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# Within-population variation in demography of *Taraxacum officinale*: season- and size-dependent survival, growth and reproduction

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## Summary

**1** Lefkovitch transition matrices were used to determine vital demographic rates of a natural population of *Taraxacum officinale* in Morgantown, WV, USA. Separate size transition matrices were calculated for each of four seasons, October–January, January–April, April–July, and July–October, to test if demographic rates vary as a function of season and if size-specific rates vary differentially among seasons. Season-dependent demography was also compared for four phenotype classes segregated by cluster analysis of leaf morphology.

**2** The finite rate of increase for the entire population was largest in autumn (October–January) and declined throughout the rest of the year. Overall, there was a small reduction in the population size. Size-specific probabilities of survival, growth and fertility varied dramatically among seasons. Sensitivity analyses showed that small individuals were particularly important to population growth from autumn to spring. Larger individuals were more important during summer.

**3** Highly season-dependent demographic rates have large implications for population distribution and persistence since increased vulnerability to perturbation during particular seasons may constrain population growth and stability. Although *T. officinale* is a long-lived perennial, annual censuses may mask the importance of certain individuals or life history traits for maintenance of genetic variability and population viability.

**4** Seasonal and annual finite rates of increase also varied as a function of phenotype class. Of two phenotype classes which had identical annual growth rates, one grew better in cool seasons while the second performed better in warm seasons. Direct competition for resources should be reduced by such inverse patterns of demography across seasons.

**5** If phenotype classes are to some degree genetically determined, the differential responses observed here suggest that temporal variation in the environment could explain the maintenance of genetic diversity within populations.

**Keywords:** genetic diversity, Lefkovitch transition matrices, temporal heterogeneity, warm and cool seasons

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## Introduction

Plant populations exist in a heterogeneous environment. Vital rates respond to both spatial (e.g. Werner & Caswell 1977; Huenneke & Marks 1987) and temporal heterogeneity (e.g. Bierzychudek 1982; Mack & Pyke 1984; Huenneke & Marks 1987; Aberg 1992; Kalisz & McPeck 1992). Even fine-scale environmental heterogeneity has been shown to influence demography (Moloney 1988; Stratton 1992). This environmental control of demography has impli-

cations for population stability and persistence, e.g. fluctuations in population size may increase a population's vulnerability to extrinsic disturbance.

Differential responses of individuals within populations to spatial environmental heterogeneity have been demonstrated together with variations in their fitness (e.g. McNeilly & Antonovics 1968; McGraw & Antonovics 1983) and this is a mechanism which potentially contributes to the maintenance of genetic diversity (Endler 1986). Studies of biotypic or geno-

typic responses to temporal heterogeneity and their consequences are rare for plant populations (Bell 1987), although differential genotypic fitness among seasons has been demonstrated for animals including ascidians (Grosberg 1988), cladocerans (Black 1980), and amphibians (Merrell & Rodell 1968; Dapkus 1976). There is significant potential in plants for individuals to show differential responses to temporal heterogeneity as fluctuations in the environment at one location can be large. In particular, in temperate climates seasonal differences in precipitation and temperature are large relative to annual differences. Analysis of temperature variance for a typical site in east-central North America (NOAA 1980–1990; Morgantown, West Virginia, USA), for example, yields no effect of year ( $F = 0.58$ ,  $P = 0.8244$ ), but a large effect of season ( $F = 122.45$ ,  $P < 0.0001$ ). In addition, seasonal variation in the environment may encompass altered rates of mineralization (Williams 1969; Davy & Taylor 1974; Morecroft *et al.* 1992), evapotranspiration (Caprio 1974), predation (e.g. Black 1980), pollinator abundance (e.g. Schemske & Horvitz 1989), and presence of pathogens (e.g. Jacome & Schuh 1992). If survival, growth, and reproductive rates for different genotypes or phenotype classes shift in rank across seasons, but are similar on an annual basis, then temporally varying selection may also contribute to the maintenance of genetic diversity.

In this study, Lefkovich transition matrices (Lefkovich 1965) were formulated for a natural population of *Taraxacum officinale* Weber censused over the course of one year to examine its demographic response to seasonality. Many studies of *T. officinale* have investigated the inter and intrapopulation responses to single environmental factors and to spatial heterogeneity. Distinct ecological differences separate many of the phenotype classes ('biotypes' *sensu* Solbrig & Simpson (1974)) and genotypes (considered microspecies or agamospecies in *Taraxacum*) in terms of response to disturbance (Solbrig & Simpson 1974; Oosterveld 1983; Sterk, Groenhart & Mooren 1983), nutrients (Oosterveld 1978, 1983; Sterk *et al.* 1983; Ford 1985; Cox & Ford 1987), competition (Solbrig & Simpson 1974, 1977; Mølgaard 1977; Ford 1981a; Sterk *et al.* 1983), soil type (Oosterveld 1983; Sterk *et al.* 1983) and soil moisture (Oosterveld 1978). These differences in response to factors that vary over space may be important in explaining the persistence of genetic variability found within populations (Van Loenhoud & Duyts 1981; Sterk *et al.* 1983; Lyman & Ellstrand 1984; Ford 1985). Few studies of *Taraxacum*, however, have addressed the response of genotypes to environmental fluctuations through time and its consequences for genetic diversity. However, Ford (1981b, 1985) demonstrated a seasonal pattern in establishment and growth of *Taraxacum* while Sterk & Luteijn (1984) examined flowering phenology. Neither study found strong evidence for sea-

son  $\times$  genotype interactions. Early growth, time to reproduction and thus population turnover rates did, however, differ between two genotypes (Ford 1985). This study investigates the possibility that a response to seasonal environmental fluctuations may play a role in the coexistence of genotypes within the population.

Differential responses of genotypes to a temporally fluctuating environment could contribute to the maintenance of genetic diversity for both sexually and asexually reproducing species. This mechanism may be particularly important in determining the genetic composition of a population of an asexually reproducing species because in the absence of such a mechanism, the genotype with the greatest fitness would, theoretically, rapidly dominate the population (Williams 1975; Janzen 1977; Sebens & Thorne 1985). In the USA, *T. officinale* obligately reproduces asexually (Lyman & Ellstrand 1984), in contrast to some European species of *Taraxacum* in which sexual reproduction may occur (e.g. Richards 1970a,b; Den Nijs & Sterk 1980, 1984; Menken *et al.* 1989; Den Nijs, Kirschner, Stepanek & van der Hulst 1990; Morita, Menken & Sterk 1990). This study of a natural population of *T. officinale* was designed to test if differential demography of phenotype classes in response to seasonality could contribute to the maintenance of genetic diversity. We had two specific objectives: to demonstrate and quantify the sensitivity of demography to environmental seasonality and to test whether the patterns of seasonal demography of phenotype classes are inversely related between seasons, but are similar annually.

## Methods

### EXPERIMENTAL ORGANISM

*Taraxacum officinale* is a ubiquitous, herbaceous perennial commonly found in lawns, meadows, and disturbed areas. *T. officinale* generally maintains foliage throughout the entire year in West Virginia, USA. Only in extreme cold, or heat combined with drought, will plants become dormant, i.e. lose all above-ground biomass. Seed production (by diplospory) may occur throughout the year, but flowering peaks in April and September/October (Gray *et al.* 1973). Maturation of achenes requires from two (Solbrig 1971) to 12 days (Beach 1939). Gray *et al.* (1973) observed that maturation may require 20 or more days in November. Achenes do not persist in a long-term seed bank (Grime 1988), but may exhibit short-term enforced dormancy (Van Loenhoud & Duyts 1981).

*T. officinale* tends to be plastic in form and leaf morphology (Oosterveld 1983; Cox & Ford 1987; Taylor 1987). Nevertheless, leaf morphology has been successfully used to identify biotypes and microspecies (e.g. Wivagg 1975; Oosterveld 1983).

## RESEARCH SITE

A natural population of *T. officinale* at the West Virginia University Horticultural Farm, Morgantown, West Virginia, USA was selected for demographic study. The population was located in an open meadow with a southern aspect. The meadow had previously been mown once every one to three months during the growing season. During the census period, plots were mown once per month to a height of  $\approx 7$  cm for the entire year so that seasonal differences were not confounded with the effects of a change in mowing regime. Additionally, this mowing regime was established to prevent decline in the *T. officinale* population as a result of overtopping since *Taraxacum* is sensitive to shading by competitors (Timmons 1950; Mølgaard 1977; Bakker, Dekker & De Vries 1980; Oomes & Mooi 1981; Van Loenhoud & Duyts 1981).

## CENSUS PROTOCOL

Four  $1 \times 3$  m blocks were delineated within the population of *T. officinale*. The blocks were separated into two pairs and were quasi-randomly located (randomization was limited by farm use and management). All *T. officinale* individuals within these blocks were identified by aluminium tags secured to the ground with floral pins. Two of the four blocks were censused in October 1990. Then each month from November 1990 to October 1991, number of leaves, leaf lengths, leaf widths, and number of scapes (flower bud, flower or seed stage) were censused on every plant for all four blocks. New seedlings which appeared were also tagged and censused for the remainder of the year. Initially, 715 individuals were tagged in the four blocks.

## PHENOTYPE CLASSIFICATION

Leaves ( $n = 305$ ) were randomly removed from each mature tagged plant within the population in spring (May) and pressed (plants exhibiting juvenile characteristics, i.e. leaves with entire margins, were excluded). Leaf length, greatest width, narrowest width between lobes, length from the base to the widest portion of leaf, number of lobes, length of the largest lobe, length from the base to the first lobe, number of teeth on the largest lobe, and leaf area were measured on all pressed leaves. Variables were made relative by dividing by total leaf length when leaf size was clearly confounded with morphological traits. Individuals within the population were segregated into phenotype classes based on these morphological traits using cluster analysis (Proc Cluster, SAS 1986).

## MATRIX MODEL AND PARAMETERIZATION

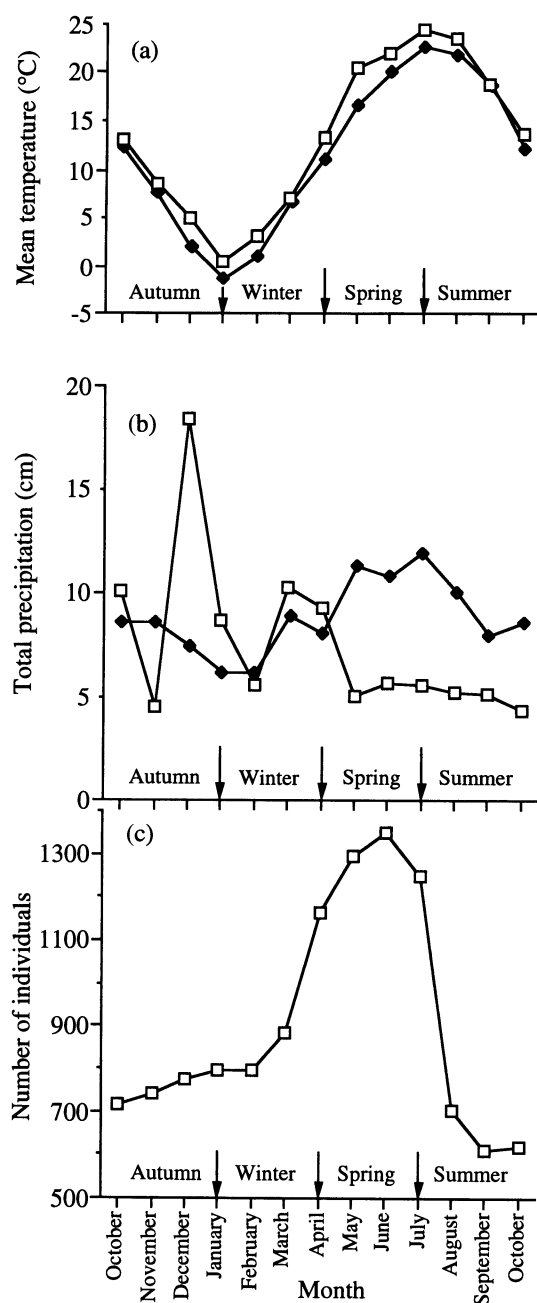
Matrix models of population growth are used to explore the consequences of the current population

structure and environment rather than to predict future population size (Caswell 1989). The models are useful as a way of integrating survival, growth, and reproduction to compare temporal or spatial patterns of population dynamics. The Lefkovich model (Lefkovich 1965) incorporates the size- or life-history stage-structure of the population in order to aid understanding of demographic rates. In plants, individual fates are often better correlated with size or stage rather than age (Harper 1977; Werner & Caswell 1977; McGraw & Wulff 1983; Van Groenendaal, De Kroon & Caswell 1988). In addition, it is often difficult or impossible to determine the age-structure of a plant population (Werner 1975; Werner & Caswell 1977).

In the present study, transition matrices (**A**) were formed with elements ( $a_{ij}$ ) which summarize the probabilities of individuals of size  $i$  arising from individuals of size  $j$  via survival or recruitment. Individuals may grow ( $i > j$ ), remain the same size ( $i = j$ ) or regress to a smaller size ( $i < j$ ).

Parameters were obtained to form separate transition matrices for the population as a whole and for individual phenotype classes. Matrices were constructed for each of four seasons, autumn (October–January), winter (January–April), spring (April–July), and summer (July–October). These seasons were determined by climate (Fig. 1). The transition matrix for the first season (October–January) was calculated using two blocks, while the remaining seasons included four blocks. The reduction in population size ( $N$ ) for the first season did not limit inferences about seasonal variation since seasonal differences were large.

In order to express plant size as total leaf area, leaf area was determined for each phenotype class and for juveniles; this was based upon regression of the product of leaf length and width on leaf area with an intercept constrained at 0 ( $R^2 = 0.96$ – $0.98$ ). Leaf area was determined for a sample of leaves ( $n = 349$ ) with a portable area meter (Li-Cor LI-3000; Lincoln, Nebraska, USA). Four size classes based on total leaf area were determined for the population using Vandermeer's algorithm (Vandermeer 1978). The algorithm minimizes errors produced by decreasing sample size with decreasing category size, and skewed distributions of individuals within large size classes. Size classes were determined using transitions across all seasons to address Moloney's (1986) criticism that the algorithm examines a population only over a single time interval. Size classes were 0.01–8.50, 8.51–23.0, 23.01–51.0, and  $\geq 51.01$  cm<sup>2</sup> leaf area. A separate seedling class was not used because identification of initially tagged individuals as seedlings would have been impossible. Size class based on diameter of taproot might have provided a better estimate of individual size, but exposing the root could potentially alter growth and survival rates. Moreover, in *Taraxacum* the seedling stage grades continuously



**Fig. 1** (a) Temperature and (b) precipitation for Morgan-town, WV from autumn 1990 to summer 1991. Open squares refer to average monthly temperatures and total monthly precipitation. Solid diamonds are mean temperatures and precipitation from 1975 through 1990 (Morgantown FAA Airport, NOAA 1991). (c) Monthly population size of *Taraxacum officinale*, beginning with all individuals originally tagged. Censuses to calculate seasonal demographic rates were performed during 1990 and 1991.

into the adult size classes and thus an arbitrary separate class of first-year plants was unnecessary.

A size transition matrix was then created for each season, phenotype class, and season/phenotype class combination. Elements of the size transition matrix ( $g_{ij}$ ) were based on the probabilities of increasing or decreasing in leaf area from one size class to another (MATLAB, The MathWorks, Inc. 1989). This transition matrix implicitly includes mortality because an

individual which dies does not grow or remain in a size class, and thus the summed probability values of these transitions are less than unity.

To form an overall population projection matrix ( $A$ ), per capita rates of reproduction were added to the growth transition matrix. Fertility [seedling recruits of size  $i$  ( $i = 1$  in this study in every case) per adult of size  $j$ ;  $f_{ij}$ ] was estimated by multiplying recruitment per capitulum [estimated as total number of seedlings which survived to the end of the season ( $S$ ) divided by the total number of capitula produced during the season ( $\Sigma C$ )] times the average number of capitula produced ( $C$ ) per individual present at the start of the season:

$$f_{ij} = \left( \frac{S}{\sum_{\text{all individ.}} C} \right) C \quad (1)$$

To form each transition probability ( $a_{ij}$ ), then:

$$a_{ij} = g_{ij} + f_{ij} \quad (2)$$

Recruitment was based on number of capitula produced rather than number of seeds because few seed heads contained all seeds at collection, in spite of the fact that seed heads were collected as often as twice per day during peak flowering. No good surrogate for seed number (e.g. seed head weight or diameter) could be found that accurately estimated the number of seeds per seed head. The mean  $\pm$  SE number of seeds per seed head for those heads collected containing all seeds was  $138.51 \pm 7.52$  ( $n = 37$ ). *Taraxacum* seeds generally exhibit 90–100% viability (Wivagg 1975). The fertility estimate assumes that the recruitment rate is invariant among capitula and from capitula of differently sized individuals (in a separate study, number of seeds per capitulum was unaffected by size class,  $P = 0.29$ ,  $n = 96$ ; unpublished data). The estimates also assume that an equal proportion of seeds are dispersed into and out of the plots (no net immigration or emigration of seeds, e.g. Oostermeijer *et al.* 1996). This assumption is reasonable because *Taraxacum* fruits generally disperse near the parent plant (Ford 1985). Lastly, in order to determine fertility by phenotype class, we assumed that seed dormancy, viability and germination were equal among classes. Seed viability per capitulum and establishment have been found to be the same within populations for different genotypes in other studies (Ford 1985) and specifically for a representative genotype from each of the phenotype classes used in this study (Vavrek *et al.* 1996). No data is available for persistence of the different phenotype classes within a short-term (within-year) seed bank.

The finite rate of increase,  $\lambda$ , was calculated for each transition matrix using MATLAB. The finite rate of increase per season is the dominant eigenvalue of the full seasonal transition matrix. To estimate the annual finite rate of increase, the four seasonal tran-



sition matrices were multiplied to form a product matrix (Skellam 1966; Sarukhan & Gadgil 1974; Huenneke & Marks 1987; Caswell 1989). The product matrix accurately reflects the schedule of survival, growth and reproduction occurring throughout the year, i.e. the product matrix contains all the demographic information from each of the seasons. However, because of the multiplication process that produces them, particular transition probabilities within the product matrix represent a complex product of growth and survival probabilities and summed fertilities and are difficult to interpret (Tuljapourkar 1985; Caswell & Trevisan 1994). Therefore, the discussion of the data and the importance of particular transitions to population growth will generally be limited to the seasonal matrices.

The reproductive value of an individual of size class  $i$  ( $v_i$ ) is the relative value of potential future reproduction (including the probability of surviving to reproduce). The set of such values is given by the left eigenvalue ( $v$ ) (Caswell 1982). The left eigenvalues for each season were calculated from the permuted product matrix so that the season under consideration was the first matrix to be multiplied.

#### STATISTICAL COMPARISONS OF MATRICES AND ELASTICITY ANALYSIS

Differences in fate (survival or growth to size class at end of census period) as a function of state (size class at beginning of census period) and season were analysed with log likelihood analysis (SAS JMP, Statistical Analysis Systems Institute 1994, e.g. Caswell 1989; McGraw 1989).

Standard errors were assigned to  $\lambda$  for each season and for each phenotype class/season combination with Tukey's Jackknife method (Sokal & Rohlf 1995, e.g. Lenski & Service 1982; Meyer *et al.* 1986; Stemberger 1988). For this method, a pseudovalue ( $\phi_i$ ) for  $\lambda$  was determined separately for each of  $n$  data sets per season and phenotype class and season combination with a different individual removed each time ( $n$  = number of individuals present at the start of the season):

$$\phi_i = n\lambda - (n-1)\lambda_{-i} \quad \text{then } \bar{\lambda} = \phi \quad (3)$$

and

$$SE = \sqrt{\frac{\sum (\phi_i - \bar{\phi})^2}{n(n-1)}} \quad (4)$$

Elasticity analysis provides a method for evaluating the relative contribution of growth transitions and fertility to population growth (Caswell, Naiman & Morin 1984; de Kroon *et al.* 1986; van Groenendael *et al.* 1988):

$$e_{ij} = \frac{a_{ij}}{\lambda} \cdot \frac{\partial \lambda}{\partial a_{ij}}, \quad (5)$$

where

$$\frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle} \quad (6)$$

Elasticity ( $e_{ij}$ ) analysis of each season would reveal the relative effect that a small perturbation of each transition element, holding all other elements constant, would have on the seasonal  $\lambda$ . The effect of these perturbations on the annual growth rate, however, is more appropriate because transitions occurring at each season are not independent of transitions from other seasons (Caswell & Trevisan 1994). Caswell & Trevisan (1994) provide a method for examining sensitivity of annual growth at particular time points in the annual cycle while incorporating transitions occurring both before and after that time reference, thus:

$$e_{ijk} = \frac{b_{ijk}}{\lambda_{\text{annual}}} \cdot \frac{\partial \lambda_{\text{annual}}}{\partial b_{ijk}}, \quad (7)$$

where refers to the  $i^{\text{th}}$  element of the  $k^{\text{th}}$  season transition matrix.

Elasticity matrices were calculated at each season and were compared to examine size-specific and season-specific differences in relative importance of particular transitions to  $\lambda_{\text{annual}}$ .

Differential phenotype class response to season was tested with Spearman Rho correlation coefficients (SAS JMP). These coefficients compared cross-season, phenotype class rank using mean  $\lambda$  for each phenotype class in each season.

## Results

### PHENOTYPE CLASSIFICATION

Cluster analysis separated five phenotype classes based on leaf morphology. Multivariate analysis of variance (SAS JMP) confirmed separation of the phenotype classes (Wilks' Lambda,  $F = 69.50$ ,  $P < 0.0001$ ). The differences among phenotype classes are illustrated as a canonical centroid plot using three of the morphological variables (Fig. 2). The first canonical axis discriminated individuals according to the degree of leaf dissection. The second

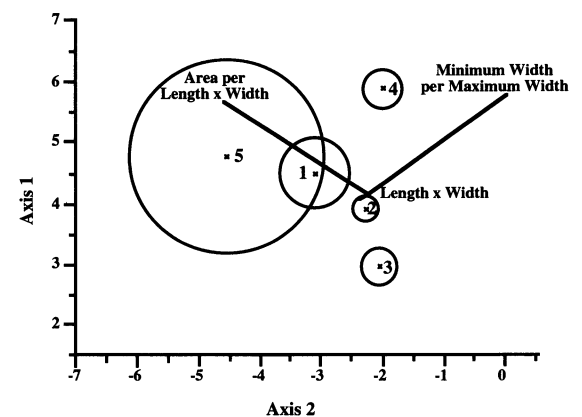


Fig. 2 Canonical centroid plot presenting multivariate least squares means (with 95% confidence region) for five biotypes of *Taraxacum officinale*. Only three of the variables from the original cluster analysis are presented to show best separation of the means.

axis primarily contrasted individuals on the basis of leaf lobe shape. Leaf morphology was variable over time, but under a given environment (e.g. an experimental common environment garden), morphological differences continued to be detectable among phenotype classes (Vavrek 1994).

#### POPULATION RESPONSE TO SEASONALITY

The pattern of temperature change during the censuses was typical for a temperate climate (Fig. 1a). Mean monthly temperatures were slightly higher than the norm (mean difference between current year temperature and the 15 year average =  $1.85 \pm 0.33$  °C). Precipitation was greater than usual during autumn, but averaged  $3.85 \pm 0.81$  cm less per month over the whole year because of low precipitation in spring and summer (Fig. 1b). The total population size of *T. officinale* responded to these climatic patterns with the greatest number of individuals occurring in mid-spring (Fig. 1c). Following the spring peak, population size declined rapidly during the summer drought.

Underlying the overall seasonal patterns in population size were shifts in size-dependent demographic rates ( $\chi^2 = 37.02$ ,  $P < 0.001$  and  $\chi^2 = 31.16$ ,  $P < 0.01$ , for season and size class, respectively). Autumn (October–January) was a season where survival was greatest in larger size classes, surviving individuals regressed in size, and most size classes produced seeds (Tables 1 and 2a). In winter (January–April), plants of all size classes survived at high rates, growth produced plants which advanced into all larger size classes by the end of the period, and reproductive rates were low. In spring (April–July), both survival and reproduction were positively related to size, and nearly all size transitions occurred. In summer (July–October), survival was at its lowest level and again positively related to size, all size transitions occurred, and no seed production occurred.

Reproductive values were season-dependent. In general, the expected contribution of individuals to population growth was highest for larger size classes (Table 2b). The values reflect high rates of survival for larger size classes during winter and spring, in addition to high recruitment during spring. Summer values are lowest among all seasons, reflecting only survival rates and the potential for reproductive contribution in the following seasons.

The finite rate of increase,  $\lambda$ , varied as a function of season (jack-knifed  $\lambda \pm \text{SE} = 2.1191 \pm 1.2977$  for autumn,  $1.0230 \pm 0.1352$  for winter,  $0.8175 \pm 0.0178$  for spring, and  $0.7688 \pm 0.0472$  for summer). Thus, population numbers were declining in two of the four seasons and were slightly declining overall with a growth rate per year of 0.9128 (based on the product matrix of all four seasons). The population declined despite producing  $\approx 125\,000$  seeds over the year: only

**Table 1** Lefkovich transition matrices for (a) autumn; (b) winter; (c) spring; and (d) summer for a natural population of *Taraxacum officinale* censused at the West Virginia University Horticultural Farm, Morgantown, WV. Seasons refer to October 1990–January 1991, January–April 1991, April–July 1991, and July–October 1991, respectively. Size classes are based on leaf area, 0.01–8.50, 8.51–23.00, 23.01–51.00, and  $\geq 51.01$  cm<sup>2</sup>. Matrix elements may include survival, growth and fertility

To size class (i)	From size class (j)			
	1	2	3	4
(a) Autumn				
1	2.1191	0.7500	1.0054	1.4436
2	0	0	0	0.0086
3	0	0	0	0
4	0	0	0	0
(b) Winter				
1	1.0226	0	0	0
2	0.1647	0	0	0
3	0.1049	0	0	0
4	0.1580	1.0000	0	0
(c) Spring				
1	0.5975	0.5908	1.0845	2.2515
2	0.1055	0.3901	0.3171	0.3770
3	0.0053	0.1277	0.1098	0.1967
4	0	0	0.0244	0.0328
(d) Summer				
1	0.1719	0.2155	0.0536	0.1429
2	0.0912	0.2500	0.1607	0.0952
3	0.0363	0.2457	0.3036	0.2381
4	0.0058	0.0905	0.3214	0.4286

**Table 2** (a) Individual fertility and (b) reproductive values for each size class per season of a natural population of *Taraxacum officinale*. Seasons refer to October 1990–January 1991, January–April 1991, April–July 1991, and July–October 1991, respectively. Size classes are based on leaf area, 0.01–8.50, 8.51–23.00, 23.01–51.00, and  $\geq 51.01$  cm<sup>2</sup>. All seedling recruitment occurred as size class 1 individuals only, i.e. no recruited seedlings grew to size class 2 or larger between germination and censusing

	Parent size class			
	Autumn	Winter	Spring	Summer
(a) Individual fertility				
1	1.4525	0.5458	0.0020	0
2	0	0	0.2362	0
3	0.0660	0	0.6211	0
4	0.4695	0	1.9482	0
(b) Reproductive values				
1	1.0000	1.0000	1.0000	1.0000
2	1.8622	2.0325	2.1520	0.3539
3	0	2.4669	2.1114	0.4744
4	0	4.2652	2.5948	0.6888

116 seedlings were recruited (less than 0.1%) from the seed rain.

Elasticity analysis revealed that during autumn and winter,  $\lambda_{\text{annual}}$  is primarily determined by the survival

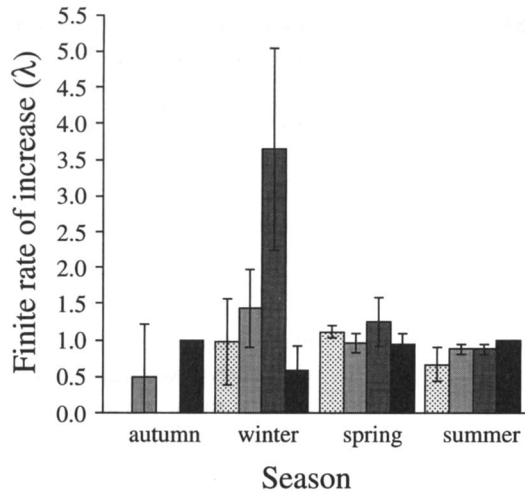
and reproduction of size class 1 individuals (Table 3). Although rapid growth of size class 1 individuals also contributes to  $\lambda_{annual}$  in winter. The transitions affecting  $\lambda_{annual}$  to the greatest extent in spring and summer are also concentrated in the upper left corner of the matrix with the exception of recruitment from size class 4 individuals in spring. Again, the survival and reproduction of small individuals disproportionately affect  $\lambda_{annual}$  and although this is generally true throughout the year, each seasonal elasticity matrix illustrates small season-dependent differences.

DEMOGRAPHY OF PHENOTYPE CLASSES

The annual finite rate of increase varied as a function of phenotype class. Phenotype classes 2 and 4 exhibited rapid growth ( $\lambda_{annual} = 2.5171$  and  $2.5868$ , respectively) while phenotype class 1 exhibited a net loss in number of individuals ( $\lambda_{annual} = 0.8203$ ). The growth rate of phenotype class 3 was intermediate ( $\lambda_{annual} = 1.6872$ ). A complete transition matrix could not be constructed for phenotype class 5 which was represented by only two individuals. Sample sizes were larger for the other four phenotype classes ( $n = 20, 112, 56$ , and  $57$ , respectively, for phenotype classes 1–4).

**Table 3** Elasticity values for overall transition matrices of a natural population of *Taraxacum officinale* for (a) autumn; (b) winter; (c) spring; and (d) summer. These values indicate the relative effect a small perturbation of each transition element independently of all other elements would have on  $\lambda$ . Transition elements include survival, growth and fertility. Seasons refer to October 1990–January 1991, January–April 1991, April–July 1991, and July–October 1991, respectively. Size classes are based on leaf area, 0.01–8.50, 8.51–23.00, 23.01–51.00, and  $\geq 51.01$  cm<sup>2</sup>

To size class (i)	From size class (j)			
	1	2	3	4
(a) Autumn				
1	0.6126	0.1524	0.1444	0.0896
2	0	0	0	0.0010
3	0	0	0	0
4	0	0	0	0
(b) Winter				
1	0.4493	0	0	0
2	0.1400	0	0	0
3	0.1137	0	0	0
4	0.2960	0.0010	0	0
(c) Spring				
1	0.3216	0.0442	0.0599	0.1879
2	0.1217	0.0725	0.0375	0.0674
3	0.0060	0.0234	0.0128	0.0347
4	0	0	0.0035	0.0071
(d) Summer				
1	0.4679	0.1334	0.0087	0.0026
	0.0879	0.0548	0.0092	0.0006
3	0.0469	0.0722	0.0233	0.0020
4	0.0109	0.0386	0.0358	0.0053



**Fig. 3** Seasonal finite rates of increase ( $\lambda$ ) for five biotypes of *Taraxacum officinale* growing in a natural population, biotype 1 (□), 2 (■), 3 (▒), 4 (■). Biotype 5 was represented by too few individuals to estimate  $\lambda$ .

Demographic responses of the phenotype classes were season-specific (Fig. 3). Ranks of finite rate of increase of phenotype classes 2, 3, and 4 changed between seasons, for example (Spearman Rho correlation coefficient =  $-0.95$  between autumn and spring,  $P = 0.051$ ). Large errors, however, partially mask seasonal demographic patterns. Phenotype classes 2 and 4 had nearly identical annual finite rates of increase but showed marked seasonal differences. Phenotype class 2 appears to be a ‘cool season’ phenotype class exhibiting a larger  $\lambda$  in winter and a reduced  $\lambda$  in summer. In contrast, growth of phenotype class 4 was high in the warm summer and autumn months and was reduced in winter. The response of phenotype class 3 was similar to that of phenotype class 2 except that responses were more exaggerated with an exceptionally low  $\lambda$  in autumn and high  $\lambda$  in winter. Phenotype class 1 tended to grow during spring and decline in population size during the hot, dry summer and autumn months. This response, intermediate between the cool and warm season phenotype classes resulted in a net loss in population size.

Discussion

POPULATION RESPONSE TO SEASONALITY

The demographic rates of a natural population of *Taraxacum officinale* were, not surprisingly, highly season-dependent. During autumn (October–January), virtually all plants declined in size. This senescence of leaves, resulting in a reduction in plant size, allows retranslocation of nutrients and carbohydrates prior to freezing. The small leaves which do persist on plants may be continually replaced or may be insulated near the ground by the grass canopy. Free sterols and fructose have also been implicated in



resistance to damage by low temperatures in *T. officinale* (Westerman & Roddick 1981; Nelson & Spollen 1987; Cyr *et al.* 1990) and may enable it to maintain above-ground biomass. For these plants, photosynthetic capability is continuously available to support winter maintenance, growth and reproduction during brief warm periods.

Maintaining a larger size throughout winter enhanced survival ( $P < 0.01$ ; quadratic regression of survival on leaf area). With additional reserves, large plants were also able to respond more quickly and vigorously to warming trends resulting in higher growth rates. Greater leaf area, however, may increase the risk of freeze injury. This may explain why so few plants maintained large leaf areas during winter.

Despite the reduction in above-ground biomass of larger individuals and relatively high mortality of small individuals, a high level of recruitment occurred during autumn, resulting in the highest population growth rate of any season. High rates of recruitment in autumn may have been due to favourable weather conditions (Fig. 1, e.g. temperature (Mezynski & Cole 1974; Van Loenhoud & Duyts 1981) or precipitation). *T. officinale* exhibited a low establishment rate in autumn at the research site 3 years later (Vavrek *et al.* 1996). Gray *et al.* (1973) were unable to correlate number of capitula or seeds per flower head with temperature, precipitation or day length even though flowering appeared season-dependent. Plants, however, may have been responding to a large number of factors including population density (Ford 1985), day length (Solbrig 1971), ground cover density (Reader 1991a), disturbance (Sterk *et al.* 1983), and seed predation (Reader 1991b). Autumn recruitment may allow early growth of offspring in spring before grass canopy closure. Early growth may then enable these individuals to dominate environmental resources early in the year (Van Loenhoud & Duyts 1981).

Spring and summer demographic rates resulted in population decline. Specific conclusions cannot be drawn explaining this decline since environmental factors were not varied experimentally, but the spring and summer of 1991 were exceptionally dry and warm for West Virginia (Fig. 1). Therefore, heat and drought stress may have increased mortality rates and precluded reproduction. Survival of *T. officinale*, however, was also lowest in summer two years later (Vavrek *et al.* 1996). Larger plants were less affected by these stresses. Presumably these individuals possess longer and larger tap roots, thereby reaching deeper into the soil profile for water and having greater storage reserves. Both of these traits would promote survival during the drought.

The consequences of the changes in demographic rates across seasons are potentially significant. The seasonal pattern of survival and recruitment will affect population growth. For example, early reproduction

often results in a larger annual  $\lambda$ , i.e. offspring produced early in the year are potentially able to contribute to population growth more quickly than offspring produced late in the year. More importantly, temporal variation in demographic rates may have consequences for population longevity. In this population, for example, the large standard errors associated with the autumn and winter  $\lambda$ -values were the result of the influence of a few individuals upon  $\lambda$ . The removal of these few reproducing or dying individuals caused large changes in  $\lambda$ . Individuals of size class 1 in winter may have different impacts on  $\lambda$  because size class 1 was comprised of an array of individuals of varying age and size. The importance of these individuals to annual growth is also reflected by the elasticity analysis. Perturbation of the survival and reproduction of size class 1 individuals in autumn has potentially large effects upon annual growth. Thus, vulnerability of this population to external forces may be greatest during autumn and winter and be determined by the response of a few individuals in a particular size class. Annual as opposed to seasonal censuses would entirely hide this vulnerability.

#### DIFFERENTIAL PHENOTYPE CLASS RESPONSE TO SEASONALITY

Five phenotype classes of *Taraxacum officinale* were characterized in the natural population by cluster analysis of leaf morphology. Demography of the five phenotype classes differed across seasons, e.g. a negative cross-season, rank correlation of  $\lambda$  between autumn and spring. The differential seasonal responses can be illustrated by the classification of phenotype classes 2 and 3 as 'cool season' phenotype classes and phenotype class 4 as a 'warm season' phenotype class. The differential demography in response to seasonal environments results in differential resource use, and thus may reduce competition for resources among these phenotype classes during times of rapid growth and recruitment. Similar niche differentiation among *Taraxacum* genotypes within a population has been found in terms of germination (Van Loenhoud & Duyts 1981) and early growth (Ford 1985). Despite the seasonal differences among these phenotype classes, the net outcome for the 'cool season' and 'warm season' phenotype classes is similar rapid annual growth. The combination of contrasting seasonal demography and similar annual growth of the seasonal phenotype classes suggest that their genetic differences will be maintained in the population over the short-term and potentially over long periods of time.

Temporal environmental variation has been suggested as a causal factor in the maintenance of species diversity within communities (e.g. Fowler & Antonovics 1981; Chapin & Shaver 1985), which is an extension of the principle demonstrated here. The differential response of genotypes within a population is

directly analogous to species responses within a community (Seger & Brockmann 1987). Many species are adapted differentially to a combination of environmental factors in time and space resulting in different phenologies as well as resource use. The timing and control of recruitment by different species may be particularly important for species richness. Grubb (1977) summarizes the consequences of variation in regeneration ecology for the maintenance of species diversity. Genetic differences among species in physiological control of the release from dormancy, for example, contribute to the separation of specific niches within a year (Grubb 1977). The greater number of niches allows for the coexistence of a greater number of species within a community. Thus, species-specific demography influences community composition in the same manner that genotypic differentiation influences within-population diversity. Additionally, the diversity within populations determines the environmental limits of species within communities (Antonovics 1976). The processes occurring within populations therefore are not only similar to community processes, but are interrelated.

Our data suggest that phenotype classes within a population may also show temporal specialization in resource use as exhibited by distinct demographic patterns. Temporal heterogeneity thus affects population structure as well as community composition. If phenotype classes are, in fact, genetically distinct (as described by others in classification of agamospecies; Wivagg 1975; Oosterveld 1983), the differential response of phenotype classes to cyclic seasonal fluctuations may be particularly important for the maintenance of genetic diversity. Rapid production of identical offspring by a clone with an adaptive advantage would allow that clone eventually to dominate the population (Sebens & Thorne 1985). However, if selective forces change with seasons, relative fitness of individual clones will also change. For example, two morphological clones of *Bosmina longirostris* (a cladoceran) are maintained by their differential relative fitness in response to seasonal change in the dominant predator species (Black 1980). If only one predator were present throughout the year, the clone with the lower fitness would be lost from the population. Selective forces may also change between years. Timing of establishment, for example, can differ between years (Ford 1985). Thus, phenotype class rank fitness may also fluctuate among years. The basic pattern of annual growth among phenotype classes found here, however, is similar to that found two to three years later in an experimental population of clones derived from the natural population (Vavrek *et al.* 1996).

Spatial environmental heterogeneity has been found to be important across gradients from kilometres to centimetres in length (e.g. Clausen *et al.* 1940; McNeilly & Antonovics 1968). Others have demonstrated interannual fluctuations in demography (e.g. Klemow & Raynal 1983; Mack & Pyke

1984). Similarly, we have shown temporal variation to be important across seasons (of three months) within a year. Plant genotypes may respond differentially to temporal fluctuations on an even smaller scale, across months or weeks. Ultimately, we may discover that different genotypes may be responding differentially to hour by hour changes in the environment since these changes can be on the same order of magnitude as seasonal changes.

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