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DEMOGRAPHIC CHANGE AND MICROHABITAT VARIABILITY IN A GRASSLAND ENDEMIC, *SILENE DOUGLASII* VAR. *ORARIA* (Caryophyllaceae)[1]

SUSAN R. KEPHART[2] AND CHRISTY PALADINO[3]

Department of Biology, Willamette University, Salem, Oregon 97301

Variable spatial and temporal environments are known to affect the population dynamics of plants, but studies of local-scale variability and its relationship to demographic change within a population remain limited. Using mapped plants, we examined the population dynamics of a coastal grassland endemic, *Silene douglasii* var. *oraria,* in two habitats over 10 yr. We hypothesized that ecological differences between rocky and grassy habitats might influence demographic parameters, including adult survival, growth, and density. Soil pH, soil moisture, and other abiotic variables differed little between habitats, but microsite differences in light, soil depth, and vegetation height were related to variation in *Silene* density and plant circumference. We also found significantly higher population densities, lower adult mortality, and more juvenile recruitment in rocky areas. Finite rates of population growth varied across years and habitats (λ = 0.82–1.12), with different patterns evident in the two habitats. In both, observed population sizes in 1992 were similar to matrix projections using 1982–1985 data. Populations declined in size in some years despite high adult survivorship and variable recruitment. More intensive study of seedlings is needed, including experimental evaluation of the role of light and competition. However, the habitat-specific differences we observed imply that ecological studies and conservation plans developed for rare plants should consider the effect of local scale variability on demography.

Key words: demography; endemism; microhabitat variability; population dynamics; rarity; *Silene.*

Local-scale spatial and temporal variability in environmental conditions can markedly influence plant populations, affecting parameters as diverse as seedling and adult survivorship, clonal architecture, and growth form (e.g., Lovett Doust, 1981; Hutchings and Slade, 1988; Moloney, 1990; Herben et al., 1993; Horvitz and Schemske, 1995). Spatial factors that are linked to demographic performance include locally variable substrates (e.g., for the swamp tree, *Nyssa sylvatica* ; Huenneke and Sharitz, 1990) and differences in plant cover (e.g., for biennial and perennial herbs; Hartnett and Bazzaz, 1985; Klemow and Raynal, 1985). Similarly, temporal patterns in rainfall influence survival and reproduction in winter and summer annuals (Klemow and Raynal, 1983, Wagner and Spira, 1994). Yet despite our knowledge of plant performance under varying abiotic and biotic conditions, patterns of plant response to environmental heterogeneity at small spatial scales remain little studied (Bell and Lechowicz, 1994).

For rare species requiring conservation, explicit evaluation of the effects of spatial and temporal environmental heterogeneity is essential (Fahrig and Merriam, 1994). However, too often time or resource-intensive demographic studies are neglected or de-emphasized relative to genetic aspects of conservation (Lande, 1988; Simberloff, 1988; Pavlik, 1994). As a consequence, many ecological studies of rare plants lack sufficient information to evaluate population vital rates and to apply conservation models accurately enough for effective management (Doak and Mills, 1994; Schemske et al., 1994). Also, very few demographic studies measure the long-term response of adults to local variability in habitat or climate (e.g., Menges 1990), despite the importance of these factors to population stability and differentiation (Turkington and Aarssen, 1984; Goodman, 1987; Moloney, 1988).

This study documents long-term demographic variability and its relationship to spatiotemporal environmental factors in a rare grassland endemic known from only three sites in coastal Oregon. *Silene douglasii* var. *oraria* is a state-threatened taxon and formerly a federal candidate taxon; both its geographic range and morphometric studies support its separation as a distinct entity (Kephart and Sturgeon, 1993). Endemism and rarity are of particular importance in *Silene* where 15 of ≈45 native perennials in North America were listed as candidate threatened or endangered taxa until recently redefined as taxa of "special concern" (Federal Register 1993, 1996). Demographic studies are underway for *S. spaldingii* and *S. regia* (personal communication: P. Lesica, University of Montana; E. Menges, Archibold Biological Station), but the population dynamics and conservation biology of most species are unknown. Published studies of rare *Silene* species document patterns of genetic variation with isolation, and the factors influencing fecundity and seed germination (Menges 1991, 1995; Lesica, 1993; Dolan, 1994; Westerbergh and Saura, 1994).

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[2] Author for correspondence. (email: skephart@willamette.edu).

[3] Current address: P. O. Box 3603, Salem, OR 97302–0603.

Our primary goal was to determine if the demographic characteristics of an herbaceous perennial, *S. douglasii* var. *oraria*, varied temporally or spatially in two grassland microhabitats. Secondarily, we sought to identify distinguishing features of these habitats that may influence the population biology of this rare *Silene*. To provide habitat-specific information, we measured and mapped individuals in permanent quadrats within rocky and grassy habitats over 10 yr. We asked: (1) Do population numbers vary temporally (and are they increasing, decreasing, or stable)? (2) Do characteristics such as plant size, density, and population growth rates differ with habitat? (3) What biotic or abiotic factors differ between grassy and rocky areas and are potentially related to measures of *Silene* performance (e.g., survival, growth, density)? Temperate grasslands and rock outcrops are often rich in rare and endemic plants (e.g., Baskin and Baskin, 1988); the knowledge that the demographic characteristics of these plants vary within heterogeneous environments has important ecological and conservation management implications.

Study site—We conducted research at Cascade Head, a Nature Conservancy preserve and UNESCO biosphere reserve located ≈ 130 km southwest of Portland, Oregon (45° 3.5′N, 124° 1.5′ W; Gonor, 1984). The preserve was ideal for this study since the grassland habitat is heterogeneous, and *S. douglasii* var. *oraria* is both protected and locally abundant. The plants occur on a steep basaltic promontory that rises 161 m above the Pacific Ocean at the mouth of the Salmon River Estuary. Mild temperatures, strong winds, and marked seasonality in precipitation characterize the local climate, with monthly rainfall averaging over 30 cm in winter but often only 2–10 cm in May-September (NOAA reports for Otis, OR, 1982–1992). Soils are acid clay-silts or clay-loams.

On the promontory, the two major habitats, grassy meadows and rocky outcrops, support a biotically rich prairie where grazing was minimal to absent historically because of fencing and steep cliffs. Shallow soils, exposed bedrock, and low vegetation characterize the westernmost rocky cliffs, whereas the adjacent hillsides have deeper soils with higher percent cover. The diverse rocky and grassy areas support communities dominated by native grasses and forbs (e.g., *Koeleria nitida, Festuca rubra, Delphinium menziesii, Castilleja litoralis, Clarkia amoena, Eriophyllum lanatum*).

Plant life history—*S. douglasii* var. *oraria* is a taprooted herbaceous perennial with a subterranean caudex. The base often branches just below the soil surface, creating a compact cluster of leafy stems aboveground that delimits each clump, or genet. Although stems of these "plants" can root at the nodes, our observations suggest they usually remain attached to the tap-rooted genet. Large clumps sometimes die off in segments, however, creating what appear to be several plants aboveground. A similar fragmentation into smaller modules occurs in other perennials with multiple shoots (Falinska, 1991). This growth habit makes genet identification less certain, but comparative estimates are possible using coordinate mapping, marked clumps, and permanent quadrats.

New foliage on adults emerges as early as late March and flowering begins in late April to early May. Plants are self-compatible and regularly set fruit at Cascade Head (Kephart and Nebenzahl, 1983). New seedlings are evident by May.

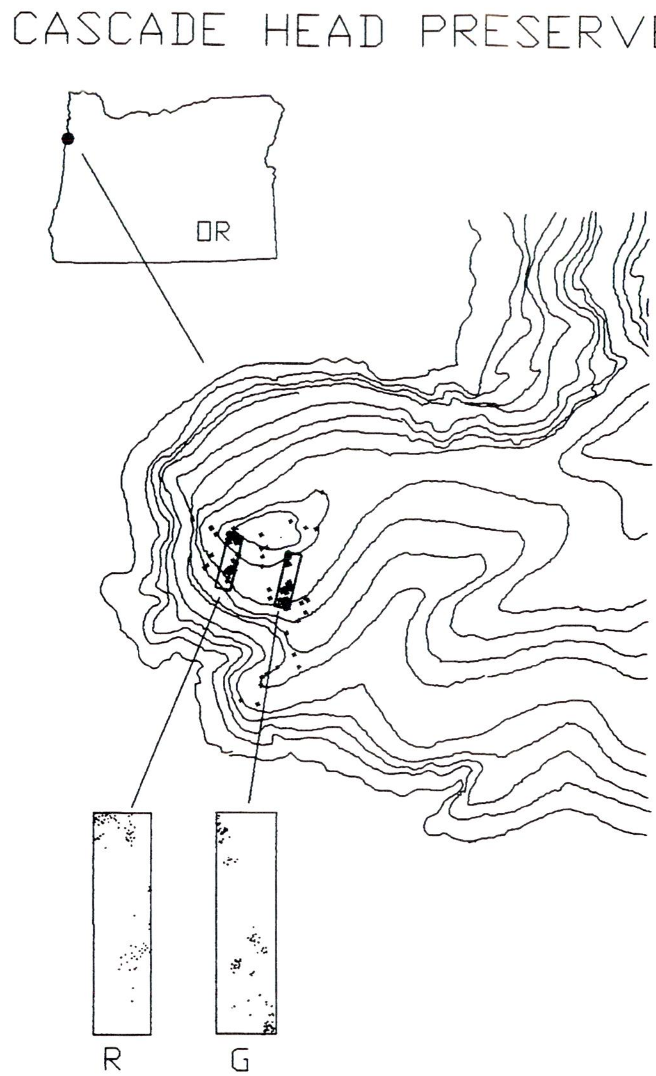

Fig. 1. The topography of Cascade Head and locations of grassy (G) and rocky (R) grids, enlarged to show the dispersion of plants mapped in 1982. The two habitats form a patchwork with rocky areas concentrated in steep western and southernmost regions and near rock formations. Dots outside the grids mark positions of *Silene* patches on the headland.

MATERIALS AND METHODS

Demographic studies—To assess population densities and growth rates in grassy and rocky habitats, we counted and measured adults and juveniles annually for three demographic transitions from 1982 to 1985, and in 1992. We also monitored survivorship of seedlings and juveniles monthly in 1984 and from 1990 to 1992.

Population sampling and adult survivorship by habitat—In 1982, we mapped all established clumps of *Silene* within two permanent 17 × 68 m grids (Fig. 1) to determine population dispersion and density, and to provide data for evaluating demographic change in different microhabitats. We located these macroplots randomly with two constraints:

(1) we used the same compass bearing to orient the long dimension of each, and (2) we located one grid in steep, "rocky" areas and one in "grassy," gently sloping portions of the promontory. Excavations were not possible, so we treated tap-rooted clumps as distinct plants if stem clusters were separated from one another by at least 2 cm. We used *x,y* coordinates to map and record the positions of individual clumps in all 1-m^2 quadrats.

For four consecutive years, and in 1992, we measured the number, size, and reproductive status of adults and new recruits, in 48 permanent quadrats selected randomly from those previously mapped with *Silene* in grassy and rocky grids. We monitored 32 additional, random "non-*Silene*" quadrats for possible invasions of formerly unoccupied sites by *Silene*. We measured the mapped and tagged plants once per year, in late June or July, when plants were green but no longer adding leaf biomass. We based size estimates on clump circumference, which worked well for the compact form of the plants; we avoided stem counts because of the potential effect of browsing on such size estimates. Plant densities and sizes were statistically analyzed across years and habitats using repeated-measures ANOVAs. If data did not meet the assumptions of homoscedasticity and normality, directly or by transformation, we used nonparametric tests.

Seedlings and juveniles—New juvenile recruits were marked annually during population censuses of all permanent quadrats in July; we distinguished them from seedlings by the absence of cotyledons and the presence of several sets of true leaves. We also followed new seedlings monthly from May to July 1984 by marking and relocating all seedling cohorts germinating in permanent quadrats. Finally, Pickering (personal communication, The Nature Conservancy) followed 80 marked seedling-derived juveniles monthly for two seasons beginning in July 1990; 23 were in previously burned plots in grassy areas outside our study grids.

Population structure and dynamics—We used Lefkovitch stage-based matrices to estimate the rate and direction of population growth (Caswell, 1989). We generated three, 1-yr demographic transitions spanning 4 yr of empirical data (1982–1985) gathered from permanent quadrats. Although small sample sizes and deterministic matrices limit the reliability of long-term projections, the mathematical properties of transition matrices allow useful estimates of finite rates of population growth at equilibrium (λ) and the contributions of life stages or processes to population viability (Menges, 1990; Schemske et al., 1994). We used RAMAS stage (Ferson, 1991) to compute statistical properties for yearly transitions among four stages: seedlings, juveniles (1st-yr recruits from seedlings or vegetative offshoots), vegetative adults (nonflowering), and reproductives. Reproductive adults produced flower buds, flowers, and/or fruits in census years; their circumferences typically exceeded 20 cm. Seeds were not included in matrices (i.e., seed dormancy was not observed or studied but most viable seeds are assumed to germinate within a single year; e.g., Silvertown et al., 1993). Elasticities calculated for matrix elements estimate the relative contribution of each life stage to λ (de Kroon et al., 1986).

Matrix coefficients for the life stages were empirically derived from quadrat censuses of marked plants in grassy and rocky sites; in the reproductive to seedling transition, we used constants estimated from seedling counts in quadrats where the number of reproductive adults was also known. This approach assumed constant numbers across years within habitats, but elasticities were low for such transitions, suggesting that small changes in these values had little effect on lambda (λ).

Rates of population increase for *S. douglasii* var. *oraria* do not reflect the reappearance of dormant individuals, a phenomenon documented in other perennial species, including *S. spaldingii* (Lesica and Steele, 1994). A few marked plants seemed to reappear after a year of dormancy. We treated these as new recruits, and simulations in which we varied their treatment in the matrix had little effect on λ. Little is known about the conditions that might induce or break prolonged dormancy in *S. douglasii,* but plants can initiate new buds from desiccated stems (S. Kephart, unpublished data).

Total numbers of juveniles were directly assessed each year, but some uncertainty is associated with the relative importance of the life stages contributing to new juveniles (e.g., a rare seedling appearing after the July census would be unmarked prior to its appearance as a juvenile in spring). Excavations were inappropriate, so we estimated whether juvenile recruits came from seedlings or vegetative offshoots based on morphology, proximity to adults, and prior knowledge of seedlings mapped in the same position. Estimates of population growth were little affected by altering ratios of juveniles derived from these pathways, but levels of genetic diversity could vary markedly depending on the source of recruitment.

To estimate the effect of environmental stochasticity on population sizes and growth rates, we computed average transition probabilities and variances from the three, 1-yr transitions. From these we projected population sizes over the 10-yr duration of our study (RAMAS stage, 1000 iterations), and compared them to empirical values obtained during census years.

Microhabitat assessments—We also sought to provide a first approximation of some of the habitat differences that might influence *Silene*. However, routine measurements that accurately assess environmental heterogeneity may be nearly impossible in principle (Bell and Lechowicz, 1994), and we could not sample the entire range of microhabitat variability among sites. Thus we used several independent measurements of environmental parameters to assess relative differences between habitats. We assumed that differences detectable in at least two of the three assessments, or which varied consistently across habitats over time, might be important distinguishing features. We then explored the possible relationship of these differences to the size and density of *Silene* plants.

In the first comparison of rocky and grassy sites conducted twice in June and July 1983, we measured soil temperature, moisture, and pH in the same 48 random quadrats that contained *Silene*. We typically averaged three measurements per quadrat using probes inserted at 15 cm depths, but shallow soils or bedrock sometimes prevented replication. We determined soil moisture and pH with an OSK-215B soil tester (Forestry Suppliers, Inc., Jackson, MS).

Second, as an independent assessment of possible between-habitat differences, we measured the same microclimatic variables on 15 June and 29 July 1983 at the base of 60 clumps of *Silene* . The four transects (B-E; 15–17 plants each) were oriented downslope and spanned the distance from west-facing, rocky sites (B, C) to deeper soiled, grassy areas (D, E). Plants in adjacent transects were 15–25 m apart.

In a third comparison of rocky vs. grassy sites, we measured a wide range of abiotic factors over 5 wk of the growing season beginning in late June 1992. In this survey, we located two replicate pairs of elongate study plots (3.2 $\times$ 34 m; N = 4 plots) in the intervening areas between the rocky and grassy grids; each pair included adjacent plots of each microhabitat type. All variables were measured in random, 1-m^2 quadrats located within the larger plots. We determined soil moisture as before and recorded soil depth. Aboveground parameters included relative humidity, air temperature, and photosynthetically active radiation (PAR), which we measured in situ at the average maximum height of *Silene* stems. (We postulated that evident differences in vegetative cover and slope between rocky and grassy sites might influence microclimatic variables.) We measured air temperature and relative humidity at vegetation height using a psychrometer. A LI-COR 190SA quantum sensor detected instantaneous PAR in 40, 1-m^2 quadrats (under sunny conditions only). For all variables, we measured plots in contrasting habitats at midday of the same day to minimize effects of solar position.

As part of the above survey in 1992, we directly compared *Silene* abundance and size with light, soil depth, and two measures of co-occurring vegetation (height, cover). We measured *Silene* abundance (SAB; plant density per square metre) and clump circumference (SCC)

TABLE 1. Mean density per square metre (± 1 SE) and number of *Silene* plants present in random quadrats (N = 24) of each 17 × 68 m grid in rocky and grassy sites. Asterisks denote significant interaction effects of habitat and year using log-transformed data (SPSS ANOVA repeated-measures test, $P < 0.05$).

Year	No. plants sampled		Mean density (no./m^2)	
	Rocky	Grassy	Rocky	Grassy
1982	76	52	3.1 ± 0.45	2.2 ± 0.31
1983	97	46	4.2 ± 0.61	1.9 ± 0.31*
1984	97	48	4.2 ± 0.59	2.1 ± 0.36*
1985	77	47	3.2 ± 0.48	2.0 ± 0.34
1992	71	46	3.0 ± 0.58	1.9 ± 0.45

within ten, 1-m^2 random quadrats in each of the same four plots used to determine light and soil depth. To infer aboveground competition, we measured the maximum height and percentage cover of the vegetation in each quadrat (N = 40). Associations between variables were determined using Pearson's product-moment correlation coefficients (Sokal and Rohlf, 1969).

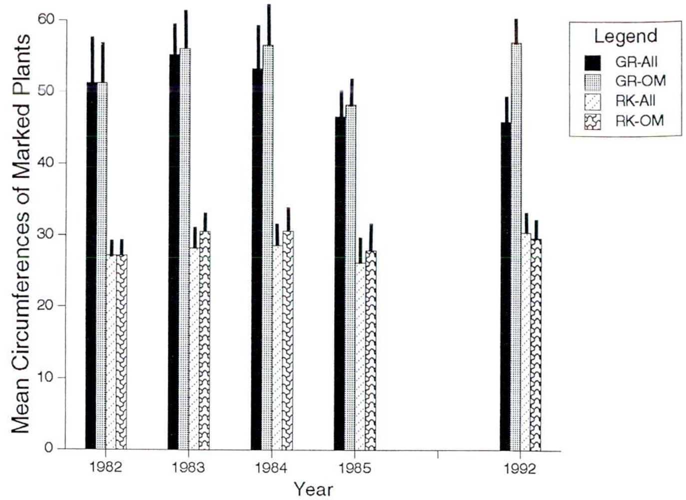

Fig. 2. Mean circumferences (± 1 SE) of all marked plants including new recruits (ALL) and those originally marked (OM) in 1982 that remained each year in grassy (GR) and rocky (RK) sites.

RESULTS

Population size and density—Plant distribution differed with habitat: 63 % of 411 plants mapped in 1982 occurred in rocky habitat (X^2 = 26.8, df = 1, $P < 0.001$). Plant dispersion was highly clumped relative to an expected Poisson distribution (X^2 = 58, 153 in each grid; $P < 0.001$). We detected *Silene* in 6.1 and 7.9% of 1156 quadrats in grassy and rocky areas, respectively.

Plant density also varied significantly with habitat, with mean values of 2.0 and 3.5 plants/m^2 across years for grassy and rocky areas, respectively (Table 1). We detected among year differences within a habitat and interaction effects of habitat and year. ($P < 0.05$, RMANOVA, Table 2).

Size and survival of marked plants: rocky and grassy sites—Plants growing in different habitats differed in mean circumference. In grass- and forb-dominated sites with deeper soils, plants were larger than in rocky habitats (Friedman Test, habitat blocked by year, $P < 0.05$; Fig. 2). Differences among years at a site were not significant (Kruskal-Wallis, H = 0.9, $P > 0.05$). Annual mortality for marked plants in grassy sites ranged from 9.8 to 10.9% during 1982–1985 and ≈ 33% of the 1982-marked plants were alive after 10 yr. Based on a 10% annual mortality, the predicted number of these marked plants agreed closely with that observed in 1992 (17 plants observed; 18 expected).

Plants in rocky habitats showed generally lower and more variable annual and 10-yr mortality rates, declining by < 2% in 1983 and 1984, and 16.2% in 1985; 48.7% of those marked in 1982 remained in 1992. Individual log-rank tests were used to compare each interval of the survivorship (i.e., depletion) curves for plants in rocky and grassy sites (Hutchings, Booth, and Waite, 1991). Residual differences were significant for two of the three yearly intervals, giving lower than expected mortality for rocky sites and higher mortality for grassy sites (Table 3). One exception occurred after vigorous growth of *Lupinus* overtopped *Silene* in a large patch of rocky habitat prior to the 1985 census; the proportion of vegetative plants becoming reproductive declined by more than one-third from previous years.

TABLE 2. Repeated-measures ANOVA of the effects of habitat and year on density of established plants of *Silene* censused in 1-m^2 quadrats.

Source of variation	SS	df	MS	F	P
Habitat	113.2	1	13.2	5.41	0.025
Year	12.5	4	3.1	2.64	0.036
Habitat × Year	13.2	4	3.3	2.79	0.028

Population structure and dynamics—In the stage structure for both habitats, reproductives comprised 58–76% of established plants, exceeding vegetative adults by 1.5 times or more (Fig. 3). Matrix probabilities show high survival for these two life history stages, which mostly maintain the same state between years (Table 4). Juveniles varied among years, constituting 1.3–22.7% of established plants (Fig. 3).

Finite rates of population growth (λ) varied across years and habitats, yielding values that individually would predict either rapid growth (1.12) or decline (0.82). Rates were higher for rocky (λ = 0.98) vs. grassy sites (λ = 0.94) overall and within years except for 1984–1985 (Fig. 4). Furthermore, the highest growth rates in

TABLE 3. Proportional survival (P) and expected mortality (E) for plants in rocky (R) and grassy sites (G) for 1-yr intervals in 1982–1985 and a single interval from 1985–1992. Residuals (RS) depict the difference between the observed and expected deaths for plants during that interval. See Hutchings et al. (1991) for computation of logrank statistic (LR). Asterisks denote significant differences; (χ^2 at $P < 0.05$); subscripts denote habitat types.

Interval	P_G	P_R	E_G	E_R	RS_G	RS_R	LR
1982–1983	0.41	0.59	2.84	4.16	+3.16	−3.16	5.3*
1983–1984	0.38	0.62	2.28	3.72	+2.72	−2.72	5.2*
1984–1985	0.36	0.64	5.38	10.30	−1.38	+1.70	0.6
1985–1992	0.37	0.63	16.82	28.18	+3.18	−3.18	1.0
Overall	E_G = 27.3			E_R = 46.4		3.30	

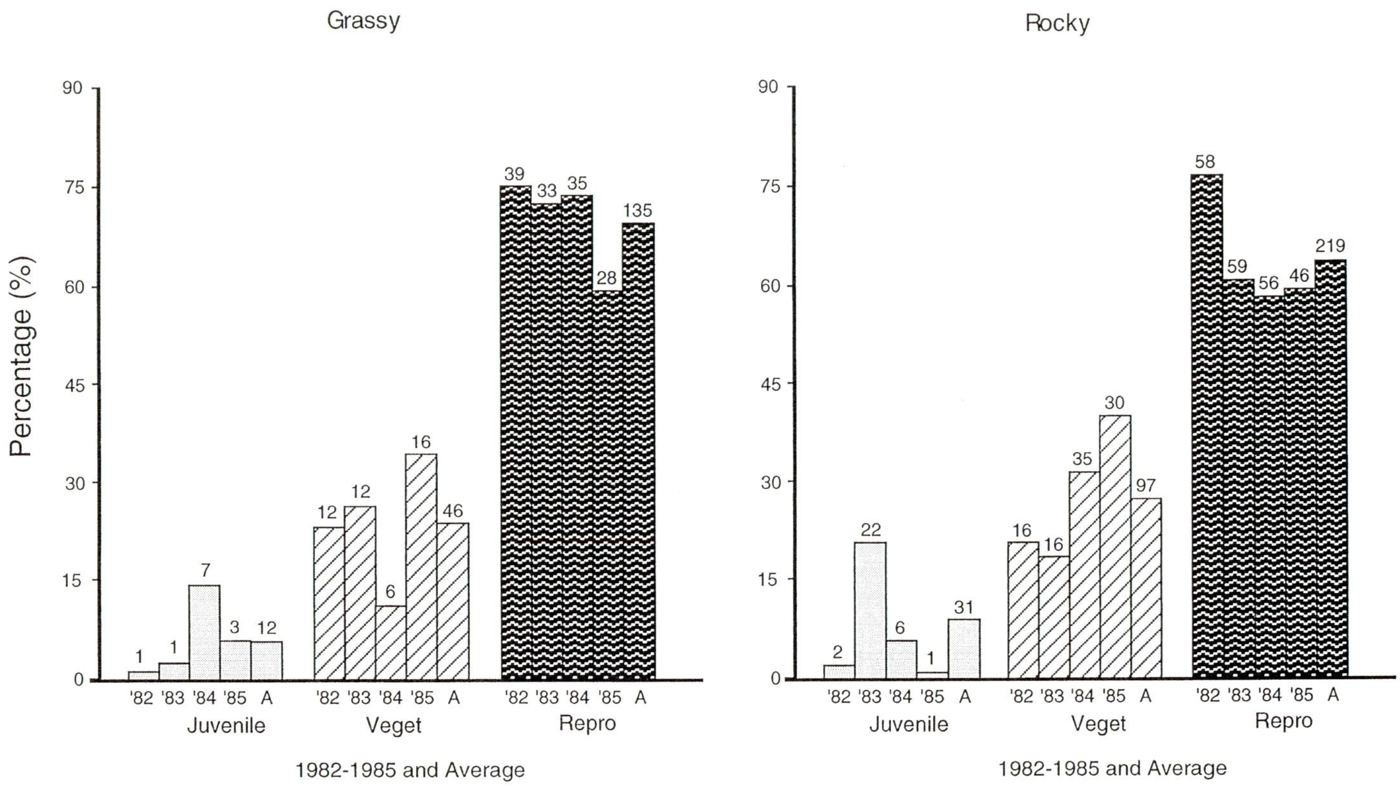

Fig. 3. Population structure of established plants of *S. douglasii* var. *oraria* in juvenile (juv), vegetative (veget), and reproductive (repro) stages. Included are plant numbers (above bars) and mean percentages (A) for 1982–1985.

grassy sites occured in years with low values in rocky areas. Stochastic simulations (Fig. 5.) also demonstrated somewhat different patterns in the two habitats: moderate population stability (rocky site) vs. declining numbers (grassy site). Observed population sizes in 1992 fell within 1 SD of those projected from transition matrices for 1982–1985.

TABLE 4. Summary stage-based matrices for three transitions from 1982 to 1985 in rocky and grassy sites. Numbers in parentheses are variances for mean transition probabilities (RAMAS-stage).

	Seedling	Juvenile	Vegetative	Reproductive
A) Rocky site				
Seedling	0	0	0	0.199
Juvenile	0.077 (0.001)	0	0.042 (0.001)	0.074 (0.010)
Vegetative	0	0.419 (0.050)	0.599 (0.011)	0.162 (0.006)
Reproductive	0	0.364 (0.037)	0.240 (0.001)	0.803 (0.013)
$\lambda_{82\text{-}85}$ = 0.978, rocky site				
B) Grassy site				
Seedling	0	0	0	0.121
Juvenile	0.054 (0.001)	0	0.037 (0.002)	0.040 (0.002)
Vegetative	0	0.405 (0.134)	0.528 (0.155)	0.131 (0.006)
Reproductive	0	0.429 (0.265)	0.389 (0.176)	0.758 (0.004)
$\lambda_{82\text{-}85}$ = 0.936, grassy site				

Elasticities depict the relative contribution of each life-cycle stage or pathway to the population growth rate (Fig. 6), and are summed to examine their relative impact (deKroon et al., 1986; Silvertown et al., 1993; Schemske et al., 1994). For both matrices, reproductives had the largest effect on λ, with elasticities averaging 68% (range = 49–97%). Among life cycle pathways (Fig. 6), survival (S1-S3) was most important: vegetative and reproductive clumps remaining in the same stage gave the largest summed elasticities in rocky (71.7%) and grassy (70.6%) habitats. A small proportion of reproductives survived, but failed to reproduce the next year (S3, Fig. 6).

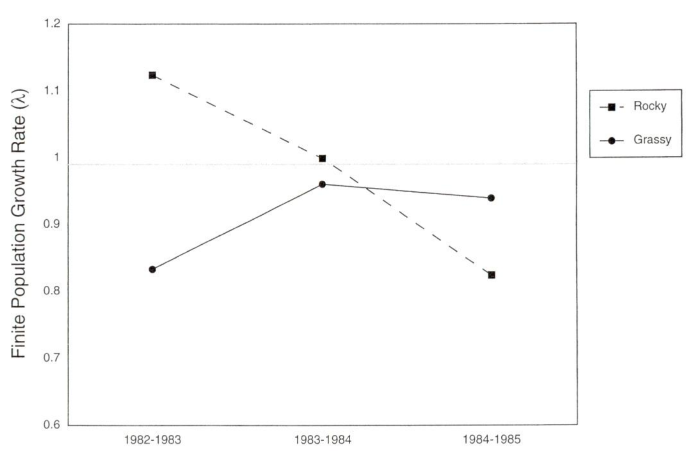

Fig. 4. Finite rates of population growth (λ) across years in rocky and grassy habitats.

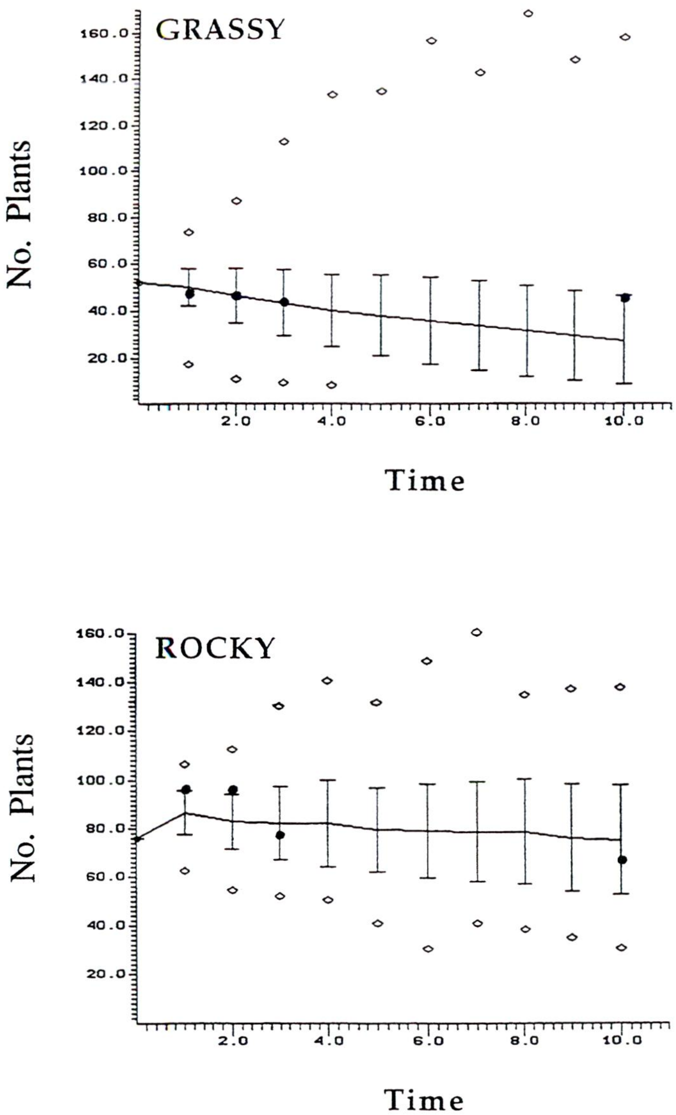

Fig. 5. Sample simulations of population projections over 10-yr periods for grassy and rocky subpopulations. Lines depict mean values (± 1 SD) for population size after 1000 iterations. Open symbols are extremes based on stochastic effects; solid circles denote observed population sizes for 1982–1985 and 1992.

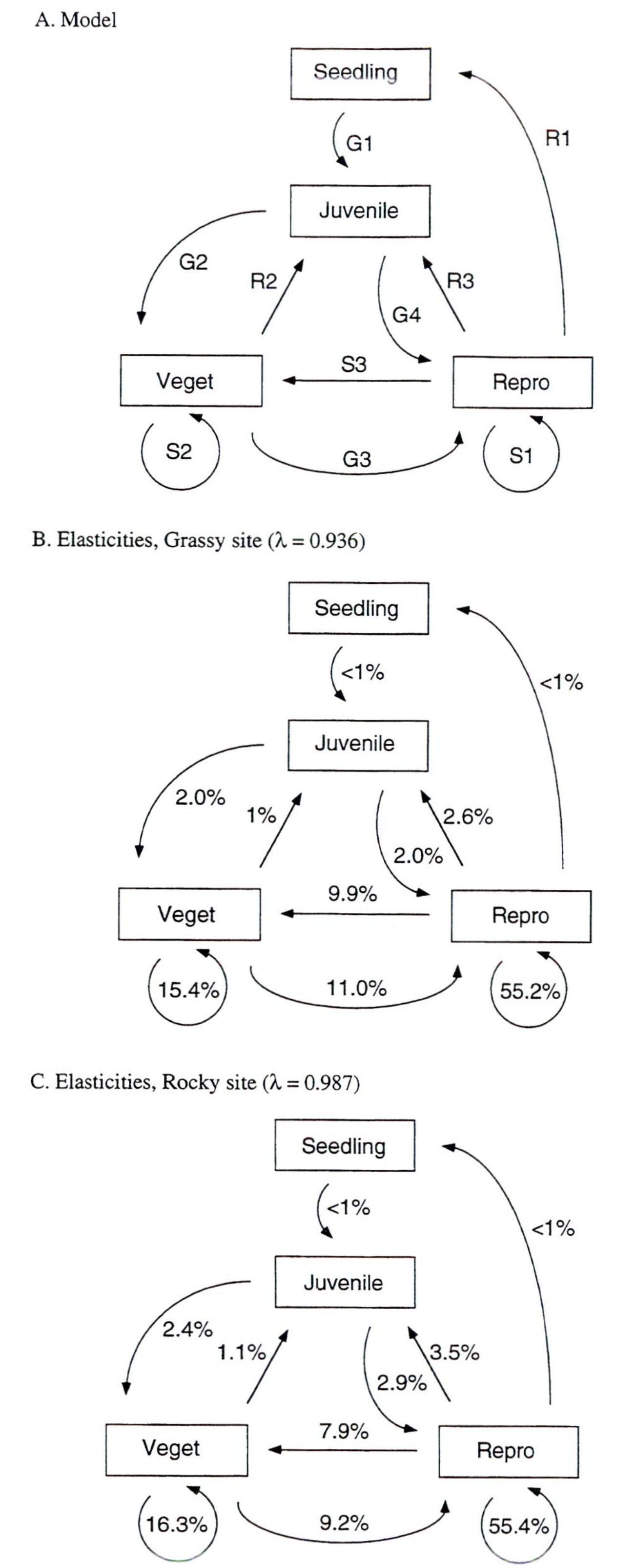

Fig. 6. Life cycle diagrams showing pathways between various stages of the model and the percentage elasticities computed from data in transition matrices of Table 4. Curved lines indicate progressive elements involving growth (G1-G3) or sexual and asexual reproduction (R1-R3); circles and straight lines depict survivorship (S1-S2) and regression (S3), respectively.

Survival and recruitment of seedlings and juveniles—Juveniles detected in midsummer censuses included both seedling-derived recruits and asexual offshoots of vegetative or reproductive adults. Over 3 yr, we observed only 43 new recruits within the 80 quadrats, with approximately equal representation of asexual offshoots (48–55%) and seedling-derived juveniles (45–53%). Significantly more juvenile recruits appeared in rocky than grassy areas ($X^2 = 8.4$, $P < 0.005$), but recruitment was limited to *Silene* quadrats; we detected no colonization by *Silene* juveniles or immigration of adults via offshoots into non-*Silene* quadrats in either habitat type (1982–1992).

Seedling survival varied seasonally and spatially. Of 61 seedlings we tracked during their first months of growth, from early May to July 1984, 45.9% survived. However, the survival rates of seedling cohorts germi-

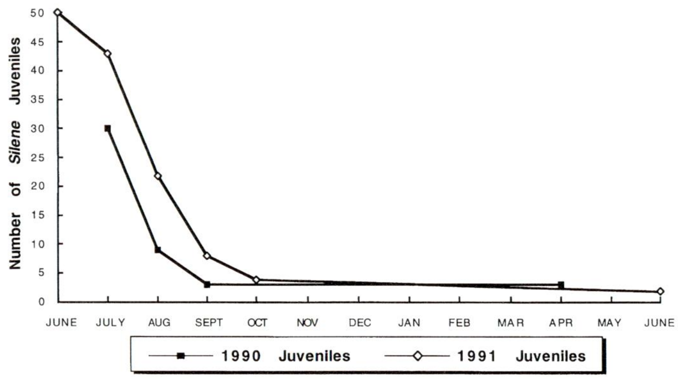

Fig. 7. Number of surviving juveniles of *Silene* for cohorts marked in 1990 and 1991. (Data contributed by D. Pickering.)

nating in different quadrats were highly spatially variable, ranging from 0 to 86%. In addition, only 5.4 and 7.7% of *Silene* seedlings survived their 1st yr to become juveniles in grassy and rocky areas, respectively (Table 4). For the seedling-derived juveniles marked in 1990 and 1991, mortality was also high late in the season, during July and August (Fig. 7).

Microclimatic variation in rocky and grassy sites—Mean values ± 1 SD for soil moisture in *Silene* quadrats were similar in grassy and rocky sites averaging 40.7 ± 8.2% and 43.9 ± 14.1% in early June and 78.0 ± 13.2% and 75.3 ± 15.6% in early July (two-sample t tests, $P > 0.05$, df = 50, 68). In fact, monthly differences were significantly different within a habitat for both rocky and grassy sites and were greater than between-habitat comparisons.

Our second estimate of between-habitat differences used abiotic measurements taken next to *Silene* plants along four transects ($N = 64$ plants). Relative to other transects, July moisture levels were significantly lower in transect B, which occurs on the steepest, rocky slope ($P < 0.05$, Student-Newman-Keuls test, SNK). Differences between other transects were not significant, and differentials between transect B and other areas may have been accentuated by record high temperatures and a precipitous drop in rainfall in late July. Wilting and desiccation were evident for some plants. Soil temperatures declined slightly from westernmost, rocky transects (B, C) to easternmost transects (D, E), but differences were significant only for nonadjacent transects ($P < 0.05$, SNK test). Soil pH values were indistinguishable across habitats, except for somewhat lower values in transect E.

Relationships among biotic and abiotic variables—In our third measure of microsite variability, adjacent grassy and rocky microsites differed significantly (Table 5) only for parameters related to soil depth and light availability (vegetation height, PAR). *Silene* was absent from grassy quadrats with dense vegetative cover; in plots containing *Silene,* exposed bedrock averaged 7% of quadrat area. Also, for quadrats with *Silene,* light availability (PAR) and *Silene* abundance were positively correlated (SAB:, $r = 0.43$, df = 18). In contrast, SAB within quadrats was negatively correlated (df = 18) with soil depth ($r = -0.47$, $P < 0.05$), vegetative cover ($r = -0.82$; $P < 0.001$) , and vegetation height ($r = -0.65$; $P < 0.01$).

TABLE 5. Mean (± 1 SE) for biotic and abiotic factors in adjacent grassy vs. rocky sites for 1992. Asterisks denote significant differences (two-sample t test, $P < 0.05$).

Measure	N	Grassy	N	Rocky
Vegetation height (cm)	20	31.0 ± 2.3	20	12.6 ± 1.1*
PAR ($\mu mol \cdot s^{-1} \cdot m^{-2} \times 10^{-6}$)	20	3.4 ± 0.4	20	14.0 ± 0.9*
Temperature (°C)	25	19.2 ± 0.4	25	18.7 ± 0.4
Relative humidity (%)	25	72.3 ± 1.7	25	74.1 ± 1.8
Soil depth (cm)	20	14.4 ± 0.8	20	9.1 ± 1.6*

To explore further the interrelationships among soil depth, light, and *Silene* performance, we sorted the 20 quadrats with *Silene* into categories of high and low PAR (< or > 1.6×10^7 $\mu mol \cdot s^{-1} \cdot m^{-2}$) and deep vs. shallow soils (< or > 3.6 cm). We found a significant, negative correlation between soil depth and *Silene* circumference ($r = -0.75$, $P < 0.05$) at low PAR but only a negligible or slightly positive relationship between these variables ($r = 0.10$, $P > 0.05$) under high PAR. Thus, in areas of low light availability but supporting *Silene,* clump size varied with soil depth and vegetation height, whereas plant size was unrelated to these parameters at high PAR levels.

DISCUSSION

S. douglasii var. *oraria* shows significant spatiotemporal variation in its demography and growth characteristics. Below we discuss: (1) the patterns and significance of this variability for population stability, (2) the possible relationship of the observed habitat-specific demography to environmental factors, and (3) the ecological and conservation implications for plant populations.

Variability in population size and dynamics—We detected significant microhabitat differences in *Silene* densities, which were consistently greater in rocky soils by 1.5–2.0 times. We also estimated population stability within habitats by the extent of temporal variation in population densities and growth rates, and by using empirically derived matrix transition probabilities to generate stochastic projections. Overall, populations varied less temporally within habitats over 10 yr (Table 1), particularly for grassy sites. Significant among-year differences largely reflect fluctuations in rocky areas (i.e., cv = 17.3% relative to 6.4% for grassy habitats); the significant interaction effect of habitat by year further suggests habitat-specific patterns of among-year variability.

Rates of population increase varied markedly ($\lambda = 0.82$–1.12) across habitats and years. Optimistic estimates, which omit the lowest, most extreme annual values, give means for rocky (1.06) and grassy (0.95) sites that imply moderately stable to declining populations, respectively. A similar pattern of somewhat higher vulnerability for plants in grassy habitats is evident in the models incorporating environmental stochasiticity (Fig. 5), and provides the first quantitative documentation of the potential for population losses since Siddall and Chambers (1978) noted declining numbers of *Silene* in the 1970s. Population sizes in 1992 are surprisingly close

(±1 SD) to projections using mean probablities and variances for 1982–1985 data, and might be more similar had we sampled in 1988–1990 when ecologists recorded increases in grassy plots (D. Pickering, personal communication, The Nature Conservancy). However, the high among-year variability in finite rates of population increase in *Silene,* and in plants generally (e.g., Bierzychudek, 1982; Horvitz and Schemske, 1995), highlight the importance of multiple estimates over time and the difficulty of projecting population trends.

Patterns of mortality—In general, declining populations ($\lambda < 1$) have a high extinction risk related to environmental stochasticity, whether reflected in growth, mortality, or reproductive status (Menges, 1992). At Cascade Head, low but variable, adult mortality (i.e., with survivorships typically exceeding 80%) and low survival of established seedlings and juveniles (< 10%) characterized plants in both microhabitats. Proximal explanations for variable mortality among years and habitat patches include local effects occurring in small patches and natural catastrophes affecting an entire region (e.g., drought). The rampant growth of lupine in one sector of the rocky grid probably contributed to the 16% decline in annual survival rate in 1985, while, in the grassy area, the survival of 1982-marked plants and total numbers were unaffected. The lowest survivorship for grassy areas occurred in 1982–1983 and may be related to heavy browsing; deer can damage as much as 87% of plants in grassy areas (S. Kephart, unpublished data).

The drought in 1992 afforded insight into the response of *Silene* to extreme climatic conditions. Soil moisture ranged from 0 to 10% that year, but the most striking change in the plant community at Cascade Head was the stark contrast of the relatively green clumps of *Silene* against the brown, dry landscape of most forbs and grasses. Although some clonal plants translocate resources between distant ramets under adverse conditions (e.g., Hartnett and Bazzaz, 1985), in *Silene* the long taproot may allow use of deeply held groundwater, as in other perennial forbs (Weaver, 1958).

Relative contributions of life-history stages to population stability—Elasticity values suggest that, for both habitats, high adult survivorship is important for population stability, ensuring that a large population of reproductives is maintained until replacement can occur via recruitment. This reflects a general pattern among herbs and other plants, particularly those with clonal growth: in 44% of herbs and 60% of clonal herbs tabulated by Silvertown et al. (1993), the highest elasticities occurred in survivorship categories. However, the number of life stages modeled varies among studies, and can affect the importance of survival or stasis relative to growth (Enright, Franco, and Silvertown, 1995). Since we used the same number of stages for plants in rocky and grassy sites, this factor should not affect relative comparisons between habitats.

Sometimes a stage with greater natural variation may limit population growth more than the one with the highest elasticity (Schemske et al., 1994). *Silene* juveniles had low elasticities but the greatest among-year variability (Fig. 3) and the least certainty in numbers; thus we need larger samples over longer time periods to discern episodic patterns and to resolve the within-season dynamics of seedlings and juveniles. Low survivorship is common in seedlings (Harper, 1977), but our sampling efforts were further thwarted by the spatial irregularity of their dispersion, high and variable mortality, and time constraints. Microclimate may be also important: gregarious germination of ≥ 28 seedlings occurred beneath large adults where plant cover may reduce desiccation in xeric summers. However, shading could limit recruitment in these microsites even if germination is successful, and the high densities near adults may reflect just the limited range of gravity dispersed seeds. Thus far, longitudinal studies of seedling emergence in *Silene* are mostly of widespread taxa with different life histories (e.g., *S. dioica* and *S. alba*; Matlack and Harper, 1986, Roberts, 1986). In the rare prairie species, *S. regia* , light appears to be critical to seed germination, which is enhanced by soil disturbance and prior burning (Menges, 1995).

Plant performance in relation to microhabitat variability—Significant habitat-specific variation in plant density and circumference, population growth rates, adult mortality, and juvenile recruitment all suggest the importance of site quality to the growth and survival of *S. douglasii* var. *oraria.* However, in identifying some of the biotic and abiotic characteristics of grassy and rocky habitats that may influence *Silene,* we discovered that different subsets of environmental parameters vary in their effectiveness as descriptors between sites. For example, most abiotic variables (e.g., subset of soil moisture, air and soil temperatures, relative humidity) were insignificantly different or varied more seasonally within a habitat than between grassy and rocky areas. Exceptions occurred during xeric periods in late July–August when we detected significant differences in soil moisture and temperature for widely spaced transects. Such differences may reduce juvenile recruitment, but are unlikely to directly affect adult survival in most years since leaf expansion, flowering, and seed production typically precede the onset of seasonal drought.

In contrast, we found significant microhabitat differences for a second set of environmental parameters, including light, soil depth, and characteristics of the surrounding vegetation. The survival, abundance, and circumference of *Silene* varied predictably with habitat for these variables. While not conclusive, our findings clearly support light availability and/or plant competition as potentially important factors affecting the distribution and density of *Silene.* First, in areas supporting *Silene,* PAR and *Silene* abundance (SAB) are positively correlated, with SAB decreasing significantly with increasing vegetation height, cover, and soil depth, parameters that provide an indirect measure of competing vegetation. Second, the relationship of *Silene* circumference (SCC) to soil depth varied with light availability. Whereas soil depth and SCC were unrelated at high light levels, plant size decreased significantly with soil depth under low PAR. Experimental studies would allow a fuller evaluation of the importance of light and competition, but it appears that light may limit *Silene* growth mainly in deeper soiled areas with more vegetation (i.e., low PAR), whereas other unidentified factors may restrict plant size in rockier sites. That shallow, rocky soils are not optimal for *Silene* growth is implied by the higher mean circumferences of plants in grassy sites, once established.

The significant, positive association between *Silene* abundance and both poor soil development and high light availability is a pattern typical of colonizers that are poor competitors for light (Tilman, 1985; Tilman and Wedin, 1991). If competition for light is important, however, one might also predict differences in the magnitude of size variation for plants under varying levels of competition. Weiner (1986) found greater size variance for *Ipomea tricolor* grown in competitive regimes; he argued that asymmetric competition for light led to variability in plant size. *Silene* adults assumed to grow under competitive conditions in grassy sites also had more variable circumferences (cv = 55–80%) in 5 yr of measurement than plants in rocky sites (cv = 38–57%), but further study is needed.

Low densities and relative high mortality characterize adults in grassy habitats, but light and competing vegetation may also influence juvenile recruitment, an aspect needing experimental study. Although *Silene*'s absence in and inability to invade sites with high cover could reflect unforseen differences in herbivory or other factors, shading is a likely possibility (Grubb, 1977). In the grassy grid, the percent cover of 40, ¼-m^2 quadrats was highest in non-*Silene* plots (Bergen, 1985), and Pickering and Macdonald (1993) found that more *Silene* juveniles survived in plots that were previously burned. A plausible alternative explanation for both juvenile and adult patterns is that litter accumulation in areas of high vegetative cover reduces survival or recruitment. Litter is known to influence seedling establishment, growth, and survival in plants (e.g., Gross and Werner, 1982); it may also increase rates of species extinction in productive communities (Tilman, 1993).

Ecological and conservation implications—Successful efforts to understand and protect rare plants must necessarily consider the ecological and evolutionary contexts in which rarity occurs and the pragmatic aspects of population management. For instance, the discovery of significant habitat-specific variability in *S. douglasii* var. *oraria* for demographic attributes (e.g., plant size, density, and population growth rate) implies that we need to consider single-site habitat heterogeneity when designing both ecological studies and conservation plans. Temporal and/or spatial variation in the growth rates of natural populations is well known, but most of our understanding of these habitat differences rests on data from multiple sites separated by 12 km or more (e.g., Bierzychudek, 1982; Menges, 1990; Lesica and Shelly, 1995). In naturally heterogeneous and fragmented landscapes, however, proximal habitat choice among patches within a locality (sensu Bazzaz, 1991; Schupp, 1995) may be just as important in influencing successful growth and recruitment. Recent evidence for this includes demographic differences linked to differences in light and substrate for tropical and temperate herbs (Horvitz and Schemske, 1995; E. Guerrant, personal communication, Berry Botanic Garden) and to edge effects for *Trillium ovatum* in forest fragments (Jules, in press).

The long-term observations of adults in different habitats at Cascade Head provide guidelines for managing populations of *Silene,* and suggest that its demographic characteristics and the amount and distribution of remaining habitat are likely to strongly influence population viability. Minimizing the encroachment of shrubs and other cover or reducing litter accumulations may be crucial for sustaining suitable habitat since the probability of seedlings, juvenile recruitment from seedlings, and adult survivorship were highest in open, rocky sites with low vegetative cover. However, the larger clump size of surviving plants in grassy areas suggests these individuals may provide an important source of seeds for dispersal to rocky microsites. In addition, many potentially interacting factors are important in determining plant rarity (Fiedler, 1986), and analyses of herbivore pressure and genetic systems in *Silene* are still in progress (S. Kephart, unpublished data).

At Cascade Head, the relatively low values of λ in grassy sites (< 1.0, Fig. 4) bolster recognition of *S. douglasii* var. *oraria* as a state and federally threatened taxon: in common and rare herbs tabulated by Silvertown et al. (1993) only eight of 45 estimates of λ fell below 1.0. The total population of *S. douglasii* var. *oraria* on Cascade Head exceeds 1000 individuals, falling within estimates for minimum viable population size in plants (Lynch, Conery, and Burger, 1995), yet further monitoring is critical given differential mortality among habitats and years and the possibility of infrequent extreme events. Ideally, one would estimate population growth rates, elasticities, and stage structure for two or more 3–4 yr cycles, allowing a longer time span for assessing stochastic variance than is possible using 2–3 transitions in consecutive years (e.g., Bierzychudek, 1982; Fiedler, 1987; Menges, 1990). However, follow-up studies of a decade or more can be of tremendous value in evaluating population trends and establishing the limits of various projection methods. Long-term appoaches that combine trend analysis with data on factors affecting the variability of critical life history stages (sensu Pavlik, 1994; Schemske et al., 1994) are still relatively rare; their success will determine the usefulness of demographic monitoring as a pragmatic tool for conservation management.

Definitions of rarity vary (e.g., Rabinowitz, 1981; Kunin and Gaston, 1993), but *S. douglasii* var. *oraria* fits most criteria applied to narrow endemics, including restricted habitat specificity, and a limited areal range and site occupancy. Historical records and ecological assessments of coastal sites suggest significant range fragmentation and habitat deterioration for grassland species due to anthropogenic disturbances and succession (Ripley, 1983). The current distribution of *S. douglasii* var. *oraria* beyond Cascade Head is limited to Cape Lookout and Neahkannie Mountain ($\approx$ 50–120 km north), but surveys in the 1800s depict extensive prairie from Cape Falcon south to Humbug Mountain, a distance of $\approx$ 400 km. On Neahkannie Mountain this habitat type is now limited to a few small patches on south-facing slopes. Only broad-scale conservation strategies that limit tree invasions and human disturbances are likely to address this deficit; successful programs would necessarily involve re-introductions of self-sustaining populations of native grasses and forbs (e.g., Guerrant, 1992; Pavlik, Nickrent, and Howald, 1993; Falk, Millar, and Olwell, 1996).

Because population sizes are small at the two remaining localities supporting *S. douglasii* var. *oraria,* demographic stochasiticity should be incorporated in future efforts to understand its biological status. Less than 100 plants are known at these sites, placing them below minimum values for population viability (Mace and Lande, 1991), and increasing the possibility that demographic and environmental effects might act synergistically in extinction vortices (Gilpin and Soule, 1986; Guerrant, 1992). Limited dispersal mechanisms will also restrict the likelihood of these populations functioning as elements of a larger metapopulation.

We also detected patterns in *Silene* populations that may parallel those of other endemic species in grassland communities. For example, the abundance and size of *S. douglasii* var. *oraria* varied significantly with microsite differences in light, soil depth, and vegetative cover. Similarly, among 29 rock outcrop endemics in unglaciated regions of the eastern United States, a high light requirement emerged as the most important contributing factor to their rarity (Baskin and Baskin, 1988). Although the generality of such patterns is often widely acknowledged, most of these taxa, like *Silene,* have not been rigorously tested relative to hypotheses of light competition. In one case, further study did not support the hypothesized low competitive ability for rare *Echinacea tennesseensis* (Baskin and Baskin 1988, Synder et al., 1994). However, its competitive ability was tested relative to a widespread congener rather than to potential competitors within the same habitat. The comparison chosen reflects the common assumption that evolutionary, not ecological factors, provide the likely explanations for rarity even when both are plausible (Kunin and Gaston,1993). Future experimental studies of *Silene* and other endemics might be designed to clarify the role of environmental and evolutionary factors in determining rarity among plants that occupy diverse microhabitats.

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