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Author(s): Diego J. Rodríguez
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A method to study competition dynamics using de Wit replacement series experiments

***Diego J. Rodríguez**, Instituto de Zoología Tropical, Universidad Central de Venezuela, Apartado 47058, Caracas 1041-A, Venezuela (drodrigu@dino.conicit.ve).*

The methodology of the replacement series experiments designed by de Wit (1960) has been extensively used in ecological studies of competition between two species of plants (see references in Firbank and Watkinson 1990). It has also been used in some competition studies in *Drosophila* (Ayala 1971, Ayala et al. 1973, Mather and Caligari 1981). The method has proven to be useful to detect the existence and measure the magnitude of competition, as well as to find the combination of two species which maximizes the total yield of a mixture (Harper 1977). However, it has also been subject to many criticisms, mainly because of the dependence of the results on the density chosen for the experiments (Marshall and Jain 1969, Firbank and Watkinson 1985, Connolly 1986). As shown by some authors (e.g. Law and Watkinson 1987) this dependence can lead to erroneous conclusions about the outcome of competition. There are reasons, however, not to abandon the method. For example, the above criticisms have been challenged recently (Cousens and O'Neill 1993). Also, in plant ecological literature there is a large amount of data obtained with the replacement series method, and it is worthwhile devising alternative procedures oriented to obtain useful information concerning the ecological dynamics from these data. The purpose of this study is to propose one such procedure, showing that, in spite of all its shortcomings, replacement series data can in some cases be used to make valid ecological inferences on the competition between two species.

The replacement series method

The method of the replacement series experiment is the following. Two species are put in known initial densities to grow together, and their final densities are recorded. By comparing these results with those of experiments where only one species at the same density has been grown, the existence and intensity of competition can be detected. Also it is possible to obtain the combintion of initial densities which maximizes the total final density, which is called total yield. All this is performed with the calculation of various indices (Harper 1977). Let I_i and O_i be initial and final densities, respectively, of species i ($i = 1, 2$). The total initial density, $I_1 + I_2$, is kept constant and will be denoted d. The experiment is repeated with different combinations of I_1 and I_2. Then a plot is made of $\log(O_2/O_1)$ vs $\log(I_2/I_1)$. If the curve of this plot crosses the straight line of slope 1 then at such a point there is supposedly an equilibrium point of the system whose stability depends on the slope of the curve: the equilibrium will be stable if the slope is lower than one, and unstable if it is larger than one (Harper 1977).

One of the main problems with the inferences made with the replacement series method is that the equilibrium obtained corresponds to an artificial dynamical system in which at the start of each interval, or generation, of growth, the total initial density is kept at d and the relative initial densities of each species correspond to those of the final densities of the previous interval. The question arises: what would happen in a real ecological system where the species are allowed to grow without any manipulation of initial densities? I will show that there is a way of analyzing replacement series data to answer this question.

A new analysis of replacement series data

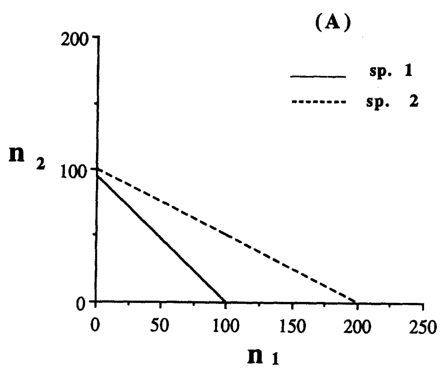
Let us assume that we know the mathematical model which governs the growth of the two-species system. Let this model be

$$n_{1,t+1} = n_{1,t} \exp(r_1 - a_{11}n_{1,t} - a_{12}n_{2,t})$$

$$n_{2,t+1} = n_{2,t} \exp(r_2 - a_{21}n_{1,t} - a_{22}n_{2,t}). \tag{1}$$

In this model $n_{i,t}$ is the number of individuals of species i at the start of generation t, r_i is the intrinsic rate of increase of species i, and a_{ij} is the strength of competition of species j on species i. Now I will show with a hypothetical example of a system growing according to eq. (1) that the stability inferences made with the traditional method in a replacement series experiment can be wrong. Fig. 1A shows the zero growth isoclines of a system (1) with a particular set of parameters in which species 2 outcompetes species 1. However, Fig. 1B shows the results of a replacement series experiment of the same system, with a curve crossing the straight line of slope 1 at a point of slope lower than one, which would lead to the conclusion that the species can coexist.

Now I will show that if the equations of growth are known, a different analysis of curves like that of Fig. 1B can help making valid inferences concerning the ecological stability. Again assume that eq. (1) governs the growth. A plot of $\log(O_2/O_1)$ vs $\log(I_2/I_1)$ is equivalent to a plot of $\log(n_{2,t+1}/n_{1,t+1})$ vs $\log(n_{2,t}/n_{1,t})$. Let us call $x = \log(I_2/I_1)$ and $y = \log(O_2/O_1)$. An expression of y as a function of x can be obtained as the equation for the curve of Fig. 1B. This equation is



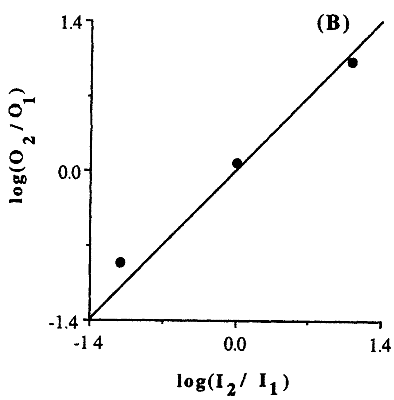


Fig. 1. (A) Zero growth isoclines of system (1) with parameters $r_1 = 4.0$, $a_{11} = 0.04$, $a_{12} = 0.042$, $r_2 = 2.0$, $a_{12} = 0.02$, $a_{21} = 0.01$. (B) Results of a replacement series experiment of the same system with $d = 80$; the three points correspond to species ratios 20:60, 40:40, and 60:20.

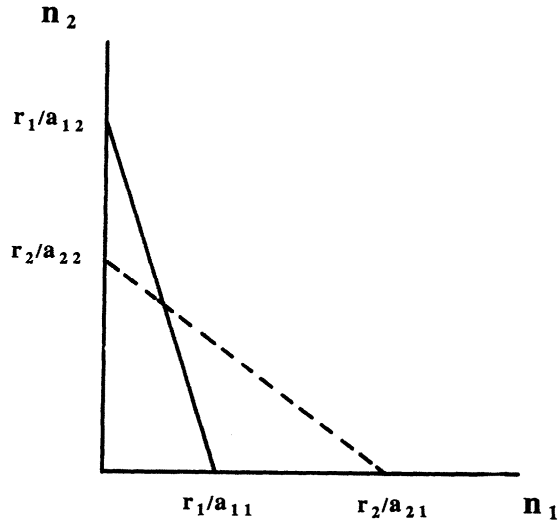


Fig. 2. Zero growth isocline for a system (1) with $r_1 = r_2$, $a_{12} < a_{22}$, and $a_{21} < a_{11}$. In this case there will be stable coexistence.

$$y = x + (r_2 - r_1) - (a_{21} - a_{11}) \frac{d}{1 + \exp(x)} - (a_{22} - a_{12}) \frac{d \exp(x)}{1 + \exp(x)}. \tag{2}$$

Having experimental data of x and y it should be possible with regression techniques to obtain estimates of the parameters of (2). From these estimates it is possible to make inferences about the results of the competition process. That these inferences can be made is clearly seen in Fig. 2, which shows the zero growth isoclines of a hypothetical system (1).

Now I will apply this method to a data set taken from Mather et al. (1982). These authors worked with three genotypes of ryegrass, *Lolium perenne*. They performed two types of experiments: monocultures in which the yield of plants of a genotype was measured for increasing initial densities, and duocultures which are replacement series experiments with a pair of genotypes. Table 1 shows the results of the monocultures experiments with genotypes C and E in the infrequent cutting regime, and Table 2 shows the results of the duoculture experiment with these two genotypes in the same regime. If these plants grow according to system

Table 1. Data from monocultures of two genotypes of ryegrass, *Lolium perenne*. Values shown correspond to two replicates of yield per plant (from Mather et al. 1982).

Initial density	Genotype C		Genotype E	
5	11.69	9.50	8.41	6.42
10	5.23	4.16	6.10	4.38
15	4.43	3.58	3.08	2.12
20	2.94	1.78	2.79	2.31

Table 2. Data from duocultures of two genotypes, C and E, of ryegrass *Lolium perenne*. Values shown correspond to mean yield per plant (from Mather et al. 1982).

Initial densities		Replicate 1		Replicate 2	
C	E	C	E	C	E
5	15	2.00	2.63	4.03	2.05
10	10	1.83	2.20	1.86	1.76
15	5	3.16	1.39	2.45	1.01

(1), the growth of a monoculture of genotype i should obey the equation

$$\frac{n_{i,t+1}}{n_{i,t}} = \exp(r_i - a_{ii}n_{i,t}), \qquad (3)$$

where $n_{i,t}$ is the initial density and $n_{i,t+1}/n_{i,t}$ represents mean yield per plant. The parameters of (3) can then be estimated by linear regression of log mean yield density per plant on initial density of the monocultures. As there are replicates of mean yield per plant for each initial density this regression allows the testing of the significance of lack of fit. The regressions were done following Draper and Smith (1981). In both genotypes there was no significant lack of fit. Fig. 3 shows the experimental data of mean yield per plant for each

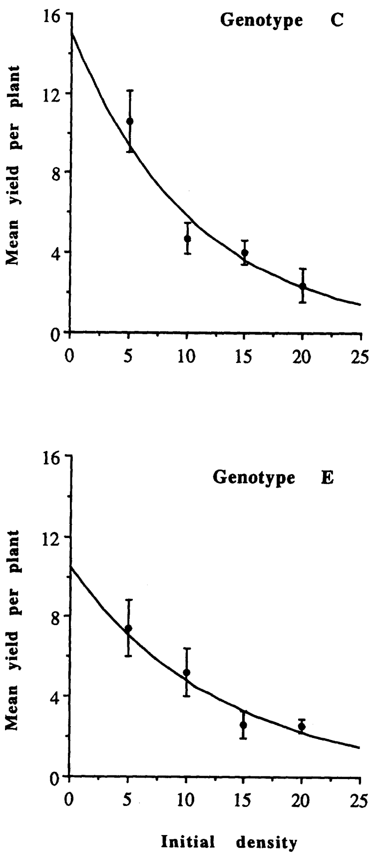


Fig. 3. Data of monocultures from Table 1, and the curve of eq. (3) corresponding to parameters of Table 3.

Table 3. Estimates of parameters of eq. (3) obtained with linear regression of log mean yield per plant on initial density in the monocultures (Table 1). Values shown are means and standard deviations. Subindices 1 and 2 correspond to genotypes C and E, respectively. Also shown are the estimates of the parameters of interspecific competition in eq. (1) obtained with nonlinear regression which fits eq. (2) to the data of duocultures (Table 2).

$r_1 = 2.711 \pm 0.207$	$r_2 = 2.350 \pm 0.209$
$a_{11} = 0.0948 \pm 0.0151$	$a_{22} = 0.0779 \pm 0.0153$
$a_{12} = 0.0937 \pm 0.0371$	$a_{21} = 0.1438 \pm 0.0371$

initial density as well as the curve of eq. (3) whose parameters were fitted with the regression mentioned above. There is good agreement between the experimental data and the fitted curve, indicating that the exponential model well describes the growth of monocultures.

If the interspecific interaction is also governed by system (1) then the relations between the quotient of final densities of genotypes, y, as a function of the quotient between initial densities of genotypes, x, should follow eq. (2). Knowing the values of r_{ii} and a_{ii} ($i = 1, 2$) from the regressions with monoculture data, it is possible to estimate a_{12} and a_{21} by fitting eq. (2) to the experimental points of x and y with nonlinear regression. This regression was performed using the method of Nelder-Meade (MATLAB 1989). The results of the estimates are shown in Table 3. The experimental data and the fitted curve are shown in Fig. 4. There seems to be good agreement between the experimental data and the fitted curve, suggesting that the competition process is adequately described with model (1). From the relationships between parameters in Table 3 it is now possible to infer the dynamic properties of the experimental system. An analysis of covariance (Sokal and Rohlf 1981) was performed to check for differences

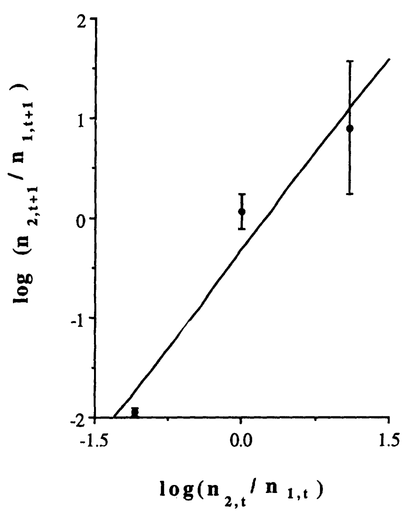


Fig. 4. Data of duocultures derived from Table 1, and curve of eq. (2) corresponding to parameters of Table 3.

between the two regression lines fitted to the logarithm of eq. (3). Such analysis detected no statistically significant differences between r_1 and r_2 ($F = 1.597$, $0.10 < P < 0.25$). Assuming that the estimates of Table 3 are normally distributed, the application of a Student's t test allows the following conclusions: a_{11} is significantly lower than a_{21} ($t = -1.869$, $0.025 < P < 0.05$); and a_{22} does not differ significantly from a_{12} ($t = -0.603$, $P > 0.25$). Then, performing a zero growth isocline analysis like that of Fig. 2, these conditions imply that, in the hypothetical case that the genotypes behave as different species, genotype 1 (C) would outcompete genotype 2 (E) in an ecological system growing according to eq. (1).

Discussion

The replacement series experiments method was devised to study the competition between two species. It has been widely used in plant ecology. It has also been criticized by several authors. Marshall and Jain (1969) and Firbank and Watkinson (1985) observed that the existence, position and stability of the equilibrium point depends on the density d. Inouye and Schaffer (1981) lucidly showed how this dependence can arise. Connolly (1986) detected a dependence of the indices obtained from replacement series experiments on the density d. Using response-surface graphs Law and Watkinson (1987) showed how a replacement series experiment can give misleading conclusions on the outcome of two-species competition. All these criticisms severely preclude the applicability of the replacement series method to study competition. Cousens and O'Neill (1993), however, report that the results of replacement series experiments are much less dependent on density variations than previously reported, so revindicating the method.

The present study further stresses the risks of using traditional analysis of replacement series data to infer the outcome of competition. I also developed a methodology of analysis of such data that can give valid inferences on the result of competition. An assumption of this methodology is that what we measure as input and output represent numbers of individuals of the same stage in consecutive generations. This is not the case in many experimental studies, as occurs with the example in the present work, in which the measurements are not done during an entire life cycle. To apply the method in these cases it would be necessary to assume that the competing species do not differ in their survivorship and/or fecundity through the portion of the life cycle which is not monitored.

The method requires knowledge of the model which governs the dynamics of the system. This knowledge can be obtained from previous studies, or can be inferred from the goodness of fit of an equation derived from the model to experimental data of monocultures and duocultures. When an experiment of replacement series is repeated for different values of d, there can be a set of estimates of the parameters of the growth model for each value of d. If the model chosen is adequate these sets of estimates should coincide, and this can be used as a check for the goodness of the model. It is important, however, to remember that significance of fit can never be taken as demonstration of any underlying dynamics. As the methodology depends critically on the selection of the dynamic model, such selection has to be properly made. There are several density dependent models different from (1) used for plants (Firbank and Watkinson 1990) and animals (Mueller and Huynh 1994). With any of these models it is also possible to find the corresponding formulas relating x and y, as well as the relationships between parameters of the growth model which ensure species coexistence.

To test the approach proposed in this study it would of course be necessary to apply it to the data of a de Wit experiment, and compare the results obtained with the observation of a longer term experiment. However, studies are rarely done with both a de Wit design and several generation monitoring simultaneously. Such studies can be done as a calibration for the methodology of the present study.

It would be interesting to apply the methodology to the abundant data collected with the replacement series method in order to infer on the coexistence of competing species, so assessing the potential of competition interactions as a structuring force in ecological communities.

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