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THE EFFECTS OF NEIGHBORS ON THE DEMOGRAPHY OF A DOMINANT DESERT SHRUB (*AMBROSIA DUMOSA*)

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Abstract. We used patch-specific matrix models to test the influence of neighboring plants on the demography of *Ambrosia dumosa*, a dominant perennial shrub of the Colorado Desert in southern California. In the desert literature, the presence or absence of neighboring plants is reported to influence plant growth and survival and has long been associated with plant–plant interactions that range from extreme competition to facilitation. Here we consider the less addressed question of how neighbor-defined population subsets contribute differently to overall population dynamics.

Demographic data collected from >6000 individual plants from a permanently mapped hectare over 10 yr were used to divide this *A. dumosa* population into subsets that were defined by the presence or absence of neighbors. By partitioning the population in this way, we documented differences in population growth, elasticity structure, and stable size structure among the distinct patch types, and evaluated the contributions of each patch type to overall population dynamics. Population growth was consistently higher for population subsets of plants that were isolated throughout their ontogeny, compared to those with close neighbors throughout their ontogeny. Further, overall population growth was proportionally more sensitive to perturbations involving isolated adults, despite the projected persistence of plants with close neighbors. In short, changes in survival of isolated adults had a greater influence on population growth than changes in survival of adults with neighbors.

We used life table response experiments (LTREs) to test for spatiotemporal effects of neighbors. The LTRE was consistent with the elasticity analyses in showing that dynamics among adult members made the greatest contribution to the observed differences in population growth among the neighbor-defined population subsets during each census period. Neighbor effects among adults were greater and more important than temporal variation in drought levels in decreasing population growth relative to a pooled 10-yr reference matrix that ignored neighbor effects. Although neighbor effects contributed greatly to differences in population growth among the models projected, the LTRE revealed that, relative to the reference matrix, transitions among juvenile size classes decreased population growth for the predominantly drought free 1984–1989 census interval and increased population growth for the 1989–1994 interval, which included four winters of extreme drought. We hypothesize that higher mortality during periods of high rainfall was due to increased competition among plants, especially in favor of adults at the expense of juveniles. The drought period was also characterized by increased recruitment of new adults, probably reflecting diminished competition from adults for well-established juveniles capable of growing into reproductive condition after elimination of smaller juveniles during 1984–1989.

Our habitat-specific partitioning of this population revealed dramatic differences in the demographic behavior of this population and showed that neighbor status is a structuring force in this plant community. Neighbor effects were shown to be dependent on plant size and suggest that conspicuous clumped distributions of adults reflect leftover individuals with diminished demographic influence remaining in a population that is largely driven by isolated adults.

Key words: Ambrosia dumosa; *desert plants; elasticity; habitat-specific modeling; life table response experiment; matrix projections; neighbors; plant demography; plant population biology; spatial and temporal variation.*

INTRODUCTION

Because plants do not move, access to soil, water, and light is locally restricted, requiring each individual to depend on a local microenvironment that is strongly influenced by surrounding vegetation (Harper 1977). Consequently, interactions among plants are most intense among near neighbors. Neighbor influence can dictate spatial distributions of plants within and among species, and spatial distributions offer clues to processes that regulate plant populations and communities (e.g., Greig-Smith and Chadwick 1965, Janzen 1970,

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Connell 1971, Mack and Harper 1977, Hubbell 1979, Phillips and MacMahon 1981, Wright and Howe 1987, Miriti et al. 1998, Barot et al. 1999). Further, the effects of spatial distribution on the overall distribution and abundance of plants may be inferred from the effects of neighbors on growth, survival, and fecundity.

Desert plant communities provide a convenient system in which to study neighbor effects because species assemblages are small, and a large literature associates the spatial distributions of desert plants with plant–plant interactions (Beals 1968, Barbour 1969, 1973, Yeaton and Cody 1976, Fonteyn and Mahall 1981). Competition among plants tends to exclude neighbors, and, in time, can promote uniform spatial patterns (Beals 1968, Phillips and MacMahon 1981, Ehleringer 1984, McAuliffe and Janzen 1986, Manning and Barbour 1988). In contrast, facilitation of small by large plants (e.g., organic nutrient deposition under large plants, amelioration of abiotic factors, and protection from herbivory) can promote clumped spatial patterns (Turner et al. 1966, McAuliffe 1986, Callaway 1995, Holzapfel and Mahall 1999). In practice, pattern in desert plant populations or communities derives from an interplay of positive and negative interactions, the magnitude of which depends on proximity to conspecifics or other influential plants (Turner et al. 1966, 1969, Callaway 1995, Miriti et al. 1998, Miriti 1999). What is not clear is the extent to which plants growing in the presence or absence of neighbors contribute differentially to overall population dynamics.

The contributions to population dynamics of plants growing in different spatial configurations cannot be evaluated from the analysis of pattern alone because (1) the spatial pattern exhibited by a species at one point in time may not persist indefinitely (Clark and Clark 1984, Miriti et al. 1998) and (2) plant responses to biotic and abiotic processes are often size- or stage-dependent. Juveniles and adults within a species often do exhibit contrasting spatial patterns (Greig-Smith and Chadwick 1965, Wright and Howe 1987, Miriti et al. 1998, Barot et al. 1999) and nonrandom mortality occurs over time as a function of spatial pattern (Wiegand et al. 1995, Miriti et al. 1998, Miriti 1999). Spatial structure is known to influence such key demographic variables as individual growth and mortality (Wiegand et al. 1995, Miriti et al. 1998, Miriti 1999), which in turn may influence species composition and diversity (e.g., Kobe 1996, Harms et al. 2000). To understand population level consequences of positive and negative neighbor effects, these effects must be incorporated into models of plant demography. Mapped data can be used to isolate population members with or without neighbors in order to ascertain differential demographic behavior of these distinct population subsets. In this way, the contribution of plants facing different spatially defined environments to overall population dynamics can be evaluated.

Although spatial demographic variation associated with the habitat type of subpopulations has been incorporated into some studies of plant population dynamics (e.g., Horvitz and Schemske 1986, 1995, Alvarez-Buylla 1994, Valverde and Silvertown 1997, Parker 2000), the effects of neighboring plants are generally not included in otherwise comprehensive studies of plant demography (e.g., Sarukhàn and Gadgil 1974, Goldberg and Turner 1986, Valverde and Silvertown 1997). At the population level, the contributions of plants experiencing different local neighborhoods are implicitly assumed to contribute equally to population dynamics.

We use a patch dynamics matrix projection model (Horvitz and Schemske 1986, Alvarez-Buylla 1994, Valverde and Silvertown 1997, Pascarella and Horvitz 1998) to quantitatively test the contributions of population subsets that are defined by the presence or absence of neighbors to local dynamics of the dominant desert shrub, white bur-sage, *Ambrosia dumosa* (Gray) Payne (Asteraceae), at a site in southern California. Our definition of patch differs from those used by others because our ''patches'' are defined by the presence or absence of a neighboring plant, rather than by a broader habitat indicator such as degree of canopy openness. This model offers the advantage of not only allowing for comparison of population trajectories based on habitat-specific criteria, but allows comparisons of population dynamics (i.e., elasticity structure and stable size structure) within each distinct population subset (Pascarella and Horvitz 1998). In other words, we can ask if population growth varies, and if variation in population behavior can be explained by neighbor status.

We use demographic projections based on comprehensive censuses over 10 yr of >6000 individually mapped *A. dumosa* in a permanently mapped study site in the Colorado Desert of Joshua Tree National Park (Miriti 1999). Our matrix projections test for demographic effects of neighbors among population subsets defined by the survival and growth of individuals occurring with or without adult neighbors. We quantify differences in the demography of our neighbor-defined subsets over the 10 yr of observation using several analyses. Analysis of observed and projected size distributions within neighbor-defined subsets allows us to observe whether neighbor effects are expressed differently by size class. Elasticity analyses reveal prospective sensitivities to demographic transitions among the neighbor-defined subsets (de Kroon et al. 1986, 2000). We also conduct a life table response experiment (LTRE; Caswell 1989*a*, 1996, Brault and Caswell 1993, Horvitz et al. 1997, Parker 2000). The LTRE allows us to retrospectively evaluate both the spatial influences of neighbors and temporal variation in demographic rates.

These analyses allow us to quantify the extent to which neighbors affect *A. dumosa* demography by considering a set of hypotheses. A null hypothesis is that

PLATE 1. The study site near Cottonwood Springs in Joshua Tree National Park, California. The formation is Colorado Desert on a bajada of the Eagle Mountains, ~20 km south of the transition to Mojave Desert. Light gray shrubs in the foreground are the dominant perennial of the system, *Ambrosia dumosa* (Asteraceae). Photograph by H. F. Howe.

the presence or absence of neighbors has no influence on overall population growth or local population dynamics. One hypothesis is that individuals isolated throughout ontogeny possess an overwhelmingly positive contribution to overall population dynamics, while those with close to neighbors do not. This might be expected if competition is so severe among neighboring plants that isolated individuals contribute disproportionately to population growth. An alternative is that neighboring plants possess an overwhelmingly positive contribution to population dynamics, while isolated plants do not. This might be expected if persistent nurse effects or other forms of facilitation last beyond the juvenile stages, giving the more numerous young recruits near adult plants a disproportionate influence on population processes. Differences between neighbor-explicit models and models that do not include neighbor dynamics will highlight the importance of neighbor influences to the population dynamics of *A. dumosa.*

METHODS

Study site and species

The study site is located on a gently sloping alluvial formation (bajada) northwest of the Eagle Mountains in Joshua Tree National Park, ~10 km from the transition of the Colorado Desert to the Mojave Desert (115°47′ W, 33°46′ N; elevation 1006 m; photo in Howe and Wright 1986). The bajada is almost free of topographic heterogeneity. The steepest slope parallels the bajada and is 4%. Soils averaged from nine sampling stations at a depth of 10 cm consist of sand (62.4%), gravel (29.8%), and clays (7.8%). Rainfall averaged 18.5 cm/yr at the Cottonwood Spring ranger station (2 km distance) from 1970–1984. The most conspicuous species within the study site are *Ambrosia dumosa* (~60% of stems) and *Larrea tridentata* (~3% of stems; Miriti et al. 1998).

Ambrosia dumosa (Gray) Payne (Asteraceae), is a low, intricately branched, monoecious, drought-deciduous, perennial shrub, usually 20–60 cm high. This species is characteristic of well drained soils below 1061 m, but occasionally occurs up to 1667 m, and is associated with Creosote Bush Scrub (Munz 1974). Leaves are pinnatifid, mostly clustered, 5–20 mm long, ovate in shape, and have 1–3 short obtuse lobes. Flower and fruit production usually occur from March through May. The life span of *A. dumosa* has been described from 35–50 yr to >200 yr (Bowers et al. 1995). Most seedlings occur close to conspecific adults, but many also occur in open spaces (Wright and Howe 1987, McAuliffe 1988, Miriti et al. 1998).

The Palmer Drought Severity Index (PDSI) for the overall region (NOAA interactive database), which is a gross indicator of rainfall at our study site, shows drought conditions from 1984 to 1994, with 1989 and 1990 as the most severe drought years (Fig. 1). Index values <-3 indicate extreme drought. During 1984–1989, PDSI values fell below -3 during the spring and summer months coinciding with the characteristic drought periods for the study site, while extreme drought conditions occurred during the winter months during 1989–1994 when precipitation normally occurs at our study site (Went 1949). Therefore, drought impacts are potentially greater for the 1989–1994 census interval.

Data collection

Demographic data for *Ambrosia dumosa* were obtained from ongoing censuses of woody perennials in a permanent study hectare in Joshua Tree National Park (Wright and Howe 1987, Miriti et al. 1998). Shrubs and cacti were tagged, measured, and mapped on a fixed grid in 1984. The hectare was recensused in 1989 and 1994, during which time growth and mortality were noted for tagged plants, and new individuals >5 cm in height were tagged and measured. Reproductive status was noted by the presence or absence of flower buds, inflorescences, or infructescences. As of the 1994 cen-

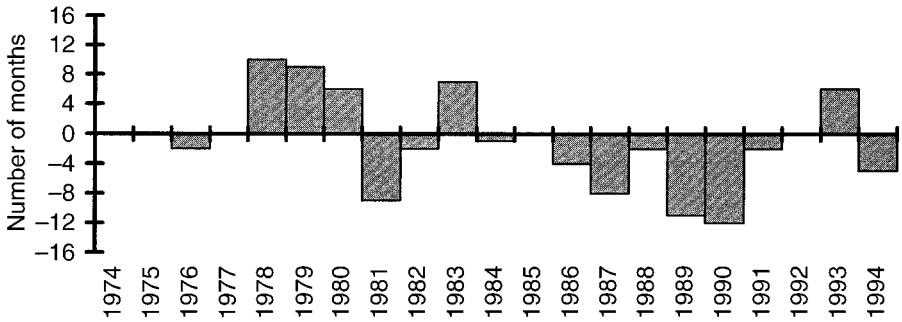

FIG. 1. Palmer Drought Severity Index values for the Southern California region from 1974 to 1994. The number of months of extreme or severe drought (index = −3 or less) are indicated by the bars below zero, and the number of months with the value above +3 are indicated by bars above zero. So categorized, our 1984–1989 census transition had ''normal'' seasonal precipitation, while the 1989–1994 transition included four winters of extreme drought.

sus, data are recorded for >6000 individuals of *A. dumosa* and of 10 000 individuals over all species.

Plant size and reproductive status

Plant size was determined by measuring the height and the major and minor axes of the canopy. Plants were considered oblate spheroids (Phillips and MacMahon 1981), with a volume (V) of

$$V = \frac{\pi p^2 q}{6}$$

where p is the smaller and q the larger of the height and the mean of the major and minor axes.

Our analyses grouped plants according to size; we separated adults and juveniles as a function of plant volume. By plotting the proportion of individuals with reproductive structures as a function of plant volume, we identified the cutoff size distinguishing reproductives (adults) and juveniles as the point of sharpest inflection in the resulting curve (Wright and Howe 1987). This method included some small reproductives in the largest juvenile category, but the reproductive contribution of these small individuals is minimal, both in absolute numbers of seeds produced and in the likelihood of survival (see Werner and Caswell 1977). For this reason, we do not feel that significant bias is introduced.

Neighbor definition

Our analyses focus on the impact of the presence or absence of a neighboring plant on overall population dynamics, assuming that the size of an individual governs its influence on the growth and mortality of a neighbor (e.g., Harper 1977, Werner and Caswell 1977, Crawley 1990). Adults disproportionately influence the growth and mortality of small juveniles, and juveniles individually have a negligible effect on adults. Log-linear analyses of juvenile fate as a function of the presence or absence of juvenile or adult neighbors showed a significant influence of adults on the survival of juveniles ($P < 0.001$), but inconclusive effects of juveniles on juvenile neighbors and no effects of juveniles on adults (Miriti 1999). We conservatively define a neighbor as an adult located within the canopy space of a focal individual. This definition is accurate for most adult plants in this population; only ~7% of adults with neighbors have more than one neighbor (M. N. Miriti, *unpublished data*). Further, the physical growth form of these shrubs is such that if canopies are touching, there is probably some overlap in root space. The space a plant occupies underground may extend beyond the canopy space, but the dimensions of this space are dynamic and are difficult to consistently define. Our conservative definition is useful because effects detected at this scale can confidently be attributed to an overwhelming neighbor effect. Canopy space is defined by the area of a circle using the major axis of the focal individual as the diameter. For juveniles, an adult is a neighbor if the juvenile is located within that adult's canopy space. Because the individual effects of juveniles on adults is negligible (Miriti 1999), we define ''neighboring plant'' as ''neighboring adult''.

To explore whether demographic variation is attributable to the presence or absence of adult neighbors, we organized the *A. dumosa* population into four neighbor-defined subsets (Fig. 2). These subsets allow neighbor status to persist or for a neighbor to appear (e.g., recruitment of juvenile into reproductive size class) or disappear (death of a neighboring adult) during the course of a 5-yr census interval. Juveniles establish and grow either under or away from adult canopies. The subsets are: (1) neighbor absent at the beginning and end of a census interval; (2) neighbor present at the beginning, but absent at the end of a census interval; (3) neighbor absent at the beginning, but present at the end of a census interval; and (4) neighbor present at both the beginning and end of a census interval. Because the effects of juveniles on adults are minor, we do not consider such potential states as juveniles germinating under isolated adults. So defined, population subsets (1) and (4) allow examination of neighbor ef-

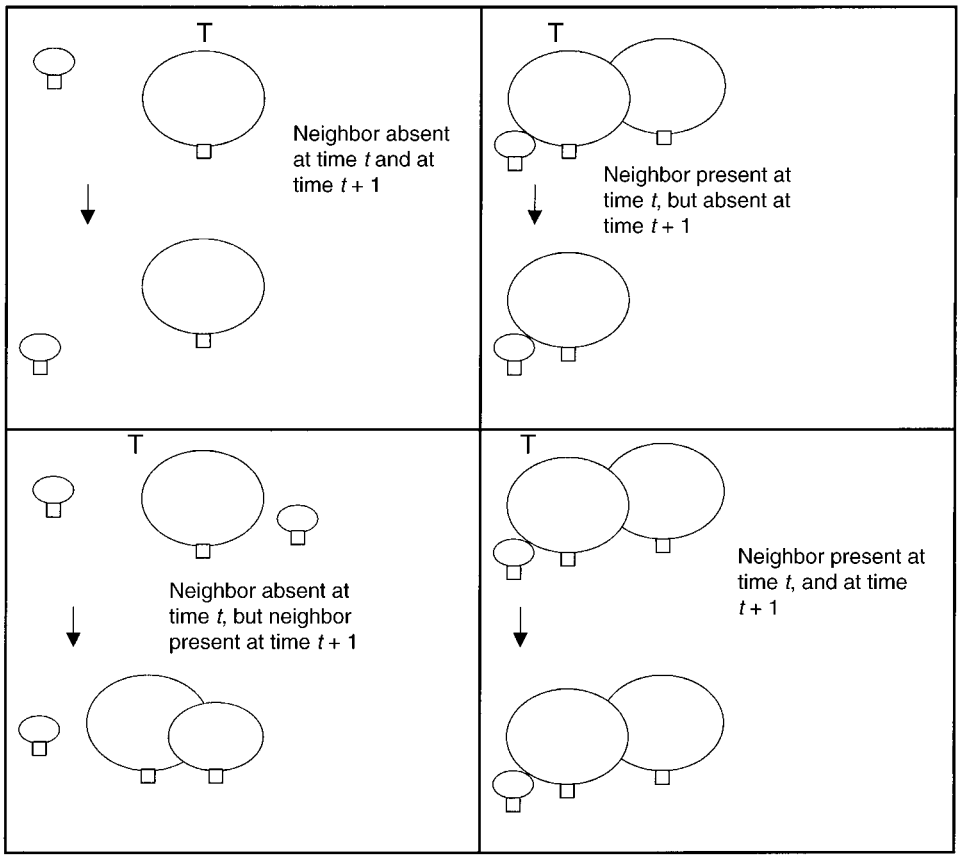

FIG. 2. Schematic diagram of the dynamics within patch types. Focal individuals are labeled with a "T." The arrow within each population subset directs the dynamics of individuals from time t to time $t + 1$

fects by contrasting the extreme states of isolation or close proximity to neighbors throughout the ontogeny of a plant. Subsets (2) and (3) are transitional and allow examination of dynamic effects such as competitive exclusion or recruitment of adult neighbors, respectively.

POPULATION DYNAMICS

Introduction and model parameterization

The standard projection matrix model is

$$\mathbf{n}_{(t+1)} = \mathbf{A}\mathbf{n}_{(t)}$$

TABLE 1. Size boundaries for the six categories used in the projection matrices.

Stage category	Log(plant volume)	Plant volume (cm^3)
Juvenile I	0–9.5	0–720
Juvenile II	9.5–10.6	720–1550
Juvenile III	10.6–15	1550–32770
Reproductive I	15–16.7	32770–106460
Reproductive II	16.7–17.5	106460–185360
Reproductive III	>17.5	>185360

Notes: Plant volume is calculated in units of cm^3. Log_2-transformed values which were used in the analysis are also presented in the table. Reproductive status is determined by remnants of inflorescences or infructescences.

in which $\mathbf{n}_{(t+1)}$ is a vector of the number of individuals within defined size categories at time $t+1$, and $\mathbf{n}_{(t)}$ is the population vector at time t. $\mathbf{A}$ is a square matrix in which the entries a_{ij} represent the transition probabilities of an individual within a given size class at time t, to a particular size class at time $t+1$. The a_{ij} values then are the size-based probabilities of growth and reproduction (Caswell 1989*b*, Horvitz and Schemske 1995). Growth can be either positive, negative (regression), or zero (stasis) for long-lived *A. dumosa.*

We used size-based Lefkovitch matrix models (Lefkovitch 1965) to evaluate the demography of *A. dumosa.* Because size is often a more reliable predictor of survival and reproduction than is age in plants (Caswell 1989*b*), size-based models have proven useful in understanding population dynamics in both short-lived (Sarukhàn and Gadgil 1974, Caswell and Werner 1978) and long-lived (Huenneke and Marks 1987, Alvarez-Buylla and García-Barrios 1991, Florez-Martínez et al. 1994, Horvitz and Schemske 1995) plant species. Data from the two census intervals, 1984–1989 and 1989–1994, were analyzed separately.

Populations were divided into six size classes using both biological and quantitative criteria. We first used algorithms that minimize distributional error associated

with the similarity of the behavior of individuals within a size class, and sampling error associated with the total number of individuals within each size class (Vandermeer 1978, Moloney 1986). Distributional error occurs when individuals within a category do not behave in a similar manner, often due to wide category bounds, whereas sampling error is common if one or more categories contain few individuals. The size classes so defined were adjusted in two instances. In one case, a suggested interval was divided into two based on reproductive criteria, and in the other case, all new juveniles (defined as plants recruited within the 5-yr interval between censuses) were combined into one size class. The six size categories include three juvenile categories and three reproductive categories (Table 1).

This longitudinal study allowed us to follow the fates of focal individuals from the start of one census period (time t) to the start of the next census period (time $t+1$). A transition frequency table of state at time t vs. state at time $t+1$ was constructed to calculate the a_{ij} entries of individual transition matrices. Dividing each entry of the frequency table by its column total yielded a maximum likelihood estimate of the transition probabilities (Caswell 1989*b*). This procedure was followed for each matrix of the two census periods under study.

Reproduction and fecundity

We define fecundity as the potential per capita contribution of reproductives to the new juvenile category. Fruits of *A. dumosa* are borne at the ends of branches in terminal and lateral spikes (MacMahon 1992), allowing the surface area of a reproductive plant to give a reasonable approximation of the relative number of seeds produced per individual. The surface areas of all reproductives, and the mean surface areas of each reproductive size class, allowed us to estimate the proportional contribution of each reproductive size class. Each proportional value was multiplied by the number of new juveniles produced within the transition interval including the position relative to an adult canopy to give the fecundity value assigned to the size class. These values, represented by the last three entries in the first row of the transition matrix, differ between matrices because the number of new juveniles varies with census date and neighbor conditions.

Seed bank dynamics (Venable and Brown 1988, Kalisz and McPeek 1993) are not included in our analyses. The absence of seed bank dynamics does not introduce significant bias since they are not directly relevant to adult plant interactions or adult–juvenile competitive asymmetries. Seed dormancies can be as long as 80 yr with unknown rates of attrition (see Rundel and Gibson 1996); adult *A. dumosa* are estimated to persist for a mean of 700 yr at this site (Miriti 1999) with low attrition therefore increasing the likelihood that the adults observed parented observed seedlings.

Population growth and the stable size distribution

The transition matrix **A** contains demographic information about the population under study. The dominant eigenvalue, or λ, gives the asymptotic growth rate of a population or a subset population, and is related to the intrinsic growth rate, r, by

$$r = \ln \lambda.$$

Therefore, $\lambda > 1$ indicates positive population growth, $\lambda = 1$ indicates stable population size, and $\lambda < 1$ indicates population decline. When a population reaches equilibrium, it will grow, remain stable, or decline at a constant rate, λ, and the proportion of individuals in each size category remains constant. The scaled right eigenvector of λ gives this stable size distribution of the population being projected. Discrepancies between observed and projected stable size or stage distributions offer insights into the fit of a population to current environmental conditions.

Elasticity analysis

It is often useful to compare the relative contributions of particular transitions, stages or demographic processes such as growth or reproduction to the population growth rate, λ. Similarly, it may be useful to evaluate which demographic process, such as growth or reproduction, contributes proportionally more to overall population growth. Elasticity analysis is a common method used to explore these differences, computed as

$$e_{ij} = \frac{a_{ij} v_i w_j}{\lambda \langle \mathbf{w}, \mathbf{v} \rangle}$$

where v_i is the ith element of the reproductive value vector (the left eigenvector of λ), w_j is the jth element of the stable stage vector, and $\langle \mathbf{w}, \mathbf{v} \rangle$ is the scalar product of the right and left eigenvectors (de Kroon et al. 1986, 2000). Elasticities give the relative contribution of nonzero transition probabilities (a_{ij}'s) to λ and are scaled such that the sum of all values equals 1; small perturbations to a_{ij}'s with high elasticity values will have strong impacts on population growth.

Neighbor interactions and population dynamics

We used a patch dynamics model (Horvitz and Schemske 1986, Valverde and Silvertown 1997) to test for potential long-term effects of neighbors on the demography of *A. dumosa*. Matrix projection of the dynamics of individuals occurring within each neighbor-defined subset gives information about the demographic effects of neighbors. The neighbor-defined matrices can be combined to form a single ''mega-matrix'' (Pascarella and Horvitz 1998) that presents information about overall population dynamics. Fig. 3 presents a life cycle diagram of the transitions within this matrix. Transition probabilities for the combined matrix were determined using a transition frequency table.

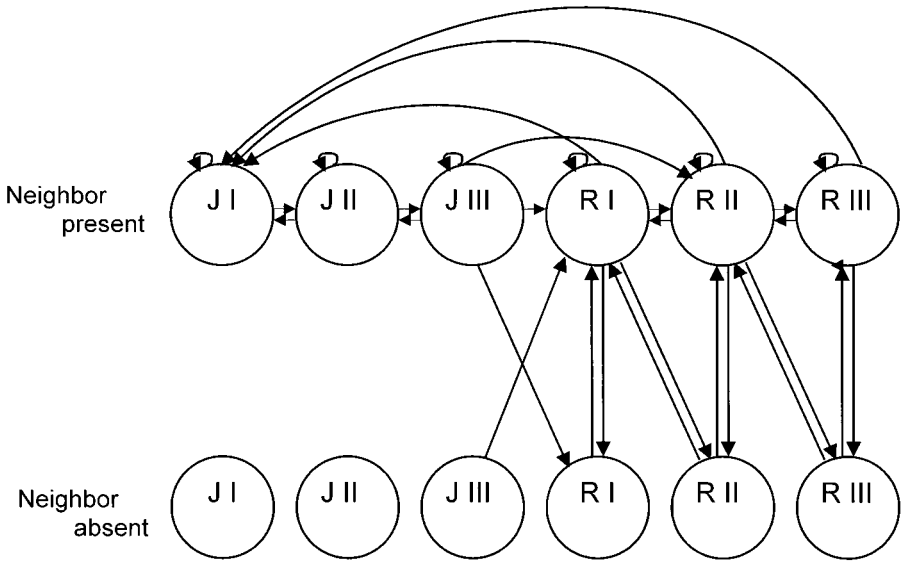

FIG. 3. Life cycle diagram depicting the major transitions between size classes and patch types that are included in the combined population model. The top diagram includes the most common transitions observed within a population subset. These transitions are omitted on the lower diagram for clarity and to enhance the transitions that occur between neighbor states. The resulting 12 × 12 mega-matrix therefore includes both transitions within subsets with constant neighbor status and transitions between neighbor states.

The plant population may be described as a series of dynamic transitions among neighbor states, with the death of or recruitment of an adult neighbor resulting in a change in the probabilities of growth and survival of the focal individual. By incorporating the dynamics between neighbor states and the demography within each neighbor state, the combined model presents a complete model for overall population dynamics. Observation of the stable stage structure and elasticities of the combined matrix yields information about the relative contributions of the various population subsets to overall population demography (Pascarella and Horvitz 1998). Observation of the subsets in isolation allows evaluation of the effects of neighbors on plant demography. If neighbor effects are predominantly negative, growth and survival should be lower for individuals with neighbors compared to those without neighbors.

Analysis of spatial and temporal variation: life table response experiments (LTREs)

We conducted a life table response experiment (LTRE; Caswell 1989*a*, *b*, 1996, Horvitz et al. 1997) to evaluate spatial and temporal variation in the demographic response of *A. dumosa* to the presence or absence of neighbors. Such analyses have proven useful in understanding the demographic responses among populations or subsets of populations that are geographically distinct or exposed to specific treatments or suites of conditions (Levin et al. 1987, Walls et al. 1991, Brault and Caswell 1993). LTREs are a method for decomposing variance in life history parameters such as λ or net reproductive rate (R_o) among two or more populations that are categorized by one or more variables such as time or location.

While elasticity analyses are ''prospective'' in that they project sensitivity relations of a future population growing at constant transition probabilities, LTREs are retrospective in considering how differences among populations have contributed to differences in life history parameters (see Horvitz et al. 1997, Caswell 2000). Similar to analysis of variance, LTREs differentiate between random and fixed effects with two different analyses. Exploration of random variables is similar to an elasticity analysis in that it points out the effects of size classes or transitions (a_{ij}'s) that strongly influence differences in demographic parameters across multiple variables; exploration of fixed variables quantifies the relative importance of focal variables or treatments to observed differences in demographic parameters such as λ.

We evaluated the effects of two fixed variables, patch type (neighbor-defined subset) and census period, and, as random variables, we evaluated variation in the transitions among size classes (a_{ij}'s) over all eight neighbor-defined projection matrices. In order to evaluate differences among treatments or transition values, it is necessary to determine a baseline matrix, $\mathbf{A}^{(\cdot)}$. A mean (mean or pooled) matrix or a nonmanipulated control matrix serves this purpose (Caswell 1996). We pooled the data over 10 yr, ignoring neighbor effects and census intervals, to calculate our baseline matrix. Such a matrix incorporates spatial differences associated with neighbors while keeping the same matrix dimensions as our individual patch matrices.

LTRE random effects.—In order to evaluate the ef-

fects of transition values among the eight neighbor-interaction/census matrices on differences in population growth, we followed Horvitz et. al (1997) in decomposing the variance in lambda ($V(\lambda)$):

$$V(\lambda) = \sum_{ij} \sum_{kl} C(ij, kl) s_{ij} s_{kl}$$

in which $C(ij, kl)$ is the covariance among all 36 matrix entries a_{ij} and a_{kl}, over the eight observed neighbor-interaction/census matrices, and s_{ij} and s_{kl} are the sensitivities of the ij, kl transitions evaluated at the reference matrix, $\mathbf{A}^{(..)}$. Covariances are calculated by converting each matrix into a single column vector and calculating the covariance among the transition probabilities among the eight vectors. Each term in the summation gives the contribution of paired transition values to variance in λ.

Similarly, we evaluated the contributions of individual matrix entries to $V(\lambda)$ using the ''covariance method'' (Horvitz et al. 1997):

$$\chi_{ij} = \sum_{kl} C(ij, kl) s_{ij} s_{kl}$$

which sums the contributions of all covariances involving the transition a_{ij}.

LTRE fixed effects.—To evaluate the effects of patch type and census, we constructed a two-way model considering population growth in patch type m and census n following Horvitz et al. (1997):

$$\lambda^{(mn)} = \lambda^{(..)} + \alpha_m + \beta_n + (\alpha\beta)_{mn}$$

in which $\lambda^{(..)}$ refers to the population growth of our reference matrix $\mathbf{A}^{(..)}$ and α_m, β_n, $(\alpha\beta)_{mn}$ are the plot, census, and interaction terms. These are calculated as:

$$\alpha_m = \lambda^{(m.)} - \lambda^{(..)} \qquad \beta_n = \lambda^{(..n)} - \lambda^{(..)}$$

$$(\alpha\beta)_{mn} = \lambda^{(mn)} - \alpha_m - \beta_n - \lambda^{(..)}$$

where $\lambda^{(m.)}$ and $\lambda^{(.n)}$ are evaluated at matrices in which transition values were calculated using data pooled over patch type and census, respectively.

Finally, the treatment effects on λ are decomposed into the contributions from the effects of each matrix element:

$$\alpha_m \approx \sum_{ij} (a_{ij}^{(m.)} - a_{ij}^{(..)}) s_{ij},$$

$$\beta_n \approx \sum_{ij} (a_{ij}^{(.n)} - a_{ij}^{(..)}) s_{ij},$$

$$(\alpha\beta)_{mn} \approx \sum_{ij} (a_{ij}^{(mn)} - a_{ij}^{(..)}) s_{ij}.$$

To control for changes in the sensitivity structure that may occur from one treatment to another, sensitivity matrices are evaluated at a matrix that is intermediate between the particular treatment being considered and the reference matrix. Following Horvitz et al. (1997), we used the mean matrix of the relevant pooled treatment matrix and our reference matrix for these calculations. We used the student edition of MA-

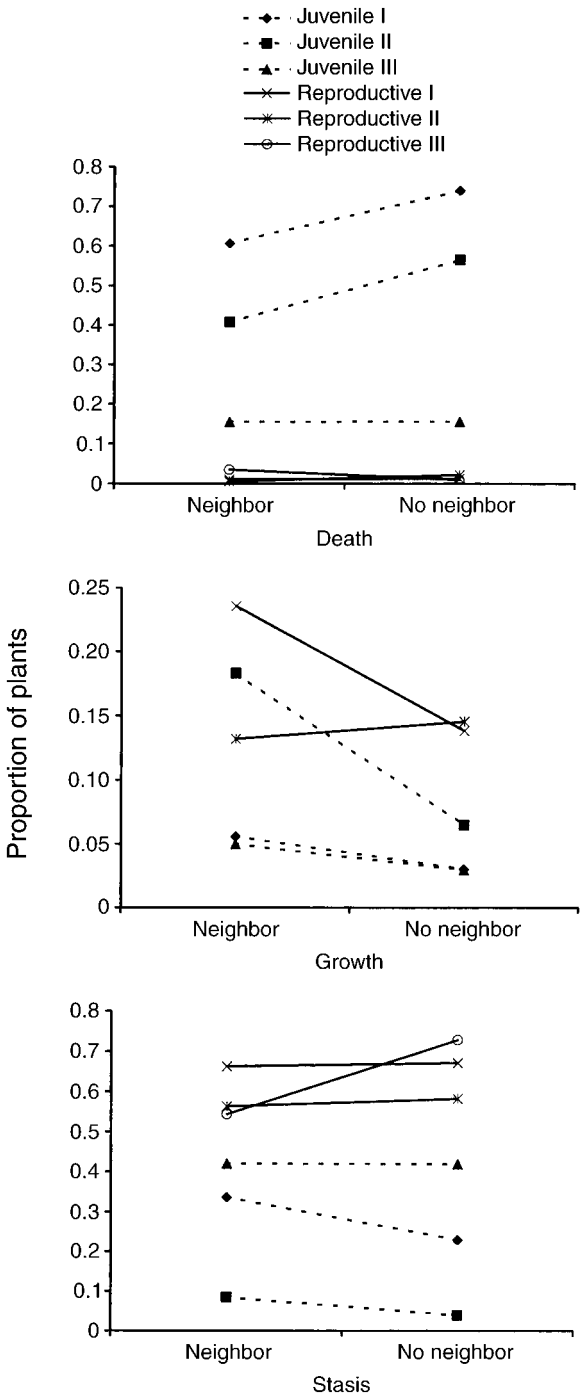

FIG. 4. The proportion of plants within each size class that experienced the indicated transition during a given census interval plotted as a function of neighbor presence or absence for the 1984–1989 census interval. Juvenile mortality increased in the absence of adult neighbors, and neighbor status more greatly influenced juvenile mortality than adult mortality. Neighbor effects for adults most strikingly influence adult growth and regression. The general pattern was similar for the 1989–1994 census interval (not pictured).

TABLE 2. Projected population growth rates for population subsets within each 5-yr census interval.

Census interval	Neighbor present at time t and time $t + 1$	Neighbor present at time t but absent at time $t + 1$	Neighbor absent at time t but present at time $t + 1$	Neighbor absent at time t and time $t + 1$
1984–1989	0.781	0.460	0.568	0.893
1989–1994	0.610	0.559	0.471	0.877

Note: Population growth is consistently highest in subsets where neighbors are absent throughout the projection interval.

TLAB version 5.0 (The MathWorks, Natick, Massachusetts, USA) for all calculations.

RESULTS

Population growth

The response of the growth and mortality of plants in the six size classes over the two census periods to the presence or absence of neighbors shows that adult neighbors had a stronger impact on growth and mortality of juvenile size classes than on adult size classes (Fig. 4, Appendix A). Small juveniles experienced enhanced growth and survival in the presence of an adult neighbor, while adults in the presence of an adult neighbor tended to remain static in size or shrink. All λ values were <1, projecting negative population growth within each neighbor-defined subset. In general, size-based growth and recruitment were higher for population subsets in which the presence or absence of a neighbor was constant from time t to $t+1$ (subsets 1 and 4). Lambda ranged from 0.4603 to 0.8927 (Table 2) with the highest λ values projected in subsets in which neither adults nor juveniles had neighbors during a census period. The lowest λ values occurred when the presence or absence of an adult neighbor differed from time t to $t + 1$ (neighbor death or recruitment). Therefore, a change in neighbor status during a transition interval is associated with decreasing population growth.

Elasticity analyses

Elasticity analyses within each subset revealed that, under most circumstances, population growth was most sensitive to stasis, compared to growth, regression, or fecundity (Fig. 5). The transition with the highest elasticity value varied among the population subsets. For those subsets in which neighbor status varied from time t to $t + 1$ (subsets 2 and 3), stasis of the largest juvenile size class consistently had the highest elasticity value, with values greater than 0.5 in all cases and as high as 0.87 in one case. In other words, under circumstances in which the spatial relations of adults vary, population growth is sensitive to the dynamics of large juveniles. For subsets in which neighbor status did not vary with time (subsets 1 and 4), stasis of one of the reproductive size classes consistently held the highest elasticity value. When spatial relations among adults are stable, population growth is most sensitive to the stasis of adults.

Elasticity analysis of the combined population was consistent with the above result showing high elasticity values for stasis of adults within population subsets where neighbor status did not vary with time (Fig. 6). During the 1984–1989 interval, the highest transition value was for stasis of the largest reproductive size class within subset 1, in which neither adults nor juveniles had neighbors. During the 1989–1994 interval, stasis of the smallest reproductive size class within this same subset held the highest elasticity value, again suggesting that under stable population growth, λ is most sensitive to the dynamics of adult individuals, with greatest sensitivity of the overall population to isolated adult plants. Altogether, population growth of *A. dumosa* was insensitive to the dynamics of plants in which the neighbor relations of adults were in flux. This difference was less pronounced during the 1989–1994 census period.

Stable size structure

Analysis of the stable size structure gives information about the relative proportions of size classes (Table 3) and the stability of a population. Comparisons of projected and observed stable size structures revealed that projected size structures significantly differed from observed structures for all models during both transition periods (Figs. 7 and 8, Table 4). Significant differences between observed and projected size distributions indicate that none of the population subsets is at equilibrium over the observed intervals, and therefore the population is not growing (or regressing) at the projected lambda values.

The observed populations for each transition period differ in that a greater proportion of individuals is in the smallest size class during the 1984–1989 interval. During the 1989–1994 interval, a greater proportion of individuals was observed in the largest juvenile size class. Both observed and projected size structures show greater variation between the two census intervals than among the different population subsets within a census interval.

Observation of the combined patch models shows

TABLE 3. Number of individuals in each size class considering neighbor status at the start of each census interval.

	1984†		1989†	
Size class	Neighbor	No neighbor	Neighbor	No neighbor
Juvenile I	588	758	989	1438
Juvenile II	71	154	109	117
Juvenile III	384	609	270	408
Reproductive I	178	390	165	408
Reproductive II	174	357	162	376
Reproductive III	114	395	83	351

† Total mortality was 1200 plants during the 1984–1989 interval and 1419 plants during the 1989–1994 interval.

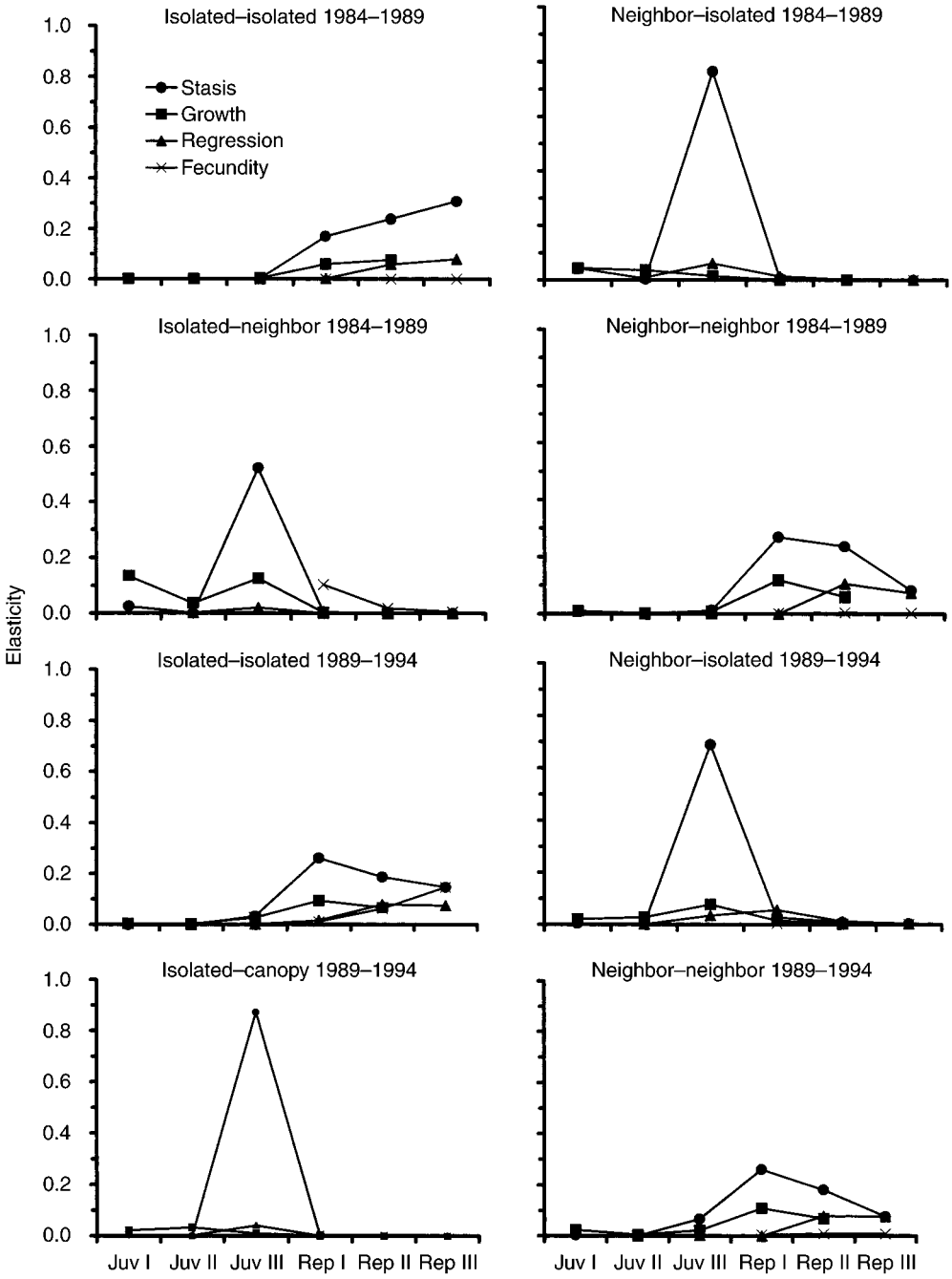

FIG. 5. Elasticity values for stasis, growth, regression, and fecundity for the neighbor-defined population subsets projected within the two census intervals 1984–1989 and 1989–1994. Peaks indicate the demographic parameter with the highest elasticity value, which contributes proportionally more to population growth. In all cases, the most important parameter is stasis, either of stage III juveniles or of reproductives. Fluctuations in numbers of small juveniles contribute little to population growth.

that a larger proportion of both the observed and projected populations occurs in isolation than with a neighbor. This is especially interesting for the smallest juvenile size class because it suggests that survival of new recruits over a 5-yr interval is not greatly reduced away from the protection of an adult canopy.

Spatiotemporal variation

All neighbor-interaction/census matrices show slower population growth rates when compared to a 10-yr pooled reference matrix $\mathbf{A}^{(\cdot)}$ ($\lambda = 0.9928$). The life table response experiment (LTRE) examines which variables (neighbor status, temporal variation, or their interac-

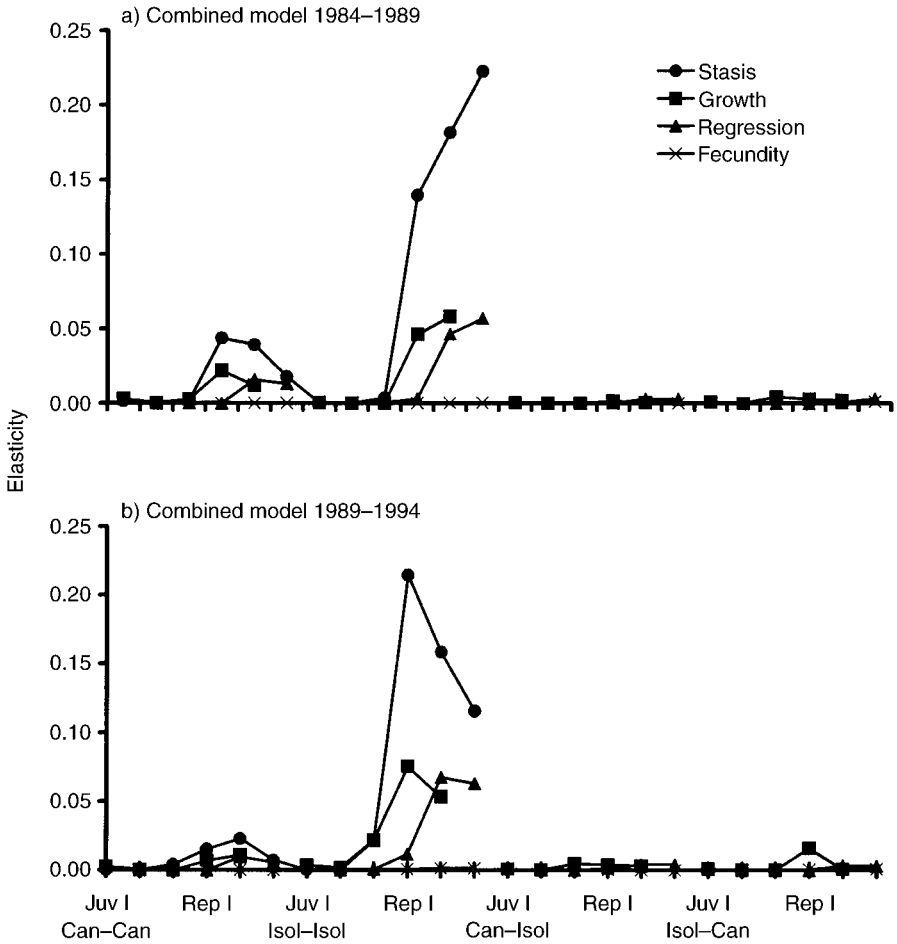

FIG. 6. Elasticities for the combined matrix models, which allow for changes in neighbor status. Patches within the matrices are in the order canopy–canopy, isolated–isolated, canopy–isolated, and isolated–canopy. All six size classes within each submatrix are represented in order with only the first juvenile and first reproductive size classes labeled. (a) Elasticity values for stasis, growth, regression, and fecundity for the combined matrix for 1984–1989; (b) elasticity values for the combined matrix for 1989–1994. Peaks indicate the demographic parameter with the highest elasticity value, which contributes proportionally more to population growth. Stasis of reproductives plays the greatest role.

tion) contribute to this reduction in population growth rate.

A detailed presentation of the LTRE is presented in Appendix B. To summarize these results, analysis of random effects, which explored variation associated with the actual transition probabilities (a_{ij}'s), were consistent with the elasticity analyses in that stasis of adults contributed most to the observed variation in projected population growth among the eight neighbor-interaction/census matrices (see Appendix B). However, analysis of the fixed treatment effects of neighbor status and census period showed that although the dynamics of adults consistently influenced population growth more than those of juveniles, the contributions of juvenile dynamics reversed sign over the two census intervals (Fig. 9). Adult plants consistently reduced population growth (λ) when compared to the baseline matrix. Juveniles on the other hand presented negative contributions to λ during the 1984–1989 census period and positive contributions to λ during the 1989–1994 census interval. These variable contributions of juveniles are likely attributable to temporal variation in abiotic variables (Fig. 9, Appendix A), which influence juvenile density and the interaction between adults and juveniles.

DISCUSSION

Matrix projections of two cohorts of plants over 10 yr documented the spatial and temporal effects of neighbors on the population dynamics of *Ambrosia dumosa*. We first examined differences in the demography of groups of plants located in population subsets that differed by the presence or absence of an adult neighbor during two 5-yr census intervals. Individual growth, recruitment, and mortality, as well as population growth, varied greatly among these four neighbor-defined subsets during both census periods, with the consistent result that neighbors were projected to decrease

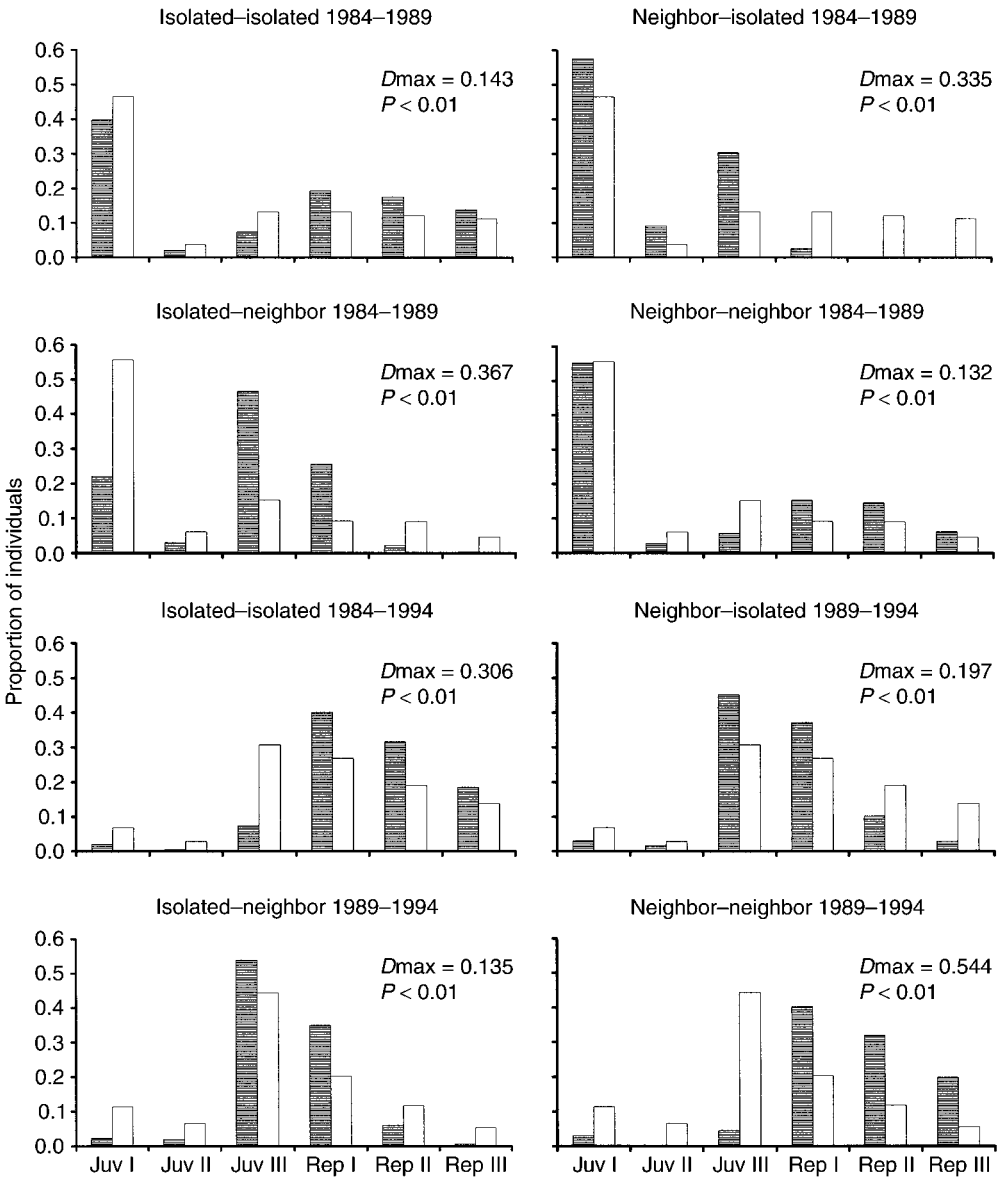

FIG. 7. Stable stage distributions for each census period and population subset. Differences in the proportions of plants within each size class are due to neighbor effects. Projected values are represented by open bars, and the observed distributions are represented by hatched bars. The Kolmogorov-Smirnov statistic, *D*max is presented with the level of significance.

population growth (Table 2, Fig. 4). Temporal variation was shown in demographic rates by differences in the stable size structures projected among all population subsets over the two census periods. Between-census variation in demographic variables was greater than within-census variation (Appendix B, Fig. B3).

We then evaluated the relative contributions of spatial and temporal effects to observed differences in population growth reflecting the four neighbor-defined population subsets and two census periods. The most striking differences were seen between juvenile contributions to population growth during the two census periods, with negative contributions from 1984–1989 and positive effects from 1989–1994. Interaction of spatial and temporal factors was not evident.

Population dynamics

Spatial factors have previously been recognized in plant dynamics, but they have been used for different purposes. The effects of plant spatial distribution on plant dynamics has been most widely recognized in ''neighborhood'' models that explore the role of density-dependent processes in determining the relative abundance of species within a community (Pacala and Silander 1985), in the role of plant resource use in regulating plant competition (Goldberg 1990), and

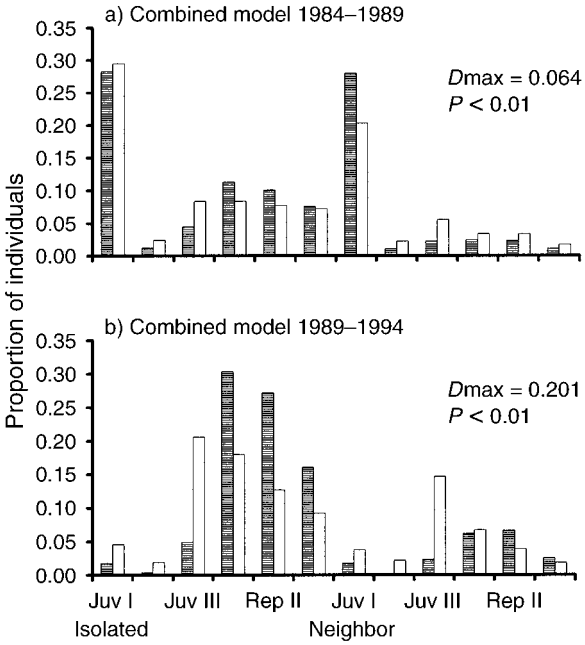

FIG. 8. Stable age distributions for the combined matrix models that allow for changes in neighbor status. Projected values are represented by open bars, and the observed distributions are represented by hatched bars. Combined models for both census intervals project a greater proportion of adults to occur in isolation than with a neighbor, although adults with neighbors are projected to persist in the population. (a) Stable stage distributions for the combined matrix for 1984–1989; (b) Stable stage distributions for the combined matrix for 1989–1994. *D*max is the Kolmogorov-Smirnov statistic.

more recently in the use of community-level SORTIE models (Pacala et al. 1996) that model community composition as a function of species-specific responses to such factors as light availability and nutrient levels. In contrast, our methods for partitioning demographic effects attributable to local variation in neighbor presence or absence in time are intended to dissect demographic variation within a single population. Our objective is to determine the relative contributions of different components of a spatially and temporally partitioned population to population growth or decline.

Neighbor effects

The apparent uniform spatial distribution of desert plants stimulated a large number of ecological studies of spatial pattern within and among desert plant species (Greig-Smith and Chadwick 1965, Beals 1968, Barbour 1969, Woodell et al. 1969, Anderson 1971, Cody 1986, Manning and Barbour 1988) and of the nature of interactions among neighboring plants (e.g., Turner et al. 1966, Barbour 1973, Yeaton and Cody 1976, Steenbergh and Lowe 1977, Wright 1982, McAuliffe and Janzen 1986, Manning and Barbour 1988, McAuliffe 1988, Brisson and Reynolds 1994, Holzapfel and Mahall 1999). These studies illustrate the extent that spatial pattern may or may not reflect direct interactions among neighboring plants. Matrix projections allow tests for long-term effects of spatial relations among individuals by permitting comparison of population trajectories for subsets of the population defined by the presence or absence of close neighbors. The focus shifts from the extent to which near neighbors cause competitive thinning to whether near neighbors significantly influence growth and survival, with the ultimate objective of determining whether these demographic differences influence overall population dynamics. Large differences in projected population growth and the elasticity structure among neighbor-defined subsets demonstrate that neighbor status does affect the local demography of *A. dumosa* at our study site. The negative impact of neighbors was evident in consistently higher population growth in subsets in which juveniles germinated and grew in isolation, and in which established adults remained isolated (Table 2). Population growth was consistently lowest in subsets in which an adult recruited next to a previously isolated adult, or in which a neighboring adult died. Both results suggest antagonism among neighboring adult plants.

Interestingly, population growth was not lowest in population subsets in which an adult neighbor was present both at the beginning and end of a census interval, which might be expected if belowground competition is most intense among near neighbors. The lowest growth was for subsets of plants experiencing addition or loss of an adult neighbor. To our knowledge, the influence of neighbor distance on competition intensity has not been directly tested, but is implicit in studies associating spatial pattern and competition in desert systems (e.g., Greig-Smith and Chadwick 1965, Phillips and MacMahon 1981, Fowler 1986), and is further suggested by positive associations between competition intensity and plant density in desert plants (Inouye et al. 1980). Projected stable size structures of our combined models indicate that neighboring plants are expected to persist in this population of *A. dumosa* despite their lower contribution suggesting that factors other

TABLE 4. Kolmogorov-Smirnov analysis of projected and observed size structures.

Years	Model	D_{max}	*P*
1984–1989	Isolated–Isolated	0.143	**
	Neighbor–Isolated	0.335	**
	Isolated–Neighbor	0.367	**
	Neighbor–Neighbor	0.132	**
	Combined	0.064	**
1989–1994	Isolated–Isolated	0.306	**
	Neighbor–Isolated	0.197	**
	Isolated–Neighbor	0.135	**
	Neighbor–Neighbor	0.544	**
	Combined	0.201	**

Note: D_{max} is the maximum difference between observed and projected values.

** $P < 0.01$.

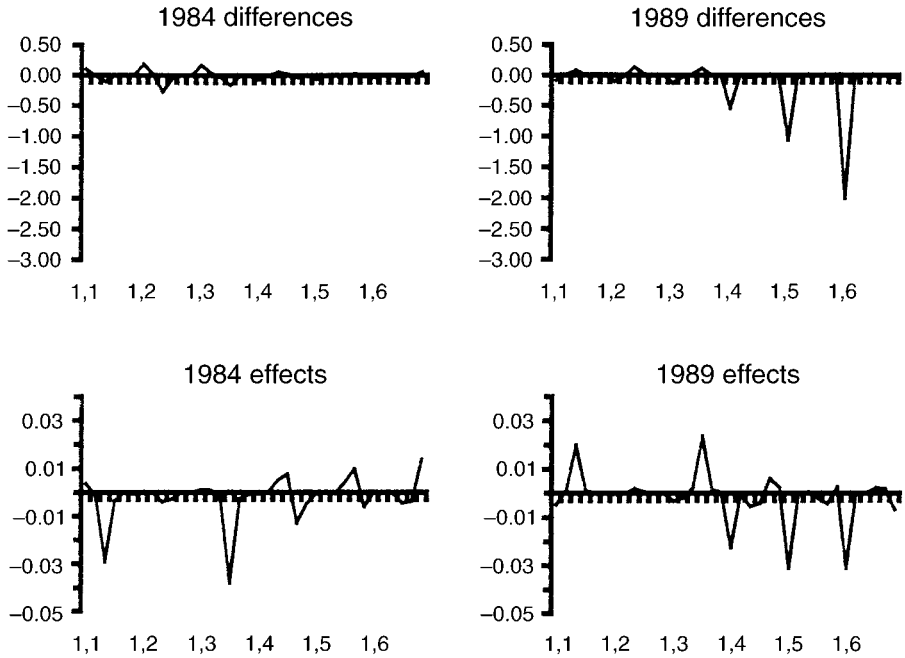

FIG. 9. Contributions of the individual matrix entries to year effects based on the results from the LTRE of fixed effects. Points labeled on the *x*-axis refer to the top entry of each of the six columns of the 6 × 6 transition matrix and are followed by the remaining entries down that column. For example, the first six entries refer to the growth of the Juv I size class. Peaks indicate transitions that made a positive contribution to population growth relative to a reference matrix that did not incorporate neighbor status. Troughs indicate transitions that made a negative contribution to population growth relative to the standard matrix. The top plots indicate the difference between the pooled year matrix and our 10-yr reference matrix; the bottom plots show the contribution of differences between the treatment and reference matrix to variation in population growth. Points above 0 represent positive contributions; points below zero represent negative contributions.

than direct competition for soil resources influence the persistence of neighboring plants.

Recent studies of conspecific interactions support the hypothesis that near neighbors need not be intense competitors (Brisson and Reynolds 1994, Toft 1995). Brisson and Reynolds (1994) found that neighboring *L. tridentata* allocated greater root development in areas of lesser competitive pressure, i.e., in the direction opposite a neighboring plant. Where this compensation does not exist and plant roots overlap, plant performance was expected to decrease (Brisson and Reynolds 1994). Mahall and Callaway (1991) experimentally demonstrated that, upon contact with roots of neighboring conspecifics, *A. dumosa* target roots decreased growth rate. This mechanism would diminish overlap of root zones of neighboring plants and allow increased allocation to unimpeded roots. This general pattern contrasts with unusual situations in which neighboring plants reach groundwater (Toft 1995), and therefore do not compete directly for one key limiting resource. For *A. dumosa,* greater reductions in population growth when neighbor dynamics change imply that recruitment of a new competitor may upset established root allocation, while loss of a neighbor may indicate ineffective allocation that resulted in competitive exclusion.

The persistence of neighboring plants in this *A. dumosa* population may also be related to the balance of competition and facilitation in plant communities (Callaway 1995, Callaway and Walker 1997). The relative roles of competition and facilitation are expected to vary with amounts of abiotic stress and life history stage, among other factors (Callaway and Walker 1997). Evidence for facilitation was seen most strongly by enhanced seedling establishment underneath adult canopies (Miriti 1999) and is suggested by the overall clumped distribution of *A. dumosa* at this study site (Wright and Howe 1987, Miriti et al. 1998). An exclosure experiment indicates that vertebrate herbivory is a major source of mortality for small plants (Miriti 1999), and this is likely to be greater for isolated juveniles and less for those under adults. The persistence of neighbors to the adult stage probably reflects the history of nurse effects that adults provide to numerous members of smaller size classes rather than continuing facilitation.

Elasticity analyses of the two combined models consistently projected that population growth was proportionally more sensitive to the stasis of isolated adults. In general, high elasticity values for stasis or survival of reproductive individuals have been observed in a number of long-lived animals and plants (Crouse 1987, Silvertown et al. 1993, Doak et al. 1994). In particular, Silvertown et al. (1993) found that population growth of woody plants was characteristically most sensitive

to stasis of adult members. The high elasticities associated with isolated adults compared to neighboring adults illustrates that all adults are not of equal significance in the population dynamics of *Ambrosia dumosa.* Mortality of isolated adults has a greater impact on population growth than disturbances involving any other size class in any other population subset.

Evaluation of elasticities for the subsets in isolation showed that when the neighbor status of adults was in flux, population growth was proportionally more sensitive to stasis of the largest juvenile size class (Fig. 5). Large juveniles in these subsets may, in fact, be in a fortuitous situation because death of an adult plant creates an opportunity for rapid growth and recruitment into reproductive size classes. Recruitment of adults involves being in the right place at the right time (e.g., Hubbell and Foster 1986, Tilman 1997, Hubbell et al. 1999). This effect was diluted for our combined model, which was largely insensitive to dynamics within the transitional subsets, thereby illustrating the advantages of partitioning demographic effects.

Temporal effects

An important aspect of population dynamics is the extent to which environmental variation affects demographic rates, and how variation in demographic rates influences population trajectories and life history (Hastings and Caswell 1979, Horvitz and Schemske 1995, Pfister 1998, Doak and Morris 1999, Sæther and Bakke 2000). Desert plant demography is commonly characterized by episodic events driven by variation in the timing and amount of rainfall (Beatley 1974, MacMahon and Wagner 1985). Consistent with findings in other arid systems (Turner 1990, Watson et al. 1997*a*), temporal variation in demographic parameters are likely to be related to drought levels recorded over the two census intervals (Fig. 1). Drought occurred in Southern California from 1985 to 1990 with the most severe drought years in 1989 and 1990. Regional drought indicators are consistent with our study site, which experienced several years with almost no rainfall (JTNP staff, *personal communication*). Drought would be expected to decrease germination, establishment of seedlings, survivorship of smaller individuals, growth, and seed production.

Noticeable differences in size structures were observed over the two census intervals. Independent of the model considered, both observed and projected size structures consistently showed a greater proportion of juveniles for the 1984–1989 census interval than for the 1989–1994 census interval (Figs. 7 and 8). Two demographic components are likely to contribute to this difference in size structure. First, the number of new juveniles produced during the two census periods differed by two orders of magnitude (1882 new juveniles produced during 1984–1989 vs. 63 produced during 1989–1994 despite particularly wet periods in 1993). Second, the probability for juvenile recruitment into reproductive size classes was over an order of magnitude greater for the 1989–1994 census interval than for the 1984–1989 interval (Appendix B, Fig. 4).

The probability of seedling establishment increased under conditions that were quite different from those that increased the probability of adult recruitment, suggesting that the biotic and abiotic conditions that enhance recruitment of large juveniles to adult size classes do not reflect those conditions that enhance establishment of seedlings (Schupp 1995; M. N. Miriti, H. F. Howe, and S. J. Wright, *unpublished manuscript*). This result may influence the observed differences among the size distributions for each census period. Such differences in conditions that promote key demographic transitions are relevant to the discussion of continuous vs. episodic processes in arid plant systems (Wiegand et al. 1995, Watson et al. 1997*a, b*). Population growth ultimately depends on environmental factors that allow the number of births to exceed the number of deaths. If these factors are not continuous in time and space, and if, as our findings suggest, conditions that promote key demographic transitions are not synchronized, these individual demographic events will occur discretely at different times. Further, high environmental variation increases lag times in the ability to detect changing demographic rates (Doak and Morris 1999), which would compromise the ability to distinguish demographic change associated with observed pulses from continuous background events. This is probably an important contributing factor in juvenile response in our two census intervals; increased mortality of adults may have been such that recruitment in the second period, characterized by drought, was possible.

Despite temporal variation in demographic traits, there were only small differences in overall projected population growth rates, λ, over the two census periods. That this wide variation in juvenile dynamics did not translate to large differences in λ is testimony to the general observation that λ is not sensitive to highly variable life history stages (Pfister 1998, de Kroon et al. 2000). An evolutionary rationale for this demographic result is provided by Slatkin (1974), who argues that high elasticity values for transitions that are widely variable would lead to wide fluctuations in λ, which in turn would often decrease fitness.

Spatiotemporal variation

It is instructive to consider the relative contributions of neighbors and time to the demography of *A. dumosa.* The retrospective character of LTREs contrasts with elasticity analyses by quantifying how variation attributable to neighbor status and census interval have contributed to observed variation in projected population growth (Horvitz et al. 1997, Caswell 2000, Parker 2000). In our study, the magnitude of demographic responses attributable to neighbor status was greater than that associated with census interval (Appendix B,

Fig. B3). Differences between the probabilities of growth of new juveniles and recruitment of large juveniles were an order of magnitude greater during the dry 1989–1994 interval compared to the normal 1984–1989 interval. However, potential effects of drought become less clear when we consider that the contribution of juveniles was negative from 1984–1989, when many established, and positive from 1989–1994 when few new juveniles established (Fig. 9). These juvenile contributions point to the importance of temporal variation since they were independent of neighbor status (Appendix B, Fig. B5).

Van Groenendael and Slim (1988) found that young *Plantago lanceolata* suffered greater mortality in a wet site compared to a dry site and suggested that increased competition at the wet site accounted for this differential mortality. Our observed higher mortality of smaller juvenile classes during 1984–1989 is also consistent with this hypothesis of density-dependent mortality. Factors that promote juvenile establishment could potentially increase competition among juveniles, thereby diminishing their demographic contribution.

While neighbor status had the greatest overall effect on population change, temporal factors did trigger variation in the demography of *A. dumosa*. Plasticity in the demographic contributions of size classes in response to temporal variation in habitat quality may be an important mechanism for population persistence.

Conclusions

An often cited shortcoming of projection matrix analyses is that the transition probabilities are constant (discussed in Bierzychudek 1999). This assumes that environmental factors do not change significantly over time, the effects of environmental change are averaged over time, or that the individuals do not significantly respond to environmental variation. However, when dealing with structured populations, environmental variation can be quantified and matrix projection models have increased appreciation of population-level responses to such variation (e.g., Menges 1990, Kalisz and McPeek 1993, Horvitz and Schemske 1995, Oostermeijer et al. 1996). The utility of matrix projections is to forecast, rather than to predict the consequences of measurable demographic variation (Caswell 1989*b*). Simply stated in our case, population subsets perform more poorly when neighbor status is in flux, and they perform best when neighbors are absent throughout plant ontogeny. The presence or absence of an adult neighbor is a structuring force in this plant community.

Incorporation of such spatially explicit information as neighbor status in analyses of plant demography also has important general implications for plant population biology. Projected population growth was higher when neighbor status was ignored, and allowed no means of distinguishing the substantial and distinct contributions of plants within the same size classes but with different neighbor status. We found strongly fluctuating demography attributable to neighbor status that might resolve conflicting paradigms that exist in studies of desert plant interactions. Experimental studies of antagonistic interactions among neighbors predicts competitive removal of near neighbors (e.g., Fonteyn and Mahall 1981, Phillips and MacMahon 1981), which in turn should generate uniform spatial distributions among desert plants. Such patterns are rare (Beals 1968, Wright and Howe 1987, Miriti et al. 1998). We have shown that neighbors do tend to reduce population growth, and that there is a demographic cost to antagonism as seen by the extremely low population growth rates in the high competition subsets. The observation of random and clumped patterns among desert plants suggests that factors other than water-mediated plant–plant interactions are important in influencing the spatial distribution of desert plants. The most important single factors may be history and longevity, including a history of facilitation in the very early stages of plants which helps large cohorts establish near adult plants. In *A. dumosa* at this site, at least, individuals that reach adult status may live a mean of 700 yr (Miriti 1999). We expect that conspicuous clumped distributions of adults reflect leftover individuals of diminished demographic influence in populations largely driven by isolated adults.

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APPENDIX A

The transition matrices used in this study are available in ESA's Electronic Data Archive: *Ecological Archives* M071-007-A1.

APPENDIX B

A description of the life table response experiment is available in ESA's Electronic Data Archive: *Ecological Archives* M071-007-A2.