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POPULATION GROWTH RATES AND AGE VERSUS
STAGE-DISTRIBUTION MODELS FOR TEASEL
(*DIPSACUS SYLVESTRIS* HUDS.)¹

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Abstract. Mathematical models are developed to examine the population-level response of an herbaceous plant species (teasel, *Dipsacus sylvestris* Huds.) which was experimentally introduced into several habitats and monitored for 5 yr. Models based on morphological stages (size) rather than chronological age give more satisfactory results. Population growth rates (λ_m) range from 0.63 to 2.60, which are likely typical for fugitive plants. Values are interpreted as responses to both external and internal factors. Grass litter, and the presence of other dicotyledonous species, and the overall primary productivity of the rest of the community are important factors determining the success or failure of an attempted colonization by teasel. Individual plant and population-level growth rates seem to be determined independently.

Key words: Age-distribution; biennial; colonization; *Dipsacus*; fugitive species; mathematical models; Michigan; morphological stages; old-fields; plant populations; population dynamics; population growth rates; population projection matrix.

INTRODUCTION

To a large extent, ecological studies of single plant species or its populations have been concerned with elucidating evolutionary radiation within a group, the plasticity of responses to the environment, or selection and fitness for particular sites. Recently there has been a great interest in basic population dynamics, including estimates of growth rates, age-specific (or size-specific) mortality rates, birth rates, and the factors influencing these. (See reviews by Willson 1972, Harper and White 1974 and references in Werner 1976.) Studies of this type are a foundation for the development of general theory in population biology.

Populations respond to both their outer environment and their own internal state. Their response is complex and multivariate, including changes in birth, death, immigration and emigration rates, growth rates at both the individual and the population level, and ultimately genetic and evolutionary changes. In this paper we use mathematical models to examine the population-level response of a plant (teasel, *Dipsacus sylvestris* Huds.). Our effort differs from other studies of plant population dynamics (e.g., Hartshorn 1972, 1975, but see Sarukhan and Gadgil 1974) in examining several populations of a single species under different environmental conditions. Our estimates of population parameters (e.g., growth rate, transient response, reproductive value) can thus be interpreted as responses to both external and internal factors. In a related paper (Cas-

well and Werner 1977), we examine the effects of hypothetical changes in the life history of teasel, by modifying the internal structure of the models.

THE POPULATIONS

Teasel (*Dipsacus sylvestris* Huds.) is a strictly semelparous plant with no vegetative propagation. Seeds germinate mainly in the spring, producing a large-leaved rosette which requires vernalization before forming a single tall (0.5–2.5 m) flowering stalk in some subsequent summer. Although commonly classified a biennial, the length of the rosette phase is variable, and may last >5 years (Werner 1975a).

In eastern North America, teasel usually is found in the later stages of old-field succession (before shrubs), in meadows, and in ruderal habitats where periods between disturbances are >1 yr. Populations are sparsely distributed regionally, but, where found, may dominate the vegetation in terms of biomass. The regional rarity of populations may be due partly to the dispersal pattern of seeds (achenes); >99% of them fall passively to the ground within a 1.5-m radius of the parent plant (Werner 1975b). Teasel is native to Europe, where its populations are also restricted to disturbed habitats, and are regionally rare but locally very dense; the few (insect) herbivores that feed on teasel are found in both N. America and Europe. It seems unlikely that the selective pressures operating on teasel now are vastly different from those under which it has been evolving for a long time.

Research on the population dynamics of teasel was

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TABLE 1. Vegetation characteristics of the study fields. See Werner 1975c for species composition and abundances

Field	Relative levels of abundance of:				Mean ² annual net primary production (g/m ²)
	Grass	Litter	Herbaceous dicots	Woody dicots ¹	
A	Medium	Low	Low	Negligible	343
B	Medium	Low	Low-Medium	Negligible	250
C	Medium	Low	Low	High	279
D	Low	Low	High	Negligible	233
J	Low	Negligible	High	High	287
K	High	High	Negligible	None	312
L	Medium	Low	Low	Negligible	377
M	Medium	Low	Low	Negligible	245

¹ Woody dicots create an overhead shading canopy.

² ANPP of total vegetation in control plots within the fields in year 2. Method for determining ANPP is described in Werner 1977.

initiated in 1969 in Kalamazoo County, Michigan, USA, within a set of contiguous, small fields (each 25 × 25 m) which were set aside for succession studies in 1964 and monitored annually. Eight fields were used; all were 2-yr fallow (Fields J, K, L, M) or 3-yr fallow (Fields A, B, C, D), although they differed greatly in vegetative structure (Table 1). Within each of the 8 fields, 26 plots 0.5 × 0.5 m in size were permanently marked and hand-sown with teasel seed at the rate of 150 seeds per plot in the winter of 1968–69. Subsamples of the seed lot prior to counting and sowing showed a 99% viability. Upon germination, individual seedlings were marked and their fates monitored for five growing seasons. Some plots were sacrificed each year to obtain estimates of primary production (cf. Werner 1977).

It is important to note that teasel was absent from the study area from 1964 until 1972, except where it was deliberately introduced for this study. The nearest natural population was 11.2 km from the study site. In order to follow accurately the initially introduced seed cohorts, any flowering heads that were produced prior to the third year of the study were removed before their seeds could be dispersed. By the third spring, germination of seeds from the initial cohort was negligible and thereafter seed heads of flowering plants were allowed to remain.

These teasel populations are artificial only in the sense that they were purposely sown in the fields. In a more important sense, they are natural; the introductions are simulated colonizations of habitats where teasel happened to be absent but of a type which it commonly colonizes. We note that the density of seeds used (600/m²) is typical of the density of seed-rain in a natural population. The fact that colonization consisted of a specified number of seeds, sown into marked pieces of ground in order to accurately assess the fate of the various seed cohorts, is irrelevant to the subsequent growth and behavior of the populations.

THE MODELS

Because production of seeds was counted, but not allowed to feed back into the population, the repeated

counts in each quadrat provide a cohort record of both survivorship and reproduction. With this information we can construct parameters for a linear, time-invariant, matrix model of population dynamics, a so-called Leslie matrix or population-projection matrix. The form of the model is:

$$\bar{x}(t + 1) = \bar{A}\bar{x}(t) \quad (1)$$

where $\bar{x}(t)$ is a vector of state variables (age-classes or physiological stage classes) and \bar{A} is a square matrix which determines the dynamics of the population. The time unit, in our case, is 1 yr.

The linearity of this model implies that there are no effects of density on population growth. Ultimately, of course, this cannot be true. However, teasel populations are capable of surviving for long periods of time, slowly increasing to much higher densities than those encountered during the course of this experiment. It is unlikely that density had any serious effects on the population during the period in which the parameters were being estimated. How long this state of affairs would persist, were the population to continue to grow under these dynamics, is another question (Caswell and Werner 1977).

\bar{A} is a constant matrix, implying that there are no changes in the environmental conditions confronting the population. We assume that successional and other changes in the eight fields were slow relative to the year-to-year dynamics of survival and reproduction, at least over the course of this experiment. This assumption is hard to test, but is probably justified (cf. Werner 1972).

State variables

The state variables, $\bar{x}(t)$, cannot be chosen arbitrarily. They must fulfill some very distinct requirements (Caswell et al. 1972). Their role is to encapsulate the relevant history of the system so that the current environmental stimulus, together with the current state, uniquely determines the system's response. An inadequate choice of the state variable fails to satisfy this requirement, and the resulting system description will be indeterminate. There will be more than one

TABLE 2. State vectors

Age classification	Stage classification
$x(1)$ seeds	$x(1)$ seeds
$x(2)$ dead or dormant seeds, year 1	$x(2)$ dead or dormant seeds, year 1
$x(3)$ dead or dormant seeds, year 2	$x(3)$ dead or dormant seeds, year 2
$x(4)$ rosettes, year 1	$x(4)$ small rosettes (<2.5 cm)
$x(5)$ rosettes, year 2	$x(5)$ medium rosettes (2.5–18.9 cm)
$x(6)$ rosettes, year 3	$x(6)$ large rosettes (≥ 19.0 cm)
$x(7)$ rosettes, year 4	$x(7)$ flowering plants
$x(8)$ flowering plants	

response possible to a given stimulus, the particular response occurring determined by the past history of the system.

The simplest state variable for population dynamic models is the number of individuals. Much ecological theory is built on the qualitative properties of models using this state variable, but except in special situations, it is not adequate for a detailed description of population dynamics. Populations of the same total size can behave very differently, depending on their internal composition. The effect of age structure is the most obvious example; a population of prereproductive individuals responds differently to a given environment than a population of the same number of reproductive or postreproductive individuals, yet all have the same population size. Lotka (1924) showed that in a constant environment, the age distribution would eventually become stable at which point it would legitimately be collapsed into a scalar measure of population size. Leslie (1945) developed a discrete technique to deal with the dynamics of the age distribution itself when the conditions of the stable age distribution theorem are not met.

Growth plasticity, however, makes even the complete age distribution an inadequate state variable for many organisms, higher plants in particular. Individuals of the same age may respond in very different ways to the same environment, depending on their history. Morphological stages based on size may encapsulate the history of a plant more accurately than a chronological age classification.

Because we have information on both the age and the size of the individual plants in this study, we have a unique opportunity to compare 2 choices of state variables for the same populations. The first (Table 2) is an age classification, consisting of seeds, dead or dormant seeds (explained below) of 2 ages, rosettes aged 1, 2, 3, and 4 yr, and flowering plants. Our second choice for a state variable is a vector of morphological stages: seeds, dead or dormant seeds, small (<2.5 cm), medium (2.5–18.9 cm) and large (≥ 19.0 cm) rosettes, and flowering plants. Neither model subdivides the flowering plant category; all flowering plants are considered identical with regard to seed output, regardless

of size or age. In the fields, the number of seeds produced per flowering plant varied little with the age of the plant, and varied (linearly) with the size of the previous-year's rosette only across sizes within the "large rosette" category.

The age vector has 8 elements, the stage vector only 7; thus the \bar{A} matrices for the 2 models are of dimension 8×8 and 7×7 , respectively. By comparing the behavior of these 2 models, we hope to determine which of these state variables most accurately describes the dynamics of the populations.

Parameter estimation

In the \bar{A} matrix of Eq. (1), the (i, j) entry gives the number of individuals of stage i produced in year $t + 1$, per individual of stage j in year t . Estimation of these parameters requires a knowledge of the fate, in the next year, of individual plants of each stage in the current year. For the purposes of parameter estimation, each of the 26 quadrats (each 0.25 m^2) in a field were considered replicate populations. The transition probabilities in the \bar{A} matrices are means taken over these replicates. Table 3 shows the resulting matrices, for the age and stage classifications, for each field.

Probabilities of seed germination were based on germination measurements made every 3 days in each field (Werner 1977). The ungerminated seeds remaining out of the 150 sown in each quadrat were assigned to the "first-year dead or dormant seed" pool. This category contains dormant seeds capable of germinating the next year as well as a number of seeds whose fate is unknown—dead or eaten. It was impossible to separate dormant from dead seeds in the field. The "second-year dead or dormant seeds" category was calculated similarly, based on seeds in the first pool that failed to germinate their second year. Since third-year germination was negligible, it was assumed in the model that all seeds not germinating after their second year of dormancy were in fact dead.

Seed germination of teasel occurs in the spring. The figures for seed germination (the first 3 columns of \bar{A} in Table 3) give the proportion of seeds (or dormant seeds) that both germinate and survive until fall. For these columns, the difference between one and the sum of a column gives the proportion of plants that die between one autumn and the next, a year later.

The probabilities of transition from one age or size class to another were obtained by following marked individual plants in the plots from one year to the next (Werner 1977). Seed production per flowering plant was estimated from regressions of seed number on head size (Werner 1975c).

The averaging of transition probabilities over replicate quadrats within a field smooths out small-scale spatial variation and demographic stochasticity. In addition, some of the parameters (e.g., in the stage model) were estimated in more than 1 yr. Hence, the elements of the matrices in Table 3 are averages over

TABLE 3. (Continued)

Field		Age Classification								Stage Classification							
M	x(1)	635	x(1)	635
	x(2)	.634	x(2)	.634
	x(3)973	x(3)974
	x(4)	.128	.024	.013	x(4)	.013	.017	.011	.000
	x(5)128	x(5)	.109	.004	.002	.077	.212
	x(6)396	x(6)	.006	.003	.000	.038	.281	.000	...
	x(7)627	x(7)000	.063	1.000	...
	x(8)029	.259	.160	.213	...								

both small-scale spatial and short-term temporal variability, and are currently the best estimates we can make for populations of teasel.

RESULTS AND DISCUSSION

Population growth rates

The solution to Eq. 1 can be written

$$\bar{x}(t) = \bar{A}^t \bar{x}(0).$$

When the matrix function \bar{A}^t is expanded in terms of eigenvalues and eigenvectors (Frame 1964) the resulting expression for $\bar{x}(t)$ is a series

$$\bar{x}(t) = \sum_{i=1}^n c_i \bar{v}_i \lambda_i^t,$$

where the c_i are constants which express the initial conditions, and the λ_i and \bar{v}_i are the eigenvalues (assumed distinct) and right eigenvectors, respectively, of \bar{A} . The eigenvalues and eigenvectors are determined by the equation

$$\bar{A} \bar{v}_i = \lambda_i \bar{v}_i.$$

As t grows large, the contribution to $\bar{x}(t)$ of any of the λ_i of modulus < 1 will decay toward zero, while that of any λ_i of modulus > 1 will increase geometrically.

If \bar{A} has a maximal eigenvalue, λ_m , which is larger (in modulus) than all the other eigenvalues, the long-term behavior of the population is given by

$$\lim_{t \rightarrow \infty} \bar{x}(t) = c_m \bar{v}_m \lambda_m^t.$$

The population will ultimately grow geometrically at the rate λ_m per year, with a structure (age or stage) defined by \bar{v}_m .

Sykes (1969) has summarized the conditions under which the existence of such an eigenvalue can be guaranteed when \bar{A} is a Leslie matrix. In the case of more general matrices, such as ours, much of this theory does not apply. The Perron-Frobenius Theorem, in its weak form applicable to reducible nonnegative matrices (Gantmacher 1959:80), guarantees the existence of a nonnegative eigenvalue of modulus greater than or equal to that of all the other eigenvalues. The only disturbing possibilities not ruled out are a maximal eigenvalue of exactly zero or of exactly the same modulus as one or more of the other eigenvalues. However, neither of these situations is struc-

turally stable in general, and they can be neglected when the elements of the matrices are estimated from real data. Thus we are justified in applying theory based on the existence of a maximal eigenvalue, and, in fact, all our matrices possess such an eigenvalue.

The biological interest in λ_m arises partly from its identification with evolutionary fitness by Wright (1937) and Fisher (1930; Fisher actually used $r = \ln \lambda_m$). They assigned values of λ_m to the different genotypes within a population and demonstrated that those genotypes with a higher λ_m would ultimately dominate the population. Fisher's Fundamental Theorem asserts that the value of λ_m for the population (the average of the values for the different genotypes) will continue to increase under the impact of selection, at a rate proportional to the genetic variance in individual fitness. In an unlimited, competition-free, optimal environment, the per capita growth rate of a genotype is known as r or r_m , the "intrinsic rate of increase," and selection operating in such an environment will result automatically in increasing the intrinsic rate of increase of the population. This result is not incompatible with the notion of K -selection introduced by MacArthur (1962, MacArthur and Wilson 1967) to describe population growth in a limited, competitively full environment. In both environments, selection operates to increase individual fitness, and still results in an increase in population fitness, but it may do so through parameters other than r_m .

Table 4 shows the population growth rates λ_m , and the instantaneous values $r = \ln \lambda_m$, for each of the eight populations, for both the age and stage models.

TABLE 4. Eigenvalues (λ_m) and instantaneous growth rates ($r = \ln \lambda_m$) for the age and stage models

Field	Age model		Stage model	
	λ_m	r	λ_m	r
A	1.263	0.233	1.797	0.586
B	1.462	0.380	1.989	0.688
C	1.401	0.337	1.875	0.629
D	1.350	0.300	2.071	0.728
J	0.333	-1.100	0.628	-0.465
K	0.0004	-7.752	0.275	-1.291
L	0.891	-0.115	1.195	0.178
M	1.679	0.518	2.605	0.957

TABLE 5. Stable age and size distribution for stage and age models

Model	Fields					
	A	B	C	D	L	M
AGE						
$x(1)$ seeds	46.87	51.13	51.55	56.35		59.13
$x(2)$ dead or dormant seeds, year 1	27.74	26.60	27.83	23.68		22.33
$x(3)$ dead or dormant seeds, year 2	21.21	16.83	18.67	16.06		12.95
$x(4)$ rosettes, year 1	3.56	4.01	1.60	2.96		4.93
$x(5)$ rosettes, year 2	0.38	0.79	0.20	0.49		0.37
$x(6)$ rosettes, year 3	0.12	0.37	0.10	0.27		0.09
$x(7)$ rosettes, year 4	0.02	0.11	0.00	0.10		0.03
$x(8)$ flowering	0.14	0.16	0.06	0.07		0.16
STAGE (size)						
$x(1)$ seeds	58.48	61.15	61.14	68.76	58.21	71.45
$x(2)$ dead or dormant seeds, year 1	24.36	23.38	24.67	18.84	20.96	17.39
$x(3)$ dead or dormant seeds, year 2	13.09	10.90	12.37	8.33	17.01	6.50
$x(4)$ small rosettes	0.53	0.87	0.81	1.59	0.93	0.50
$x(5)$ medium rosettes	2.79	2.59	0.69	1.96	2.45	3.30
$x(6)$ large rosettes	0.50	0.88	0.23	0.40	0.31	0.56
$x(7)$ flowering	0.24	0.26	0.10	0.13	0.14	0.29

Table 5 lists the corresponding stable distributions (age or size, respectively).

A value of $\lambda_m > 1$ (corresponding to an $r > 0$) implies that the population will grow geometrically. A value less than one results in a population decline to extinction. Using either state variable, the populations in our eight fields exhibit a spectrum of growth rates from rapid extinction (J, K) through borderline persistence (L) to rapid population growth (A, B, C, D and especially M).

Clearly, the *Dipsacus* populations cannot continue growing at rates as high as $\lambda_m = 2.6$ forever. Either their own density must ultimately limit population growth, or the environment will change in such a way as to eliminate them. Both factors are probably important; density effects are considered in another paper (Caswell and Werner 1977). The nonequilibrium values of λ_m underline teasel's ecological position as a fugitive species.

There are few other valid estimates of population growth rates for natural plant populations. Hartshorn (1972, 1975) used a size class matrix model to study *Pentaclethra macroloba* and *Stryphnodendron excelsum*, 2 rain forest tree species in Costa Rica. His values of λ_m for the 2 species are 1.002 and 1.047, respectively. These are as expected for large organisms in equilibrium with a very stable environment. Sarukhan and Gadgil (1974) developed a model similar to ours to describe population growth in 3 species of *Ranunculus*. They obtained values of λ_m from 0.743–1.801 for *Ranunculus repens*, 0.095–4.665 for *Ranunculus bulbosus*, and 0.350–2.328 for *Ranunculus acris*. The ranges reported are over 5–10 quadrats in a single Welsh meadow. The occurrence of values $\ll 1$ and $\gg 1$, and the range of values found, are similar to our results for teasel and are to be expected in species living in nonequilibrium situations.

The stable age and size distribution (Table 5) are similar among fields and between models. They have been calculated before only by Hartshorn (1972, 1975) and are presented here for their possible value in later comparative studies. The stage model consistently predicts higher proportions of seeds and flowering plants in the population, and a smaller proportion of rosette plants. This is, no doubt, related to the higher population growth rates exhibited by the stage model (see below). Stable distributions are not presented for fields J and K, or for L in the age model, because these populations decline to extinction rather than grow with a stable distribution.

The high proportion of the population in the dead or dormant seed category is somewhat artificial. As mentioned earlier, there is no way of knowing what fraction of these seeds are dormant and what fraction are dead. The very low germination rates (Table 3) and the lack of long-term dormancy mechanisms suggest that most are dead, rather than dormant. Thus these components of the stable vectors are artificially inflated by the inclusion of a portion of the population that is no longer extant.

Age vs. stage as state variables

We cannot directly compare observed and predicted population trajectories using the 2 models, because reproduction was prevented by removing the seed heads before the seeds could be dispersed. There are, however, several interesting indirect comparisons to be made between the two state variables.

First, Werner (1975a) showed that, when all 8 populations are lumped together, size is a better predictor than age of plant fate from year to year. Our model supports this on a field-by-field basis as shown in Table 6. Here we examine the accuracy with which the 2 models predict the first occurrence of flowering in each

TABLE 6. Observed and predicted year of first flowering. Numbers in parentheses give the number of flowering plants predicted for that year

Field	Predicted		Observed
	Age model	Stage model	
A	2 (0.03) 8 (1.03)	2 (0.42) 3 (2.15)	2
B	2 (0.02) 8 (2.41)	2 (0.33) 3 (2.81)	3
C	3 (0.03) 9 (1.33)	3 (0.93) 7 (6.69)	3
D	3 (0.03) 9 (1.00)	3 (1.52)	4
J	2 (0.008) ¹	2 (0.42) ¹	2
K	never	never	never
L	2 (0.003) >25	2 (0.12) 15 (1.03)	2
M	2 (0.56) 5 (1.53)	2 (1.74)	2

¹ Declines thereafter.

of the fields. Since the model deals in real numbers, while fractional plants are impossible, we have shown both the time when the model predicts the appearance of the first flowering plants and the time when the predicted number of flowering plants first exceeds 1. The stage model is clearly more accurate. In only 2 cases was its prediction more than 1 yr off. One of these cases (field C) was so close (a prediction of 0.93 flowering plants) to 1 at the correct year that flowering plants would surely be expected at this time. The other (field L) is a marginally persistent population: λ_m for the age model is 0.891, for the stage model 1.195. Both the age and stage models predict a very long time to the first flowering, which actually occurred in the 2nd year. Over all 8 populations, the deviation between observed and predicted first flowering is 1.62 ± 1.64 ($\bar{x} \pm SE$) years for the stage model as opposed to 6.00 ± 2.58 for the age model.

Because of the plastic nature of growth in teasel plants, it is not surprising to discover that the stage-based models are superior to the age-based models in predicting population behavior. As with most sessile organisms, selective advantage has been conferred on those individuals able to modify growth rates, to switch from vegetative to reproductive modes, or to change age of first reproduction in response to a changing environment from which they cannot move. The large body of theory and analytical techniques developed by animal demographers cannot be applied directly to studies of plants with the possible notable exceptions of very long-lived perennials where sometimes variation in growth rates, age to first reproduction, etc., can be smoothed over long time periods, or annuals where growth and reproduction is canalized into a definite time period. Even in the case of annuals, however, stage-based models may also prove more useful than

age-based models when analyses rightly include the dynamics of seeds in the soil; for most annuals, the length of the dormancy period of seeds is plastic to some high degree and dependent upon environmental conditions.

Although the stage distribution is clearly superior to the age distribution as a state variable for teasel, this is not the complete story. The values of λ_m vary from field to field in the same way in either model (Spearman rank correlation coefficient $r_s = 0.93$), and there is only 1 case (field L) where the 2 models make contradictory predictions about population persistence. However, the maximum eigenvalues for the age model are in every case smaller than those for the stage model. If the age and stage classification were simply regroupings of one another, our use of cohort survival data should have resulted in identical values for λ_m (give or take sampling error). This is so because when the population reaches its stable distribution, at which time it is growing at the rate λ_m , any grouping of the states (including just summing all classes to obtain population size) will grow at λ_m . Thus any matrix generated by grouping categories must have a maximum eigenvalue equal to λ_m . The fact that there is a consistent pattern in which the eigenvalues of the age model are always less than those of the stage model implies that the 2 ways of classifying the population are not independent. The age-transition dynamics are affected by the size distribution, and *vice versa*. A complete population description would require at least an age \times stage classification as a state variable. Such state variables for populations have been proposed on theoretical grounds (cf. Caswell et al. 1972) and have been applied by Slobodkin (1953) and Sinko and Steiffer (1969) to invertebrate animals.

This interaction between the 2 classifications is also suggested in Table 1 of Werner (1975a) where, for example, the probability of death varies by as much as a factor of 8 (from .02 to .17) between rosettes of the same size but different ages. However, the interaction was not detectable in that paper: statistical tests cannot be used to examine age \times size interaction since the data are in the form of single numbers per block.

Further evidence for an age \times stage interaction comes from the variances of the elements of the \bar{A} matrices. Since each quadrat within a field was treated as a replicate population, these variances measure the degree of uncertainty in the prediction of the future state from the value of the current state. Eliminating the seed, dormant seed, and flowering plant categories from consideration because they are the same for both models, the average variances ($\pm SE$) for the remaining matrix elements are $.068 \pm .009$ for the age model and $.072 \pm .010$ for the stage model. The values are not significantly different. This means that the variation, from one replicate population to another, in the description of transition dynamics, is about the same whether the age or stage alone is used as a state variable.

One hypothesis is that this interaction involves an

age-dependence of mortality for large rosettes. Large rosettes older than 5 yr seem to experience a dramatically increased mortality. This effect cannot be incorporated into the stage model, which is blind to the age of a rosette, and it might account for the higher λ_m values generated by the stage model. However, if this were entirely the answer, one would expect that fields with high survivorship in large rosettes should show the largest discrepancy between λ_m (stage) and λ_m (age). In fact, this is not the case (cf. Tables 3 and 4).

It would be of considerable interest to construct a combined age \times stage distribution model for *Dipsacus*. The existence of the age \times size interaction suggests that such a model would be an improvement over either the age or stage classifications alone. Unfortunately, parameterizing the resultant 16-dimensional model would require considerably more data than we have available. Moreover, Werner's (1975a) demonstration of the superiority of size over age as a predictor of rosette transitions, and the superiority of the stage model over the age model in predicting the occurrence of flowering suggest that the improvement over the stage model might not be great. Because of the demonstrated superiority of the stage model, and the theoretical reasons for preferring size to age as a stage variable for organisms with plastic growth, we will carry out the rest of our analyses on the stage model only.

Environmental effects on population growth

The biotic environments confronted by the *Dipsacus* populations in the eight fields differ in many respects. In Table 1 we have summarized some of these differences; we relate them here to the growth rate of the populations. The direct action of the environment is on the individual plant, which germinates, grows, lives, and dies in relation to its surroundings. The results of this action appear at successively higher levels of organization; the population (through birth rates, death rates, growth and extinction), the community (dominance by particular species or lifeforms, diversity, etc.) the ecosystem (nutrient cycling, microclimate alteration, etc.), and the biosphere (atmospheric homeostasis, global element cycles and energy budgets, etc.). The population growth rate, λ_m , is a natural parameter (although only one of several) for measuring environmental impact at the population level, since it integrates the effects of birth and death rates in a way intimately related both to population dynamics (growth, extinction) and evolution (as the mean fitness of the population).

The populations in fields J and K have growth rates considerably less than one, indicating that these fields are closed to continuance by *Dipsacus*. The reasons are different for each field. Field K had a high level of grass and grass litter (*Agropyron repens* L.). Werner (1975d) has shown that *Agropyron* litter inhibits the germination of *Dipsacus* seeds in both the field and laboratory. Examination of the matrices (Table 3) reveals that the

TABLE 7. Correlation coefficients (Spearman's rank correlation coefficient, r_s) between community productivity (annual net primary production in control plots; cf. Table 1), population growth rate (λ_m) and individual plant growth rate (mean diameter of rosettes in August; Werner 1977)

	λ_m	Community productivity
Individual growth rate	0.000 ¹	.476 $P \approx .10$
λ_m	—	-.79 $P < .05$

¹ A rarity in statistics: a correlation coefficient of exactly zero.

population in Field K had the lowest germination probability (.199), and also the lowest survivorship of seedlings from spring until fall (.042) of any of the populations.

Field J had high levels of herbaceous dicots, which compete strongly with *Dipsacus* (Werner 1977), and was also heavily shaded by woody dicots (mainly *Rhus typhina* L.). Germination probability was highest (0.577) in this field, and 1st-year seedling survivorship was not unusually low (0.120, rank 5th). However, the heavy shading and dicot cover depressed the growth rates of rosettes, resulting in high mortalities and very low transition probabilities from one size class to the next (the subdiagonal terms in the \bar{A} matrix, Table 3). The result is the same as that of the germination depression in field K: ultimate extinction of the population.

Beyond these 2 extreme cases, there is no obvious relationship between the vegetation factors and λ_m . Teasel is able to colonize successfully a range of old-field communities, being barred from invasion by the combination of extreme shading and competition from dicot herbs (e.g., Field J) or by litter effects on seeds and seedlings (e.g., Field K). See Werner (1977) for further discussion of the effect of these factors on individual plants.

Another possible measure of the competitive stress faced by *Dipsacus* is the annual net primary production of the community being invaded. Table 1 shows this figure, which was measured in control quadrats for each field (Werner 1977). The productivity in an environment is inversely correlated with λ_m for *Dipsacus* (Spearman rank correlation $r_s = -0.79$, $P < .05$). Thus, there is strong indication that the growth rate of *Dipsacus* populations is suppressed by the "success" of the rest of the community.

Population growth vs. individual plant growth

There are some interesting comparisons between these results on population growth rate and the growth rates of individual plants (Werner 1977). It is well known, on mathematical grounds (Lewontin 1965), that increases in individual growth rate can dramatically increase population growth rate by shortening devel-

opmental time. It is not necessarily true, however, that individual and population growth rates in real populations always respond in the same way to the same factors.

Table 7 shows the rank correlation coefficients between λ_m , individual plant growth rates, and community productivity. Community productivity and λ_m are negatively correlated, but community productivity and individual growth rate are positively correlated. There is a correlation of exactly zero between the individual plant growth rates and population growth rates.

Over our sample of 8 environments, then, it appears that individual and population level growth rates are determined independently of one another. This does not rule out the possibility of a distinct relation between the 2, as seems to be the case in field J where low individual growth rates due to competition with other dicots are associated with a low value of λ_m . It means that such a relationship cannot be assumed as a general rule.

Correlation analysis is clearly not going to unravel the causal mechanism relating individual and population growth rates. We have spoken earlier of the integrative nature of such measures as λ_m . The price for such integration is the loss of detailed information on internal mechanisms. The point remains, however, that these analyses clearly demonstrate "emergent" properties at the population level that are not predicted by knowledge of the mechanisms operating at the individual level.

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