

# Determinants of the abundance of invasive annual weeds: community structure and non-equilibrium dynamics

R. P. Freckleton<sup>1\*</sup>, A. R. Watkinson<sup>1</sup>, P. M. Dowling<sup>2</sup> and A. R. Leys<sup>3</sup>

<sup>1</sup>Schools of Environmental and Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK

<sup>2</sup>Co-operative Research Centre for Weed Management Systems, NSW Agriculture, Agricultural Research and Veterinary Centre, Forest Road, Orange NSW 2800, Australia

<sup>3</sup>National Parks and Wildlife Service, PO Box 1967, Hutsville NSW 2220, Australia

The dynamics of an annual pasture community are described from a five-year experimental and monitoring study. The community was dominated by two grasses (*Lolium rigidum* and *Vulpia bromoides*) and a legume (*Trifolium subterraneum*). Fits of population dynamic models to *per capita* rates of population change indicate that interactions between the grasses were generally strong, while interactions between the grasses and legumes were weaker. Most, but not all, of the net effects of competition on population growth could be attributed to interactions occurring during plant growth. Phase-plane analysis indicated that, for a constant environment, a joint equilibrium of the two grasses is unstable since interspecific competition between *Lolium* and *Vulpia* is stronger than intraspecific competition. Consequently, the community will tend to a mixture of only one or other of the grass species and *T. subterraneum*, depending on the founding composition of the pasture. Analysis of data taken from a year in which a drought occurred (1993–1994) demonstrated profound effects on all three species. Modelling of the long-term impacts of the effects of repeated droughts showed that disturbance of this form overrides the founder effect observed under constant conditions. Consequently, *Vulpia* is ultimately able to invade any mixture of the other species in environments where stochastic disturbances occur.

**Keywords:** stochastic model; resource competition; long-term dynamics; competition; invasion dynamics

## 1. INTRODUCTION

Despite long-term debates over the role of competition in determining plant community structure (Grime 1977, 1979; Tilman 1982, 1988) and over the relative importance of competition and environmental variability in determining abundance (Huston 1994; Chesson & Huntly 1997), very few studies have addressed these issues together to provide an analysis of how they interact to determine community dynamics. It is only relatively recently that detailed multispecies analyses have, for example, modelled competition as a force driving successional dynamics in forests (Pacala *et al.* 1996) or measured in detail the role of competition in structuring systems of dune annuals (Rees *et al.* 1996) and perennial grasses (Law *et al.* 1997). What these models have emphasized is the variability in the strength and nature of competitive interactions across systems. Competition is a key force driving succession in forests, for example, while its role would appear to be minor in the case of dune annuals. Furthermore, in some systems such as desert plant communities, temporal variability may be a highly significant determinant of community composition (Venable & Lawlor 1980; Venable *et al.* 1993). The studies cited above tend to be the exception and there are few examples of communities for which we have a detailed description of competitive interactions as well as the impacts of temporal variability, especially the effects of extreme variability such as recurrent droughts.

One of the major issues surrounding the study of plant competition has been that of methodology (Firbank & Watkinson 1990) and it is only recently that work on the dynamics of simple plant communities has shown the power of statistical analysis of simple census data for characterizing the strengths of interactions between species in unmanipulated communities. Rees *et al.* (1996) and Law *et al.* (1997) show that analyses based on the principle of regressing rates of local population change on local population densities can be used to estimate the *per capita* strengths of population interactions. Moreover, while techniques based on plant removal and competition indices may be biased owing to the development of spatial structure within plant communities (Pacala 1997; Pacala & Levin 1997), competition coefficients estimated using regression techniques are not biased in this way when measured at an appropriate spatial scale (Freckleton & Watkinson 2000). In addition, simulation and randomization methods offer a powerful approach to assessing the efficiency of statistical techniques and the reliability of predictions based on such analyses (Law *et al.* 1997; Freckleton & Watkinson 2000).

In this paper we use this approach to analyse long-term (five year) data on the dynamics of a pasture community dominated by annual plants, and the effects of extreme environmental variability in the form of droughts (Dowling 1996). In particular we concentrate on how these processes interact to determine invasion of this community by a pernicious weed (*Vulpia bromoides*), which is typical of a variety of species that present problems to

\*Author for correspondence (r.freckleton@uea.ac.uk).

both agricultural and natural ecosystems worldwide (e.g. Usher 1988; Lonsdale 1994; Williamson 1996).

## 2. METHODS

### (a) Field experiment

The experiment was conducted at the Agricultural Research Institute, Wagga Wagga, NSW, Australia (latitude 35°3'S; longitude 147°21'E; altitude 219 m; annual average rainfall 555 mm). Pastures were established within small plots (2 m × 6 m) that consisted of combinations of two 'desirable' species, *Trifolium subterraneum* L. and *Lolium rigidum* L., as well as the weed species, *V. bromoides* (L.) S. F. Gray. Four pasture mixtures were established, comprising three densities of *Trifolium* (1, 25 and 100 kg ha<sup>-1</sup> seed of *T. subterraneum* cv. Junee) as well as a mixture of *Trifolium* and *Lolium* (25 kg ha<sup>-1</sup> of *Trifolium* plus 20 kg ha<sup>-1</sup> of *Lolium*). Each of the pasture treatments was sown with two densities of *Vulpia* (250 m<sup>-2</sup> and 1250 m<sup>-2</sup>). In 1992, after convergence of the densities of *Vulpia* across treatments, a density differential was reimposed by herbicide (simazine) application, which was applied to half of the plots, reducing the densities of the two grasses by ca. 90%. The plots were grazed over the summer following the death of vegetative parts and seed shed of all species.

Plant densities (individuals per unit area) were monitored between May 1990 and August 1994. Densities were determined by counting all plants of all species in 20 cores (4.5 cm diameter) taken from each plot in August. Biomass was estimated by the dry weight rank method by using the rising plate on eight locations of the plate per plot, and data were analysed using BOTANAL (Tothill *et al.* 1992). Estimates of dry matter production were based on eight pasture cuts calibrated against the rising plate for each sampling period.

The year 1993–1994 was exceptionally dry. The total rainfall over the growing period (April–October) was 205 mm, compared with a long-term average ( $\pm$  s.d.) of 335  $\pm$  11 mm. The data from this year are therefore important in that they can be used to assess the impact of droughts on pasture dynamics. We analysed long-term meteorological data, recorded on site since 1898, in order to estimate the long-term frequency of severe droughts.

### (b) Model development

The order of events in the life cycle is as follows: seed germination (autumn) is followed by seedling establishment, plant growth and mortality (winter), seed production and shed (spring), with seeds remaining in enforced dormancy (summer) until germination in the following autumn. The models are based on censuses of plants at flowering (i.e. in the spring). In order to fit models for population dynamics and interactions to the census data we provisionally ignored the presence of seeds in a seed bank. Seeds of *Trifolium* are in fact persistent and ultimately we used literature-derived parameter estimates to include this carry over for modelling dynamics in a stochastic environment. There is little evidence that seeds of the two grasses are persistent and inclusion of a small reserve of persistent seed had little effect on the model results in any case. The model predicts population size ( $N$ ) at time  $t + 1$  as a function of the sizes of the three populations at time  $t$  using a hyperbolic equation (e.g. Watkinson 1980; Rees *et al.* 1996):

$$N_i(t+1) = \lambda_i N_i(t) \left[ 1 + \sum_{j=1}^3 \alpha_{ij} N_j \right]^{-1} \quad (1)$$

The parameters of equation (1) are the finite rate of increase,  $\lambda$ , defined as the maximal mean rate of population increase from low densities and competition coefficients,  $\alpha$ , that model the *per capita* competitive effects of intraspecific ( $\alpha_{ii}$ ) and interspecific ( $\alpha_{ij}$ ) competitors. This formulation allows the dynamics of the species to be modelled using parameters that we are able to estimate directly from the data on counts of numbers of plants.

To examine the source of competitive effects in more detail we compared the estimated competitive reductions in *per capita* population growth with data on mean plant biomass. Specifically, we regressed mean plant biomass for each plot on the net *per capita* competitive reduction in population growth, i.e.  $1 + \sum_{j=1}^3 \alpha_{ij} N_j$ . A good correspondence between these two quantities is suggestive that effects of competition between plants during growth are primarily responsible for competitive effects on population growth.

To explore how the competitive structure of the community is likely to affect long-term dynamics in a varying rather than a constant environment, we explored the impacts of drought on community composition and dynamics and, in particular, the invasion of mixtures of *Lolium* and *Trifolium* by *Vulpia*. The effects of drought were modelled by using the parameter values from 1993–1994, which were very different from those of the other years. Specifically, we iterated a stochastic version of the model in which the parameters from the drought year were applied, rather than those from the 'normal' years, with a given probability. This probability was varied from 0 to 1. Within this range we were able to specify the likely range of values of this probability by analysis of the long-term pattern of rainfall at the site (see below).

The seeds of *Trifolium*, unlike those of the other species, tend to persist in the soil for a number of years. In order to realistically model the dynamics of the population in a stochastic environment, it is necessary to include this persistence (e.g. Ellner 1984; Rees & Long 1992). We achieved this by including new parameters in the model for *Trifolium* defining seed production, the emergence of seed from the seed bank, the proportion of seed that is dormant and the proportion of seed that survives for a year in the seed bank, respectively. The model was modified for *Trifolium* by incorporating a second equation describing the dynamics of seed in the seed pool using these parameters and based on the bottleneck model of MacDonald & Watkinson (1981) as well as the submodel for seed dynamics of *Trifolium* of Rossiter *et al.* (1985). The equations for the dynamics of *Trifolium* were modelled by:

$$N_i(t+1) = \lambda_i N_i(t) \left[ 1 + \sum_{j=1}^3 \alpha_{ij} N_j \right]^{-1} + \gamma_i S_i(t) \quad (2.1)$$

$$S_i(t+1) = \lambda'_i N_i(t) \left[ 1 + \sum_{j=1}^3 \alpha_{ij} N_j \right]^{-1} + \gamma'_i S_i(t). \quad (2.2)$$

$\lambda$  and the competition coefficients were generated from the nonlinear model fitting.  $\gamma$ ,  $\gamma'$  and  $\lambda'$  were defined as:  $\gamma$  is the proportion of seed surviving for a year, germinating and surviving to flowering (the probability of seed survival multiplied by the probability of emergence and survival);  $\gamma'$  is the proportion of seed surviving for a year in the seed bank (probability of seed surviving for a year multiplied by the probability of not germinating); and  $\lambda'$  is the maximum number of seeds per plant recruiting to the seed bank (calculated as the

maximum number of seeds produced per plant multiplied by the probability of a seed not germinating and being dormant).

To look at the sensitivity of model predictions to parameter variations, we calculated a sensitivity index for each model parameter:

$$\sigma(P) = \left| \frac{\partial \log(N_{t+1}/N_t)}{\partial \log P} \right|. \quad (3)$$

The sensitivity of the model to some parameter  $P$ ,  $\sigma(P)$ , is calculated as the differential of the logarithm of population growth rate with respect to the logarithm of the parameter. Defined this way, the sensitivity measures the relative effect of  $P$  on the model predictions. We analysed model sensitivity under a range of conditions designed to explore the sensitivity of the system to changing parameter values under a range of initial conditions and drought regimes.

### (c) Statistical methods: estimation of model parameters

We used regressions of the change in local population size on population size to estimate competition coefficients, using a technique similar to that of Rees *et al.* (1996) and Law *et al.* (1997). Although our regressions are based on a smaller number of measurements, ours are based on larger areas, and we use randomization methods to quantify directly the reliability of our predictions. Note that although the density of *Lolium* was not varied through an additive series, the contrast between the two treatments, as well as the natural variations between plots over the course of the experiment allowed the effects of *Lolium* to be assessed using regression approaches.

To ensure stationarity of the time-series, and hence eliminate autocorrelations, the data were analysed as the first order difference of the logarithmically transformed densities, i.e.  $\ln[N(t+1)/N(t)]$ . The model (equation 1) was fitted using a Levenberg–Marquardt procedure to minimize the least squares. Owing to the extremely skewed distribution of densities, leverage effects were controlled for by weighting each point by the reciprocal of the logarithm of density. Separate parameters were included for each year when the residual sum of squares for the overall model fit was significantly reduced.

The seed bank parameters for *Trifolium* were estimated from an existing model for seed bank dynamics in the literature (Rossiter *et al.* 1985). These were: the combined emergence of seed from the seed bank and subsequent survival of plants (0.50); the proportion of seed that is dormant (0.35); maximum seed production per plant (225); and the proportion of seed that survives for a year in the seed bank (0.82).

Parameters were inevitably correlated and hence standard errors for individual parameters are misleading; furthermore, in the present context of understanding community structure, we are more interested in the net reliability of the overall model predictions rather than that of individual parameters. To generate useful confidence intervals for the model predictions we therefore employed a resampling procedure. The data for each species were resampled according to the initial composition and year and the model parameters successively re-estimated to generate 5000 resampled sets of model parameters. These bootstrap parameter estimates were then used to generate the solutions to equation (1) for the three pairwise mixtures and confidence intervals (convex hull polygons) generated from these 5000 sets of parameter estimates. The estimation and analysis procedures were written using the standard procedures in *Mathematica v. 3.0* (Wolfram 1996).

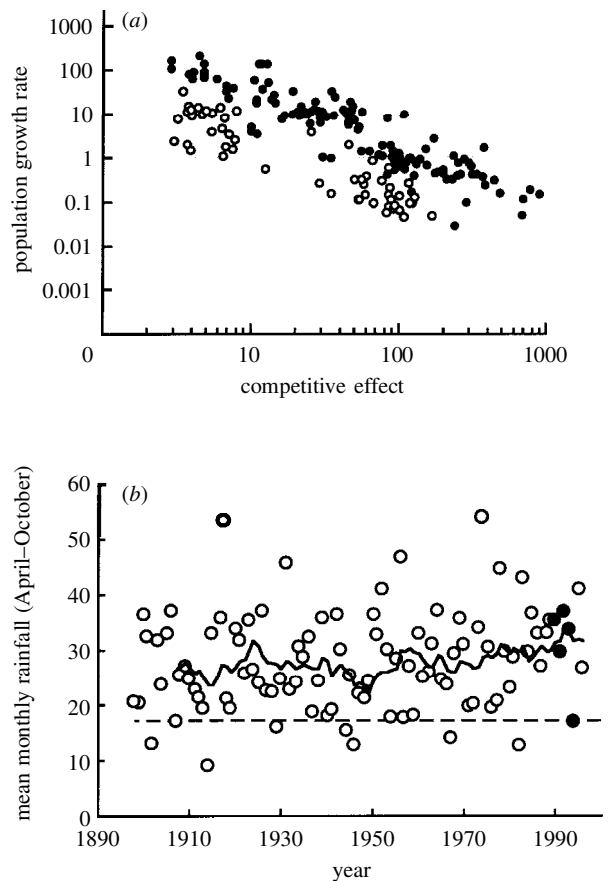


Figure 1. (a) Patterns of population growth in *Vulpia* as a function of net competitive effects in normal years (1990–1992; filled symbols) and under drought conditions (1993–1994; open symbols). (b) The long-term (1898–1996) pattern of rainfall at the experimental site; filled symbols indicate the years of study. The line indicates the ten year running average, while the dashed line shows the rainfall in 1993–1994.

## 3. RESULTS

### (a) Observed dynamics and variability

Overall the models explained 74, 66 and 77% of the variance in log-transformed population growth rates of *Vulpia*, *Lolium* and *Trifolium*, respectively. As shown in figure 1a, this high explanatory power of the models results from the large impacts of competitive effects on population growth. Table 1 shows the best fit estimates of the parameters of equation (1) to the data from the non-drought years. The first year of the experiment produced slightly higher estimates of  $\lambda$  for *Trifolium* together with a considerably higher estimate for *Vulpia* and a high estimate of the *per capita* effect of *Lolium* on *Trifolium*. Our interpretation of this pattern is that it is a consequence of the treatments being sown, rather than naturally regenerating during the first year of the experiment (as would be the case when a new pasture is established). The finite rate of increase of *Trifolium* was low in 1992–1993. This was almost certainly due to the rather late germination of *Trifolium* in this year, which resulted from low rainfall during the first three months of the growing season. This low germination was, however, compensated for (in terms

Table 1. *Fits of models for population growth and competitive interactions. Fits of parameters of equation (3) estimated from the data*

(Mean parameter values assumed for modelling are shown in bold.)

	year	$\lambda$	$\alpha_{iV}$	$\alpha_{iT}$	$\alpha_{iL}$
<i>Vulpia</i>	1990–91	304.46	<b>0.0128</b>	<b>0.00238</b>	<b>0.02203</b>
	1991–92	<b>49.04</b>	<b>0.0128</b>	<b>0.00238</b>	<b>0.02203</b>
	1992–93	<b>49.04</b>	<b>0.0128</b>	<b>0.00238</b>	<b>0.02203</b>
<i>Trifolium</i>	1990–91	30.51	<b>0.00034</b>	<b>0.01028</b>	0.04184
	1991–92	<b>25.23</b>	<b>0.00034</b>	<b>0.01028</b>	<b>0.00273</b>
	1992–93	4.98	<b>0.00034</b>	<b>0.01028</b>	<b>0.00273</b>
<i>Lolium</i>	1990–91	<b>9.73</b>	<b>0.0039</b>	< <b>0.000001</b>	<b>0.00305</b>
	1991–92	<b>9.73</b>	<b>0.0039</b>	< <b>0.000001</b>	<b>0.00305</b>
	1992–93	<b>9.73</b>	<b>0.0039</b>	< <b>0.000001</b>	<b>0.00305</b>

Table 2. *Fits of models for population growth and competitive interactions. Mean interaction matrix*(The entries are the per individual equivalence of one species to the other, calculated as  $\varepsilon_{ij} = \alpha_{ij}/\alpha_{ii}$  (e.g.  $\varepsilon_{TL} = 0.27 = 0.00273/0.01028$ .)

effect on	effect of		
	<i>Vulpia</i>	<i>Trifolium</i>	<i>Lolium</i>
<i>Vulpia</i>	1	0.19	1.72
<i>Trifolium</i>	0.03	1	0.27
<i>Lolium</i>	1.28	< 0.001	1

of biomass production) by exceptionally high rainfall in the latter part of the season. Varying the finite rate of increase for *Trifolium* had little impact on the model predictions as *Trifolium* tends to be a rather neutral part of the system (see below).

The parameters that were employed for modelling purposes are highlighted in table 1. Using these values, we can derive a net interaction matrix for the system (table 2). The entries in this matrix represent the per individual equivalence  $\varepsilon_{ij}$  (i.e.  $\alpha_{ij}/\alpha_{ii}$ ) of each species to the others. This matrix indicates that the interactions between the two grasses (*Vulpia* and *Lolium*) were strong, but that the interactions between the legume (*Trifolium*) and the grasses were much weaker.

The net life cycle probability of survival ( $\pm$  s.e. measured across the 64 plots) measured from seed production through germination and the vegetative stage was estimated for *Vulpia* as  $0.015 \pm 0.02$  for 1991–1992 and  $0.017 \pm 0.01$  for 1992–1993, which compares with a value of  $0.0015 \pm 0.0005$  for 1993–1994 when the drought occurred. This reduction in survival impacted severely on net rates of population change (figure 1a). By measuring the average deviation of population growth rates from the mean fitted model, i.e. the difference between the open and closed symbols in figure 1a, we were able to estimate the impacts of drought on all three populations. In 1993–1994 the population growth rates were reduced to levels of  $0.03 \pm 0.005$ ,  $0.06 \pm 0.010$  and  $0.09 \pm 0.015$  of the population growth rates in previous years, for *Trifolium*, *Lolium* and *Vulpia*, respectively.

In order to generate an approximate measure of the frequency of droughts as severe as that of 1993–1994,

Table 3. *Components of competitive effects on population growth as indicated by regressions of log-mean plant biomass on the log-net competitive effects (see § 3(b) for definition) predicted by the models fitted to the data on per capita population growth (tables 1 and 2)*(A slope close to  $-1$  indicates that mean plant biomass declines exactly in proportion to increasing competitive effect, the implication being that per capita effects on plant performance determine the per capita strength of competitive effects on population growth.)

	slope	s.e.	$R^2$	$n$	$p$
<i>Vulpia</i>	$-1.098^a$	0.033	0.88	155	< 0.0001
<i>Trifolium</i>	$-0.807^a$	0.117	0.33	188	< 0.0001
<i>Lolium</i>	$-0.435$	0.101	0.24	56	< 0.001
<i>Lolium</i> <sup>b</sup>	$(-0.85^a)$	(0.113)	(0.50)	(56)	(< 0.0001)

<sup>a</sup>Not statistically significantly different from unity ( $p > 0.05$ ).<sup>b</sup>Regression results when *Vulpia* was excluded from the calculation of the competitive effect for *Lolium*.

figure 1b shows the mean rainfall during the growing period (April–October) for the long-term weather data measured at the site. Over the past 100 years, eight droughts have occurred that were as bad as or worse than that of 1993–1994, while approximately 15 droughts have occurred that were nearly as bad or worse (figure 1b).

**(b) Components of competition**

Comparison of plant weights with the *per capita* impacts of intra- and interspecific densities on population growth suggested that interactions during the growth period impacting on the mean performance of plants were important determinants of dynamics in this system (table 3). In table 3 a slope of  $-1$  indicates that plant weight declines exactly in proportion to increasing *per capita* effects of competition on population growth, implying that competitive effects on mean plant performance determine effects on population growth. The values for *Vulpia* and *Trifolium* were not statistically significantly different from unity. The value for *Lolium* was statistically significantly different from unity, yet negative and significantly different from zero, indicating that interactions between plants play some role in determining net rates of population change. Since further information on the demography of this species, in particular information on plant recruitment in relation to density, is unavailable

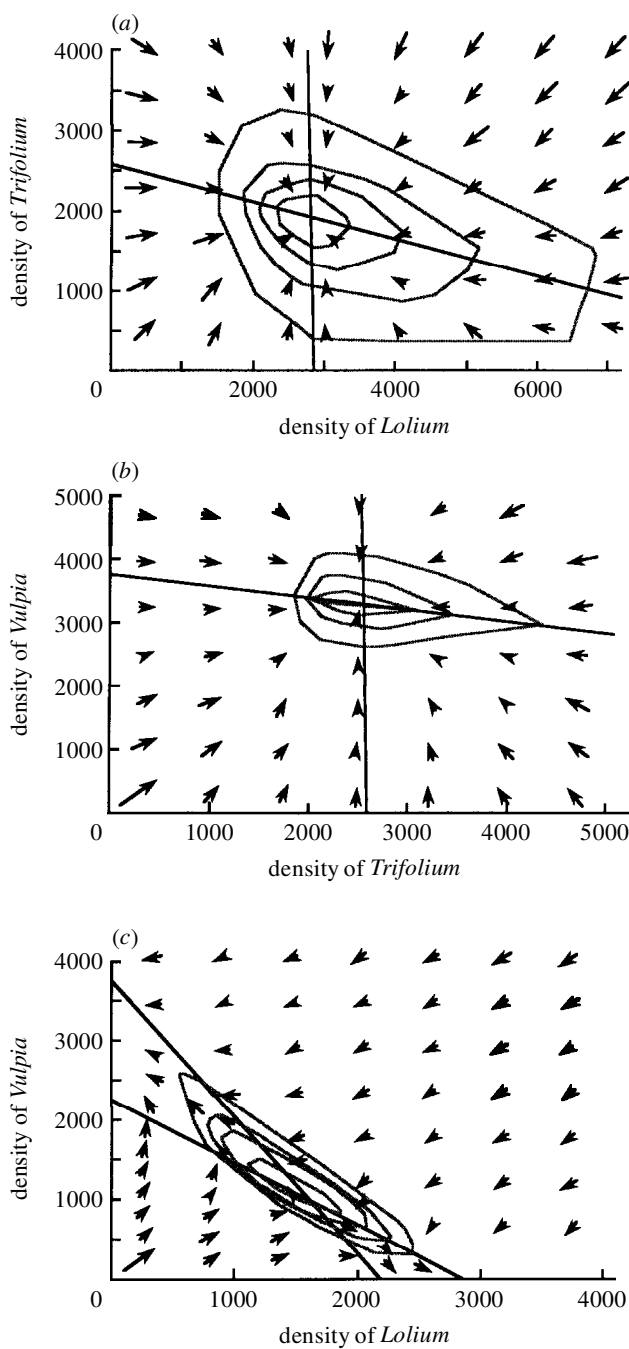


Figure 2. Phase-plane analysis of patterns of coexistence in pairwise mixtures of *L. rigidum*, *T. subterraneum* and *V. bromoides*. The solid lines show zero growth isoclines, while the arrows indicate the trajectory of the system from different initial combinations. The convex hull polygons represent 25, 50, 75 and 95% quantiles for the joint equilibrium.

we cannot narrow down the reasons for these effects. One clue as to the source of competitive effects is obtained by excluding *Vulpia* from the calculation of competitive effects. In this case, when the value of  $\alpha_j$  for the effect of *Vulpia* on *Lolium* is set to zero, so the net competitive effect is simply a function of intraspecific competition, the slope of the regression increases to a value of  $0.85 \pm 0.11$ , which is not statistically significantly different from unity. This would appear to indicate that the effect of *Vulpia* on the net population growth of *Lolium* occurs on some stage of the life cycle other than on mean plant performance.

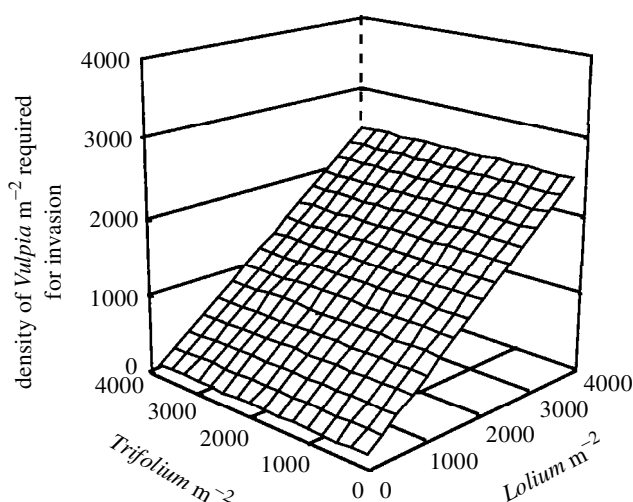


Figure 3. Effects of initial conditions on community structure. A critical density of *Vulpia* is required for invasion of the system.

### (c) Modelled dynamics and interactions

We explored the impacts of parameter error by determining the predicted equilibria in a constant environment. The 50, 75 and 95% confidence regions in figure 2 show that variability in the predictions of densities were generally confined to well within an order of magnitude, apart from the prediction of the density of *Trifolium* in combination with *Lolium*.

The interactions between the grasses and the legume are stable and essentially weak (figure 2*a,b*). The zero growth isoclines for these two pairs of species are nearly at right angles to each other, and densities at the joint equilibria are only marginally reduced relative to the monoculture equilibria. By contrast, the interaction between the two grasses is strong (figure 2*c*). In particular, since the *per capita* effects of interspecific competition are greater than those of intraspecific competition for interactions between these two species, the joint equilibrium of the two species is unstable and moves towards a monoculture of one or other of the species.

Owing to the unstable nature of the equilibrium between *Lolium* and *Vulpia*, the three-species equilibrium is unstable and the long-term composition of the community depends on the initial densities. As shown in figure 3, this means that there exists a critical threshold density of *Vulpia* that must be exceeded for invasion of a mixture of *Lolium* and *Trifolium*. Since the effect of changing the density of *Lolium* on this threshold is greater than the effect of varying the density of *Trifolium* (figure 3), the prediction from the equilibrium model is that a high enough density of *Lolium* should prevent invasion of the system by *Vulpia*. This, however, is based on analysis of the model in a constant environment.

When periodic droughts are incorporated into the system, the unstable nature of the equilibrium between *Lolium* and *Vulpia* has important consequences for community composition. Figure 4*a,b*, for example, contrasts the dynamics of two communities in which *Vulpia* invades from a high density (figure 4*a*) and a low density (figure 4*b*). When the environment is invariant, the system is eventually dominated by *Vulpia* in the former case, while

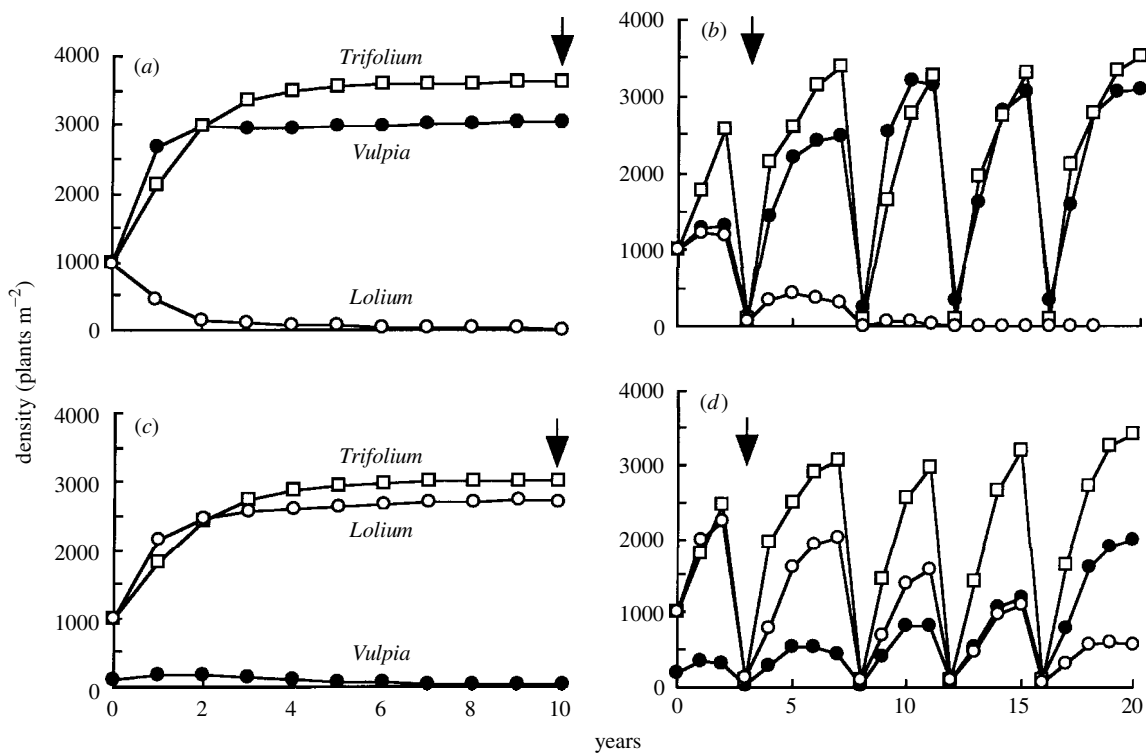


Figure 4. Effects of temporal variability and initial community composition on the invasion of *Vulpia* into mixtures of *Trifolium* and *Lolium*. Invasion in a stable environment (*a, b*); invasion when periodic droughts are applied (*c, d*). In (*a, c*) *Vulpia* is introduced at high densities, whereas it is introduced at low densities in (*b, d*). The arrows indicate points at which model sensitivity values were calculated (see table 4).

in the latter case it becomes dominated by *Lolium*. In contrast, when periodic droughts are applied, *Vulpia* is able to invade both communities (figure 4*c,d*). The invasion and dominance of *Vulpia* over *Lolium* is thus greatly facilitated by the occurrence of droughts.

More generally, figure 5*a* shows the mean density of *Vulpia* over 100 years (replicated 5000 times at each parameter combination) as a function of the initial density of *Vulpia* and the per annum probability of drought. Increasing the frequency of drought markedly increases the mean levels of *Vulpia*. In particular, as the per annum probability of drought approaches a level of 0.1–0.2, *Vulpia* is able to invade from even very low levels.

#### (d) Sensitivity of model predictions

To examine how parameter sensitivity varied with initial conditions and environmental variability we calculated the sensitivities for model parameters at the points indicated by arrows in figure 4. Parameter sensitivities (table 4) tended to be similar for drought and non-drought conditions, the main effect of drought being to decrease the sensitivities of the competition coefficients, except in the case of *Lolium* where sensitivity increased in the drought years at high initial densities of *Vulpia* or remained the same at low initial densities. The sensitivities of the model predictions to the *per capita* effects of *Vulpia* ( $\alpha_V$  and *Lolium* ( $\alpha_{iL}$ )) varied in proportion to their abundance. We also explored the effects of inclusion of a small reserve of dormant seed for the grasses, as well as analysis of the sensitivity of the model predictions to the seed bank of *Trifolium*. These sensitivities were found to be small, however (results not presented).

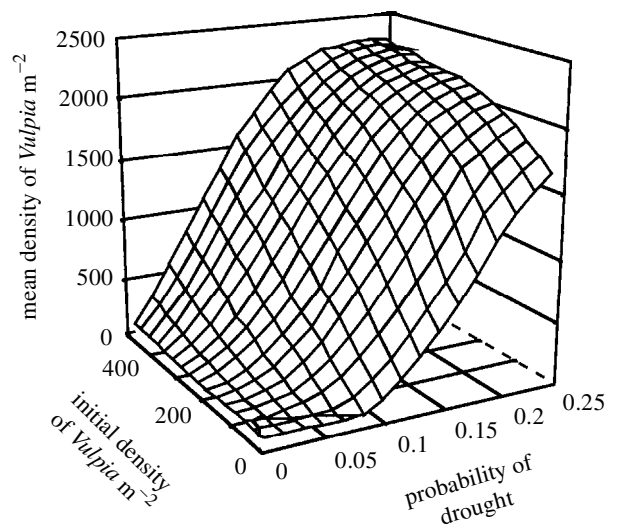


Figure 5. Effects of initial conditions and temporal variability on community structure through the invasion of stable mixtures of *Lolium* and *Trifolium* by *Vulpia*.

## 4. DISCUSSION

The main results to emerge from this analysis are that competition plays a key role in determining the composition of these communities, and that the outcome of competition is modulated by the long-term frequency of droughts. Furthermore, we predict that it is not only drought that could increase the probability of

Table 4. Sensitivity analysis of the model predictions in constant and varying environments

(Model sensitivity values were calculated at the points indicated by arrows in figure 4, corresponding to: high initial densities of *Vulpia* (a, b) and low initial densities of *Vulpia* (c, d), in constant conditions (a, c) or in a drought year (b, d).)

	$\lambda$	$\alpha_v$	$\alpha_T$	$\alpha_L$
(a) favourable conditions/high density of <i>Vulpia</i>				
<i>Vulpia</i>	1.000	0.842	0.122	0.015
<i>Trifolium</i>	0.905	0.035	0.835	0.003
<i>Lolium</i>	1.000	0.917	0.002	0.008
(b) drought conditions/high density of <i>Vulpia</i>				
<i>Vulpia</i>	1.000	0.332	0.106	0.541
<i>Trifolium</i>	0.914	0.015	0.756	0.110
<i>Lolium</i>	1.000	0.514	0.002	0.380
(c) favourable conditions/low density of <i>Vulpia</i>				
<i>Vulpia</i>	1.000	0.007	0.067	0.911
<i>Trifolium</i>	0.903	$4.133 \times 10^{-4}$	0.626	0.245
<i>Lolium</i>	1.000	0.015	0.002	0.879
(d) drought conditions/low density of <i>Vulpia</i>				
<i>Vulpia</i>	1.000	0.014	0.067	0.905
<i>Trifolium</i>	0.911	$7.919 \times 10^{-4}$	0.632	0.246
<i>Lolium</i>	1.000	0.029	0.002	0.865

communities becoming dominated by *Vulpia*. What happens is that *Vulpia* populations recover more rapidly following perturbation than the other species because *Vulpia* has a higher finite rate of population increase ( $\lambda$  in table 1). As a consequence the potential exists for a range of non-selective disturbances to increase the probability of *Vulpia* invasion. These could, for example, include the effects of overgrazing and non-specific herbicides. Such an emphasis on the impacts of severe negative conditions, rather than positive ones, relates to the fact that the abundance of populations in stochastic environments responds more to poor conditions than to very good conditions, since the relationship between geometric population growth and environmental conditions is highly nonlinear (e.g. Freckleton & Watkinson 1998).

It is commonly argued that the analysis of plant functional types is an appropriate framework with which to explore the impacts of climate variability and change on plant communities (e.g. Grime *et al.* 1997; Smith *et al.* 1997). Our results demonstrate that such a broad approach may be inadequate for many practical applications. The competition matrix that we generated (table 2) clearly defines two functional groups within the community: the legume component (*Trifolium*) and the annual grass component (*Lolium* and *Vulpia*). While this grouping is intuitive and indeed is often used (e.g. Hobbs 1997), for practical purposes (i.e. farm management) it would not be satisfactory to make predictions of community structure at this resolution, i.e. just at the level of broad species groups. In this system, it is critical to be able to predict which of the annual grasses occurs in the community since one of the species is a desirable component whereas the other is not.

The experimental design employed in this study has allowed us to produce the first phase-plane diagrams

illustrating the outcome of competition on the dynamics of a plant community in the field. It was not aimed at exploring competition in a mechanistic manner or to explicitly link population dynamics to resource competition and hence falls short of the strict criteria for the design of such experiments (e.g. Grover 1997, p. 71). Yet we are nevertheless able to make a number of statements concerning the mechanisms of competition between the species in this experiment and to go some way towards addressing the criticism that simple empirical approaches tell us little about how competition affects community dynamics (e.g. Tilman 1988). The comparison of the effects of competition on net population change and on mean plant performance (table 3) suggests that inter- and intraspecific interactions during the period of vegetative growth were important components of population growth for *Trifolium* and *Vulpia*. In contrast, only intraspecific effects during plant growth were important for *Lolium*, with interspecific effects on population change arising from interactions occurring at another stage in the life cycle. This could arise in a number of ways, such as inhibition of seedling emergence through the development of cover and altered red-to-far-red ratios, as has been suggested in the case of *Anisantha sterilis* (Lintell Smith *et al.* 1999) or even through allelopathic effects (An *et al.* 1997). Indeed simple models of allelopathic interactions predict the occurrence of founder effects (Durrett & Levin 1997).

While the analysis of long-term census data for the detection of intraspecific interactions (or intraspecific density dependence in the broadest sense) is common, albeit fraught with problems (Shenk *et al.* 1998; Freckleton *et al.* 2000; Rothery 1998), analyses of the dynamics of multispecies systems are less common. The analytical components of the work by Rees *et al.* (1996) and Law *et al.* (1997) have demonstrated how the principle of regressing rates of population change onto local population densities can be employed to analyse interactions and dynamics in multispecies plant populations. Importantly their analyses demonstrate how the spatial structure that develops naturally within plant populations may be used in lieu of manipulations. Indeed while the natural development of such spatial structure within plant communities may thwart attempts to detect or measure interspecific interactions using simple removal methods (Pacala 1997; Pacala & Levin 1997), regression methods are robust under these conditions (Freckleton & Watkinson 2000). The power of this approach is evidenced by the ability of the models to separate the patterns of competition and dynamics in the first year of the experiment from those in the later years. Indeed, experiments based on sown rather than naturally regenerating mixtures have suggested that competitive interactions between grasses and legumes are stronger (e.g. Willoughby 1954).

Apart from the variability arising from the establishment of the species during the first year of the experiment, the main source of temporal variability was the drought in 1993–1994. As shown in figure 1, droughts are an important characteristic of the climate of the region and their impacts on plant performance and long-term community dynamics can hardly be doubted. The importance of our analysis is that, while the equilibrium

between the two grasses that is predicted in a constant environment is unstable, and hence may make it appear unlikely that *Vulpia* will be able to invade established pastures, the invasion of *Vulpia* will be almost inevitable when droughts occur. While previous work has highlighted the importance of temporal variability on the finite rate of increase of annual weeds (Freckleton & Watkinson 1998) this analysis further demonstrates how temporal variability may then interact with the process of competition to determine abundance.

Despite the long interest and success of ecologists in analysing two species systems, studies of the dynamics of multispecies systems have been less common (Shorrocks *et al.* 1997). Our analysis has highlighted the power of simple demographic approaches for analysing the dynamics of multispecies communities in stochastic environments. We have for the first time been able to produce phase-plane diagrams illustrating Lotka–Volterra dynamics in the field. The combination of long-term data and the use of simple population models has allowed us to tease out components of population and community dynamics and to predict the impacts of changing climatic conditions on community composition.

We thank Birgitte Verbeek for help with the field experiment and Gordon Murray for supplying and discussing the weather data. We thank Bob May, Mark Rees, Bryan Shorrocks, Bill Sutherland and Katriona Shea for their comments on previous versions of this manuscript. The work was supported in part by Natural Environment Research Council grant GR3/11458 to A.R.W.

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