# EFFECTS OF COMPENSATORY GROWTH ON POPULATION PROCESSES: A SIMULATION STUDY

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*Abstract.* The spatial extent of the canopy or root system of a plant is often used as an index of its potential to acquire resources, such as water and nutrients. This has given rise to the area of influence (AOI) and neighborhood concepts for quantifying competitive interactions between neighboring plants. Both are based on a circle of fixed radius centered on a plant, which presupposes that two plants in close proximity are always strong competitors. There is evidence that this is not always the case. In this paper, we present a simple model of plant population dynamics that extends the concept of AOI by considering "compensatory" growth of root systems. The ability of a plant to grow roots into soil zones free of neighbors in response to competitive pressures is expressed by the value of a single parameter, λ. Effects on population attributes resulting from competition in plants with compensatory growth are compared with populations with noncompensatory growth.

Simulations show that compensatory plants are better able to utilize available space, have greater biomass, and outcompete noncompensatory plants. The change from a clumped to a regular distribution of individuals due to density-dependent mortality is delayed in noncompensatory plants. These theoretical results suggest that growth plasticity and the resulting asymmetry in space acquisition may play an important role in plant population dynamics.

*Key words: area of influence; competition;* Larrea tridentata; *neighborhood; pixel; self-thinning; simulation model; spatial distribution.*

## INTRODUCTION

Competition in plants is restricted between individuals in each other's immediate vicinity. Thus, the spatial extent of the canopy or root system of a plant is often used as an index of its potential to acquire resources, such as water and nutrients (Czárán and Bartha 1992). This has given rise to two major approaches for quantifying competitive interactions between neighboring plants: (1) the "area of influence" and (2) "neighborhood" indices. Both of these are based on a circle of fixed radius centered on a plant.

Area of influence (AOI) is generally defined as the circular area around a plant where it is effectively able to acquire resources, and is based on the combined size of its crown, stem, and roots (Bella 1971). Overlap in AOI of neighboring plants is used to estimate competitive pressure. This approach is used extensively in experimental studies of intraspecific competition (Daniels et al. 1986, Tomé and Burkhart 1989) and in individual-based simulation models of population dynamics (Firbank and Watkinson 1985, Leps and Kindlmann 1987, Bonan 1988, Judson 1994, Bart 1995). A "neighborhood" is generally defined as the circular area around a plant that contains all neighbors that affect its performance. Numerous indices have been proposed that are based on size, distance, and/or numbers of neighbors within a plant's neighborhood (Mack and Harper 1977, Weiner and Conte 1981, Pacala 1985).

The restriction that AOIs and neighborhoods be circular areas with plants in their center presupposes that two plants in close proximity compete strongly. There is evidence that this is not always the case. Roots of many plants preferentially grow into areas of high resource concentration (de Kroon and Hutchings 1995) or into areas with less competition to compensate for close neighbors (Harper 1985). The overlap between neighboring tree canopies is often reduced, producing asymmetry in their shape (Ng 1980, Franco 1986, Young and Hubbell 1991). In such cases, a fixed circular AOI or neighborhood will not adequately describe competitive interactions. Ross and Harper (1972) found that for *Dactylis glomerata* the specific position of a plant within a patch of conspecific neighbors had little influence on its overall performance, a result they attributed to its ability to expand into directions of lesser interference. Harper (1985) and Franco (1986) reported that several species of modular organisms exhibited a regulatory mechanism to avoid overlap between modules of the same or different individuals. Asymmetry in plant AOI may also indicate a compensation for the negative effect of neighborhood interactions (Hutchings 1988, Ford and Sorrensen 1992, Sorrensen-Cothern et al. 1993).

Brisson and Reynolds (1994) found spatial asym-

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metry in the horizontal extent of root systems in the desert shrub *Larrea tridentata*. The resulting lack of overlap between neighboring root systems is likely the result of growth reduction in the root zones due to resource depletion or to the effect of chemical compounds released in the soil (Mahall and Callaway 1991). We proposed a "compensatory" model of neighborhood interactions to explain such patterns: assuming that the overlap of AOI between neighbors is minimal, the growth of individuals is symmetric (circular) until neighboring root systems meet; thereafter, asymmetric growth occurs into areas free of neighbors to compensate for the "loss of resources" in the zone of interaction. Thus, if space is available in its immediate vicinity, a plant may not necessarily be negatively affected by the presence of close neighbors.

In this paper, we present a simple heuristic model of plant population dynamics that extends the concept of AOI by considering "compensatory" growth of root systems. The ability of a plant to grow roots into soil zones free of neighbors in response to competitive pressures is expressed by the value of a single parameter. Effects on population attributes resulting from competition in plants with compensatory growth are compared with populations with noncompensatory growth. Although the development of this model was influenced by our observations of the natural populations of *L. tridentata,* we present it as a general theoretical model to account for morphological plasticity in response to competition.

## MODEL DESCRIPTION

### Assumptions

Our model simulates the development of an even-aged, monospecific population of plants distributed in a plot of $Y$ equal-sized pixels. Armstrong (1993) discusses advantages of using pixel-based over index-based models of intraspecific competition. In particular, a pixel-based approach is well suited to simulate asymmetric growth (Armstrong 1993). The structure of the model is inspired from a model developed by van Tongeren and Prentice (1986).

The growth of a plant is represented by increases in the number of contiguous pixels it occupies. Interaction between neighboring plants is represented by competition for horizontal space; overlap of neighbors is not allowed—a pixel may belong only to one plant. The need for empirical parameters to characterize neighborhoods (e.g., mass of plant distance, size of neighborhood, dispersion, etc.) is eliminated since the negative effect of neighbors is accomplished via the direct effect of space availability, a surrogate for resource availability. The simulated plot is assumed to be homogeneous whereby each pixel contains identical resources.

The AOI of a plant has two characteristics: (1) total surface area ($A$, number of occupied pixels) and (2)

geometric shape. For a plant growing in the absence of competitors, the AOI will be circular and its actual or realized surface area ($A_{rel}$) will always be equal to the potential surface area ($A_{pot}$). A plant growing in close proximity to neighbors will usually have an asymmetric AOI and its realized surface area will always be less than or equal to potential surface area (i.e, $A_{rel} \leq A_{pot}$).

Initially, to simulate germination and establishment, a population of $N$ individuals is spatially distributed throughout a plot of $Y$ pixels. We do this according to a defined spatial distribution: regular, random, or clumped, using a modified version of LPOINT, a computer program that generates two-dimensional point patterns (Penridge 1986, Wu et al. 1987). Plant $i$ is assigned to a single pixel, $Z_i$, the location of the main stem. As plant $i$ grows and, hence, occupies more pixels, $Z_i$ may or may not coincide with the centroid of the total surface area the plant occupies.

### Potential and realized surface growth

The radius ($\rho$) of a circular AOI of an isolated plant increases by a constant amount, $c$, each time step:

$$\rho_{t+\Delta t} = \rho_t + c. \tag{1}$$

To express Eq. 1 in terms of total surface area ($A$), we substitute $\sqrt{A/\pi}$ for $\rho$ and rearrange:

$$A_{t+\Delta t} = A_t + 2c\sqrt{\pi A_t} + \pi c^2. \tag{2}$$

We define the potential increase in surface area at this time step, i.e., $A_{t+\Delta t} - A_t$, as the potential surface growth ($\Delta A_{pot}$) of a plant (of any shape):

$$\Delta A_{pot} = 2c\sqrt{\pi A_t} + \pi c^2. \tag{3}$$

Eq. 3 is computed for each plant in the population and represents potential growth in the absence of neighbors. Next, realized surface growth ($\Delta A_{rel}$) is computed with an iterative scheme whereby each plant is assigned a single pixel until either $\Delta A_{rel} = \Delta A_{pot}$ or no more pixels are available, in which case $\Delta A_{rel} < \Delta A_{pot}$. During each iteration, the order in which a plant is assigned a pixel is random. A pixel is considered available for assignment to an individual plant if it meets the following three conditions: condition 1—it is the closest unoccupied pixel to the plant main stem ($Z_i$); condition 2—it is adjacent to a pixel already occupied by the plant; and condition 3—it is within an area around $Z_i$ given by radius $r_{max} + \lambda c$, where $r_{max}$ is the distance from $Z_i$ to the farthest pixel occupied by the plant at the previous time step and $\lambda$ is a compensation parameter (Fig. 1). Condition 3 prevents an individual from having an unreasonably high growth rate in a single direction when the existence of neighbors in the other directions restrict growth.

The AOI of a plant growing in complete isolation will approximate a circle, regardless of the value of $\lambda$ (Fig. 1A). For plants with noncompensatory growth, $\lambda = 1$, i.e., growth is restricted to the area $r_{max} + c$. In
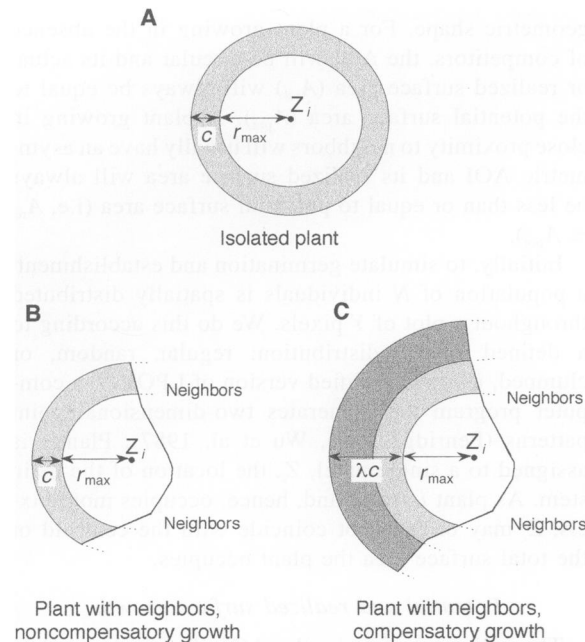
FIG. 1.   Increases in size for: (A) an isolated plant, (B) a plant with no compensatory growth in the presence of neighbors, and (C) a plant with compensatory growth in the presence of neighbors. $Z_i$ is the plant center, $c$ is the radial increase of a circular plant in the absence of neighbors, $r_{max}$ is the distance between a plant center its most distant edge, and $\lambda$ is a compensatory parameter.

the presence of neighbors, a plant with noncompensatory growth will not realize its potential growth (i.e., $\Delta A_{rel} < \Delta A_{pot}$) (Fig. 1B). A plant with a compensatory growth ($\lambda > 1$) may compensate for the lack of available pixels at the region of contact with neighbors by accessing available pixels (given by Conditions 1–2) within the area delimited by $\lambda c$ (Condition 3) (Fig. 1C). Thus, plasticity in growth is completely determined by the value of the single parameter $\lambda$, which may be defined as the ratio of maximum radial growth of a plant to radial growth of a plant in isolation.

Mortality is deterministic, determined solely by plant interference, through the indirect effect of competition for space. Death of an individual occurs if $\Delta A_{rel}/\Delta A_{pot} < M$, where $M$ is a minimum growth threshold. Thus, we assume that a slow-growing individual has a lower survivorship than a fast-growing one. This assumption follows several other models (Monserud 1976, Hamilton 1990, Kobe et al. 1995). Pixels previously occupied by a dead individual are immediately available to neighboring plants.

In Fig. 2 we present a simulation using Eqs. 2–3 and conditions 1–3 in a small population of 40 individuals capable of compensatory growth (i.e., $\lambda = 3$). At $t = 0$, the population is randomly distributed. This simulation illustrates the spatial dynamics of the AOIs over time. The form of Eq. 3 per se is not critical to the results presented in this paper. Rather, it is a heuristic
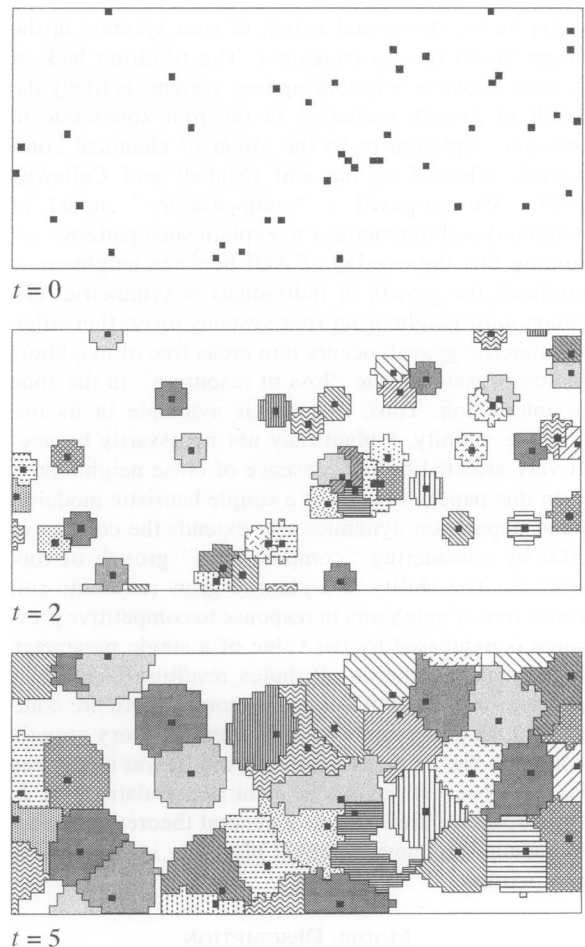


FIG. 2.   Small population of 40 individuals capable of compensatory growth (i.e., $\lambda = 3$). At $t = 0$, the population is randomly distributed.

tool that allows us to examine the effects of compensatory growth on neighborhood interactions.

### Simulation conditions

Simulations were conducted for an initial population of $N_0 = 400$ plants in a $400 \times 400$ pixel plot. The plot is bounded by similar plots on each side to avoid edge effects, i.e., the plot is folded onto itself such that plants growing on the left margin of the plot have access to pixels on the right side of the plot. LPOINT was parameterized to generate a clumped initial distribution, which is often observed in monospecific populations under natural conditions (Schlesinger et al. 1982, Kenkel 1990). We used the same initial distribution of plants in all simulations to permit direct comparisons.

Pixel length is arbitrarily set to length $L$; hence, area is in units of $L^2$. For computational simplicity, we set $c = L$. Simulations were run for 30 time steps (unless otherwise stated), where time has arbitrary units. This combination of plot size, initial population size, and length of simulation is representative of model dynam-

ics observed from a much larger set of simulation conditions.

Several population attributes were calculated. The spatial distribution was estimated using the Clark-Evans $R$ statistic, with the Donnelly correction for edge effect (Donnelly 1978, Sinclair 1985):

$$R = \frac{\bar{r}}{E(\bar{r})} \qquad (4)$$

where $\bar{r}$ is the average distance between a plant and its nearest neighbor, and $E(\bar{r})$ is the expected value of $\bar{r}$ for a population with random distribution. With the Donnelly correction,

$$E(\bar{r}) = 0.5\sqrt{\frac{A}{n}} + \left(0.051 + \frac{0.041}{\sqrt{n}}\right)\frac{D}{n} \qquad (5)$$

and

$$\text{SE}(\bar{r}) = \frac{\sqrt{0.07A + 0.037D\sqrt{\frac{A}{n}}}}{n} \qquad (6)$$

where $D$ is the length of the boundary of the region. Eq. 4 has a standard normal distribution under the hypothesis of complete spatial randomness (Sinclair 1985). The Clark-Evans $R$ has an expected value of 1 for random distributions, $<1$ for clumped, and $>1$ for regular distributions.

Size inequalities of individuals in a population were calculated using the Gini ($G$) coefficient (Weiner and Solbrig 1984):

$$G = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n}|g_i - g_j|}{2n^2 g} \qquad (7)$$

where $g$ is a measure of size. $G$ varies from 0, when all individuals are of equal size, to 1 when all but one individual of an infinite population has a size of 0 (Weiner and Solbrig 1984).

To express simulation results in terms of total plant biomass ($B$, arbitrary units of mass per plant), we assume a constant relationship between the AOI of a plant and biomass, i.e.:

$$B = \sqrt{A^3/k} \qquad (8)$$

where $k$ ($L^6$ mass$^{-2}$) is set to 1.

For the simulations presented here, we set $\lambda = 1$ (noncompensatory), 2, 3, or 4 (compensatory), and $M = 0.66$. These combinations resulted in appreciable self-thinning under all circumstances. Simulations not reported here showed that the rates of change in population attributes were sensitive to values of parameters $\lambda$ and $M$ but, in general, the patterns per se remained unaffected.
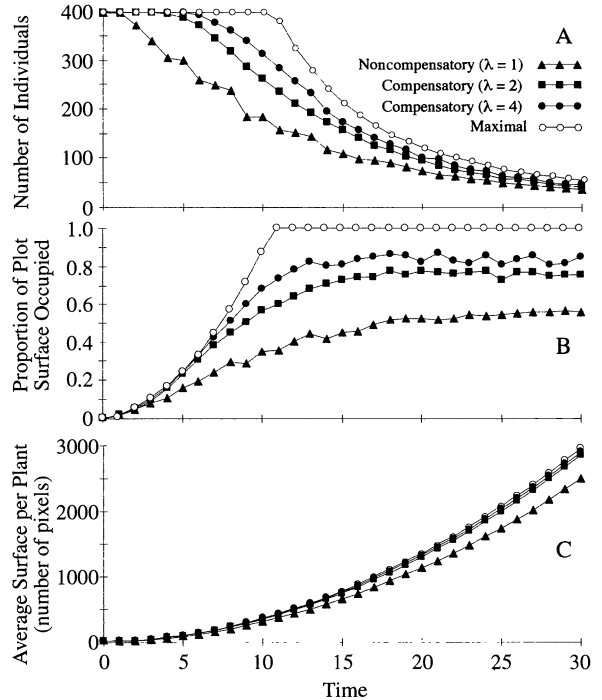


FIG. 3. Change in population size, proportion of plot surface occupied, and average surface area occupied by a plant over time, for simulated plants with compensatory and noncompensatory growth, and for a population of plants with maximum growth, as determined by Eqs. 6–7.

### Plants with optimal growth

From Eq. 1, it can be shown that the radius $\rho$ of the circular area occupied by a plant with unimpeded growth is

$$\rho_t = \rho_0 + ct \qquad (9)$$

We substitute $\sqrt{A/\pi}$ for $\rho$ and rearrange to show that the surface occupied at time $t$ by a plant with optimal growth is

$$A_t = A_0 + 2ct\sqrt{\pi A_t} + \pi c^2 t^2. \qquad (10)$$

Eq. 10 holds for plants with a noncircular area if they show compensatory growth. In a closed surface, all plants grow at their full potential and the population size remains constant at $N_0$ until the surface becomes saturated. At this point, mortality occurs such that the maximum number of plants with unimpeded growth that the plot may contain is

$$N_t = \frac{S}{A_t} \qquad (11)$$

where $S$ is the surface area of the plot.

### Results

In both compensatory and noncompensatory plants, population size decreases from 400 individuals to ~40 individuals at $t = 30$ (Fig. 3A). However, mortality
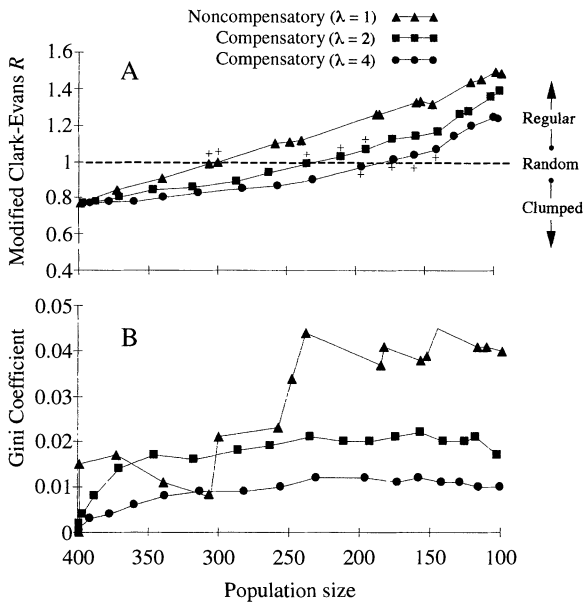
FIG. 4.    Change in spatial distribution and size inequalities as a function of population size, for simulated plants with compensatory and noncompensatory growth. A plus symbol (+) indicates a spatial distribution nonsignificantly different from a random distribution.



FIG. 5.    Change in population size for a mixed population having an equal number of plants with compensatory and noncompensatory growth.

during the early stages of population development is higher in noncompensatory plants, despite the fact that a larger proportion of the plot is unoccupied (Fig. 3B). Noncompensatory plants tend to be slightly smaller than compensatory plants, and this difference increases with time (Fig. 3C). As $\lambda$ increases in a population, maximal plant size and area occupied are approached (Eqs. 10–11) (Fig. 3A–C).

The spatial distributions of all populations gradually change from clumped to random to regular, although the rate of change is much higher in populations of the noncompensatory plants (Fig. 4A). At any population size, the value of Clark-Evans $R$ is larger in noncompensatory plants. The transition from a clumped to a random distribution in noncompensatory plants occurs after ~100 individuals die, whereas in a compensatory population (with $\lambda = 4$) this transition occurs only after the mortality of ~200 individuals (Fig. 4A). Statistically significant regularity occurs at a population size of ~235 in the noncompensatory population compared to ~175 and 130 in the compensatory populations with $\lambda = 2$ and $\lambda = 4$, respectively.

The size inequalities in populations with compensatory growth gradually increase, reaching a plateau as the number of individuals decrease (Fig. 4B). In the noncompensatory population, there are pronounced fluctuations before the Gini coefficient levels off, oscillating around a value of ~0.4. Size inequalities remain low for all populations ($G < 0.05$ in all cases), although the plateau is 2–3 times higher for noncompensatory plants (Fig. 4B).
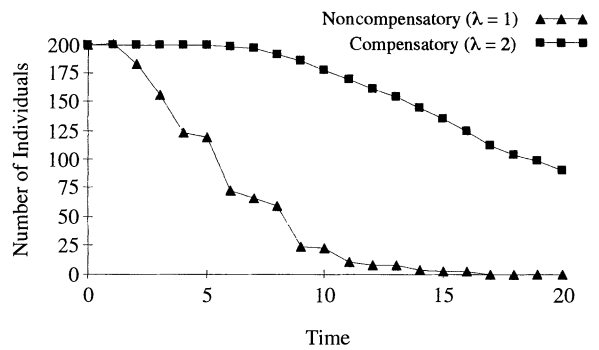
In a separate simulation, we randomly assigned half of the initial population of 400 plants as noncompensatory ($\lambda = 1$) and the other half as compensatory ($\lambda = 2$). The results are shown in Fig. 5. Mortality rates in noncompensatory plants were substantially higher, leading to their complete elimination from the population by $t = 17$ (Fig. 5).

## DISCUSSION

Our simulations show that growth plasticity in individuals, here defined as the compensatory growth of root systems, has an effect on population dynamics. These effects appear to be mainly on the *rates* and *magnitudes* of changes in population attributes over time and on the competitive ability of individuals.

The high rates of mortality in the population of noncompensatory plants is due to local crowding, despite the fact that a large proportion of the overall plot is unoccupied (Fig. 3). Mortality in early stages of growth is delayed in plants with compensatory growth because of their ability to access available space outside their ecological neighborhood as defined by a circle with a fixed radius. However, even for compensatory plants, mortality affects the population long before the site is saturated (Fig. 3B). Compensatory plants appear to utilize the available space better, generally occupying ~80% of the simulated plot, while noncompensatory populations never occupy >60% of the total area. This difference stems from both fewer individuals and the smaller average size of noncompensatory plants (Fig. 3C).

Factors such as uneven initial size distribution, genetic variation in growth rates, or nonsimultaneous germination contribute to size inequalities in populations (Bonan 1988). Since these factors are not considered in our model, the observed size inequalities are the direct result of differing competitive pressures due to neighborhoods. Our results suggest that, in general, when individuals have the capacity for compensatory growth, such factors may be less important determinants of overall population dynamics. Plants that are able to exploit a greater available space, even in the

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presence of neighbors, tend to reduce differences between them and isolated plants. Consequently, differences in size hierarchy in the population are reduced (Fig. 4B).

In even-aged plant populations where competition is intense, it is expected that distributions will shift towards a regular spatial pattern over time as mortality occurs (Kenkel 1988). For compensatory populations, this change (from clumped to regular) occurs over a longer time period (Fig. 4A). Advantages of compensatory growth appear to include a more complete utilization of the available space, allowing more plants to survive or grow in a specified area, regardless of the spatial distribution of their stems. Yet, since the differences in population dynamics observed between compensatory and noncompensatory plants are mainly in terms of magnitude, it is doubtful that population attributes measured in natural populations will provide empirical evidence for or against compensation.

At the individual level, the advantages of compensatory growth are clearly evident. In a mixed population of compensatory and noncompensatory plants, noncompensatory ones are rapidly outcompeted (Fig. 5). The possibility that plants in heterogenuous environments may preferentially grow resource-acquiring structures into patches of high resources has received wide attention in recent years, leading to the development of the "foraging concept" (de Kroon et al. 1994, de Kroon and Hutchings 1995). Compensatory growth resulting from competitive pressure may be considered a specific case of foraging, which is affected by the proximity of neighbors. If this morphological plasticity results in similar advantages in resources, a full appreciation of the selective advantage of compensatory mechanisms must include a consideration of the physiological costs of plasticity (de Kroon and Hutchings 1995), an aspect not addressed in our model.

This modeling work was motivated by our recent study of a population of the desert shrub *Larrea tridentata,* where we found that asymmetry in the horizontal extent of root systems was related to competitive pressure of neighbors (Brisson and Reynolds 1994). This particular population nicely fits the two-dimensional structure of our model since lateral roots are extensive, but occur within a narrow range of depth, and overlap between neighboring root systems is minimal. In the southwestern deserts of the United States, *L. tridentata* frequently occurs in nearly pure stands over large areas. Early studies concluded that these shrubs appeared to be evenly distributed, an observation later confirmed by statistical analysis (reviewed in Barbour 1973). This was hypothesized to be the result of density-dependent mortality resulting from competition for water, an hypothesis that became generally accepted until Barbour (1973) showed that regular distributions in this species were not as common as generally thought. Others concluded that regular distributions were artifacts caused by mathematical biases

(Ebert and McMaster 1981, Cox 1987, but see King and Woodell 1987). Density-dependent mortality may produce the development of a regular distribution of the surviving individuals. However, several factors may prevent or delay the development of regularity in *L. tridentata* populations where competition is presumably severe. The factors most commonly cited are soil heterogeneity and unevenness in age distribution (Anderson 1971, Barbour 1973, Phillips and MacMahon 1981). Our results suggest that morphological plasticity in growth of individuals could also reduce the possibility that a population exhibits a regular distribution. In our simulations, there is no heterogeneity, the population is even-aged, and mortality is due entirely to competition. Yet, a regular distribution of shrubs is delayed when plants exhibit compensatory growth. Lack of observed regularity in the field may therefore be partially attributed to the biology of the species, in addition to the confounding factors generally cited.

Despite its simplicity, our pixel-based model of competition for space is able to mimic fundamental elements of population dynamics that are commonly observed in nature, including a decrease in population size with time due to competition, self-thinning, and the change from clumped to regular spatial distribution resulting from density-dependent mortality. It can be easily implemented to include continuous regeneration and dispersal. The pixel-based approach does, however, have some disadvantages. From a technical viewpoint, pixel-based models are necessarily discrete in both time and space, despite the continuous nature of competition, which may potentially introduce undesirable effects (van Tongeren and Prentice 1986). Also, pixel-based models require more computer memory and take much more time to solve than comparable index-based models.

Another limitation of our approach is that we consider horizontal space to be a surrogate for all resources. We assume that neighbors compete for the same resources at the same location. While this may be a reasonable assumption for conspecific neighbors, neighboring plants of different species may be limited by different resources, or obtain their resources at different locations (e.g., root exploration at different depths) or at different times.

Despite these limitations, our model overcomes the restriction that two plants in close proximity always be strong competitors. It is generally recognized that the primary mechanism of plant competition is spatial interaction. Although the significance and generality of compensatory growth require more empirical evidence, Ford and Sorrensen (1992) state that models that do not account for morphological plasticity in response to competition may be limited, a conclusion we support.

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