bar{X}	16.8	47.6	29.4	13.0	25.6	44.8	48.5	3.6	2.4
	(SD)	(13.6)	(32.2)	(19.0)	(14.8)	(25.1)	(30.4)	(29.4)	(3.8)	(2.9)
C	\bar{X}	11.4	40.6	21.6	12.6	18.8	21.0	41.0	1.6	1.2
	(SD)	(15.5)	(53.3)	(27.4)	(9.8)	(24.6)	(13.0)	(48.1)	(1.8)	(0.8)
D	\bar{X}	38.0	152.4	52.6	—	70.6	85.0	100.7	2.0	1.0
	(SD)	(18.4)	(59.0)	(29.5)	(—)	(28.7)	(44.2)	(38.7)	(0.0)	(1.0)
E	\bar{X}	12.6	151.2	52.6	20.2	65.4	48.6	159.0	3.8	0.8
	(SD)	(9.6)	(92.5)	(30.3)	(10.6)	(35.8)	(18.9)	(114.5)	(1.6)	(1.0)

Two problems arise in using sensitivity values to identify vital rates having the greatest potential impact on population growth (de Kroon et al. 1986). The first problem is that a large sensitivity may be associated with transitions not observed in natural populations. The second problem is that vital rates associated with reproduction (the first row of the transition matrices) may take on values much greater than unity, whereas all other rates are constrained to lie between values of 0 and 1, inclusive. An equal change in the absolute value of these two types of parameters may, therefore, have unequal effects on the magnitude of λ_1 . de Kroon et al. (1986) have suggested the use of the elasticity index, e_{ij} , to avoid these problems. Elasticities are obtained by multiplying s_{ij} by a_{ij}/λ_1 . This provides a measure of the effect of a proportional change in a_{ij} upon λ_1 . Also, since as shown by de Kroon et al. (1986),

$$\sum_i \sum_j e_{ij} = 1, \tag{6}$$

the value of e_{ij} can be taken to represent the proportional contribution of a_{ij} to overall population growth. I have used elasticity analyses to determine the relative importance among size classes of the various demographic processes, i.e., survivorship, growth, sexual reproduction, and year-to-year stochastic variation, in producing change in population structure among study locations.

RESULTS

General demographic patterns

One of the most striking demographic patterns I found was the level of year-to-year variation in the number of individuals recruited into the population (Table 1). With the exception of the 1984 census, recruitment, determined as g_{kt} for census t , was extremely low each year of the study. (In addition to the data reported, I also observed low recruitment levels during 1983 and 1987.) During the 1984 census period, values of g_{kt} were 10 to 167 times the rates observed during other years. These high values for g_{kt} cannot be attributed to a previous increase in reproductive output. In fact,

there is a statistically significant, negative Spearman rank correlation between the number of culms produced during 1983, 1984, and 1985 ($\sum c_{ikt}$) and levels of recruitment the following years ($g_{k(t+1)}$): $r_s = -0.54$; $P < .05$; and $n = 14$.

The number of individuals at locations B and C was consistently lower than in the other three locations, although location E did have few individuals during 1983 (Table 1). During the late spring and early summer of 1983, there was an extended drought within the study site, which apparently caused a decline in the number of individuals in the intermediate size classes of locations B and C by June 1984 (Fig. 1). There was little change in the number of individuals in the largest size classes during that same time period; in fact, none of the individuals initially censused in the two largest size classes died during the course of the study. The high germination rates of 1984 resulted in a marked increase in the number of individuals in the intermediate size classes in June 1985. This effect was least at location D, where most of the individuals germinating in 1984 and surviving to 1985 remained within the smallest size class.

Transition matrices

With the exception of the first two columns, the entries in the first row of the transition matrices derive entirely from recruitment of new individuals into the population through germination of seed (Table 2). Since there was no reproduction by individuals in the smallest size class, the first column, first row transition values were due solely to individuals remaining in the smallest size class over the transition period. The second column, first row transition values were due primarily to recruitment through seed production by the next to smallest size class, not to declines in size.

There was considerable site-to-site and year-to-year variation in demographic transition rates (Table 2). With the exception of location A, vegetative growth rates were generally higher during the 1984–1985 transition period. This was, in part, counterbalanced by a decline in reproduction during 1984–1985 (Table 2).

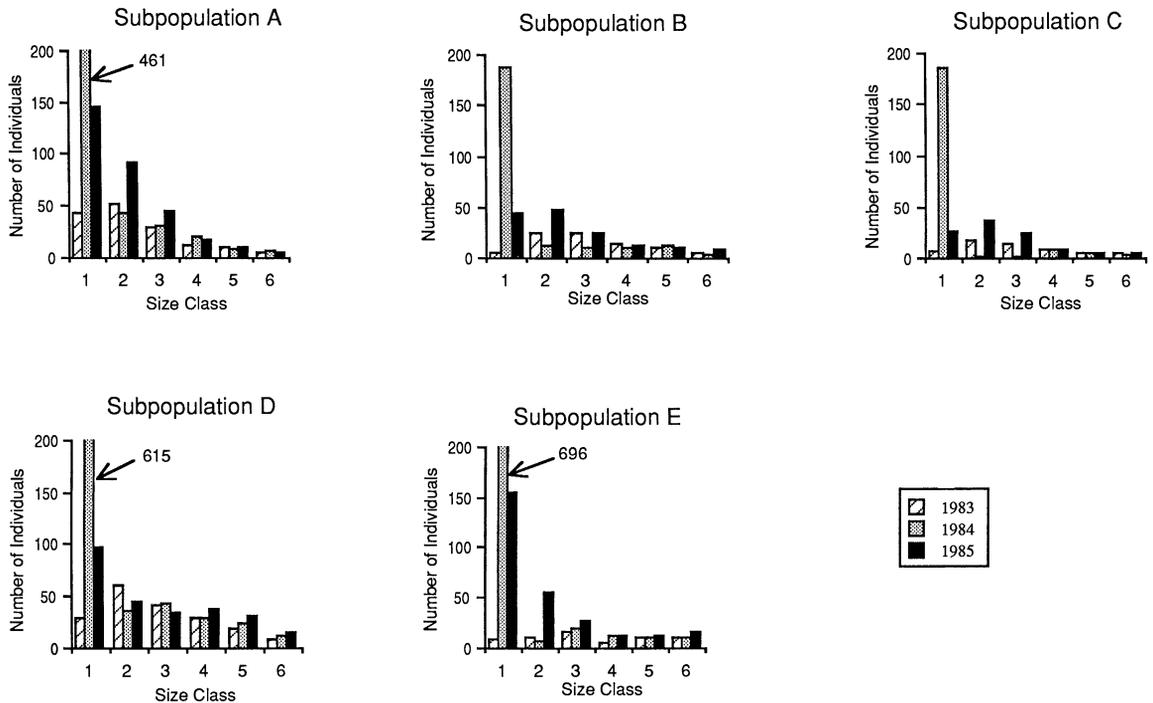


FIG. 1. Number of individuals in six size classes for a *Danthonia sericea* population at five locations during three June censuses.

TABLE 2. Transition matrices for six plant size classes in *Danthonia sericea* populations at five locations during two census periods. Broken lines (---) indicate transition elements equal to zero.

Location	Size class	Transition period											
		June 1983–June 1984						June 1984–June 1985					
		1	2	3	4	5	6	1	2	3	4	5	6
A	1	.21	.47	1.89	6.57	15.10	21.75	.27	.07	.05	.25	.76	.76
	2	.19	.55	.10	---	---	---	.13	.56	.22	---	---	---
	3	.02	.19	.57	---	---	---	.01	.37	.72	.19	---	---
	4	---	.02	.27	.77	.30	---	---	---	.06	.67	.22	---
	5	---	---	---	.23	.60	---	---	---	---	.14	.67	.29
	6	---	---	---	---	.10	1.00	---	---	---	---	.11	.71
B	1	---	.20	.46	2.43	7.36	12.44	.43	.09	.04	.39	.69	1.50
	2	.17	.12	.20	.07	---	---	.34	.50	.09	---	---	---
	3	---	.12	.16	.14	.10	---	---	.42	.64	---	---	---
	4	---	---	.20	.36	---	---	---	---	.27	.60	---	---
	5	---	---	---	.14	.80	.60	---	---	---	.40	.23	---
	6	---	---	---	---	.10	.40	---	---	---	---	.77	1.00
C	1	---	---	---	.94	10.01	25.30	.10	---	---	.04	.30	1.97
	2	---	.05	---	---	---	.20	.20	---	---	---	---	---
	3	---	---	.07	---	---	---	.12	1.00	---	---	---	---
	4	---	---	.29	.33	---	---	.02	---	1.00	.62	---	---
	5	---	---	---	.11	.20	.40	---	---	---	.38	.25	.33
	6	---	---	---	---	.20	.40	---	---	---	---	.75	.67
D	1	.07	.89	1.76	4.09	9.21	21.15	.14	.09	.03	.06	.13	.26
	2	.17	.39	.17	---	---	---	.03	.53	.16	.03	---	---
	3	.13	.23	.46	.20	---	---	.004	.28	.43	.07	---	---
	4	---	.05	.29	.50	.05	---	.003	.08	.36	.60	---	---
	5	---	---	---	.27	.68	.11	---	.03	.03	.30	.79	.15
	6	---	---	---	---	.26	.89	---	---	---	---	.21	.85
E	1	.11	.52	2.29	5.59	17.25	30.77	.19	.02	.07	.13	.33	1.21
	2	---	.27	.06	---	---	---	.08	.38	---	---	---	---
	3	---	.59	.53	---	---	---	.02	.62	.42	.17	---	---
	4	---	.09	.29	1.00	.09	---	---	---	.42	.33	---	---
	5	---	---	.12	---	.82	---	---	---	.05	.50	.54	---
	6	---	---	---	---	.09	1.00	---	---	---	---	.45	1.00

TABLE 3. Log-linear analysis of the effect of location (*L*) and year (*Y*) on the demographic fate (*F*) of *Danthonia sericea* in six initial size classes. Data show chi-square approximations using a G^2 test, with degrees of freedom in parentheses (Fienberg 1977).

Initial class	Marginal association				Partial association		
	<i>FLY</i>	<i>FY</i>	<i>FL</i>	<i>LY</i>	<i>FY</i>	<i>FL</i>	<i>LY</i>
1	28.3** (8)	32.5*** (2)	335.9*** (8)	65.6*** (4)	4.2 (2)	307.7*** (8)	37.4* (4)
2	5.1 (8)	34.8*** (2)	58.2*** (8)	6.8 (4)	29.7*** (2)	53.1*** (8)	1.7 (4)
3	10.0 (8)	11.6* (2)	47.8*** (8)	20.4*** (4)	0.6 (2)	37.8** (8)	10.4* (4)
4	17.8* (8)	21.0*** (2)	23.6*** (8)	22.9*** (4)	3.2 (2)	5.8 (8)	5.1 (4)
5	4.3 (8)	7.7 (2)	16.5* (8)	4.6 (4)	3.4 (2)	12.2 (8)	0.3 (4)
6	2.0 (4)	2.1 (1)	14.2* (4)	3.2 (4)	0.1 (1)	12.2* (4)	1.2 (4)
Culm production	57.5*** (16)	70.9*** (4)	274.4*** (16)	98.8*** (4)	13.4** (4)	216.9*** (16)	41.3*** (4)

* $P < .05$, ** $P < .01$, *** $P < .001$.

Most changes in size did not involve growth through more than one size class over a census period. However, the two smallest size classes at locations C, D, and E (columns one and two of the appropriate matrices) did have relatively high growth rates during the 1984–1985 transition period, with many individuals passing through one or more size classes. In no instance did an individual starting in the largest size class at the beginning of a census period die during that period (Table 2).

Location C had the most extreme variation in transition rates. Mortality was very high during the 1983–1984 census period. In contrast, growth rates were very high and mortality was very low during 1984–1985.

There was a strong interaction between location and year affecting transition rates of the smallest size class ($P < .01$, size class one, FLY, in Table 3). The FLY interaction was also significant for size class four, but only at the .05 probability level. Overall, the strongest factor affecting transitions was location (the FL interactions of Table 3). This factor was significant at the .05 probability level in the more conservative partial association analysis for four of the six initial size classes. In the marginal association analysis, location was a significant effect for all initial size classes. Year-to-year variation was less important, but had a significant effect on transition rates within the smaller size classes (FY interactions of Table 3). (A significant LY interaction indicates that the rank order of the number of individuals within a size class changed from year to year among locations and is not of general interest within the context of this study.) In all cases, significant effects of year-to-year variation and location on demographic fate were strongest among the smallest size classes and declined in importance among the larger individuals. This is due in part to a decline in sample size among the larger size classes.

Log-linear analysis indicates that location, year-to-year variation, and interactions between location and year all have a very significant effect on the relative contribution to reproduction by the different size classes (Table 3). Care must be taken in interpreting this result. The log-linear analysis cannot be used to determine whether the number of culms produced per individual within each of the size classes differed among locations or between years. It only indicates a difference in the relative distribution of culms among size classes.

Asymptotic properties

During the 1983–1984 transition period, long-term population growth was predicted to be positive ($\lambda_1 > 1$) at locations A and D, static ($\lambda_1 = 1$) at location E, and negative ($\lambda_1 < 1$) at locations B and C (Table 4). Negative growth rates at locations B and C can be attributed to high levels of mortality in the intermediate size classes and to a low probability of survival in the smallest (Table 2). The only reason that growth rates were not lower is that there was no mortality among the largest individuals.

TABLE 4. Predicted growth rates (λ_1) for *Danthonia sericea* at each of five locations.

Location	λ_1		
	1983–1984	1984–1985	1983–1985*
A	1.33	1.01	1.17 (1.16)
B	0.94	1.18	1.09 (1.05)
C	0.60	1.20	1.07 (0.85)
D	1.43	1.01	1.15 (1.20)
E	1.00	1.07	1.28 (1.03)

* Normalized to a 1-yr growth rate by taking the square root of the predicted growth rate calculated as the matrix product of the 1983–1984 and 1984–1985 Lefkovich matrices; numbers in parentheses are square roots of the product of the predicted 1983–1984 and 1984–1985 growth rates.

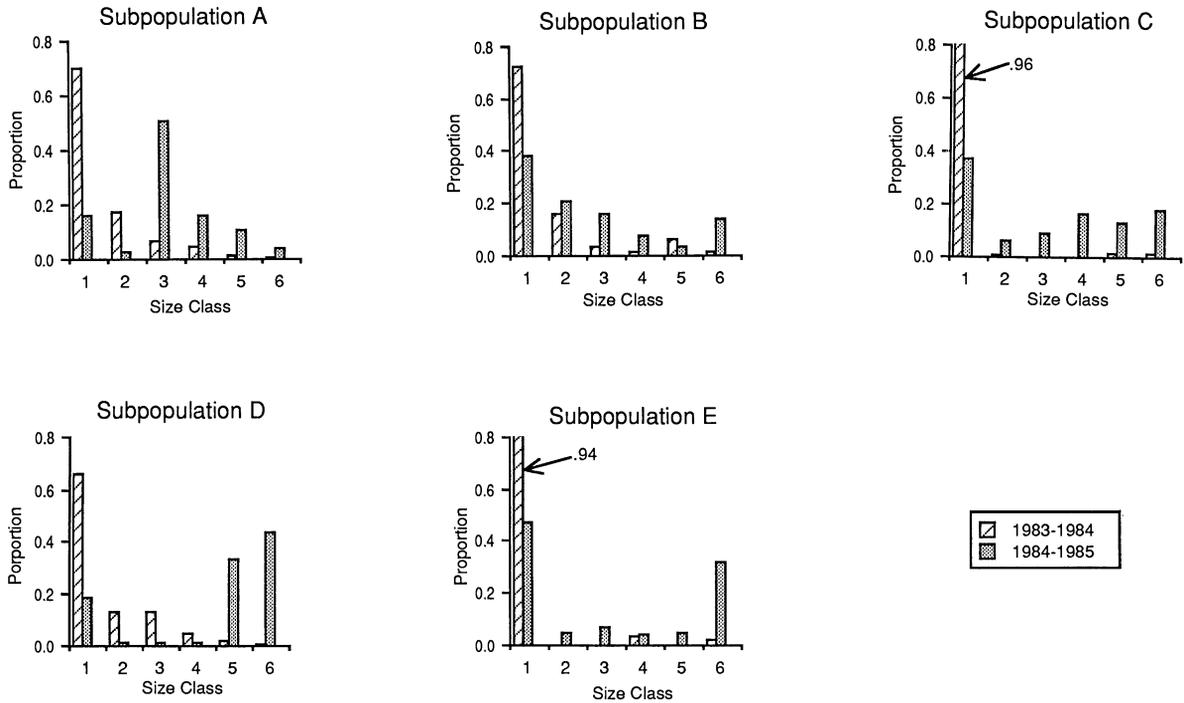


FIG. 2. Predicted stable size class distributions for two transition periods at five locations for a *Danthonia sericea* population (see Asymptotic Properties subsection of Methods for an explanation of the derivation of the predicted distributions).

Stable size class distributions, as predicted from the 1983–1984 transition matrices, were dominated by the smallest size class (Fig. 2). The most interesting distribution is seen at location C, with virtually no individuals in the intermediate size classes and only a few in the largest. It must be kept in mind that the growth rate at location C was negative and that there was no survival by individuals in the smallest size class over the transition period, effectively severing any connection between reproduction and recruitment into the population.

Although there was very little recruitment during the 1984–1985 transition period, predicted growth rates at all the locations were positive (Table 4). In contrast to the 1983–1984 results, locations B and C had the highest growth rates. This was due to a marked increase in survival and growth within the smaller size classes. The low population growth rates predicted for locations A and D ($\lambda_1 = 1.01$) were most likely due to a combination of high mortality among individuals within size class one (0.59 and 0.82 over the year, respectively) and a low rate of recruitment.

Stable size class distributions predicted from the 1984–1985 transition matrices show two basic patterns (Fig. 2). Location A has a bimodal distribution produced as follows: low levels of reproduction produce few recruits into the smallest size class; mortality of recruits is moderate, producing a decline in numbers for size class two; individuals in the three largest size classes have low levels of mortality and build up in number by gradual recruitment from the two smallest

size classes (Table 2). Locations B, C, D, and E all have U-shaped, stable size class distributions predicted from the 1984–1985 transition matrices. There are two key processes involved: (1) low levels of recruitment into the smallest size class, and (2) no mortality among individuals attaining the two largest size classes. There are relatively high levels of growth within the intermediate size classes, producing a strong connection between initial recruitment and subsequent growth into the largest size classes. It is the details of this growth that dictate the actual shape of the distribution for each location. I would like to point out that none of the predicted distributions match the distributions observed in the field (compare Figs. 1 and 2).

An analysis of 1983–1985 transition matrices, obtained for each location as a matrix product of the 1983–1984 matrix post-multiplied by the 1984–1985 matrix, predicts that growth rates for locations A, B, and D will be similar in magnitude to the geometric mean of the 1983–1984 and 1984–1985 growth rates (Table 4). In contrast, substantially greater growth rates are predicted for locations C and E using the former method. High rates of recruitment during the spring of 1984 act synergistically with high survivorship and growth in the intermediate size classes during the 1984–1985 census period to produce this difference.

Elasticity analysis

A majority of the larger elasticity values are associated with the diagonal elements of the transition matrices, particularly those corresponding to the two larg-

TABLE 5. Transition matrix elasticities for *Danthonia sericea* populations at five locations during two census periods. Elements marked by a broken line correspond to transition elements equal to zero.

Location	Size class	Transition period											
		June 1983–June 1984						June 1984–June 1985					
		1	2	3	4	5	6	1	2	3	4	5	6
A	1	.02	.01	.02	.05	.04	.01	.01	.00	.00	.00	.01	.00
	2	.10	.07	.00	---	---	---	.02	.11	.07	---	---	---
	3	.03	.07	.08	---	---	---	.01	.09	.27	.02	---	---
	4	---	.02	.08	.16	.02	---	---	---	.04	.12	.02	---
	5	---	---	---	.07	.06	---	---	---	---	.04	.10	.02
	6	---	---	---	---	.01	.04	---	---	---	---	.02	.04
B	1	---	.00	.00	.00	.01	.00	.04	.00	.00	.01	.01	.05
	2	.02	.00	.00	.00	---	---	.07	.06	.01	---	---	---
	3	---	.02	.01	.00	.01	---	---	.08	.09	---	---	---
	4	---	---	.02	.00	---	---	---	---	.07	.07	---	---
	5	---	---	---	.02	.62	.09	---	---	---	.06	.01	---
	6	---	---	---	---	.09	.07	---	---	---	---	.05	.30
C	1	---	---	---	.00	.00	.00	.08	---	---	.00	.01	.08
	2	---	.00	---	---	---	.00	.05	---	---	---	---	---
	3	---	---	.00	---	---	---	.03	.05	---	---	---	---
	4	---	---	.00	.00	---	---	.01	---	.08	.10	---	---
	5	---	---	---	.00	.11	.22	---	---	---	.09	.04	.08
	6	---	---	---	---	.22	.44	---	---	---	---	.16	.20
D	1	.01	.02	.04	.05	.03	.04	.10	.00	.00	.00	.00	.00
	2	.06	.03	.01	---	---	---	.00	.01	.00	.00	---	---
	3	.11	.04	.08	.01	---	---	.00	.00	.00	.00	---	---
	4	---	.02	.11	.07	.00	---	.00	.00	.00	.01	---	---
	5	---	---	---	.07	.07	.01	---	.00	.00	.01	.32	.08
	6	---	---	---	---	.04	.07	---	---	---	---	.09	.45
E	1	.00	.00	.00	.00	.00	.00	.01	.00	.00	.00	.00	.04
	2	---	.00	.00	---	---	---	.04	.02	---	---	---	---
	3	---	.00	.00	---	---	---	.01	.04	.03	.01	---	---
	4	---	.00	.00	.27	.00	---	---	---	.05	.02	---	---
	5	---	---	.00	---	.00	---	---	---	.01	.04	.04	---
	6	---	---	---	---	.00	.73	---	---	---	---	.04	.61

est size classes (Table 5). This indicates that a large contribution to population growth comes from individuals that remain within the same size class from year to year. Another category of elasticities that have large values correspond to transition elements associated with an increase in size among the smaller size classes, indicating the importance of early establishment success to continued population growth. This is not a consistent pattern, but occurs only at locations A and D for the 1983–1984 transition period, and in all but location D for the 1984–1985 transition period (Table 5).

Few of the elasticity values associated with recruitment into the population (the first row of the transition matrices) are of appreciable size. Only the elasticity for recruitment associated with the largest size class at location B for the 1984–1985 transition period contributes >5% to the long-term population growth rate (a value greater than 0.05 in Table 5). The elasticity analysis indicates that the greatest contribution to population growth comes from individuals that remain in the same size class from year to year or increase in size. Because of high mortality among recruits and the low levels of germination success, the reproductive success of an individual depends upon being able to pro-

duce seed for several years; this is only possible for individuals attaining a large size, at which point they are effectively buffered from year-to-year demographic variation.

DISCUSSION

I found that population growth rates by *Danthonia sericea* differ over small spatial and temporal scales. This can be attributed, in part, to differences in the rates of growth and mortality among newly germinating seedlings and among the smaller individuals in the population. It is the demographic transition rates among these individuals that exhibit the strongest, statistically significant differences among locations and between years. However, the lack of significant differences among transition rates for the larger individuals might be the result of the smaller sample sizes associated with the two largest size classes. Elasticity analysis, which provides a measure of the potential contribution of differences in various demographic processes to differences in overall population growth, paints a slightly altered picture from the one just presented. It attributes to the smaller individuals only an intermediate contribution to differences in population growth and attributes the greatest potential contribution to the larg-

est individuals, primarily through their ability to persist in the population over a very long period of time. However, there is little contribution to differences in overall population growth by reproductive output of the largest individuals. In fact, elasticity analysis indicates that, for all size classes, population growth rates are relatively insensitive to the raw rate of recruitment through sexual reproduction. This can also be seen by examining the data more closely. With two exceptions, population growth rates predicted from the 1983–1984 data were at or below replacement rate, although recruitment rates were relatively high. In contrast, growth rates predicted from the 1984–1985 data were all above replacement levels, although there was very little recruitment. The difference was due primarily to low survival among newly germinating seedlings during the 1983–1984 census period.

Since mortality is generally high among seedlings and plants in the smaller size classes, there is an extremely low probability that germinating individuals will be recruited into the largest size classes. However, once an individual attains a large size, it becomes an important component of the population, producing copious amounts of seed over a long period of time. Large individuals have a very low probability of dying. In fact, none of the individuals that began the study within the two largest size classes died over the two transition periods investigated, even though there was a serious drought during 1983. Large size can be seen as an effective refuge buffering the individual from environmental stress. This aspect of the demographic process, however, does not differ markedly among locations or between years, and therefore does not play a major role in producing demographic differences within the population. What is important in producing differences is the rate at which small individuals are recruited into the larger size classes.

Temporal patterns of recruitment from seed may be more important in determining long-term population growth rates and in determining the proportional distribution of individuals among size classes, i.e., population structure, than was indicated by elasticity analysis. Overall, low rates of recruitment by *Danthonia sericea* are the rule, but years in which recruitment is high may play a major role in periodically replenishing populations, particularly when followed by good growth years. The demographic dynamics observed at location C provide a case in point: Individuals of intermediate and small size at location C had high mortality rates during the 1983–1984 transition period, coupled with a high rate of recruitment. Even with substantial recruitment into the population, the long-term prediction under these demographic conditions was for a fairly rapid decline in the size of the population. In contrast, during the 1984–1985 transition period, rates of recruitment into the local population were low, but the long-term prediction was for rapid growth due to low rates of mortality among individuals in the smaller size classes. When the two transition periods are con-

sidered together in a matrix analysis, i.e., a good year of recruitment always followed by a good year of growth, the long-term prediction for population growth ($\lambda_1 = 1.07$) is greater than if the geometric mean of the long-term trends predicted for the two separate transition periods is used ($\lambda_1 = 0.85$). In the latter case, the prediction is that the population is actually declining in size. The situation is, in some ways, even more extreme at location E. There, when both transition periods are considered together, population growth is predicted to be extremely rapid ($\lambda_1 = 1.28$), whereas the geometric mean of population growth rates over the two transition periods predicts that the population is growing very slowly ($\lambda_1 = 1.03$). Unfortunately, since such a large year-to-year difference in the amount of recruitment was found, it is hard to generalize about the impact of differential recruitment rates on long-term population growth and on the overall maintenance of differences in population size among locations without knowing more detail about long-term trends in rates of recruitment by the population.

If recruitment rates were high every year, population growth rates would be substantially higher given the present demographic relationships. However, there is some circumstantial evidence for density-dependent control of recruitment. High rates of recruitment by *Danthonia sericea* in 1984 were observed after a general decline in vegetative cover during the 1983–1984 growing season due to extreme drought conditions. If successful recruitment increases with a decline in cover by the surrounding vegetation, it could serve to replenish the population at a time when establishment success is greater due to lower density-dependent mortality. I have presented some experimental evidence for density-dependent control of germination elsewhere (Moloney 1986a). If real, it could confer some level of stability upon the *Danthonia sericea* population, particularly in more marginal habitats, as found at location C.

With high year-to-year variation in demographic parameters, as observed with *Danthonia sericea*, the Lefkovich transition matrix model can provide some understanding of the general trends controlling population processes during the period of study. However, an implicit assumption of the analysis is violated. It is assumed that the demographic parameters are time invariant, and any predictions of the expected distribution of individuals among size classes or predictions of long term population growth depend upon this assumption (Keyfitz 1968, Caswell 1978). There is a need to develop models explicitly incorporating year-to-year variation in predicting long-term demographic processes.

One theoretical prediction that is applicable to populations with varying demographics is derived from the property of weak ergodicity. This states that populations governed by the same demographic parameters, whether time invariant or not, will converge in population structure over time, independent of initial

conditions (Searle 1966, Charlesworth 1980). While of interest, this property does not yield much insight into predicting long-term population trends for specific applications. An area of research that does show promise in developing a theory of time-variant population demography is the study of stochastic matrices (see Gourley and Lawrence 1977, Cohen 1979*a, b*, Slade and Lenenson 1982, Cohen et al. 1983, Tuljapurkar 1984). By obtaining accurate estimates of year-to-year variation in demographic parameters and their frequency distributions, simulation studies of population change governed by a series of transition matrices might be used to understand the long-term consequences of environmental variation on population stability. The problem with this type of study will be the difficulty in obtaining accurate estimates of transition probabilities, particularly for life history stages with very low mortality or gradual transition rates. I would argue that, although there is some value to studying a population such as *Danthonia sericea* with models developed to study time-invariant phenomena, further understanding of population processes will need to incorporate an explicit consideration of temporal, as well as spatial, variation.

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APPENDIX

Since culm production by size class during 1983 was not known for location D, I had to make estimates of $r_{iD(1983)}$ using the following information: (1) number of individuals in each size class; (2) number of seeds germinating and surviving to be included in the 1984, 1985, and 1986 censuses; and (3)

mean number of culms produced per individual per size class during the 1984 and 1985 censuses. (Notation is defined in the Methods section.) The major assumption I employed was that the number of culms produced by an individual *Danthonia sericea* plant is related allometrically to the size of the individual. Since the average size of an individual in a given size class is approximately double that of the next smallest size class, I made the further assumption that the allometric relationship for culm production by individuals within size classes can be represented best by a geometric progression.

The expected number of culms, C_{ikt} produced by individuals in size class i from location k for census t can be defined by the allometric relationship

$$C_{ikt} = \alpha_{kt} \cdot X_{ikt} \cdot \Theta^{(i-2)}, \quad (\text{A.1})$$

where $i = 2, \dots, 6$. (Individuals in the smallest size class do not produce culms.) The parameter Θ is the allometric constant specific to the individual location. The parameter α_{kt} , which may change from year to year, is a constant of proportionality for location k at census t . The total number of culms, C_{kt} produced by a population will be related to the distribution of individuals among size classes by

$$C_{kt} = \alpha_{kt} \cdot \sum_i [\Theta^{(i-2)} \cdot X_{ikt}] \quad i = 2, \dots, 6. \quad (\text{A.2})$$

It can be shown, using the definition of r_{ikt} presented in Eq. 1 of the Methods section, that

$$r_{ikt} = \frac{g_{k(t+1)} \cdot \Theta^{(t-2)}}{\sum_i [\Theta^{(i-2)} \cdot X_{ikt}]} \quad i = 2, \dots, 6. \quad (\text{A.3})$$

An estimated value of the allometric constant for subpopulation D was obtained using Eq. A.4:

$$\hat{\Theta} = \frac{\sum_i \sum_t [r_{(i+1)D} / r_{iD}]}{n} \quad i = 2, \dots, 5, \quad (\text{A.4})$$

with $n = 8$ and $t = 1984, 1985$. The estimated value of Θ was found to be 2.29 with a standard deviation of 0.53. Estimates of population growth rates, size class distributions and reproductive values differed very little among analyses using estimates of $r_{iD(1983)}$ made with values of Θ at the mean, at one standard deviation above the mean, and at one standard deviation below the mean.