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Suppression and hierarchy in a competition experiment between populations of *Lolium perenne* and *Trifolium repens*: a comparison of two methods of measurement

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Abstract. Suppression and hierarchy are two concepts associated to plant population structure. Two methods of measurement, one for each concept, are compared on the same data set. It appears from the results that the degree of suppression does not necessarily indicate the strength of the size hierarchy. Thus, it seems that both suppression and hierarchy are complementary aspects of the structure of plant populations.

Resumen. *Supresión y jerarquía en un experimento de competencia entre poblaciones de* Lolium perenne *y* Trifolium repens: *una comparación de dos métodos de medida.* Dos conceptos que van asociados a la estructura de las poblaciones vegetales son los de supresión y jerarquía. Para cada uno se ha propuesto un método de medida y el objetivo de este trabajo ha sido el de comparar el comportamiento de ambos en un mismo conjunto de datos. De los resultados se desprende que el grado de supresión de una población no indica necesariamente el nivel de jerarquización de dicha población; de aquí, que los dos conceptos puedan ser considerados aspectos complementarios de la estructura de las poblaciones vegetales.

Introduction

Growth studies of plant populations of annual species have shown that yield per unit area is relatively constant for a wide range of densities (law of constant yield, see White 1981 and references therein). In this situation mean plant weight decreases as density is increased. However, interesting aspects expressed by the shape of the weight frequency distribution of individual plants may be concealled by the use of means since usually the mean is not representative of the most common plant in the population (Harper 1977). The weight frequency distribution of individual plants in a population changes from a normal distribution in early stages of plant growth to a lognormal one in later stages as a consequence of the exponential nature of plant growth (Koyama & Kira 1956). The concept of suppression is applied to the intensity of interference among plants in a population and

it is assumed that it exagerates the shape of the initial size distribution. A concept related to suppression is that of hierarchy (Weiner & Solbrig 1984). Three elements conform the degree of hierarchy in a population, that is, (1) a great variation of individual plant weight; (ii) occurrence of few large plants and many small ones; and (iii) a high proportion of total mass and seed output concentrated in a few large plants. Both the degree of suppression and the level of hierarchy within a population are influenced by population density, kind of competitors, predators, habitat differences, etc. so a measure of both concepts would be interesting when comparing the population dynamics of the same or similar species.

It is interesting to comment a methodological difference between hierarchy and suppression. The degree of hierarchy gives account of the population structure in a single point of time, and it is assumed that two unrelated populations may be scaled along an axis of hierarchy. On the other hand, because the degree of suppression refers to the interference exerted within the population during a period of time, two stages (or phenological phases) are required no provide a measure of the strength of interference. Both measures should be viewed as intuitive tools which may be useful in field studies of demography rather than an objective to be measured in itself. Since a deeper understanding of the behaviour of both measures in plant populations is needed, the purpose of this paper is to constrast both approaches using the same data set.

Methods

The data used in this study come from a replacement series experiment (de Wit 1960) carried out by Di Tella (1983) to study competition between *Lolium perenne* and *Trifolium repens*. The proportion and densities of both species were: 16L:0T; 12L:4T; 8L:8T; 4L:12T; OL: 16T where L indicates *Lolium* and T, *Trifolium*. The design was replicated four times and was conducted in a greenhouse. Plants were harvested when *Lolium* was at ripening stage, dried in the owen and weighed. The different mixtures will be labeled as L4, L3, L2 and L1, and T4, T3, T2 and T1 which correspond to population densities of 16 (pure cultures), 12, 8 and 4 plants per pot for each species respectively.

I have estimated the degree of suppression in each population as expressed in Soria (1985). In short, the method consists in the calculation of the cummulative function of the Shannon index (H') on each consecutive weight frequency class, starting from the lowest one. The representation of the cummulative H' values gives a sigmoidal curve for a gaussian distribution of weights, and a rectangular for a skewed one. The statistical comparison of these curves were done by a Kolmogorov-Smirnov test applied to the distributions of individual weights, dividing the range of weights in 500 equal intervals. The strength of population hierarchy was measured acording to

Weiner & Solbring (1984). The procedure requires first the ordenation of plants according to increasing size, and second the representation of the cummulative percentatge of population mass versus the cummulative percentatge of population. This plot is called a Lorenz curve by economists, and is a straigth line (the diagonal of a square) for a population composed of plants of equal weight, and a hollow curve when the parent distribution is lognormally distributed. The degree of hierarchy is reflected by the departure of the curve from the diagonal, and is measured by the Gini coefficient (see Sen 1973), that is:

$$G = 1 + (1/n) - (2/n^2 \cdot u)\,(x_1 + 2x_2 + \ldots + nx_n); \quad x_i \geqslant x_{i+1}$$

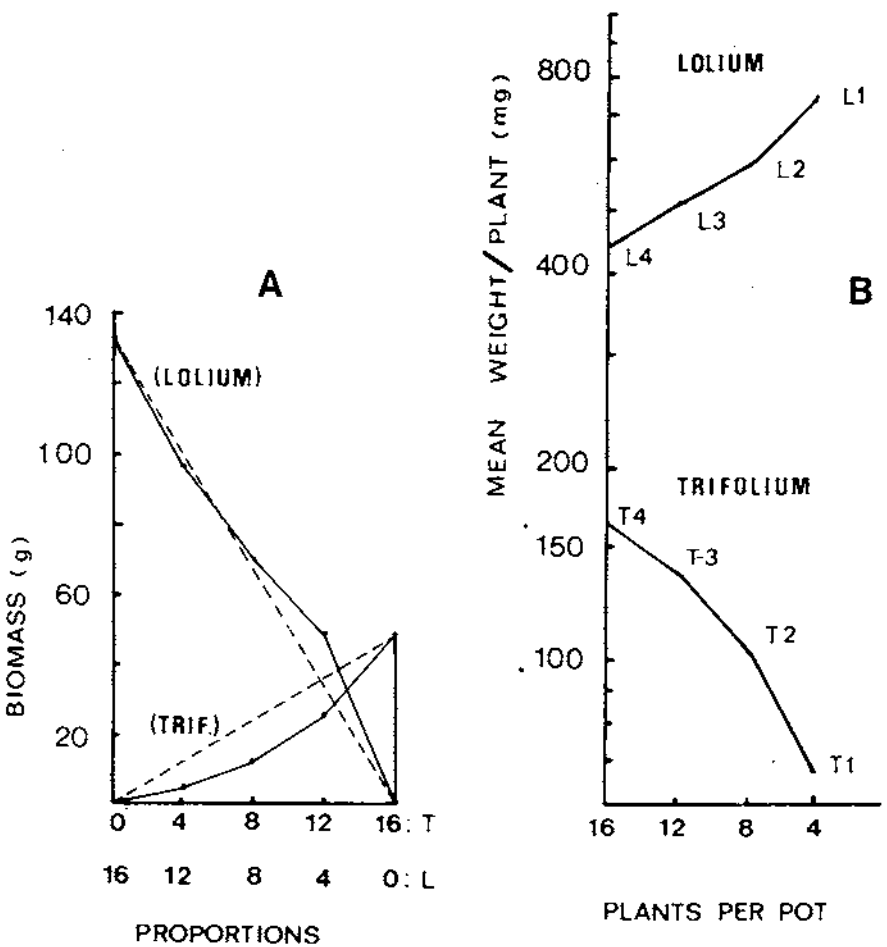

Figure 1. (A) Population performance of *Lolium perenne* and *Trifolium repens* in the sowing mixtures. The broken line is the expected mass of monocultures of the same density. (B) mean weight per plant versus the population density in each mixture.

where n is sample size, u the mean plant weight and x the weigth of individual plants.

In order to compare two Lorenz curves the jacknife method was used, (Higgins et al. 1984) obtaining first an error estimate of the coefficients, and then applying a t-test.

Results

The species performance at the different mixtures are represented in Figure 1 and corresponds to a case of compensation (de Wit 1960). The production of *Lolium* in the 12L:4T and 8L:8T mixtures is equivalent to that expected from monocultures if planted at the same total density (broken line in Figure 1a). However, the production at the 4L:12T combination is higher than that of monocultures. In contrast, the production of *Trifolium* is lower than expected in all sowing proportions, the reduction being about 8 to 10 g in presence of either 12 or 8 plants of *Lolium*. Figure 1b shows that as the proportion of *Trifolium* is decreased the mean plant weigth of *Lolium* increases in a linear form; and, conversely, the mean weight of *Trifolium* decreases when the proportion of *Lolium* is increased.

Table 1 shows that both the pure culture, t4, and the T1 mixture present a similar degree of hierarchy (Gini coefficient of 0.26 and 0.27 respectively); the same applies to the pair T2, T3 (Gini coefficient of 0.32); that is, the «extreme» populations, T1 and T4, were less hierarchical than those of the two intermediate mixtures. In addition, the difference between T2 and T4, and T3 and T4 were statistically significant (Table 2). In the population of *Lolium* the degree of hierarchy seemed to decrease with the purity of the mixture (Table 3); that is, the L1 mixture was the most hierarchical, while

Table 1. Gini coefficient, mean weight per plant, and coefficient of variation (C. V.) for the four *Trifolium* populations.

	Population [a]			
	T1	T2	T3	T4
g_j (Gini coef.)	0.260	0.320	0.320	0.270
s.e. (g_j)	0.027	0.019	0.015	0.010
d.f.	61	115	181	301
mean weight ($\bar{x}$) (mg)	66. 37	103. 83	138. 75	162. 33
s.e. ($\bar{x}$)	4. 11	5. 66	5. 85	4. 58
C.V. %	48. 14	58. 73	56. 99	49. 04

[a] T1, T2, T3 and T4 contain, respectively, 4, 8, 12 and 16 plats of *Trifolium repens* and 12, 8, 4 and 0 plants of *Lolium perenne* per pot.

Table 2. Pair comparisons of the four *Trifolium* populations: t-test compares size hierarchy; and K-S, degree of suppression. For symbols, see Table 1.

Populations compared	t-test	d.f.	K-S test	K-S (5 %)
T1, T2	–1.963	176	0.138	0.214
T1, T3	–1.923	242	0.122	0.200
T1, T4	–0.338	362	0.086	0.190
T2, T3	0.206	296	0.069	0.162
T2, T4	2.520*	416	0.115	0.149
T3, T4	2.664*	482	0.112	0.128

* ($P < 0.05$)

Tabla 3. Gini coefficient, mean weight per plant, and coefficient of variation (C. V.) for the four *Lolium* populations.

	Population [a]			
	L1	L2	L3	L4
g_j (Gini coef.)	0.322	0.274	0.229	0.233
s.e. (g_j)	0.024	0.015	0.011	0.010
d.f.	63	118	191	316
mean weight ($\bar{x}$) (mg)	756. 23	591. 93	504. 33	420. 08
s.e. ($\bar{x}$)	56. 08	27. 55	14. 76	10. 26
C.V.(%)	59. 33	50. 77	40. 56	43. 49

[a] L1, L2, L3 and L4 contain, respectively, 4, 8, 12 and 16 plants of *Lolium perenne* and 12, 8, 4 and 0 plants of *Trifolium repens* per pot.

Tabla 4. Pair comparisons of the four *Lolium* populations: t-test compares size hierarchy; and K-S, degree of suppression. For symbols, see Table 3.

Populations compared	t-test	d.f.	K-S test	K-S (5 %)
L1, L2	1.636	181	0.148	0.211
L1, L3	3.494	254	0.339 *	0.196
L1, L4	3.335 *	379	0.180	0.186
L2, L3	2.383 *	309	0.272 *	0.159
L2, L4	2.160 *	434	0.114	0.146
L3, L4	0.304	507	0.303 *	0.124

* ($P < 0.05$)

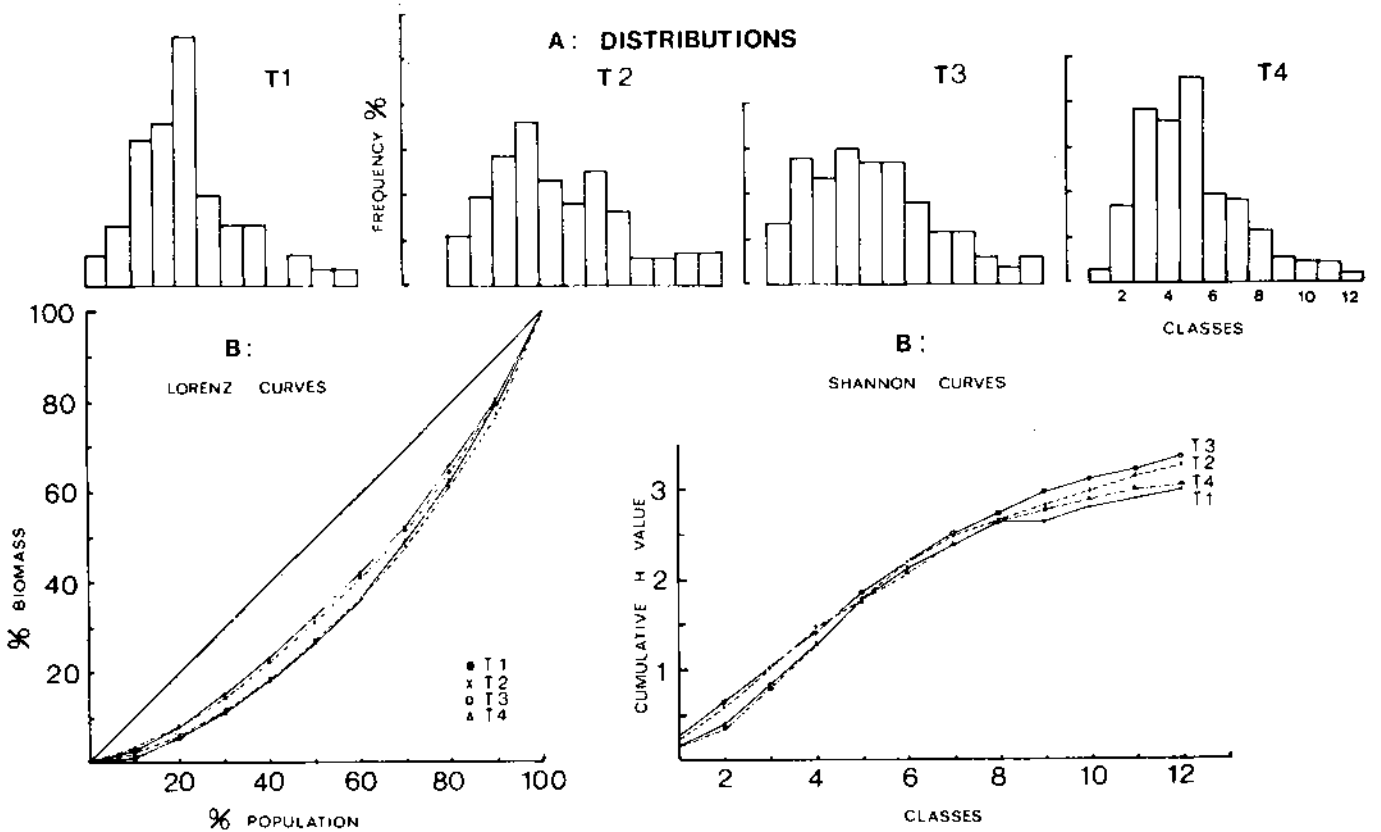

Figure 2. (A) *Trifolium repens*. Weight frequency distribution of individual plants in each mixture. The classes depicted are ordinal classes. (B) Lorenz and Shannon curves generated from the distributions of (A). The diagonal in the left figure represents the perfect equality among members of an ideal population. For symbols, see methods section.

L4 had the lowest value; and the pairs L2, L3; L1, L3 were also significantly different. Nevertheless, the comparisons between L1 and L2, and L3 and L4 were not significant. (Table 4).

The populations of *Trifolium* presented a similar level of suppression since all comparisons were statistically not significant (Table 2). The two pairs most alike were T2, T3, while the pair T1, T2 was the most dissimilar (the highest K-S values in Table 2). In the case of *Lolium* only comparisons involving L3 were significantly different (Table 4).

Discussion

The interpretation on the results on suppression merits a methodological comment. The comparison provided by the K-S test can tell us wether or not the degree of suppression exerted within different populations are of similar magnitude, as indicated by the Shannon (SH) curves. Thus the case of T1 and T4 tells us that the presence of 12 plants of *Lolium* results in an equivalent degree of suppression as that of a pure culture of 16 plants of *Trifolium* per pot. From the point of view of hierarchy, both T1 and T4 show the same (low) level of hierarchy (Fig. 2b). Thus in this case suppression and hierarchy are congruent. On the other hand the non significance of the calculated K-S value in the pair L1, L4 implies that the presence of 12 Trifolium plants are equivalent in their suppresive action as that exerted within a pure population of 16 plants of Lolium per pot. The same argument applies to the pair L2, L4. However L1 is more hierarchical than L4 (see Lorenz curves in Figure 3b, and the coefficient of variation or Gini coefficient in Table3); and L2 is also more hierarchical than L4.

In other terms, L1, the population with the greatest level of interspecific interference, gives a Lorenz curve that indicates a higher hierarchy than that of L4, the population with nil interspecific interference; yet, both L1 and L4 give similar SH curves (Fig. 3b). Comparison of L2 and L4 follows the argument above in the same direction: L2, the population with higher interspecific interference is more hierarchical than the pure population L4, but both present equal SH curves. However the case of the pair L3, L4, is reverse, since both show similar levels of hierarchy but L4, the pure culture, shows a higher degree of suppression than L3. Thus two populations may show similar levels of suppression but not necessarily the same degree of hierarchy (and viceversa); or, in other terms the more suppressed population does not necessarily correspond to the more hierarchical one. Although the construction of histograms depends on an arbitrary decision, we only appreciate the intuitive value of suppression in a population by the shape of the frequency distribution. However, comparisons of two distributions, although spurious in appearance, are perfectly correct since they are contrasted after dividing the range in many intervals (see methods section). Thus it seems that suppression and hierarchy would tell us complementary aspects

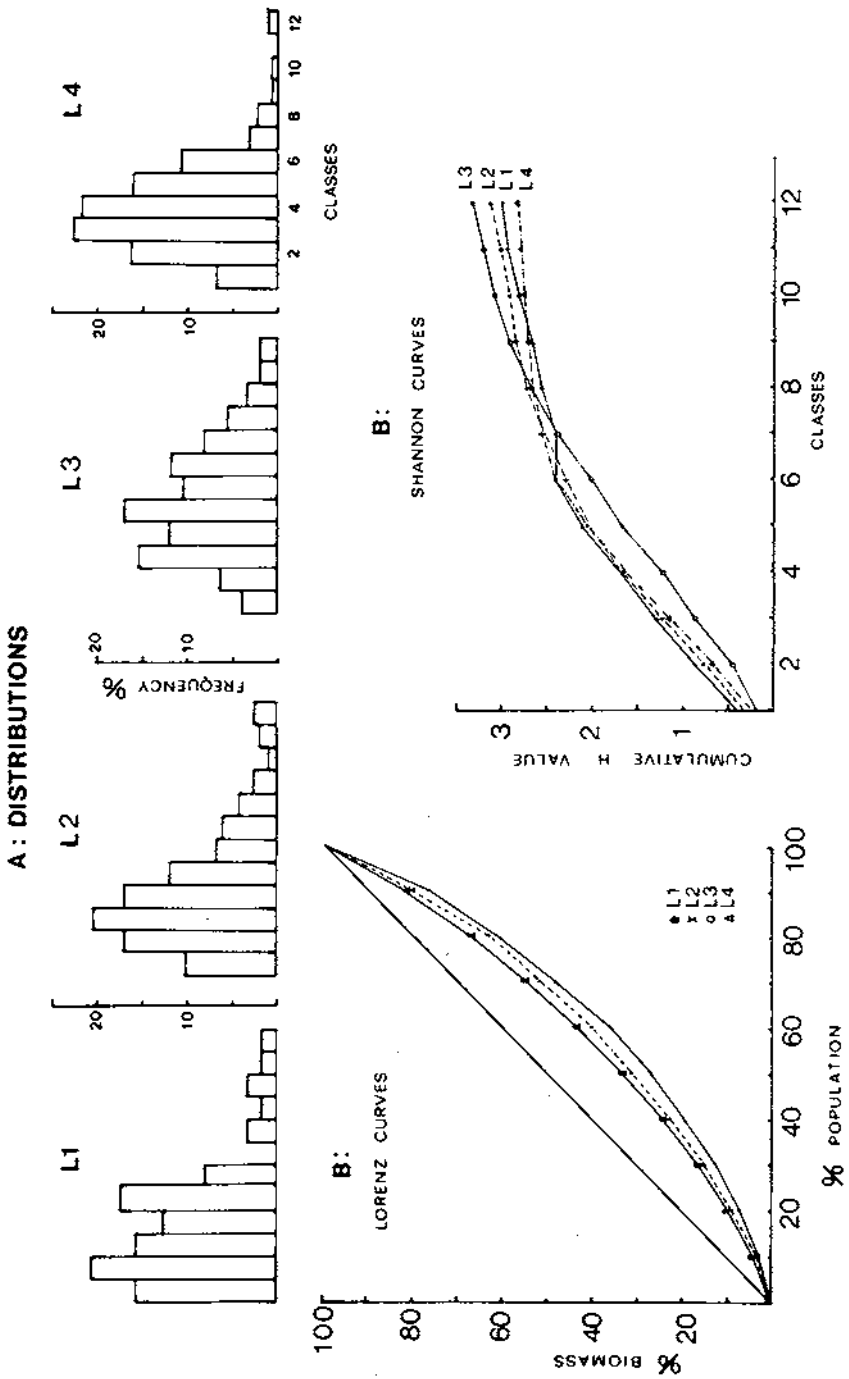

Figure 3. *Lolium perenne*. Same legend as in Figure 2.

of plant population structure: the first associated with the particular sequence of ordered individual weights; the second, with the variation around the mean plant weight. Nevertheless, more data are needed to ascertain the relevance and utility of both measures in field studies of plant populations.

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