Non-manipulative estimates of competition coefficients in a montane grassland community

RICHARD LAW*, TOMÁŠ HERBEN† and ULF DIECKMANN‡

Wissenschaftskolleg zu Berlin, Wallotstrasse 19, D-14193 Berlin, Germany

Summary

1 A method is given for estimating competition coefficients in multispecies grassland communities without manipulation, using the natural turnover of individuals at a fine spatial scale. The method requires a detailed map of the spatial distribution of plants documented at several points in time, and uses non-linear regression of the local density of the plants on their densities in small neighbourhoods at a previous time.

2 The method is tested by generating realizations of two spatiotemporal stochastic processes for which the true parameter values are known. It is shown that non-linear regression successfully recovers the major features of the competition matrices.

3 The method is applied to a montane grassland dominated by four species of grass, for which spatial data on four plots are available for an 11-year period, and for which results of manipulation experiments are also available.

4 The results show that competitive interactions between species are as strong as interactions within species. There are strong asymmetries in the competition coefficients of species pairs, but little sign of species specificity. Intransitivities of the interaction matrix are not evident. The competition coefficients obtained show a good measure of agreement with the results of manipulation experiments that have been carried out on the community.

5 It is argued that non-manipulative methods of the kind described here hold a useful key to understanding interactions in plant communities.

Keywords: competition coefficient, grassland, plant community, spatial pattern, spatiotemporal dynamics

Journal of Ecology (1997) **85**, 505–517

Introduction

Interactions between species lie at the heart of community ecology. It is through them that species are coupled to one another, and their dynamics become more than the sum of independent processes operating within species. A fundamental problem for community ecologists has been the difficulty in measuring how strong these interactions are.

This problem applies as much to groups of plants living together as it does to other taxa (Law & Watkinson 1989), and has led to three kinds of research programme in plant ecology. One approach has been to measure surrogate properties that might indicate how one plant species affects another. These may be either plant traits deemed to be important for the outcome of competition such as biomass (Gaudet & Keddy 1988), or properties that might stem from competitive interactions such as spatial patterns of plant species (Wilson, Gitay & Agnew 1987; see also Lepš 1995). A second approach has been to try to estimate the strength of interactions from the response of species to experimental perturbations of communities (Aarssen & Epp 1990; Goldberg & Barton 1992). While such manipulation experiments have much to recommend them, they are hard to carry out in a controlled manner (Wilson 1995). A third approach has been to measure competitive interactions of subsets of species grown under artificial conditions (*ex situ* experiments). Illuminating though such experiments are, it is inherently difficult to assess how relevant they are to the field, because of the different culture conditions under which the plants are grown (Grace, Guntenspergen & Keough 1993).

*Present address: Department of Biology, University of York, PO Box 373, York YO1 5YW, UK.

†Present address: Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic.

‡Present address: International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria.

In this paper we suggest an alternative way of estimating the interaction strengths in grassland communities without manipulation, simply using the natural turnover of individuals at a fine spatial scale. This is motivated by the knowledge that, in these communities, a single physical location may be visited by many if not all the plant species in the community, even though the macroscopic state of the community may appear to change little (van der Maarel & Sykes 1993). If the dynamics are followed through time with a sufficiently detailed spatial resolution, the fine-scale turnover as one species replaces another should become measurable. Analysis of the dynamics of plant communities using this approach has been tried before (Watt 1947; Thórhalsdóttir 1990), but we know of only one previous analysis leading to quantitative estimates of interaction strengths for models of community dynamics (Rees, Grubb & Kelly 1996). We use non-linear regression for estimation, first demonstrating that the method can recover the interaction structure of artificially generated spatiotemporal data. The method differs from that of Freeman & Emlen (1995), which measures yield and local densities at a single point in time and obtains estimates of competition coefficients from regression of the former on the latter.

To make use of fine-scale turnover, one needs a detailed map of the spatial distribution of each species and how this distribution changes through time. Data of this kind, from a montane grassland in North Bohemia (Herben *et al.* 1993a), form the basis of this paper. The use of this community also has the advantage that it has been the subject of certain manipulation experiments (Herben *et al.* 1997), from which independent qualitative checks on the estimated interactions can be made. We show that there is a good measure of agreement between our non-manipulative estimates of interaction strengths and results of the manipulation experiments, and that the interactions between species are highly asymmetric and as strong as those within species.

Methods

FIELD SITE AND DATA

The study site was located in a montane grassland in the Krkonoše Mountains in the northern part of the Czech Republic (Severka settlement, *c.* 3 km northwest of Pec pod Sněžkou, latitude 50°41′42″N, longitude 15°42′25″E, altitude approximately 1100 m). The whole area has a harsh climate; mean temperature in the warmest month (July) was 13.6 °C (1988), 13.7 °C (1989) at the nearby climatic station (Pec pod Sněžkou, *c.* 900 m a.s.l.). There is a long winter with thick snow cover at the study site, usually lasting from November until the end of April. The grassland was established in about the 17th century and has a long history of management by mowing (Krahulec 1990).

The traditional management of the meadows before the study began consisted of mowing once a year in the second half of July and occasional manuring.

Four permanent plots of 50×50 cm were established at the site in 1984–85. The plots were marked by vertical plastic tubes inserted to a depth of 20 cm. A sampling frame was used, the position being set by fitting steel rods into these plastic tubes. This allowed the frame to be fitted every year with precision better than 0.5 cm. In these plots, the number of tillers of each species within a grid of 15×15 cells (each 3.3×3.3 cm) was counted in mid-July every year. Here we use data up to 1995.

To simulate traditional management, the plots and their surroundings were clipped to a height of 1 cm after each recording. Since the reported study was part of a larger experimental study of grasslands, two plots (S1 and S3) were manured in autumn 1985 and again in 1989 (cow manure of pH = 7.7, the traditional treatment for these grasslands). This addition of nutrients is equivalent to total N = 17, NO_3-N = 0.2, NH_4-N = 3.8, PO_4-P = 2.4 (all values in g m^{-2}). However, the differences between the manured and non-manured plots are minor, both at the large scale and at the fine scale (V. Hadincová, T. Herben & F. Krahulec, unpublished data), and here we treat them as replicates.

There were only four principal species in the plots: *Anthoxanthum alpinum* Á. Löve and D. Löve, *Deschampsia flexuosa* (L.) Trin., *Festuca rubra* L., and *Nardus stricta* L. These species form the basis of the analysis in this paper, and we use subscripts A, D, F and N, respectively, to refer to them in the equations below. Other species occurring at a much lower abundance were *Polygonum bistorta* L., *Deschampsia cespitosa* (L.) Beauv., *Vaccinium myrtillus* L., *Potentilla aurea* L., *Agrostis capillaris* L., *Campanula bohemica* Hruby, *Juncus filiformis* L. and *Solidago virgaurea* L. ssp. *alpestris* (W. and K.) Hayek. The number of modules (leaves) of most frequent species of these (*Polygonum*) in all four plots was less than one-sixth of that of the least frequent species (*Festuca*) in our analysis. Although the system was species-poor at the large scale, the species coexisted at the fine scale, with two to four species present per 11 cm^2 cell. According to the Braun–Blanquet classification of the Krkonoše grasslands (Krahulec 1990), the study area should be classified as belonging to the *Sileno–Nardetum pleurozietosum* (*Nardo–Agrostion, Nardetalia*). Figure 1 illustrates the dynamics of the spatial pattern of the four principal species in one of the plots.

INDIVIDUAL-BASED STOCHASTIC PROCESS

Here we describe an individual-based stochastic model, the parameters of which include the interaction strengths we wished to estimate.

The model assumes that space is apportioned into discrete cells in a lattice; this is dictated by the way in
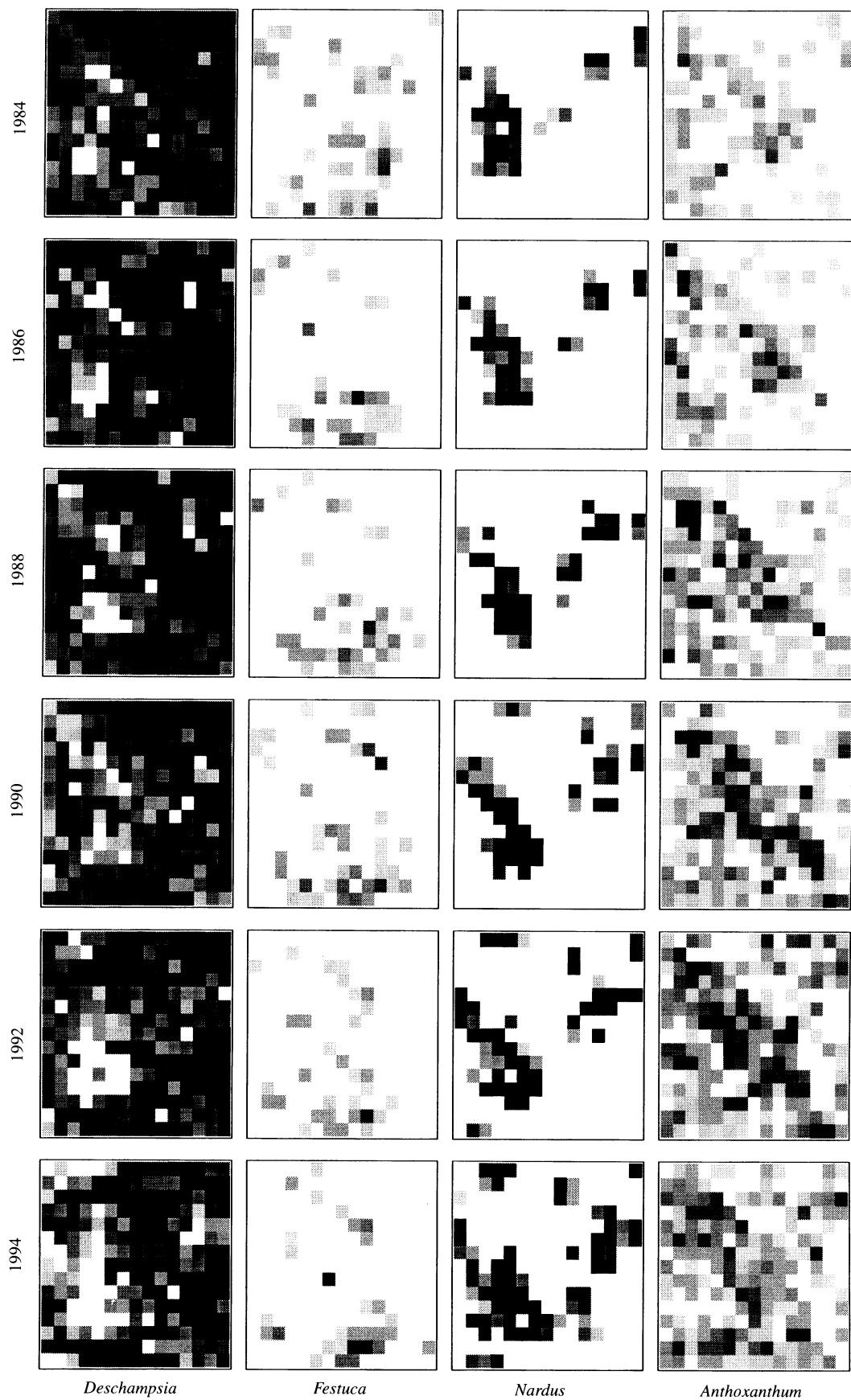
Fig. 1. Observed spatial patterns of four grass species from a single plot in a montane grassland, from 1984 to 1994; patterns are shown for alternate years. The depth of shading of cells is proportional to the number of tillers of a species (white indicates absence of the species). The species are shown in separate columns; a row shows the spatial pattern of all species at a single time.
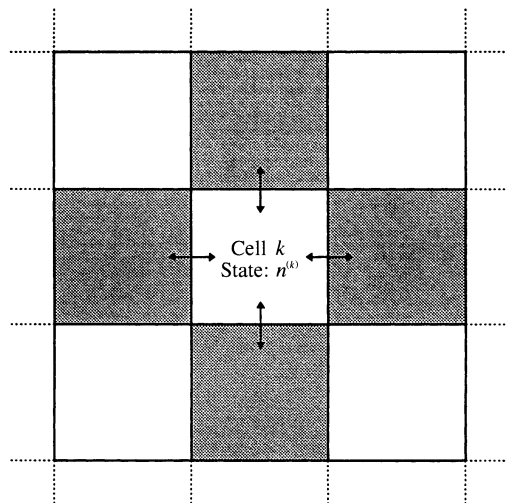
Fig. 2. Cell k, and its set of neighbours $S^{(k)}$ shown as shaded. The state of cell k is given by the number of tillers of each species it contains $n^{(k)}$. Coupling of cells comes about through movement of tillers between cell k and its neighbours in the model. Coupling of species is due to dependence of daughter tiller production in cell k on $n^{(k)}$.

which the data were collected, and is clearly no more than an approximation to the underlying process, which must be spatially continuous. The primary unit on which the analysis is based is a focal cell, k, and its set of neighbouring cells $S^{(k)}$; $S^{(k)}$ is taken to be the north, east, south and west neighbouring cells of k (Fig. 2). The four-cell neighbourhood is used because, given the small distances moved by tillers of the species in this study, movement across an edge is much more likely than movement across a corner into a diagonal neighbour cell. Cell k takes discrete states determined by the number of tillers of each of the four abundant grass species it contains; we write the number of tillers as the vector $n^{(k)} = (n_A^{(k)}, n_D^{(k)}, n_F^{(k)}, n_N^{(k)})$, using the letters A, D, F, N to denote species. The corresponding vector for a neighbour cell is written $n^{(l)}$, and the vectors of all cells in the neighbourhood of k are collected together into a set $N^{(k)}$.

The primary events acting on tillers are births, deaths and movements. *Births* bring about a coupling of species through a dependence of tillering on the number (and identity) of neighbour tillers; this is in keeping with the observation that interactions between plants tend to have much more effect on tiller births than deaths (e.g. Jónsdóttir 1991; Duralia & Reader 1993; V. Hadincová, T. Herben & F. Krahulec, unpublished data on *Festuca rubra* from the studied community). These interactions are assumed to be sufficiently localized for the dependence to apply only within cells. For cell k, the per capita number of daughter tillers $b_i^{(k)}$ produced by species i is assumed to be a Poisson-distributed random variable with mean:

$$b_i^{(k)} = c_i \cdot \exp\left(\sum_{j=A,D,F,N} a_{ij} \cdot n_j^{(k)}\right), \qquad \text{eqn 1}$$

and similarly for cells l in the neighbourhood of k. Here parameter c_i is the mean number of daughter tillers produced by a parent tiller in the absence of any other tillers, and a_{ij} is a species-specific weighting for the effect of a tiller of species j on this number. A negative value of a_{ij} implies that species j reduces tillering by species i. It is through this weighting that one species affects another, and a_{ij} values for species pairs can thus be thought of as interaction coefficients.

Regarding *deaths*, tillers are assumed to have a survival probability s_i from one year to the next that is independent of age and neighbourhood. *Movement* of tillers across the boundary of cell k and its four neighbouring cells induces a local coupling of cells, and deals with most aspects of the dispersion process in so far as it is tiller-dependent. The probability m_i that a tiller of species i moves out of one cell and into another from one year to the next is taken to be independent of tiller state and neighbourhood. Both parent and daughter tillers are known to change location as they grow. We assume that tillers are the major participants in movement on the assumption that, even in *Anthoxanthum*, the species showing the greatest recruitment from seed, establishment did not exceed 10 plants per 225 cells (V. Hadincová, T. Herben & F. Krahulec, unpublished results).

To describe the individual-based community dynamics, the lattice of cells is updated in three steps. First each tiller on the lattice gives birth to a random number of daughter tillers using equation 1. Second, each tiller (mother and daughter) survives with probability s_i. Third, each surviving tiller moves with probability m_i to a neighbour cell, the choice of cell being random with a uniform distribution. The order in which deaths and movements occur is immaterial for the dynamics. A complete cycle of births, deaths and movements constitutes a single iteration of 1 year. With this information, an individual-based stochastic model for the community is fully specified.

PARAMETER ESTIMATION BY NON-LINEAR REGRESSION

The expected number $\tilde{n}_i'^{(k)}$ of tillers of species i in the cell k in year $t+1$ can be written as a function $f_i(n^{(k)}, N^{(k)})$ of the states $n^{(k)}$ and $N^{(k)}$ in year t:

$$\tilde{n}_i'^{(k)} = f_i(n^{(k)}, N^{(k)}) =$$

$$s_i \cdot \left(\underbrace{(1-m_i) \cdot n_i^{(k)} \cdot (1+b_i^{(k)})}_{(a)} \right.$$

$$\left. + \underbrace{\frac{m_i}{4} \cdot \sum_{l \in S^{(k)}} n_i^{(l)} \cdot (1+b_i^{(l)})}_{(b)} \right). \qquad \text{eqn 2}$$

Part (a) gives the contribution due to tillering within cell k and includes those tillers that do not move from this cell to one of the neighbours. Specifically, there
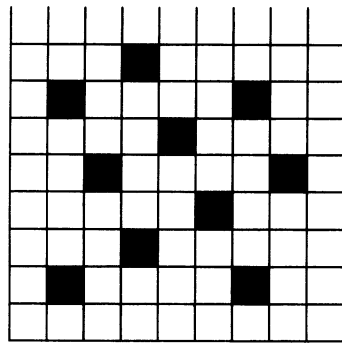
Fig. 3. Tiling of cells used for non-linear regression; cells chosen for analysis are shown as black. The starting position was displaced one cell to the right in successive years, so that each cell was revisited for sampling only after 5 years.

are $n_i^{(k)}$ tillers of species i in cell k at census in year t; this is multiplied by $(1 + b_i^{(k)})$ to get the number of tillers after reproduction, and by $s_i \cdot (1 - m_i)$ to get the number remaining in cell k after mortality and movement across the cell boundary have taken place. Part (b) deals with tiller production in the neighbourhood of cell k, followed by movement into cell k, and is obtained as follows. At the time of census in year t, there are $n_i^{(l)}$ tillers of species i in neighbourhood cell l; this is multiplied by $(1 + b_i^{(l)})$ to get the number of tillers after reproduction, and by $s_i \cdot m_i$ to get the proportion that move out of cell l and survive. Only a quarter of those moving out of cell l are expected to move across the boundary into cell k; the summation is needed to allow for the four neighbour cells, all of which contribute to movement into cell k. In writing equation 2, we assume that the dependence of tillering on neighbours is approximated by the number and identity of these neighbours at the time of census; the equation is then specified by $n^{(k)}$ and $N^{(k)}$ in year t, and the estimation of parameters below can proceed separately for each species.

Spatially extended time series, such as that in Fig. 1, are rich in information about local dynamic processes, and can be used to estimate the parameters of equations 1 and 2. The data used here, based on four plots, 225 cells per plot and 11 time intervals (10 for plot 3), provide 9675 cells on which to work. However, this set needs to be restricted in several ways. First, boundary cells have to be excluded because their neighbourhoods are incomplete. Second, since it is only

local dynamic processes that are dealt with, cell k is included only if there is at least one tiller in this cell or its neighbourhood or both at time t. Third, the spatial proximity of neighbour cells makes it likely that they are not statistically independent; to make these errors as small as possible, we have adopted the tiling shown in Fig. 3. This arrangement of cells ensures a minimum distance of over 7 cm between centre points of the cells used; it also means that, at any time, neighbour cells are being used for only one focal cell. By rotating the starting point in successive years, the same cell is revisited only after 5 years, a time lag longer than that known to give significant autocorrelations in this community (Herben, During & Krahulec 1995). Table 1 gives the number of cells that remain available for parameter estimation for each species. The amount of spatial information we are left with is insufficient to estimate parameters separately for each year and, for this reason, the data are pooled over the time period 1984–95 and a single analysis is carried out.

There are seven parameters in equations 1 and 2 for each species. One of them, s_i, is not estimated. This is because it is likely to be strongly correlated with c_i in the estimation procedure, thwarting attempts to estimate both parameters, and also because estimates of s_i are available from other research on this grassland (T. Herben, unpublished results) (Table 1). The remaining six, denoted by the vector $\boldsymbol{p}_i = (a_{iA}, a_{iD}, a_{iF}, a_{iN}, c_i, m_i)$, are estimated by non-linear regression (Draper & Smith 1988). This involves iterative adjustment of $\boldsymbol{p}_i$ until the function:

$$\sum_k (F(n_i'^{(k)}) - F(\tilde{n}_i'^{(k)}; \boldsymbol{p}_i))^2$$

reaches a local minimum. Here $n_i'^{(k)}$ is the observed number of tillers of species i at $t + 1$ and $\tilde{n}_i'^{(k)}$ is the number expected from equation 2. The function F is defined below. Notice that the regression is on the number at $t + 1$, rather than on the ratio $n_i'^{(k)}/n_i^{(k)}$, because the latter would lead to a reciprocal relationship if $n_i'^{(k)}$ were a random variable independent of $n_i^{(k)}$; in other words, a relationship would appear where none actually existed.

The analysis assumes that errors are independent and come from a normal distribution with the standard deviation independent of the mean. Preliminary

Table 1. Information on the species. Tiller biomasses are given as means, taken from V. Hadincová, T. Herben & F. Krahulec, (unpublished data)

Species	Number of cells sampled	Survival ratio (s_i)	Tiller biomass	
			Mean (g)	(SE)
Anthoxanthum	1319	0.2	0.018	(0.001)
Deschampsia	1439	0.7	0.007	(0.0005)
Festuca	1033	0.3	0.021	(0.001)
Nardus	762	0.7	0.014	(0.0007)

analysis indicated the existence of a power relationship $\sigma = a \cdot \mu^b$ between the mean μ and standard deviation σ of the dependent variable. The transformation $F(x) = x^{(1-b)}/(a(1-b))$ largely removes this, and we therefore used this transformation, obtaining the parameters a and b by prior analysis of the relationship between the mean and standard deviation based on regression with untransformed data. We checked for independence of the errors by analysis of their spatial and temporal correlations; a positive correlation over short distances could not be removed in *Anthoxanthum* and *Deschampsia*; otherwise the residuals were close to independent through time and space. Parameter estimates can be rather sensitive to the presence of outliers with large residuals. To see how serious a problem this was, we ran the regression analysis on the full data and then repeated the analysis a number of times, removing an increasing number of the most extreme points. It was evident that the estimates were affected by these points, but that the sensitivity to outliers soon decreased; by excluding 5% of the most extreme points, the estimates were made relatively stable.

Approximate confidence intervals for the parameter estimates were constructed using a likelihood inversion technique proposed by Cook & Weisberg (1990); this method accounts for asymmetry in the shape of the function being minimized. By following the contours of this function in the direction of one parameter while minimizing it for all other parameters, the method reflects the actual, often asymmetric, uncertainties in a non-linear regression. In consequence, the lower and upper confidence intervals are of different width and are computed separately. The analysis was carried out using the statistical package BMDP (Dixon *et al.* 1990). As gradient descent is local for non-linear regression, choice of starting conditions has to be made with care; we used values known to be in the correct range from other research on the community, and checked for robustness of the estimated parameter values by testing other starting conditions as well.

TEST OF THE NON-LINEAR REGRESSION

As a simple check on the capacity of the non-linear regression method to recover the interaction strengths, we generated some realizations of the stochastic model with known values of parameters s_i, a_{i1}, a_{i2}, a_{i3}, a_{i4}, m_i, c_i, for $i = A, D, F, N$. These provided time series of spatial patterns, analogous to those in Fig. 1, to which the non-linear regression could be applied; the true and estimated values could then be compared. Time series 11 years long were used, with a lattice size of 30×30 cells, so that the amount of information would be similar to that from the field site (four plots of 15×15 cells). Before extracting a time series, we allowed the realizations to run for about 50 iterations from an initially uniform spatial distribution, so that

the data would be relatively unaffected by an arbitrary initial layout. Two kinds of interaction matrices were used, with interspecific competition: (i) absent, and (ii) weak. For each kind of community, we carried out 10 independent realizations of the stochastic process.

Results

Our tests on the non-linear regression method show that it successfully recovers the underlying structure of interaction matrices of artificial time series (Table 2). The overall structure of the matrices of competition coefficients are clearly evident when the coefficients are estimated from the time series by non-linear regression. Some differences are to be expected, because the time series used are no more than stochastic realizations of the ecological model; but the ranking of estimated coefficients is correct in all cases. The method is less successful in recovering c_i and m_i; these appear to be systematically underestimated.

In view of the positive results on interactions above, we applied the regression method to investigate how the species interact in the montane grassland. The full regression model explains a high proportion of the variation in the observed number of tillers of all species at year $t + 1$ (Table 3); the highest proportion is explained for *Deschampsia*, the lowest for *Anthoxanthum*. Much of this variation is accounted for simply in terms of the number of tillers present at year t; obviously cells with small numbers of species i in year t are also likely to have small numbers at $t + 1$. For comparison, we have included regression analysis on some other models in which interactions are progressively constrained and eliminated. The variation explained by effects of conspecific and heterospecific neighbours on tiller production is much smaller (1–3.5%), the overall effects of heterospecific neighbours accounting for an additional 1–2% of the total variation (highest in *Festuca*, lowest in *Nardus*), the additional effect on the fit of making the interactions species-specific being negligible (highest in *Festuca*: 1.4%).

Despite the small amount of variation explained, the neighbourhood effects on tiller production may be deemed significant, since the approximate 95% confidence intervals of the interaction coefficients do not span zero in the majority of cases (Table 4). With one exception, statistically significant coefficients are negative, indicating a prevalence of competition. Since the exception, a_{NF}, has a lower limit very close to zero, the community can be said to be essentially competitive.

Comparison of competition coefficients along the ith row of Table 4 shows how the coefficients of species i depend on the associated species. Corresponding to the lack of species-specificity noted above, there is a broad overlap of confidence intervals for the coefficients of *Deschampsia* with heterospecific neighbours. The same applies to *Anthoxanthum*, where the

Table 2. Survival probabilities (s_i), mean daughter tiller production in absence of neighbours (c_i), mobilities (m_i) and interaction coefficients (a_{ij}) for two kinds of community with contrasting patterns of interspecific competition. (a) True parameter values used to generate realizations of a stochastic process. (b) Mean of parameter values estimated by non-linear regression on 10 realizations of the stochastic process

Species (i)	s_i	c_i	m_i	a_{i1}	a_{i2}	a_{i3}	a_{i4}
(a) *True parameter values*							
Interspecific competition absent							
1	0.3	4.0	0.2	−0.1	0.0	0.0	0.0
2	0.3	4.5	0.2	0.0	−0.1	0.0	0.0
3	0.3	5.0	0.2	0.0	0.0	−0.1	0.0
4	0.3	5.5	0.2	0.0	0.0	0.0	−0.1
Interspecific competition weak							
1	0.5	4.0	0.2	−0.1	−0.05	−0.05	−0.05
2	0.5	4.5	0.2	−0.05	−0.1	−0.05	−0.05
3	0.5	5.0	0.2	−0.05	−0.05	−0.1	−0.05
4	0.5	5.5	0.2	−0.05	−0.05	−0.05	−0.1
(b) *Estimated parameter values*							
Interspecific competition absent							
1		3.56	0.13	−0.099	0.004	0.000	0.000
2		4.08	0.15	0.002	−0.098	0.000	0.001
3		4.76	0.14	0.001	0.001	−0.103	0.001
4		5.40	0.17	−0.000	−0.002	0.000	−0.100
Interspecific competition weak							
1		3.79	0.10	−0.075	−0.071	−0.062	−0.063
2		4.32	0.15	−0.050	−0.097	−0.053	−0.056
3		4.74	0.18	−0.046	−0.046	−0.098	−0.054
4		5.12	0.20	−0.052	−0.048	−0.050	−0.096

Table 3. Coefficients of determination for different models of tiller birth processes. The models are based on equation 2 with conditions set on parameters as specified below. All parameters were estimated by non-linear regression

Model	Anthoxanthum	Deschampsia	Festuca	Nardus
Full species-specific model	0.561	0.691	0.566	0.633
(a) Competition of heterospecifics equal	0.559	0.690	0.552	0.625
(b) Competition of all species equal	0.559	0.683	0.551	0.620
(c) Only intraspecific competition	0.548	0.677	0.545	0.625
(d) No competition	0.547	0.676	0.544	0.602

The models are as follows:
(a) $a_{ij} = a_{ik}$, for $j, k \neq i$ and $i, j, k = A, D, F, N$;
(b) $a_{ij} = a_{ik}$, for $i, j, k = A, D, F, N$;
(c) $a_{ij} = 0$, for $j \neq i$ and $i, j = A, D, F, N$;
(d) $a_{ij} = 0$, for $i, j = A, D, F, N$.

overlap includes the coefficient with conspecifics as well. But *Festuca* and *Nardus* show slight signs of specificity, since the confidence intervals of a_{FN} and a_{NA} are disjunct from the intervals for the remaining heterospecific coefficients.

The competition coefficients contain information that cannot be explained fully in terms of tiller biomasses (Table 1). *Deschampsia*, which has the lowest tiller biomass, does have consistently small effects on the other species (Fig. 4). And four of the five large competition coefficients apply to a larger species interacting with a smaller one. But the coefficients for *Festuca* and *Deschampsia*, the two species with smallest and largest tiller biomasses, cannot be dis-

tinguished when in association with *Nardus*. One might also expect some deleterious response of *Nardus* to *Festuca*, but the effect is either zero or marginally beneficial.

The overall structure of the matrix of competition coefficients has several obvious features (Table 4). First, there is no strong indication of diagonal dominance; in other words, it is not the case that intraspecific competition is generally greater than interspecific competition. For example, *Deschampsia* is more strongly affected by all kinds of heterospecific neighbours than it is by conspecifics, *Festuca* is more strongly affected by *Nardus*, and *Nardus* is more strongly affected by *Anthoxanthum*. Secondly, the matrix is

Table 4. Results of regression analysis. Estimated values of parameters are shown in bold. The two rows following each estimate give approximate lower and upper 95% confidence limits of the estimate. Where these limits span zero, the estimate is shown in parentheses

Species (i)	a_{iA}	a_{iD}	a_{iF}	a_{iN}	c_i	m_i
Anthoxanthum	**−0.031**	**−0.033**	**(−0.015)**	**−0.019**	**4.889**	**0.156**
	−0.042	−0.042	−0.038	−0.031	3.972	0.119
	−0.021	−0.025	0.005	−0.009	5.985	0.198
Deschampsia	**−0.134**	**−0.037**	**−0.243**	**−0.178**	**0.983**	**0.358**
	−0.247	−0.044	−0.478	−0.790	0.697	0.311
	−0.056	−0.031	−0.117	−0.062	1.358	0.406
Festuca	**(−0.008)**	**(0.000)**	**−0.023**	**−0.135**	**2.481**	**0.066**
	−0.043	−0.011	−0.032	−0.281	1.971	0.042
	0.015	0.009	−0.015	−0.070	3.100	0.095
Nardus	**−0.151**	**(0.014)**	**0.068**	**−0.036**	**0.950**	**0.035**
	−0.311	−0.013	0.008	−0.045	0.625	0.018
	−0.045	0.030	0.112	−0.028	1.400	0.057
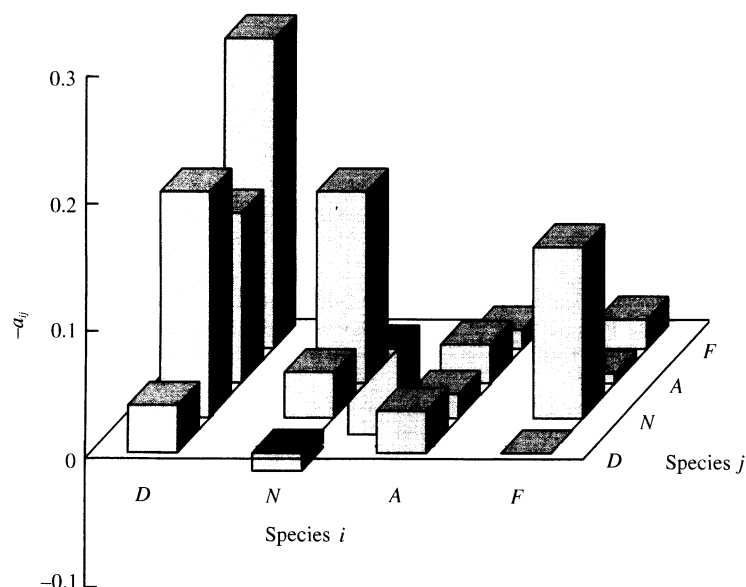
Fig. 4. Relationship of competition coefficients to tiller biomasses of species. The species are ranked in order of increasing biomass in each direction.

highly asymmetric; taking the six pairs of interaction coefficients (a_{ij}, a_{ji}), there are five in which one species has a much more negative coefficient than the other; the exception is the *Anthoxanthum–Festuca* interaction, where neither coefficient is significantly different from zero. Thirdly, there is no clear indication of a non-transitive relationship that would cause the species to replace one another in a cyclic manner.

Discussion

COMPARISON WITH MANIPULATION EXPERIMENTS

The montane grassland on which this study is based has also been the subject of certain manipulation experiments. Results of these experiments can be used to provide an independent assessment of the interaction strengths estimated by the non-manipulative method described above, to the qualitative level of presence or absence of interactions.

The manipulation experiments have been of two kinds: (i) a removal experiment, involving removal of one species at a time, followed by observation of fine-scale reinvasion of the cleared area by other species (Herben *et al.* 1997); (ii) an implant experiment, where individual tillers of *Festuca* are introduced into different neighbourhoods and growth and tillering of these implants are compared (V. Hadincová, T. Herben & F. Krahulec, unpublished results). Table 5 gives a summary of the results of the manipulation experiments. There is good agreement between the

Table 5. Overview of species interactions determined by manipulation experiments at the study site (Herben *et al.* 1997; V. Hadincová, T. Herben & F. Krahulec, unpublished results). R, removal experiment; I, implant experiment; −, negative effect; +, positive effect; 0, no effect

		Neighbour species			
		Anthoxanthum	*Deschampsia*	*Festuca*	*Nardus*
Affected species:					
Anthoxanthum	R	·	−	+	0
Deschampsia	R	−	·	−	−
Festuca	R	0	−	·	0
Festuca	I	0	0	·	−
Nardus	R	−	0	0	·

qualitative results of manipulations and the signs of the interactions estimated by non-linear regression. Comparing Tables 4 and 5 it can be seen that, of the seven significant negative effects found by regression, six are negative in at least one manipulation experiment. The odd one out is a_{AN}, where no response in *Anthoxanthum* could be observed following removal of *Nardus*; the competition coefficient estimated by non-linear regression is particularly small in this instance. Of the four coefficients found by regression to be not significantly different from zero, no effect of manipulation was observed in three cases; the other coefficient is a_{AF}, where there is some evidence from the removal experiment that *Festuca* is beneficial to *Anthoxanthum*. This leaves one coefficient, a_{NF}, found to be positive by regression, that is zero in the manipulation experiment.

Manipulation experiments have their own drawbacks (Wilson 1995) and cannot be taken as an absolute standard against which to test other methods of estimating interactions. But the measure of agreement between the two methods is great enough to give some confidence that they are uncovering similar information about the community. The regression method does evidently have some power to reveal the interactions in the grassland.

COMPARISON WITH COMPETITION INFERRED FROM PLANT TRAITS

Alternative methods of estimating interaction strengths using surrogate variables such as tiller biomass do not look promising. While some interactions appear to be correlated with biomass, others do not, and it would not be possible to reconstruct the competition matrix from knowledge of the tiller biomass alone. This is in contrast to findings of other studies (Gaudet & Keddy 1988, 1995; Goldberg & Landa 1991), which were able to identify correlates of competitive performance determined in *ex situ* experiments. However, these experiments compared species from different communities, and covered a larger range of biomasses than our study, where differences between species are rather small (Goldberg & Werner 1983;

Silvertown & Dale 1991). Competition remains important here, but less readily attributable to obvious morphological features such as tiller biomass.

STRUCTURE OF COMPETITIVE INTERACTIONS

The competitive interactions determined by the non-manipulative method yield an interaction matrix with properties well in line with those obtained elsewhere. These include (i) lack of diagonal dominance, (ii) asymmetries in pair-wise competition, and (iii) transitive competitive interactions.

Diagonal dominance of the interaction matrix would promote coexistence of species; in the extreme, when all off-diagonal terms are zero, the species would be independent of one another and limited entirely by intraspecific interactions. Yet in all but one of the species, intraspecific effects are weaker than interspecific ones; *Anthoxanthum*, in which all the confidence intervals are overlapping, is the odd one out. This finding fits into the pattern observed in the few other studies that have measured both intra- and interspecific competition (reviewed by Goldberg & Barton 1992), although matters appear to be rather different in a recent study of sand-dune annual plants (Rees *et al.* 1996).

A caveat to keep in mind about the estimated self-limitation terms is that the model (equation 2) assumes that conspecific tillers can be treated as independent. This simplifies a complex process in which clonal fragments of several tillers may remain for some time, operating as a unit with internal density regulation (Hutchings & Barkham 1986; de Kroon 1993). Ideally, the self-limitation terms would reflect two different dynamic processes: (i) density regulation within a clonal fragment, and (ii) competition between independent clonal fragments of the same species, and it is possible that the estimated intraspecific interactions would be modified if these details of clonal growth were incorporated. In a neatly designed experiment, de Kroon, Hara & Kwant (1992) showed that the effects of the two processes can be similar; but the differences themselves were species dependent,

which makes the generalization of their finding rather difficult.

Our study, like most others on plant competition, shows strong asymmetries in pair-wise competitive interactions (*e.g.* Keddy & Shipley 1989; Silvertown, Lines & Dale 1994). Such asymmetries have often been ascribed to differences in plant size (Silvertown & Dale 1991). But, as noted above, the structure of our competition matrix cannot be fully explained in terms of differences in tiller biomass. This is in line with the finding of Grace and his coworkers (Grace, Keough & Guntenspergen 1992; Grace *et al.* 1993), who found that the structure of several competition matrices persisted even after the size effects had been reduced by a refined analysis.

It appears from the competition matrix that the community is transitive; intransitivity, a tendency for one species to replace another in a cyclic sequence, is not evident. Intransitivity has been of longstanding interest to plant ecologists as a mechanism that could promote coexistence of species, since it prevents a community from becoming dominated by some small subset of species (Watt 1947, 1955; Gimingham 1988; Remmert 1991; Hendry & McGlade 1995). However, recent experimental studies on grassland communities, in keeping with our own result, have only been able to demonstrate transitive relationships (Thórhalsdóttir 1990; Silvertown *et al.* 1994; Turkington 1994).

The interaction matrix does not, on its own, provide insight into the combinations of species that persist in the long term. One cannot simply treat the matrix as though it applies to a non-spatial model, as this would be to ignore the spatial structure that develops in the community. A spatiotemporal model is needed that captures the spatial structure and how this structure changes through time. Our preliminary computations suggest that such a model would not permit coexistence of the species, suggesting that the community is in a process of change. This will be the subject of further investigations.

LIMITATIONS OF THE APPROACH

The analysis inevitably rests on certain assumptions; these may affect the parameter estimates, and it is important that they are made explicit. The assumptions are of two kinds: (i) those concerned with the ecological model (equation 2), and (ii) those to do with statistical methods involved in parameter estimation.

Three assumptions about the ecological model need to be stressed. First, the model assumes that tillers within species are independent, thereby ignoring any clonal integration of tillers that might take place. To deal with such integration would need a much more complex state-dependent model, giving rise to many more parameters none of which could be estimated at present. But it is important to appreciate that the assumption may affect the estimates of self-limitation (see structure of competitive interactions). Secondly, the model only allows movement between each cell and its four nearest neighbours. As already noted (individual-based stochastic process), this is a reasonable approximation given the cell size relative to the small distances moved by these clonal grasses. It would not necessarily apply to other systems, and would need to be checked whenever the method is used. Thirdly, the model assumes that feedback acts on tiller births rather than deaths. While it is known that births usually are more sensitive to density than deaths (e.g. Jónsdóttir 1991; Duralia & Reader 1993; unpublished data on *Festuca rubra* from the studied community), it would be interesting to estimate coefficients for deaths as well. It was not possible to do this here because the two sets of coefficients were too strongly correlated to be separated by non-linear regression.

Among the statistical assumptions, the following three need emphasis. First, to achieve a data set for which the errors could be said to be near to independent, a sacrifice of the major part of the data set was required, as can be seen from the tiling in Fig. 3. Secondly, the strong relationship between mean and variance of the data made some transformation necessary. The choice of this had some effect on the parameter estimates, although our checks on alternatives (logarithmic, untransformed) indicate that the qualitative picture is not seriously affected. Thirdly, the sensitivity of parameter estimates to outliers led to our excluding the 5% most outlying points at each tail prior to estimation. The dependence of parameter estimates on the proportion of outliers removed diminished when the most extreme data points were taken out, but it never disappeared entirely. There is perhaps no unique way to decide how best to deal with these matters, but it is important to appreciate that the parameter estimates are, to some extent at least, dependent on what decisions are made.

The analysis was based on the response of tillers to densities in their immediate neighbourhood after a time lag of 1 year. To put it another way, the analysis deals only with events that are local both in space and time, ignoring information on the global spatial structure (such as global density, size and shapes of clumps, spatial correlations between species) and on the temporal correlation structure. For this reason, it would be unrealistic to expect the statistical model to provide parameter estimates that predict accurately the global patterns. Nonetheless, it is tempting to explore the global spatiotemporal patterns generated by the local model. Figure 5 illustrates the spatial configurations that develop for one of the field plots, using the estimates from Table 4 as parameters for the stochastic realization, and the pattern in 1984 in Fig. 1 as the initial configuration. Although parameter estimation and simulation are based on local information only, many global features of the data are well reproduced. In particular, it can be seen that the
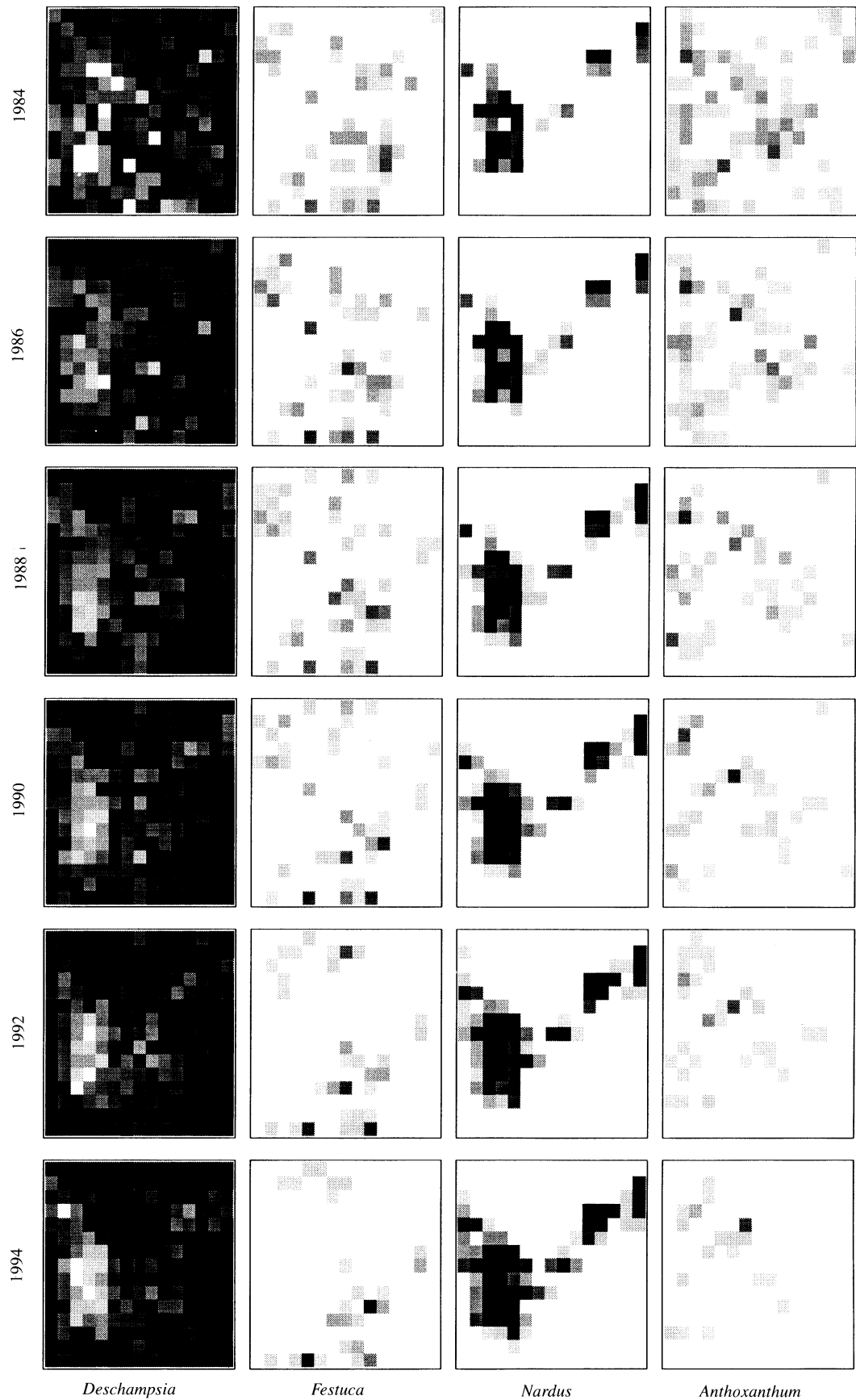
Fig. 5. A realization of the stochastic model for community dynamics, based on the parameters in Table 4, starting with the spatial pattern shown for 1984 in Fig. 1. Shading as described in Fig. 1.

spatial patterns of three of the four species (*Deschampsia*, *Festuca* and *Nardus*) are comparable with those in the field. Notice, for instance, the tendency for *Deschampsia* to become scarce in regions where *Nardus* is concentrated. The spatial pattern of the fourth species, *Anthoxanthum*, is not satisfactorily described by the model, as it undergoes a decline in the simulation, but does not do so in the field. Evidently, the local density dependence considered in our simple statistical model already succeeds in explaining a significant part of the global patterns observed in the field.

Ultimately, there must remain a limit as to how much can be read about interactions from the natural turnover of species. As a thought experiment, imagine that clumps of one species, *Nardus* say, have a tendency to move in one direction, growing at the front and dying at the back; another species of relatively high mobility, say *Anthoxanthum*, tends to fill the space left in the wake of these clumps. This could be construed as a negative coefficient a_{NA} when using the non-manipulative method because it does not indicate whether the space that becomes occupied by *Anthoxanthum* is the cause or the effect of the disappearance of *Nardus*. Manipulation of the *Anthoxanthum* density is needed to distinguish these causal pathways. The agreement between the results we have obtained and those from manipulation experiments (see: validation of estimated interaction strengths) indicates that this is not a major problem here. But the fact that such scenarios can be created argues for some caution in the interpretation of results of non-manipulative analyses.

Conclusion

Notwithstanding these reservations, we think non-manipulative methods hold an important key to learning more about interactions in plant communities. They go directly to the natural turnover of individuals within communities and measure the replacement of one species by another. In so doing, they avoid the problems of how to interpret results of manipulation and *ex situ* experiments, and the uncertainties as to how surrogate variables such as plant size are related to competitive interactions.

Having said this, there is much to be done to develop and refine the methods. To make further progress, it may help to shift the focus from the dynamics of events in single cells to the dynamics of global spatial structures. As noted above, the former deals with the spatial processes only in so far as they depend on movement in a local neighbourhood from one time to the next. The latter deals with the whole spatial structure of the system over longer periods of time, and utilizes important information inaccessible to the method given here.

References

Aarssen, L.W. & Epp, G.A. (1990) Neighbor manipulations in natural vegetation: a review. *Journal of Vegetation Science*, **1**, 13–30.
Cook, R.D. & Weisberg, S. (1990) Confidence curves in nonlinear regression. *Journal of the American Statistical Association*, **85**, 544–551.
Dixon, W.J., Brown, M.B., Engelman, L. & Jennrich, R.I. (1990) BMDP *Statistical Software Manual*. University of California Press, Berkeley.
Draper, N.R. & Smith, H. (1988) *Applied Regression Analysis*. Wiley, New York.
Duralia, T.E. & Reader, R.J. (1993) Does abundance reflect competitive ability? A field test with three prairie grasses. *Oikos*, **68**, 82–90.
Freeman, D.C. & Emlen, J.M. (1995) Assessment of interspecific interactions in plant communities: an illustration from the cold desert saltbush grasslands of North America. *Journal of Arid Environments*, **31**, 179–198.
Gaudet, C.L. & Keddy, P.A. (1988) A comparative approach to predicting competitive ability from plant traits. *Nature*, **334**, 242–243.
Gaudet, C.L. & Keddy, P.A. (1995) Competitive performance and species distribution in shoreline plant communities: a comparative approach. *Ecology*, **76**, 280–291.
Gimingham, C.H. (1988) A reappraisal of cyclical processes in *Calluna* heath. *Vegetatio*, **77**, 61–64.
Goldberg, D.E. & Barton, A.M. (1992) Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist*, **139**, 771–801.
Goldberg, D.E. & Landa, K. (1991) Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *Journal of Ecology*, **79**, 1013–1030.
Goldberg, D.E. & Werner, P.A. (1983) Equivalence of competitors in plant communities: a null hypothesis and a field experimental approach. *American Journal of Botany*, **70**, 1098–1104.
Grace, J.B., Guntenspergen, G.R. & Keough, J. (1993) The examination of competition matrix for intransitivity and intransitive loops. *Oikos*, **68**, 91–98.
Grace, J.B., Keough, J. & Guntenspergen, G.R. (1992) Size bias in traditional analyses of substitutive experiments. *Oecologia*, **90**, 429–434.
Hendry, R. & McGlade, J.M. (1995) The role of memory in ecological systems. *Proceedings of the Royal Society B*, **259**, 153–159.
Herben, T., During, H.J. & Krahulec, F. (1995) Spatio-temporal dynamics in mountain grasslands: species autocorrelations in space and time. *Folia Geobotanica and Phytotaxonomica*, **30**, 185–196.
Herben, T., Krahulec, F., Hadincová, V. & Kovárová, M. (1993a) Small scale spatial dynamics of plant species

in a grassland community during six years. *Journal of Vegetation Science*, **4**, 171–178.

Herben, T., Krahulec, F., Hadincová, V. & Pecháčková, S. (1997) Fine-scale species interactions of clonal plants in a mountain grassland: a removal experiment. *Oikos*, **78**, 299–310.

Hutchings, M.J. & Barkham, J.P. (1986) An investigation of shoot interactions in *Mercurialis perennis*, a rhizomatous perennial herb. *Journal of Ecology*, **64**, 723–743.

Jónsdóttir, G.Á. (1991) Effects of density and weather on tiller dynamics in *Agrostis stolonifera*, *Festuca rubra* and *Poa irrigata*. *Acta Botanica Neerlandica*, **40**, 311–318.

Keddy, P.A. & Shipley, B. (1989) Competitive hierarchies in herbaceous plant communities. *Oikos*, **54**, 234–241.

Krahulec, F. (1990) Nardo-Agrostion communities in the Krkonoše and West Carpathians Mts. *Folia Geobotanica and Phytotaxonomica*, **25**, 337–347.

de Kroon, H. (1993) Competition between shoots in clonal plants. *Plant Species Biology*, **8**, 85–94.

de Kroon, H., Hara, T. & Kwant, R. (1992) Size hierarchies of shoots and clones in clonal herb monocultures: do clonal and non-clonal plants compete differently? *Oikos*, **63**, 410–419.

Law, R. & Watkinson, A.R. (1989) Competition. *Ecological Concepts* (ed. J. M. Cherrett), pp. 243–284. Blackwell Scientific Publications, Oxford.

Lepš, J. (1995) Variance deficit is not reliable evidence for niche limitation. *Folia Geobotanica and Phytotaxonomica*, **30**, 455–459.

van der Maarel, E. & Sykes, M.T. (1993) Small scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. *Journal of Vegetation Science*, **4**, 179–188.

Rees, M., Grubb, P.J. & Kelly, D. (1996) Quantifying the impact of competition and spatial heterogeneity on the structure and dynamics of a four-species guild of winter annuals. *American Naturalist*, **147**, 1–32.

Remmert, H. (1991) *The Mosaic-Cycle Concept of Ecosystems*. Springer-Verlag, Berlin.

Silvertown, J. & Dale, P. (1991) Competitive hierarchies and the structure of herbaceous plant communities. *Oikos*, **61**, 441–444.

Silvertown, J., Lines, C.E.M. & Dale, M.P. (1994) Spatial competition between grasses: rates of mutual invasion between four species and the interaction with grazing. *Journal of Ecology*, **82**, 31–38.

Thórhalsdóttir, T.E. (1990) The dynamics of a grassland community: a simultaneous investigation of spatial and temporal heterogeneity at various scales. *Journal of Ecology*, **78**, 884–908.

Turkington, R. (1994) Effect of propagule source on competitive ability of pasture grasses: spatial dynamics of six grasses in simulated swards. *Canadian Journal of Botany*, **72**, 111–121.

Watt, A.S. (1947) Pattern and process in the plant community. *Journal of Ecology*, **35**, 1–22.

Watt, A.S. (1955) Bracken vs. heather: a study in plant sociology. *Journal of Ecology*, **43**, 490–506.

Wilson, J.B. (1995) Testing for community structure: a Bayesian approach. *Folia Geobotanica and Phytotaxonomica*, **30**, 461–469.

Wilson, J.B., Gitay, H. & Agnew, A.D.Q. (1987) Does niche limitation exist? *Functional Ecology*, **1**, 391–397.