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# THE ANALYSIS OF DYNAMIC INTERACTION IN A LEGUME BINARY MIXTURE UNDER CONTROLLED CONDITIONS OF IRRIGATION AND CLIPPING

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## ABSTRACT

The objective of this study was to analyse the type of interference that occurred between the annual legume species, purple clover (*Trifolium purpureum* L.) and narrow leaved crimson clover (*Trifolium angustifolium* Loisel.), growing in mixed conditions under two different watering regimes and two different clipping treatments. A replacement series experiment was conducted in pots placed in the field. The above ground biomass (gr/plant) were measured. The recently proposed Inverse Linear Model was implied in order to analyse the competitive interaction between the above species. The results suggest that *Tr. purpureum* was the superior competitor to *Tr. angustifolium* and a remarkable niche differentiation was occurred after the clipping treatment.

## KEYWORDS

Interference, replacement series, inverse linear model, resource use, grazing, density

## INTRODUCTION

The annual legume species are very widespread species which occur in almost all temperate and tropical areas of the world. *Trifolium purpureum* (L.) and *Trifolium angustifolium* (Loisel.) are very close and common annual legume species widely expanded in the Mediterranean region. There is a lack of knowledge about the type of interference involved between these two species and especially under drought and grazed conditions. Moreover, there is a lot of controversy about the approaches used in quantification of interaction outcome in mixture experiments. de Wit (1960) proposed the approach of "Replacement Series", which has accepted a strong criticism (Connolly and Nolan, 1976; Joliffe et al., 1984; Firbank and Watkinson, 1985; Connolly, 1987; Silander and Pacala, 1990; Silvertown and Dale, 1991). Spitters (1983) and Connolly (1986) have proposed the Inverse Linear Model (I.L.M.), which the particular forms, of two species grown in mixture, are:

$$1/W_1 = a_{10} + a_{11}d_1 + a_{12}d_2 \quad (1)$$

$$1/W_2 = a_{20} + a_{21}d_1 + a_{22}d_2 \quad (2)$$

where  $d_1$  and  $d_2$  the densities of species 1 and 2, respectively,  $a_{11}$  and  $a_{22}$  the intraspecific coefficients that measure the effect of the density of a particular species on itself,  $a_{12}$  and  $a_{21}$  are the interspecific coefficients measuring the effect of the density of one species on the other and  $a_{10}$ ,  $a_{20}$  present the intercept, often interpreted as attributes of spaced plants, although this is not always correct (Connolly, 1986). Besides, Vleeshouwers *et al.* (1989) have proposed the niche differentiation index of species grown in mixture, expressed by the ratio quotient:

$$R = (a_{11}/a_{12})/(a_{21}/a_{22}) \quad (3)$$

where  $a_{11}$ ,  $a_{12}$ ,  $a_{21}$  and  $a_{22}$  are the parameters obtained by the I.L.M. (eq. 2, 3). If  $R=1$  the two species compete for the same resources,  $R<1$  indicates in some way an inhibition and  $R>1$  indicates in some way a niche separation (Spitters, 1983; Connolly, 1987).

The objective of this experiment was the study and the analysis of the interference type involved between the *Trifolium purpureum* L. and *Trifolium angustifolium* Loisel. growing in several total constant and relative densities, as well as the niche differentiation, under cut and drought conditions.

## MATERIALS AND METHODS

The experiment was conducted in northern Greece, in the University farm (40°34' E, 23°43' N, at the sea level). Two annual legume species, *Trifolium purpureum* (L.) and *Trifolium angustifolium* (Loisel.) were established in pots in the beginning of 1990, at two different watering regimes ( $W_0$ ,  $W_1$ ) and three different clipping dates ( $C_1$ ,  $C_2$ ,  $C_L$ ). The pots had the same soil mixture.  $W_0$ ,  $W_1$  indicate unwatered (only the rainfall) and watered plants (watering until field

capacity). Tensionmeters had been placed in the pots to control the watering condition of the soil.  $C_1$ ,  $C_2$ ,  $C_L$  indicate the clipping dates of 19 May, 4 July and 19 August (last clipping), respectively.  $C_1$  and  $C_2$  indicate successive clippings instead of  $C_L$  which indicate that the initial plants were clipped all at once. Thus, there were 6 combined treatments ( $W_0C_1$ ,  $W_0C_2$ ,  $W_0C_L$ ,  $W_1C_1$ ,  $W_1C_2$  and  $W_1C_L$ ) and three replications in each relative density. Three total constant densities: 6, 12, 18 plants/pot and five relative densities in each total density: 1/0, 2/1, 1/1, 1/2, 0/1 (varied from monoculture of *Tr. angustifolium* to monoculture of *Tr. purpureum*) were established in a replacement series (3 replacement lines) experiment (Fig. 1). The above ground biomass (dry weight), expressed as gr/plant of the component species, after the above treatments application, were determined. The inter- and intraspecific coefficients (eq. 1, 2) and the niche differentiation index  $R$  (eq. 3), as well, were calculated.

## RESULTS AND DISCUSSION

The set of equations of the I.L.M. (eq. 1, 2) and the dry weight data (gr/plant) analysed according to the I.L.M. for six combined treatments were presented in Tables 1a and 1b.

### A. Unwatered Treatment ( $W_0$ )

a<sub>1</sub>) **Interference.** The intraspecific coefficients  $a_{11}$ ,  $a_{22}$ , suggest an expected reduction of the above ground biomass related to the successive clippings in both of the species. This reduction was significant in *Tr. angustifolium* (0.020 and 0.046 for the successive clippings instead of 0.493 for the last clipping). It means that the application of clipping on the plants of *Tr. angustifolium* improved the intraspecific effect reflected upon its above ground biomass. The interspecific coefficients  $a_{12}$  in *Tr. purpureum*, suggest that the interspecific effect of density of *Tr. angustifolium* reflected upon the above ground biomass of *Tr. purpureum*, was very small and remains rather stable at the first and at the last stage of its growth (0.016 and 0.018, respectively), indicating that *Tr. purpureum* exploit better the remaining available resources (e.g. light) and avoid the cumulative effect of unwatered conditions. The successive clipping almost remove the interspecific effect (0.0003), that permits the intraspecific effect to control the performance of *Tr. purpureum*. Conversely, the successive clipping diminished the interspecific effect ( $a_{21}=0.172$ , 0.605 for  $C_1$  and  $C_2$  instead of 4.093 for the last clipping) in *Tr. angustifolium*. However, these values remained high, indicating a remarkable suppression exerted by *Tr. purpureum* on *Tr. angustifolium* which appears to reduce its effectiveness in the preemption of the remaining available resources (e.g. light).

b<sub>1</sub>) **Niche differentiation.** The values of 0.37 and 0.57 of  $R$  (eq. 3, Table 1a) for  $C_1$  and  $C_L$ , respectively, suggest a strong inhibition of the plants' performance related with resources preemption, instead of 10.81 ( $a_{12}=0.0003$ ) for  $C_2$  that suggests niche separation between the species. In the rest clippings, the combined intraspecific effect ( $a_{11}, a_{22}$ ) is less than the interspecific one ( $a_{12}, a_{21}$ ), a fact that resulted in strong competition due to resources preemption.

### B. Watered treatment ( $W_1$ )

a<sub>2</sub>) **Interference.** The intraspecific coefficients  $a_{11}$ ,  $a_{22}$ , show that the intraspecific effect of  $C_1$  and  $C_2$  clipping on *Tr. purpureum* and *Tr. angustifolium* was greater than  $C_L$ , a fact that was probably due to the exhibition by the plants of both species to favour watered conditions for a long time period, thus they were able to exploit all the available water supply. The interspecific coefficients  $a_{12}$ , for *Tr. purpureum*, show that the intraspecific effect of density of *Tr. angustifolium* was very small, almost nonexistent, and it remains rather stable (0.003 to 0.001), suggesting that in binary mixtures the plants of *Tr. purpureum* exploit better the available water. The successive clipping didn't change this status (0.002). Conversely, in *Tr. angustifolium*, the  $C_1$  clipping diminished the interspecific effect,

from 0.138 to 0.071. The successive  $C_2$  clipping, gave higher interspecific coefficient (0.212), a fact probably due to the better resources exploitation from the plants of *Tr. purpureum*. Never the less, these values were lower than those obtained in  $W_0$  treatment. This was due to the favouring of watered conditions that reduced the intensity of interspecific effect of *Tr. purpureum* on *Tr. angustifolium*.

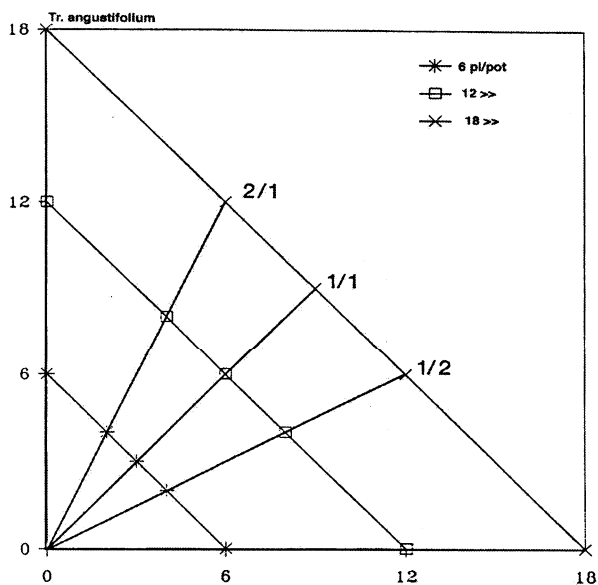
b.) **Niche differentiation.** The R values of 2.94 and 2.65 (Table 1b) for  $C_1$  and  $C_2$  clipping suggest a niche separation between the two species instead of the 0.70 value of  $C_L$  which suggests a strong inhibition of performance related with water preemption. For  $C_1$  and  $C_2$  clippings, the niche separation was due to the very low  $a_{12}$  interspecific coefficients (0.003 and 0.002, respectively). For the last clipping, the low value of  $a_{12}$  (0.001) in relation to combined effect of intraspecific coefficients ( $a_{11}, a_{22}$ ) resulted in strong inhibition. The range of niche differentiation indices (R) was greater in  $W_0$  treatment (from 0.37 to 10.81) than in  $W_1$  treatment (from 0.70 to 2.94), indicating that the differences in niche differentiation were more blunt in watered than in unwatered conditions.

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**Figure 1**

Diagram of the experimental design (3 replacement lines) showing the combinations of total and relative densities of *Tr. purpureum* and *Tr. angustifolium*.



**Table 1a** Yield (gr/plant) of *Tr. Purpureum* ( $W_1$ ) and *Tr. angustifolium* ( $W_2$ ) in the replacement series at  $C_1C_2$  and  $C_L$  clippings in unwatered treatment ( $W_0$ ). The inter- and intra-specific coefficients were calculated by I.L.M. (eq. 1, 2). The niche differentiation index (R) was calculated by eq. 3. The subscripts 1 and 2 denote *Tr. purpureum* and *Tr. angustifolium*, respectively.

Relative densities		$C_1W_0$		$C_2W_0$		$C_LW_0$	
$d_1$	$d_2$	$W_1$	$W_2$	$W_1$	$W_2$	$W_1$	$W_2$
6	0	2.504	0	1.336	0	1.143	0
4	2	3.494	0.601	2.025	0.28	1.864	0.235
3	3	3.558	1.305	2.256	0.4	2.069	0.307
2	4	5.636	1.451	3.983	0.617	3.753	0.487
0	6	0	1.926	0	0.849	0	0.626
12	0	1.528	0	1.376	0	0.966	0
8	4	2.077	0.452	1.342	0.2	1.007	0.134
6	6	2.208	0.719	1.458	0.233	1.121	0.137
4	8	2.832	0.868	1.775	0.475	1.249	0.353
0	12	0	1.166	0	0.669	0	0.452
18	0	1.078	0	0.883	0	0.556	0
12	8	1.299	0.331	1.263	0.1	0.763	0.013
9	9	1.452	0.569	1.35	0.167	0.914	0.067
6	12	1.836	0.696	1.786	0.375	1.137	0.243
0	18	0	0.883	0	0.405	0	0.272
$a_{10}$		0.0541		0.3348		0.1828	
$a_{11}$		0.05		0.0431		0.0864	
$a_{12}$		0.0161		0.0003		0.0184	
$Sa_{11}$		0.0022		0.0068		0.0079	
$Sa_{12}$		0.0027		0.0082		0.0095	
$Pa_{11}(\%)$		0		0.0001		0	
$Pa_{12}(\%)$		0.0002		0.9745		0.0859	
$R^2$		0.98		0.83		0.93	
$a_{20}$		0.456		0.51		-11.235	
$a_{22}$		0.0203		0.0455		0.4932	
$a_{21}$		0.1723		0.605		4.0933	
$Sa_{22}$		0.0231		0.078		1.096	
$Sa_{21}$		0.0277		0.0934		1.316	
$Pa_{22}(\%)$		0.403		0.5279		0.6633	
$Pa_{21}(\%)$		0.0002		0.0001		0.0125	
$R^2$		0.81		0.83		0.52	
R		0.37		10.81		0.57	

**Table 1b** Yield (gr/plant) of *Tr. Purpureum* ( $W_1$ ) and *Tr. angustifolium* ( $W_2$ ) in the replacement series at  $C_1C_2$  and  $C_L$  clippings in watered treatment ( $W_1$ ). The inter- and intra-specific coefficients were calculated by I.L.M. (eq. 1, 2). The niche differentiation index (R) was calculated by eq. 3. The subscripts 1 and 2 denote *Tr. purpureum* and *Tr. angustifolium*, respectively.

Relative densities		$C_1W_0$		$C_2W_0$		$C_LW_0$	
$d_1$	$d_2$	$W_1$	$W_2$	$W_1$	$W_2$	$W_1$	$W_2$
6	0	4.528	0	6.742	0	7.737	0
4	2	6.163	0.988	8.211	1.799	12.901	2.298
3	3	7.158	1.57	8.744	1.901	13.397	3.917
2	4	7.658	1.828	9.433	2.222	15.845	4.739
0	6	0	1.9	0	3.636	0	5.576
12	0	2.531	0	3.859	0	4.667	0
8	4	2.564	0.938	4.167	0.784	6.003	0.506
6	6	4.024	1.148	5.908	1.238	8.359	1.579
4	8	4.214	1.51	6.047	1.741	10.249	2.311
0	12	0	1.662	0	2.351	0	3.188
18	0	1.392	0	2.088	0	2.842	0
12	8	2	0.675	3.392	0.3	3.408	0.609
9	9	2.789	0.858	4.048	0.5	5.101	0.735
6	12	4.016	0.983	5.714	1.167	7.839	1.988
0	18	0	0.883	0	1.404	0	2.863
$a_{10}$		0.0213		0.034		0.0034	
$a_{11}$		0.0368		0.0224		0.196	
$a_{12}$		0.0034		0.0017		0.002	
$Sa_{11}$		0.0027		0.0018		0.0013	
$Sa_{12}$		0.0033		0.0022		0.0015	
$Pa_{11}(\%)$		0		0		0	
$Pa_{12}(\%)$		0.3179		0.4504		0.2196	
$R^2$		0.96		0.95		0.96	
$a_{20}$		0.4078		-0.2878		-0.0028	
$a_{22}$		0.0194		0.0426		0.0098	
$a_{21}$		0.0714		0.2115		0.1378	
$Sa_{22}$		0.0092		0.0294		0.0243	
$Sa_{21}$		0.0111		0.0353		0.0291	
$Pa_{22}(\%)$		0.0648		0.1812		0.6956	
$Pa_{21}(\%)$		0.0001		0.0002		0.011	
$R^2$		0.82		0.8		0.72	
R		0.37		10.81		0.57	