COMMUNITY ECOLOGY

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Assessing determinants of community biomass composition in two-species plant competition studies

Abstract A method is proposed for assessing the relative importance of species identity, neighbour species influence and environment as determinants of change in community biomass composition in two-species short-term competition experiments. The method is based on modelling the *differences* in relative growth rates (RGR) of species (hence called the RGRD method). Using a multiple regression approach it quantifies the effects of initial species' abundance, species identity and environment on RGRD and hence on change in community biomass composition. The RGRD approach is relatively simple to use and deals readily with statistical difficulties associated with correlated responses between species from the same stand. It can be easily adapted to analyse sequential harvest data. An example based on data from two-species mixtures of the annual species *Stellaria media* and *Poa annua* is used to illustrate the method. The main determinant of change in community biomass composition was species identity, reflected in the difference in growth rates between the species. Change in community composition was not, in general, significantly affected by the influence of neighbours or fertiliser level. The unimportance of the influence of neighbours in affecting the composition of these communities contrasts with the strong role of intra- and interspecific competition in determining the size of individuals of both species (Connolly et al. in Oecologia 82:513–526, 1990).

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Introduction

A central issue in the ecology and agronomy of plants is quantifying the extent to which individuals of co-occurring species both affect and respond to one another, and how these interactions influence the structure of plant communities (Schoener 1983; Connell 1983; Tilman 1988; Keddy 1989; Goldberg 1990; Grace and Tilman 1990; Bazzaz 1996; Gibson et al. 1999; Grime 2001; Connolly et al. 2001). Most short-term competition studies (and these are the norm) have inferred the outcome of competition, in terms of the likely composition of the community, from the relative sizes of estimates of intra- and interspecific effects among species or indices of competitive ability (Gibson et al. 1999; Connolly et al. 2001; Weigelt and Jolliffe 2003). These studies have generally relied solely on biomass yield at harvest to assess competitive effects (Keddy and Shipley 1989; Goldberg and Barton 1992; Gibson et al. 1999). In this paper we use the changes in species biomass over time to study the determinants of community composition at harvest. We recognise that dynamics and shifts in community composition depend on many processes other than growth, and the importance of factors such as recruitment, survival, spatial structure and scale (e.g. Watkinson et al. 2000; Freckleton and Watkinson 2000) may also need to be incorporated in a full assessment of community change.

Connolly et al. (2001) distinguished several questions in competition studies, one of which was "Which species gains (wins) in a mixture?" This question is concerned with measuring the relative changes in the abundance of species over the duration of the experiment. It focuses directly on the question of outcome: over an interval of time, is one species gaining, or winning, in a mixture (e.g. in terms of biomass, seed number, access to

resources) relative to others. If all species gain at the same per unit rate, stand composition, defined as the proportional abundances of species, will remain unchanged, while if one species gains at a faster per unit rate than another its relative proportion in the community will increase. Here we use gain to denote net gain; biomass may be lost to herbivory, senescence etc. We develop a new approach to distinguish the effects of the initial abundance of species, species growth traits and environment as determinants of "species gain" and change in community composition for two-species mixtures. The method generates specific testable hypotheses. It readily incorporates data from several sequential harvests, destructive or otherwise. Many of the ideas developed below may be readily generalised to multi-species communities (Ramseier et al., in preparation). The exposition is in terms of stand level phenomena but some of the ideas apply at the individual plant level. The experimental approach advocated includes the density series methods used by Goldberg et al. (1995) as a particular case but allows assessment of species frequency as well as density effects.

The ideas are developed for two species grown in a range of mixed stands where the outcome variable is biomass per individual at harvest and the explanatory variables include the initial biomass of each species in the stand. This is a simple case, where the presumption is that the arena for the competitive interactions between the species is determined by the initial biomass of the species and environmental factors (Connolly et al. 2001). We use the initial biomasses of the species as scaled versions of their initial densities, to allow for differences in the initial sizes of the two species. This can be generalised to include other information on initial conditions, e.g. initial relative sizes of seedlings (Connolly and Wayne 1996) or metrics for explanatory variables other than initial species' biomass (Kropf and Spitters 1991; Connolly et al. 2001).

We present an example based on experimental data (Connolly et al. 1990) in which there is evidence of strong inter- and intraspecific effects, as measured by the response models for individual species, but where these effects are not the main determinants of change in stand composition.

Materials and methods

Notation

We use the following notation, assuming an experiment with stands sown with mixtures or monocultures of the two species. For the ith species in a stand, y_i is its biomass per stand at the start of the experimental period, and $y = \sum_i y_i$ is the total initial biomass of the stand, which will vary from stand to stand according to the experimental design. Y_i is the stand biomass for the species at the end of the experimental period and $Y = \sum_i Y_i$ is the total biomass of the stand. RGR_i is the average relative growth rate for the ith species and

equals $\ln\left(\frac{Y_i}{y_i}\right)/t$, where t is the duration of the experiment and ln is the natural logarithm. x_i is the expected species biomass proportion in the stand at harvest, with $\sum_i x_i = 1$.

Relative growth rate difference models

A comparison of the change in composition for the two species is related to a difference in their RGRs. This will form the basis of the modelling approach adopted below. The stand composition at the start and end of the experiment is $(y_1/y, y_2/y)$ and $(Y_1/Y, Y_2/Y)$ respectively. To analyse the change in composition one could model the output per unit input, Y_1/y_1 and Y_2/y_2, separately for each species using a response model approach (Connolly et al. 1990) and deduce changes in composition from the two models. However, in the method proposed below, the change in composition is directly the object of analysis and leads to a much simpler approach. The final relative to initial proportion of the ith species is $Y_i y/y_i Y$. This can be written as $Y_i y/y_i Y = e^{t.RGR_i} y/Y$ from which

$$\ln\left(\frac{Y_i}{y_i}\frac{y}{Y}\right) = \ln\left(\frac{y}{Y}\right) + t.RGR_i \qquad (1)$$

From this, the difference in the natural logarithm of the final relative to initial proportions for the two species is expressible in terms of the differences between the RGRs for both species.

$$\ln\left(\frac{Y_2}{y_2}\frac{y}{Y}\right) - \ln\left(\frac{Y_1}{y_1}\frac{y}{Y}\right) = t(RGR_2 - RGR_1) \qquad (2)$$

or, where $RGRD = RGR_2 - RGR_1$,

$$RGRD = RGR_2 - RGR_1 = \frac{\ln\left(\frac{Y_2}{y_2}\right) - \ln\left(\frac{Y_1}{y_1}\right)}{t} \qquad (3)$$

The average relative growth rate over the experimental period can be calculated for a species that is present in a stand at both the start and end of an experimental period. The methods below are based on modelling RGRD, the difference in average RGRs between species. Values of RGRD are directly related to compositional changes. If the average RGR is the same for both species in a stand over a period of growth, $RGRD = 0$ and neither species gains and their position in the community relative to each other does not change over the period. If one species is initially twice as abundant as the other it will be twice as abundant at the end of the period. If $RGRD > 0$ then species 2 gains and vice versa if $RGRD < 0$. The calculation of RGRD does not require knowledge of yields of individual plants, only species' yields at the stand level. In a stand the species with the higher RGR is deemed to be more *efficient* over the course of the experiment in the sense that it has a higher output per unit input.

If output and input biomass have been determined for both species over a range of mixed stands and for several applied treatments, it makes sense to model the RGRD as a function of variables characterising the initial conditions in the mixture (e.g. y_1 and y_2) and the different environments. Suppose that the treatment is denoted by a variable T (which may have several levels but for the moment we assume only two, 0 and 1). A simple model with which to develop ideas is

$$\text{RGRD} = b_0 + b_1 y_1 + b_2 y_2 + b_3 T + \varepsilon \qquad (4)$$

where b_1 and b_2 measure the effect of changing the initial biomass of the first or second species on the difference in average RGR, and b_3 measures the effect of treatment. A positive value of b_i (for $i = 1$ or 2) means that increasing species i in the initial community will enhance the difference in average RGRs in favour of species 2 and hence will tilt the final composition more towards that species. A negative value has the opposite effect. The two coefficients b_1 and b_2 show how changes in initial abundance of the species can influence the growth differential between species and we call them *influence* coefficients. The influence of a species is the difference between its intraspecific effect on its own RGR and its interspecific effect on the RGR of the other species. A positive value of b_3 means that for a particular mixture the environmental factor increases the RGRD and hence increases the proportion of species 2 in the composition. If all three coefficients (b_1, b_2 and b_3) are zero then the difference in average RGR is not affected by initial composition or applied treatment and will be constant (b_0). This constant difference in average RGR reflects the difference in growth rates of the two species over the experimental period and will shift composition in favour of the faster growing species. If b_0 itself is also zero then community composition will not change over the course of the experiment. Thus, this model allows the effects of differences in growth rates between species (species identity), initial species' abundance and the effects of applied treatments to be examined as separate determinants of the extent of community change. Model 4 has the desired generality and simplicity. The outcome of the question "which species gains" can be predicted at all possible mixtures (within the range of the experimental design) and the relative contributions of various factors to changes in community composition can be simply assessed.

Of course the model can be more general than this and can include higher order terms in initial biomass and interactions between treatment and initial abundance. The residual term ϵ is assumed to be normally distributed with constant variance, which was checked by examination of residuals. Correlation between the outputs Y_1 and Y_2, and hence between the average RGRs for the two species in a stand, does not introduce a complication in the analysis since the model does not require the inclusion of a parameter for this correlation.

In the formulation and interpretation of the parameters of model 4 as specified, the coefficient b_0 is the difference in average RGR for zero levels of y_1 and y_2 and the lowest level of T. As zero levels of these two initial variables does not give a realistic stand it is more sensible to have b_0 represent the difference in RGR at values of $\bar{y}_1$ and $\bar{y}_2$, the mean values of initial biomass of the two species across the experiment design. This is achieved by using $y_1 - \bar{y}_1$ and $y_2 - \bar{y}_2$ as explanatory variables in the model rather than y_1 and y_2 respectively. The intercept now becomes the expected difference in RGR for a stand with initial biomass of $\bar{y}_1$ and $\bar{y}_2$ for the two species and the low level of the environmental factor. The estimates of the other parameters of model 4 remain unchanged in value and in meaning. This approach is adopted in the analysis of the example below.

Multiple harvests   Multiple harvest data may arise from multiple sequential destructive harvests at a number of time points or as repeated measurements on each stand at different times. For sequential destructive harvests the analysis can be particularly simple. Suppose that there are k harvests and that a variant of models 3 and 4 is fitted for each harvest (with harvest index $h = 1,..., k$) as follows,

$$\ln\left(\frac{Y_{2h}}{y_2}\right) - \ln\left(\frac{Y_{1h}}{y_1}\right)$$
$$= Z_h = b_{0h} + b_{1h} y_1 + b_{2h} y_2 + b_{3h} T + \varepsilon_h \qquad (5)$$

This model has the same form as 3 and 4 but the time t_h from the start to the hth harvest is omitted. Then the model for $(t_{h'} - t_h)$ times the RGRD between harvests h and h', is simply obtained by subtracting one set of coefficients from the other as

$$\text{RGRD}(t_{h'} - t_h)$$
$$= Z_{h'} - Z_h$$
$$= (b_{0h'} - b_{0h}) + (b_{1h'} - b_{1h}) y_1 + (b_{2h'} - b_{2h}) y_2$$
$$+ (b_{3h'} - b_{3h}) T + \varepsilon_{h'} - \varepsilon_h \qquad (6)$$

If the variance-covariance matrices of the estimators of the coefficients for harvests h and h' are V_h and $V_{h'}$ respectively, then the variance-covariance matrix for the difference between coefficients is $V_{h'} + V_h$ since the equations are based on independent data.

For repeated-measures data on the same stands, models 5 and 6 can also be used but the error structure should reflect the more complex nature of random variation. It should include a component reflecting stand-to-stand variation (perhaps changing over time) and a covariance structure for the repeated data within stands. Estimation of changes in inter-harvest periods would proceed as above but the variance of estimators, and inference, would be somewhat more complex. These models would lend themselves to searching for time-related patterns in the parameters, which could reduce the number of parameters in the model and provide more insight into growth dynamics.

This approach may be well adapted to the requirements of longer term experiments with perennial species, where the initial conditions may not provide the most appropriate reference point as time advances. Many of the other facets of the approach would still be useful, in particular the focus on determining community compositional change through analysis of the difference in RGRs. In Eq. 6, for assessing which species gains between two successive harvests (h and h'), the term $Z_{h'} - Z_h$ can also be written as

$$Z_{h'} - Z_h$$
$$= \left[\ln \left(\frac{Y_{2h'}}{y_2} \right) - \ln \left(\frac{Y_{1h'}}{y_1} \right) \right] - \left[\ln \left(\frac{Y_{2h}}{y_2} \right) - \ln \left(\frac{Y_{1h}}{y_1} \right) \right]$$
$$= \ln \left(\frac{Y_{2h'}}{Y_{2h}} \right) - \ln \left(\frac{Y_{1h'}}{Y_{1h}} \right) \tag{7}$$

This is the difference between the natural logarithms of the ratios of species contribution to the successive harvests and does not involve the starting conditions y_1 and y_2. It is a constant times the average difference in RGRs in the inter-harvest period. This difference can then be modelled by reference to community status at the previous harvest (Y_{1h} and Y_{2h}) and environmental variables. Using the community status at the start of a period, which incorporates the history of the community, may give a better insight into the drivers of compositional change in the period than the temporally more remote initial species' biomass. Similar approaches to modelling community dynamics have been developed by Connolly and Wachendorf (2001), Nolan et al. (2001) and Wachendorf et al. (2001). When successive harvests are taken on the same plots, RGR more properly refers to growth from a post harvest residue rather than being based on the previous harvest yield. In this case it is more appropriate to refer to the variable being analysed as the difference in relative biomass change (RBCD) rather than the difference in relative growth rate (RGRD) but the modelling may proceed as above.

Predicting composition   Community composition at the end of the experiment or at intermediate harvests can be predicted from the model. Estimates of parameters and of yields are indicated by placing a caret ($^\wedge$) over the appropriate term. The estimated equation for the difference in average RGR is, from Eq. 4,

$$
\begin{aligned}
R\hat{G}RD &= \hat{b}_0 + \hat{b}_1 y_1 + \hat{b}_2 y_2 + \hat{b}_3 T \\
&= \frac{\ln \left(\frac{\hat{Y}_2}{y_2} \right) - \ln \left(\frac{\hat{Y}_1}{y_1} \right)}{t}
\end{aligned}
\tag{8}
$$

The predicted composition is derived as follows,

$$R\hat{G}RD.t = \hat{Z} = \ln \left(\frac{\hat{Y}_2}{y_2} \right) - \ln \left(\frac{\hat{Y}_1}{y_1} \right) = \ln \left(\frac{\hat{Y}_2}{y_2} \middle/ \frac{\hat{Y}_1}{y_1} \right)$$

from which

$$e^{\hat{Z}} = \left(\frac{\hat{Y}_2}{y_2} \middle/ \frac{\hat{Y}_1}{y_1} \right)$$

Imposing the condition that proportions of a composition must sum to one, (i.e. $\hat{x}_1 + \hat{x}_2 = 1$), gives, after some elementary algebra,

$$\hat{x}_2 = \frac{(y_2/y_1)e^{\hat{Z}}}{1 + (y_2/y_1)e^{\hat{Z}}} \quad \text{and} \quad \hat{x}_1 = 1 - \hat{x}_2 = \frac{1}{1 + (y_2/y_1)e^{\hat{Z}}} \tag{9}$$

which sum to one. Approximate standard errors for predicted proportions are computed using Taylor series approximation methods (Kendall and Stuart 1977). These approximation methods are discussed in Muldowney (1999) and Muldowney et al. (2001) for a somewhat similar application.

One difficulty with the above approach is the presence of zero values in a composition since the logarithm of zero is not defined. Also, the method can only be applied to mixtures, suggesting that monocultures are irrelevant, as indeed they are to the questions on stand composition addressed here. Statistical issues to do with the precision of estimates and experimental design are the subject of another paper (Connolly and Kirwan, in preparation). As the models proposed are multiple regression models the modelling process is subject to the difficulties and methods of model fitting, testing and interpretation as described, for example, in Draper and Smith (1981).

Null hypotheses

The definitions in the preceding section form the basis for the following testable null hypotheses about the species. (1) Species composition does not change in any stand. To check this test whether RGRD = 0 for all stands, i.e. all four coefficients are zero. (2) Stand composition is not affected by species influence ($b_1 = 0 = b_2$), by environmental treatments ($b_3 = 0$) or species identity ($b_0 = 0$). To test these hypotheses fit the RGRD model and use the coefficients of the model as the basis of the tests of hypotheses. If the influence of a species is zero it means that the differential in RGRD is independent of initial species' abundance and that the intra- and interspecific effects of a species are equal. Much of the interest in competition studies lies in whether these null hypotheses are true, and, if not, the relative importance of the determinants in changing composition.

Example

To illustrate these methods we use data drawn from a competition experiment between *Stellaria media* and *Poa annua* (described in Connolly et al. 1990). The design consisted of monoculture stands at a range of densities for each species and mixtures of the two species varying in density and relative frequency. Initial size estimates were available for seedlings for both species, from which their initial stand biomasses were calculated (H1). The biomass
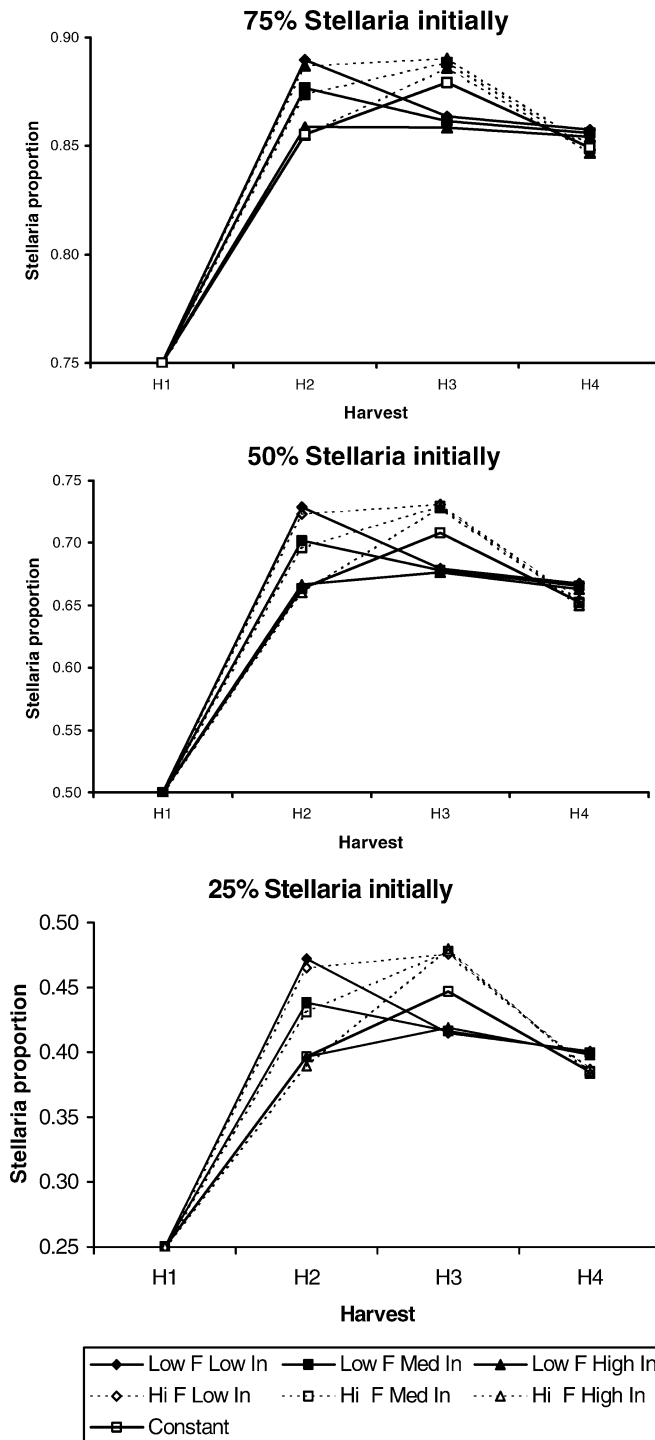
of each species was recorded at each of three sequential harvests (H2, H3 and H4). The RGRD model uses the biomass data from mixed stands for all three harvests. In separate analyses of output per unit input (Y_i/y_i) for each species Connolly et al. (1990) showed that, for both species, there were strong intra- and interspecific effects at each of harvests H2, H3 and H4.

To simplify the exposition the second and third of three fertility levels were combined. Summary data on the initial biomass and average RGR for *Stellaria* and *Poa* for various inter-harvest periods (Table 1) show that average RGR was initially quite high but declined rapidly through time. The RGR of *Stellaria* was higher on average than that of *Poa* for the first two inter-harvest periods (H12 and H23) and lower in the final period (H34). The RGRD models (RGR *Stellaria*-RGR *Poa*) fitted for H12, H13 and H14 (Table 2), included the initial biomass of *Stellaria* and *Poa* (adjusted by subtraction of their mean initial biomass) and a fertility effect. Fertility was scored 1 for low and 2 for high and the equations in Table 2 are adjusted to the mean fertility. Following this adjustment, the constants in Table 2 measure the difference in RGR at the average values of initial *Stellaria*, *Poa* and fertility. The coefficients for RGRD models in H23 and H34, derived using Eq. 6, are also shown in Table 2.

The main determinant of change in community composition was species identity, the difference in the rates of growth of the species (the constants in Table 2). Species influence and the effect of fertility were small. The intercept in the model estimates the average difference between RGRs and provides a test of this against zero. *Stellaria* gained over the three periods H12, H13 and H14, (had a higher average RGR than *Poa*, measured by the intercept) but the advantage to *Stellaria* reduced with increasing harvest number. In H23 *Stellaria* still had the advantage, on average. In H34 the average RGR of *Poa* exceeded that of *Stellaria*. There was only one significant effect other

than the constant terms, a positive response to fertility in H13 (Table 2). In this period high fertility increased the proportion of *Stellaria*.

The compositional changes predictable from these models are illustrated in Fig. 1 in which predictions are made (a) just on the basis of the intercept and (b) for the full models. *Stellaria* proportion was predicted at three harvests for a range of initial *Stellaria* proportions, for three levels of initial stand biomass and the two fertility levels. For predictions from the intercept alone (the species identity effect), composition changed strongly towards *Stellaria* in H12 and H23 but the final period somewhat redressed the balance towards *Poa*. The large change towards *Stellaria* in H12 reflects the average difference of 0.052 in RGR in its favour during this period. The constant was significantly different from zero in all inter-harvest periods and so the difference in growth rates reflected in these constants would lead to changed composition, irrespective of starting point, in all stands. The complex pattern of change in stand composition arising from just one parameter shows the richness of this very simple model. Note that it would be difficult to ensure that specific predetermined proportions of species would be achieved at the design stage. What is required is that the proportions actually achieved are well measured and that they cover the design space of interest reasonably well. When the regression models are fitted, prediction at specific values of the explanatory variables, whether design points or otherwise, is possible and this is how the predictions in Fig. 1 were made. Such predictions must be confined to points covered by the design space.

Including the effects of the other terms in the model changed these outcomes only slightly. For H12, increasing initial *Stellaria* or *Poa* resulted in a reduction in the relative importance of *Stellaria* vis a vis *Poa*, displayed by the density effect in Fig. 1 since both coefficients were negative. Over the models both positive

Table 1 Number of stands and mean initial above-ground biomass of *Stellaria* and *Poa* for three sequential harvests, and mean relative growth rate (*RGR*) for both species over several inter-harvest periods

Harvest	Number of stands	Mean initial biomass per unit area (g)		Mean RGR in inter-harvest periods			
		Stellaria	*Poa*	Periods	*Stellaria*	*Poa*	Difference
2	22	0.215	0.103	H12	0.227	0.177	0.050
3	58	0.149	0.095	H13	0.130	0.102	0.028
4	22	0.165	0.109	H14	0.091	0.078	0.013
Average		0.167	0.100	H23	0.067	0.054	0.013
Minimum		0.001	0.001	H34	0.015	0.032	−0.017
Maximum		0.450	0.282				

Table 2 Estimated models for difference in relative growth rate (*RGR*) between *Stellaria* and *Poa* over selected harvests. Values of the *t* statistic greater than or equal to 2 are indicated in *bold type*

Harvest	Constant	t	Fertility	t	Initial biomass			
					Poa	t	*Stellaria*	t
12	0.0525	**7.74**	−0.0022	−0.15	−0.0970	−0.96	−0.0829	−1.17
13	0.0269	**18.66**	0.0075	**2.45**	0.0056	0.25	−0.0088	−0.62
14	0.0126	**6.04**	−0.0012	−0.23	−0.0003	−0.01	−0.0026	−0.12
23	0.0103	**2.06**	0.0138	1.29	0.0723	0.95	0.0394	0.76
34	−0.0152	**−2.27**	−0.0180	−1.12	−0.0118	−0.10	0.0094	0.14

Fig. 1 Predicted *Stellaria* proportion at four harvests for a range of initial *Stellaria* proportions, for three levels of initial community biomass (*Low In*, *Med In* and *High In*) and two fertility levels (*Low F* and *Hi F*). Also shown are predictions from the model containing only a constant

and negative coefficients (not significant) were noted for initial *Stellaria* and *Poa*. The significant fertility effect in H13 enhanced *Stellaria* relative to *Poa*. The results suggest that, with the exception of one effect of fertiliser,

the dynamics of these stands were largely determined by species identity.

Discussion

In this paper we have developed the RGRD method to address the question "which species gains" in a mixture of plant species (Connolly et al. 2001). It has proved to be a simple but powerful tool in evaluating the relative importance of species' identity, the balance between species intra- and interspecific effects (species' influence) and environment as determinants of species' gains and hence of changes in stand biomass composition. Connolly et al. (2001) also raised the question "how do species affect each other". The RGRD analysis and example show how the answer to this question contributes to the change in community composition. The RGRD method raises several statistical issues and can be readily developed to assess determinants of change in biomass composition in communities of more than two species.

The strong intra- and interspecific competition evidenced by the competition coefficients in models of individual species (Connolly et al. 1990) was largely unimportant in determining changes in stand composition. So, although there was evidence of considerable change in community composition, this was not driven by the effects of species on each other as measured by intra- and interspecific competition coefficients. This concurs with the results of others (e.g. Firbank and Watkinson 1985; Rajanaemi and Goldberg 2000) who indicated that the outcome of competition may not be predictable on the basis of measures of competition alone. Indeed, Goldberg et al. (1999) claimed that the extension of effects of interactions on individual growth or survival to effects on population distribution and abundance or community structure is highly problematic. Why are the two questions so weakly related? Increasing the initial biomass or density of a species will generally reduce the performance of individuals of all species but may well do so in a way that leaves the differential between them in terms of RGR relatively unchanged. Thus, intra- and interspecific competition, even though intense, may have a relatively minor role in changing the RGR differential and hence, in changing stand composition, i.e. competition may be intense but not important (Weldon and Slauson 1986). This suggests that indices such as the coefficient of aggressivity and the relative crowding coefficient, which can be largely determined by the balance of intra- and interspecific competition, may not always be good predictors of competitive outcome. It is a strength of the modelling framework proposed here that the relative importance of these competition coefficients in determining the outcome of competition is explicitly tested. The non-significance of influence coefficients implies that intra- is not appreciably different from interspecific competition and that resource partitioning may not be an important

mechanism of coexistence in these species (Goldberg and Barton 1992).

The changes in RGR differential through time in the example shows how the considerable temporal change in the dynamics of species interaction can be simply described in terms of the three determinants examined, with different factors being more or less important in different phases of growth. Searching for equilibrium points, which would involve zero RGRs for both species, may be more relevant in studying the dynamics of species over several years rather than in short-term studies, particularly with annual species. It is likely that such equilibria would also involve other aspects of the population behaviour of species than their biomass accumulation.

The RGRD method avoids many of the statistical problems of model complexity and potential correlation among responses from different species in a stand. This simplification is a general feature of compositional data analysis (Aitchison 1986) of which the RGRD method is a variant. Multiple regression models sufficed rather than the more complex models generally used for the analysis of individual species responses (Law and Watkinson 1987; Firbank and Watkinson 1990; Connolly et al. 1990). The assumptions of normality and constant variance for the difference in RGR values were confirmed by residual analysis. The methods developed here generalise quite readily to more than two species (Ramseier et al., in preparation) and provide a rich environment in which to pursue the interplay between species, for example, to investigate the existence of various types of hierarchies among species (Keddy and Shipley 1989; Shipley 1993; Grace et al. 1993). The use of the average RGR as an important element in studying stand dynamics echoes the use of Rmax (Grime 2001), the maximum RGR for a species, as an indicator of species' competitive abilities and the emphasis placed on RGR in competition studies (Milthorpe 1961; Connolly and Wayne 1996). Experiment designs that allow the full implementation of the RGRD method include those that have been proposed for response surface estimation (e.g. Connolly 1987; Rejmánek et al. 1989; Roush et al. 1989; Snaydon 1991; Turkington and Jolliffe 1996; Gibson et al. 1999; Goldberg and Scheiner 2001; Inouye 2001).

The RGRD method for examining the question "which species gains" can be used even when individual plants are difficult or impossible to distinguish at harvest and/or initially, since the RGR or output per unit input can be calculated even when only stand level data are available for each species. This may be of particular value in modelling structural change in stands of perennial species in which clonal species form part of the community and where species' densities may become difficult to determine after some time. In these stands, where repeated measurements may be available, perhaps over several years, it may be useful to use the most recent measurement of stand state rather than its initial state as the reference point for change in any period (see Eq. 7 and Connolly and Wachendorf 2001; Wachendorf et al. 2001; Nolan et al. 2001). Apart from probably

giving a better fit for the models, this may provide insight into the relationship between community change over a period and its status at the start of the period. Despite the claims for the RGRD method developed here, we repeat the qualification expressed in the introduction that dynamics and shifts in community composition may depend on many processes other than growth, and their effects may need to be incorporated in a full assessment of community change.

The use of biological metrics of functional rather than, or in addition to, numerical density as initial reference points serves three purposes. It focuses attention on the importance of the initial state of a stand as a determinant of its state at a later time. It provides an analytical basis for the assessment of community processes while avoiding the potential biases associated with the use of species' densities as explanatory variables (Connolly et al. 2001). Finally, it emphasises the desirability of assessing competition over a defined time interval(s), rather than through a single final measure. Other biological metrics that have been or may be used in characterising initial community structure include the relative sizes of individuals of different species (Connolly and Wayne 1996), the ratio of initial leaf area between weed and crop species (Kropf and Spitters 1991), leaf area index and grass tiller density (Wachendorf et al. 2001), root biomass, measures of plant architecture, etc. Indeed, species' initial densities in addition to their initial biomass may explain aspects of compositional change. A detailed discussion of the implications of various measurement metrics in respect of these questions of neighbour effects and gain is contained in Connolly et al. (2001).

In relating this approach to the methods used in the biodiversity debate (Allison 1999; Hector et al. 1999; Symstad et al. 1998) we note that the designs used in such studies have largely focussed on species identity and species richness. The emphasis in the current approach on using a range of stands of differing relative frequency in the design allows examination of the effect of evenness in the stand, a third component of biodiversity, and to assess the separate effects of these three components. In addition, including a range of overall density/abundance allows the interaction of increasing competitive intensity with these factors to be evaluated. The focus on community structure in this paper, as in Goldberg et al. (1995), does not require the inclusion of monocultures in the design. An examination of community function through measures such as stand productivity or nutrient cycling would be better served by designs that included monocultures and perhaps mixtures with less than the full complement of species examined (Connolly and Kirwan, in preparation).

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