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SUMMARY

The value of grass-legume associations is still under discussion from both agronomic and breeding points of view, chiefly because of contrasting conclusions on the nature of interference effects. A set of experiments was carried out at Lodi in 1980-84, to determine the effect of interspecific interference on the single partners and on associations as a whole. The general conclusions drawn from these experiments and their consequences for breeding strategies are summarized and discussed in this paper. Comparison of different models for analysis of the experimental data suggested a possible explanation of the different opinions on the nature of interference effects.

Additional key words : *Biological density, binary mixture, competition, genetic association ability, interference, plastic response.*

RÉSUMÉ

Etude expérimentale des associations entre légumineuses et graminées fourragères.

L'intérêt des associations légumineuses-graminées est toujours en discussion, tant du point de vue agronomique que des stratégies à adopter dans la sélection ; la cause principale de ce débat est à chercher dans les différentes conclusions sur la nature des effets d'interférence au niveau inter-spécifique. Une série d'expériences a été réalisée à Lodi de 1980 à 1984 pour éclaircir ce point. Les conclusions d'ordre général et les conséquences pour la sélection sont discutées dans cette note. La comparaison entre différents modèles d'analyse des données expérimentales a permis de mettre en évidence une des causes possibles des différentes interprétations existant jusqu'à présent sur la nature des effets d'interférence au niveau inter-spécifique.

Mots clés additionnels : *Aptitude génétique à l'association, association binaire, compétition, densité biologique, interférence, réponse plastique.*

I. INTRODUCTION

The value of grass-legume associations is still under discussion, not only from the agronomic point of view of harvestable biomass, but also and chiefly from that of the nature of the interference effects produced within the associations themselves. As a consequence, breeding strategies for the creation of cultivars to be used in grass-legume associations are also under discussion. In fact, the objective of creating associations able to produce more biomass than monocultures demands different strategies, depending on the type of relationships found either between the associated partners or between the partners and monocultures.

In a series of experiments on intra-specific interference effects between lucerne, red clover, tall fescue and cocksfoot (ZANNONE *et al.* 1983) we found that the situations created inside the binary associations, as represented by the "plastic response" (JACQUARD, 1972), were generally situations of competition with one partner gaining and the other losing when compared with a pure stand. The gain made by one partner was generally compensated by the loss made by the other ; as a consequence, intra-specific binary associations did not generally present any agronomic advantage over the corresponding monocultures.

The hypothesis by which we interpreted these generalized situations of competition was that the winning partner should find in mixture a lower biological density (as defined by ROTILI, 1979) than in pure stand, while the weaker partner should find in mixture a greater biological density than in pure stand. In other words, intra-specific interference effects were manifested as "density" effects. This hypothesis was supported by the relationship which exists between the vigour of populations and the slope of the "plant weight/density" regression line. Moreover, we observed a linear relationship between the yield of binary associations and the ratio between the corresponding two monocultures : such a relationship can be explained by variation in biological density (ZANNONE, 1985).

Starting from this hypothesis, we carried out a series of experiments on binary grass-legume associations, the results of which have been partially published (ROTILI *et al.*, 1982 ; ZANNONE *et al.*, 1982 ; PAOLETTI & LOCATELLI, 1982). These experiments were analyzed by the same procedure as the intra-specific association experiments, by calculating the "plastic responses" of both partners at each cut. This allows description of the development, over the course of the season, of each partner in comparison with the other and of both in comparison with the respective monoculture. The importance of this analysis is founded on the fact that cutting is one of the principal and drastic factors affecting crop structure during the season. In addition, we observed that the analysis of "plastic responses" made on the average of several cuts gave in many cases results contrasting with those of cut-by-cut analysis. In particular, analysis based on averages showed some cases of "co-operation" despite the fact that cut-by-cut analysis always showed only situations of competition.

Following such observations, we also considered that analyses made following the GALLAIS (GALLAIS, 1970) and MAÎTRE (MAÎTRE, 1977) methods, usually applied to average data, have sometimes given results indicating situations of co-operation. So, we decided to apply such methods of analysis to our cut-by-cut data, in order to verify if the contrasting results were due to the different models or to the different way of applying them.

The GALLAIS model gives indications on the "general and specific associating ability", either in terms of mean squares or by parameters assigning to each population its proper value. A series of correlation coefficients is calculated between these parameters in order to define the nature of interference phenomena and to predict association performance (table 1). In particular, great attention is paid to the relationship between the associating and/or dominating ability parameters and the pure stand values, as well as to the relationship between the direct effect (α) and the associate effect (β). A positive correlation between these two last parameters would allow association of partners which are both stimulated and stimulating at the same time, and which therefore co-operate in the production of a higher biomass than the corresponding monocultures.

TABLE 1

Models of analysis of interference experiments.

Modèles d'analyse utilisés dans les expériences sur l'interférence.

Linear model (Gallais) - correlations :
g_i/v_i : associating ability *vs.* pure stand value
c_i/v_i : dominating ability *vs.* pure stand value
β_i/v_i : associate effect *vs.* pure stand value
α_i/β_i : direct effect *vs.* associate effect.
Proportional model
Maître (de Wit)
$\frac{Y_{i/j}}{Y_{ii}} \Big/ \frac{Y_{j/i}}{Y_{jj}}$: relative yield of i *vs.* relative yield of j
Rotili-Zannone
$\frac{nY_{i/j}}{Y_{ii}} - 1$; $\frac{nY_{j/i}}{Y_{jj}} - 1$: plastic responses (*)

(*) In the binary associations 1 : 1, n = 2 and plastic response = twice the relative yield.

The correlation between associating (or dominating) ability and pure stand performance gives indications on the possibility of predicting the association performance on the basis of the pure stand performance.

The same kind of correlation has been applied by MAÎTRE (1977) to the "relative yields » (as defined by DE WIT (1960)) of the two partners of each binary association. A positive correlation between the two relative yields would indicate "co-operation" between the two partners.

The object of this paper is to compare the results of the different methods of analysis and to bring together the conclusions from the whole series of inter-specific association experiments.

II. MATERIALS AND METHODS

The results of the series of experiments on grass-legume associations carried out at the Lodi Institute have already been published in part (cit.), and more detailed information can be found in the literature. We will discuss here some aspects of the results of grass-lucerne experiments, stressing that the conclusions on the nature of interference effects can be extended to grass-birdsfoot trefoil experiments.

The experiments with grass-lucerne associations are described in tables 2 and 3. They were carried out either in the greenhouse or in the field. The partners of each binary mixture were arranged either alternately in the same row, or in different rows, single or double.

The analysis of variance was done, according to the experimental design (randomized blocks), either cut by cut or on the average of cuts, to obtain the significance of differences between associations and pure stands and the incidence of the different partners on the performance of each population.

The agronomic value of mixture was evaluated by the formula :

$$\left(\frac{Y_{ij}}{(Y_{ii} + Y_{jj})/2} - 1\right) \times 100 .$$

Values over 10 % were statistically significant.

The nature of interference effects was expressed by the "plastic responses" (JACQUARD, 1972) calculated by the formula :

$$\frac{nY_{i/j}}{Y_{ii}} - 1$$

where the term n in the numerator is a multiplication factor relating the population in mixture to the same unit area of monoculture. For fifty-fifty binary mixtures, the $\frac{n\,Y_{i/j}}{Y_{ii}}$ term is twice the relative yield of DE WIT.

The theoretical situations created inside a mixture, as revealed by the plastic responses, are described in figure 1.

The data of experiments 1 and 2 were also analyzed using the linear parameters of the GALLAIS model ;

TABLE 2

Grass-lucerne binary assocations. Description of populations and experiments.
Associations binaires luzerne + graminée. Description des populations et des expériences.

Species	Earliness	Greenhouse		Field	
		Exp. 1	Exp. 2	Exp. 3	Exp. 4
Medicago sativa					
cv. Bresaola	early	*			
cv. Equipe	mean				*
cv. Leonicena	medium-early	*	*	*	
cv. Robot	mean	*	*	*	
Festuca arundinacea					
cv. Clarine	mean		*	*	*
cv. Manade	early	*	*	*	*
cv. Penna	early	*			
cv. Raba	early		*		
Dactylis glomerata					
cv. Chantemille	late		*	*	*
cv. Dora	early	*	*	*	*
cv. Montpellier	very early		*		
cv. Prairial	very late	*			
Bromus catharticus					
cv. Bellegarde	early		*	*	
cv. Cabro	early		*	*	
Bromus sitchensis					
cv. Lubro	late		*		

TABLE 3

Grass-lucerne binary associations. Methods and experimental designs.
Associations binaires luzerne + graminée. Méthodes et plans des expériences.

	GREENHOUSE		FIELD	
	Experiments 1 (*)	Experiment 2	Experiment 3	Experiment 4
Design	← Randomized blocs →			
Replicates	10	10	4	4
Plant position	alternated in the row	alternated single rows	alternated single or double rows	
Plot size	concrete boxes of cm 25 × 40 × 150			
	1 row of 70 cm	2 rows of 70 cm	m 4.5 × 1.8 – 12 rows	
Sample analyzed	all the plot		1 m × 8 central rows	
Date of sowing	Autumn 1979	Spring 1981	Spring 1981	Spring 1982
Stage of cutting	← 20 % flowering of lucerne →			
Cut interval	24-28 days		30-35 days	
Characteristics analyzed	← dry matter yield →			
	← stability (c.v. "among cuts") →			
	← earliness →			

(*) A replacement series was done in this experiment with 0:4, 1:3, 2:2, 3:1, 4:0 proportion of each partner.
In all other experiments only pure stands and fifty-fifty mixtures were analyzed.

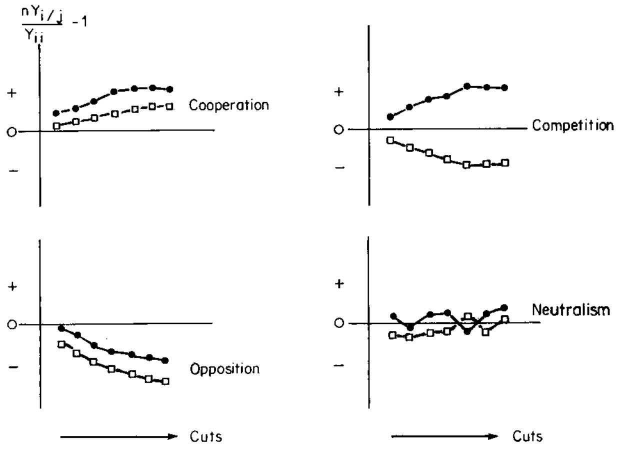

Figure 1

Theoretical situations in binary associations defined from plastic responses. In ordinate, plastic responses.
In abscissa, cuts.

Situations théoriques chez les associations binaires définies à partir des réponses plastiques.
En ordonnée les réponses plastiques.
En abscisse la succession des coupes.

these parameters and the correlations between them were calculated cut by cut.

Finally, the relationship between the two "relative yields" was also analyzed, according to the MAÎTRE procedure, either cut by cut or on the average of the cuts, on the data of experiment n.1.

III. RESULTS AND DISCUSSION

A. Agronomic value of associations

The agronomic value of binary grass-lucerne mixtures was generally high, the dry matter yield of the associations being significantly greater than the average production of the two corresponding monocultures, and often than the better of them.

The best performing associations were those between the populations performing best in pure stand. So, a rough prediction of association performance is feasible by the simple observation of pure stands. Nevertheless, as we shall see in the following paragraphs, this underestimates association value, since interference effects are not taken into account.

B. Nature of the interference effects

The interference effects, as revealed by the plastic responses cut by cut, were always represented by situations of competition (+ −). This result is in agreement with those of the intra-specific interference experiments (ZANNONE *et al.,* 1983). However in the intra-specific experiments, the trend of the plastic responses through the cuts was represented by two diverging lines (fig. 2a), indicating the progressive elimination of the weaker partner, while in the inter-specific experiments the plastic responses were characterized by two lines alternatively fluctuating around the zero value (horizontal line) (fig. 2b). Such fluctuation from positive to negative values follows the analogous fluctuation of monoculture performance through the seasons.

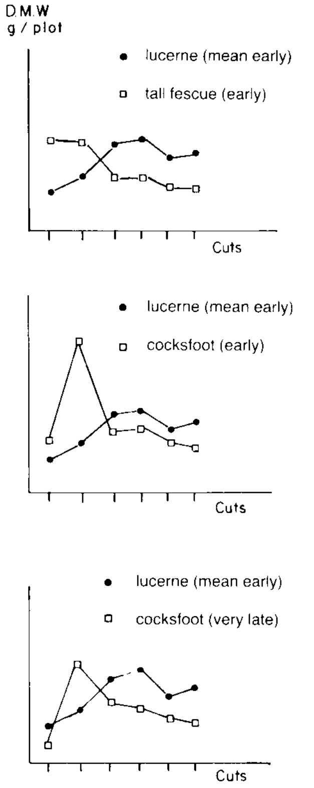

Figure 3

Dry matter per plot in monoculture (in one series of experiments with grass-lucerne binary associations).
In ordinate, dry matter per plot.
In abscissa, cuts.

Matière sèche par parcelle en culture pure (chez une série d'expériences avec associations binaires graminée + luzerne).
En ordonnée la matière sèche par parcelle.
En abscisse la succession des coupes.

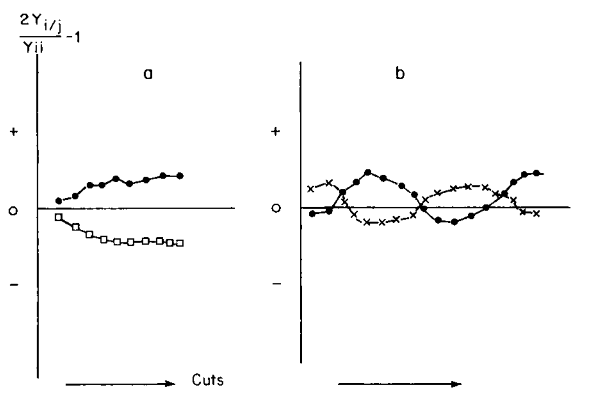

Figure 2

Type of plastic responses observed.
a) intraspecific binary associations.
b) interspecific binary associations.
In ordinate, plastic responses.
In abscissa, cuts.

Type de réponses plastiques observées dans nos expériences.
a) associations binaires intra-spécifiques.
b) associations binaires inter-spécifiques.
En ordonnée les réponses plastiques.
En abscisse la succession des coupes.

Figure 3 shows a sample of the monoculture yield trend from experiment n.1. The tall fescue cultivars in this experiment were all of the same earliness so the example represents fairly well the general trend for this grass. Concerning the cocksfoot cultivars, a very late cv. was included in the experiment ; it seemed interesting to us to show the different position of the early and late cocksfoot cv. with reference to the lucerne trend ; the lower advantage in the spring and the greater disadvantage in the summer of the late cocksfoot cv. is reflected in the "plastic responses" in the associations (ZANNONE *et al.,* 1982).

The convergent-divergent trend was enhanced when the proportions of the two partners in a mixture were different. Figure 4 represents the type of plastic responses obtained in experiment n.1 with three different proportions of the two components of each binary mixture. At the first three cuts, the grass is gaining over the lucerne ; the amount of its advantage is inversely proportional to the number of its presences (the mortality in this experiment was practically negligible at the first three cuts). In other words, 75 % of vigorous grass plants, in the presence of

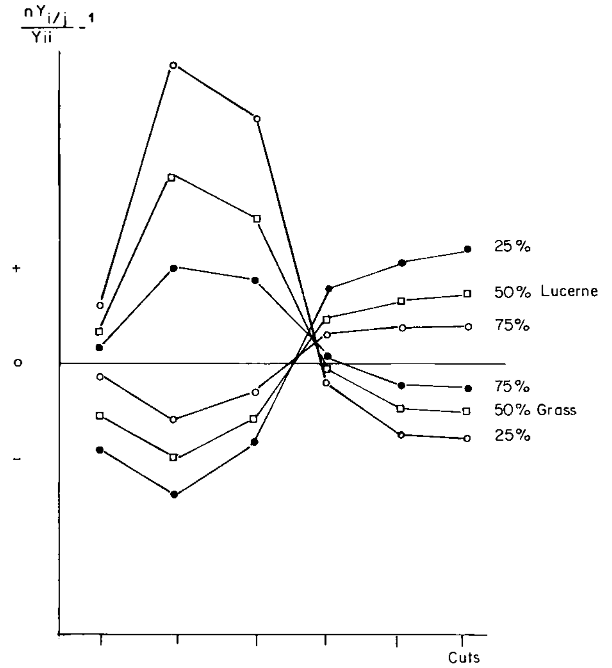

Figure 4

Plastic responses observed in grass-lucerne binary associations with different proportions of the two components.
In ordinate, plastic responses.
In abscissa, cuts.

Réponses plastiques observées chez des associations binaires graminée + luzerne avec différentes proportions des deux partenaires.
En ordonnée les réponses plastiques.
En abscisse la succession des coupes.

25 % of weak lucerne plants, performs better than 100 % pure stand plants, but worse than 25 % vigorous grass plants in the presence of 75 % weak lucerne. By contrast, these 75 % vigorous grass plants, when becoming disadvantaged, showed up a lower decrease (because in presence of 25 % of vigorous lucerne plants) than the 25 % grass plants in presence of 75 % of vigorous lucerne plants. The situation of the lucerne plants in the three different types of mixture is essentially a mirror image of this. Such a complex of plastic responses is in agreement with the hypothesis of the variation in biological density.

In our experiments, the convergence-divergence was a constant rule, but its intensity changed (for the same pair of partners) according to the type of establishment. For instance, experiments n.1 and n.2 were both done in the greenhouse, but the first with plants of both species alternated in the row, and the second with plants of each species in alternated single rows. In experiment n.1 the interference effects were more drastic than in experiment n.2, and this was revealed by more intensive plastic responses. The same was true for experiment n.3 in which the alternated single rows were compared with double rows (ROTILI *et al.*, 1982). When the species were in alternated double rows, the plastic responses were less drastic than when they were in alternated single rows. Moreover, for the same pair of partners, the succession of convergence-divergence could be inverted by changing the date of sowing (autumn or spring), or cancelled by suspending the nitrogen supply (ROTILI *et al.*, 1982).

In other words, any given population may turn out more or less dominating or dominated, in the presence of the same partner, according to the variation in environmental conditions or management techniques.

Another peculiar feature of the plastic responses observed in these experiments was that the advantage of one species was generally higher than the disadvantage of the other : there was an "over-compensation " effect in favour of the winning partner, and therefore alternatively in favour of both species. These over-compensation effects were cumulated through the cuts, bringing the associations to produce more than the average of the two corresponding monocultures, and often more than the better one. This cumulation of over-compensation effects means that association performance is underestimated, if it is based only on the average of the two monocultures.

C. Model of cultivars suitable for interspecific binary associations

The alternation of positive plastic responses of two associated species is a consequence of the displacement in time of the maximum production of the said species. The best performing associations were those between vigorous cultivars of lucerne and grass cultivars characterized by high vigour and earliness. In such associations, the grass cultivar can display its potentialities before lucerne reaches its maximum vigour (cf. fig. 3).

According to this situation, a model for association of perennial grass and lucerne cultivars can be defined as in table 4.

TABLE 4

Model of perennial grass and lucerne cultivars for binary interspecific associations.

Modèle des variétés de luzerne et de graminées pérennes pour des associations interspécifiques.

Grasses	1. Early, very early
	2. Very vigorous
	3. Very persistent
	4. High photosynthetic activity even in reduced light intensity
	5. High stability of yield through the cuts.
Lucerne	1. Early
	2. Very vigorous
	3. Very persistent (root reserve recovery at bud stage)
	4. High stability of yield through the cuts.

In a fertile and well exploited environment like the Po Valley, at least, the optimisation of such characteristics as vigour, persistence and stability in both species, and of earliness in grasses, can give good results. High persistence in lucerne can be reached by anticipating the recovery of root reserves to the blue bud stage, through selection for resistance to frequent cutting : this is precisely the method applied at the Forage Institute of Lodi.

D. Comparison between the different models of analysis

In all the inter-specific association experiments, we obtained, at every cut, plastic responses indicating situations of competition (+ −). However, when we applied the calculation of plastic responses to the average of the cuts, we obtained several responses of (+ +) type, indicating situations of co-operation (table 5, Exp. 1).

The same was true for the MAÎTRE procedure applied to the data of experiment n.1 (fig. 5). However, if applied separately cut by cut, the MAÎTRE procedure also gave results to be interpreted more as competition than as co-operation phenomena (fig. 6, *a* to *f*).

In order to clarify such apparently contradictory results, we analyzed the data of our two greenhouse experiments (Exp. 1 and Exp. 2) by applying the linear parameters cut by cut. We found that not only the parameters *per se,* but also the correlation coefficients, showed the same kind of alternation shown by the plastic responses.

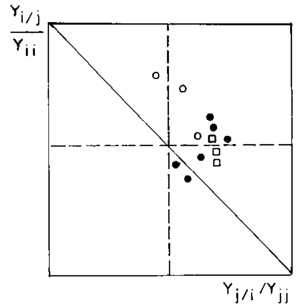

Figure 5

MAÎTRE procedure representing the mean results of a series of grass-lucerne binary associations. Mean dry matter of six cuts.
In ordinate, ratio between partner i and its monoculture.
In abscissa, ratio between partner j and its monoculture.

Représentation de MAÎTRE des résultats moyens d'une série d'associations binaires graminée + luzerne. Matière sèche moyenne des 6 coupes.
En ordonnée le rapport entre le partenaire i et sa culture pure.
En abscisse le rapport entre le partenaire j et sa culture pure.

TABLE 5

Plastic responses in grass-lucerne binary mixtures, calculated on the averages of 6 cuts.

Réponses plastiques chez des associations binaires entre luzerne et graminées, calculées sur la moyenne de 6 coupes.

	Grass species			
	Tall fescue		Cocksfoot	
LUCERNE	cv. Manade (M)	cv. Penna (P)	cv. Dora (D)	cv. Prairial (P)
cv. Bresaola (B)	B − 8 M + 23	B + 1 P + 25	B − 15 D + 18	B + 3 P + 14
	+ 15	+ 26	+ 3	+ 17
cv. Leonicena (L)	L + 1 M + 21	L + 5 P + 21	L − 6 D + 23	L + 33 P − 6
	+ 22	+ 26	+ 17	+ 27
cv. Robot (R)	R + 2 M + 26	R + 7 P + 22	R − 9 D + 16	R + 25 P + 5
	+ 28	+ 29	+ 7	+ 30

Figure 7 gives, for experiment n.2, the trend of variation through the cuts of the linear parameters : direct effect (α), associate effect (β), associating ability (g) and dominating ability (c). The direct effect (α) and the associate effect (β) were always opposite, while the direct effect (α) and the dominating ability (c) showed a very similar trend. In our opinion, this is the consequence of the nature of interference effects, characterized by situations of competition, as revealed by the plastic responses.

Figure 8 gives the correlation coefficients between the linear parameters and between them and the pure stand values (v_i). Here again we observed the opposite trend of the α and β parameters, as well as the similarity between the α and c parameters. Furtherly, we observed that the actual value of the correlation coefficients varied from significant to non-significant values and even from positive to negative values in some cases. So, the trend in variation seemed to be more indicative of the situation than the actual values

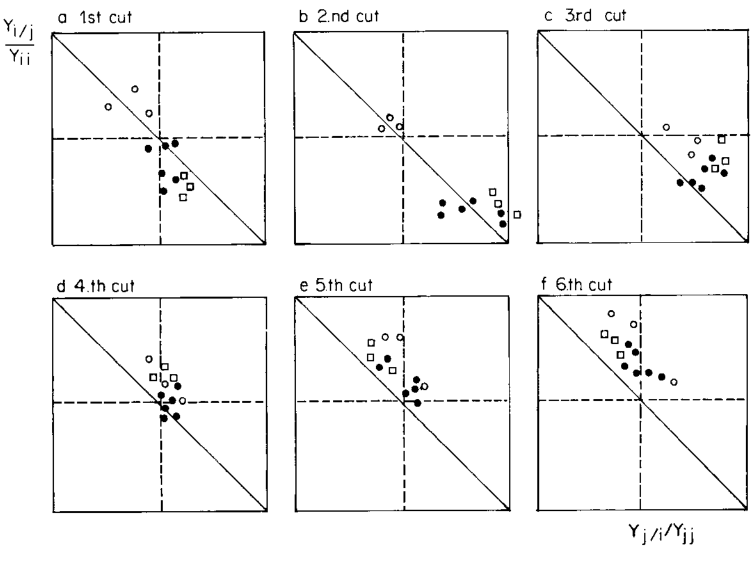

Figure 6

MAÎTRE procedure representing the results of a series of binary associations cut by cut (see fig. 5).
In ordinate, ratio between partner i and its monoculture.
In abscissa, ratio between partner j and its monoculture.

Représentation de MAÎTRE des résultats d'une série d'associations binaires considérés coupe par coupe (voir fig. 5).
En ordonnée le rapport entre le partenaire i et sa culture pure.
En abscisse le rapport entre le partenaire j et sa culture pure.

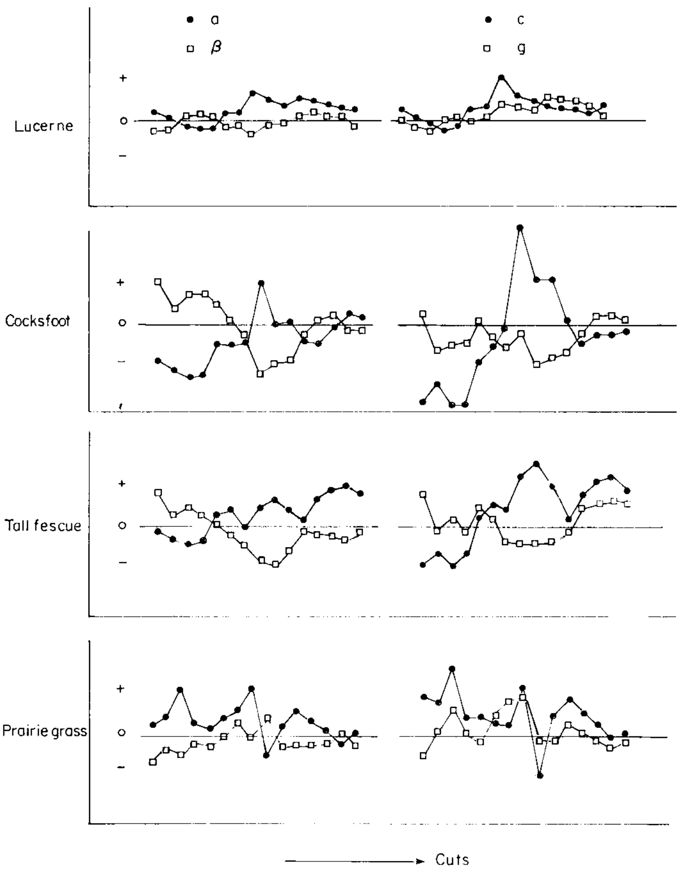

Figure 7

Variation with time in the parameters of the GALLAIS *linear model in grass-lucerne associations.*
In ordinate, parameter values.
In abscissa, successive cuts.

Variation au cours des saisons des paramètres du modèle linéaire de GALLAIS *chez des associations graminée + luzerne.*
En ordonnée les valeurs des paramètres.
En abscisse la succession des coupes.

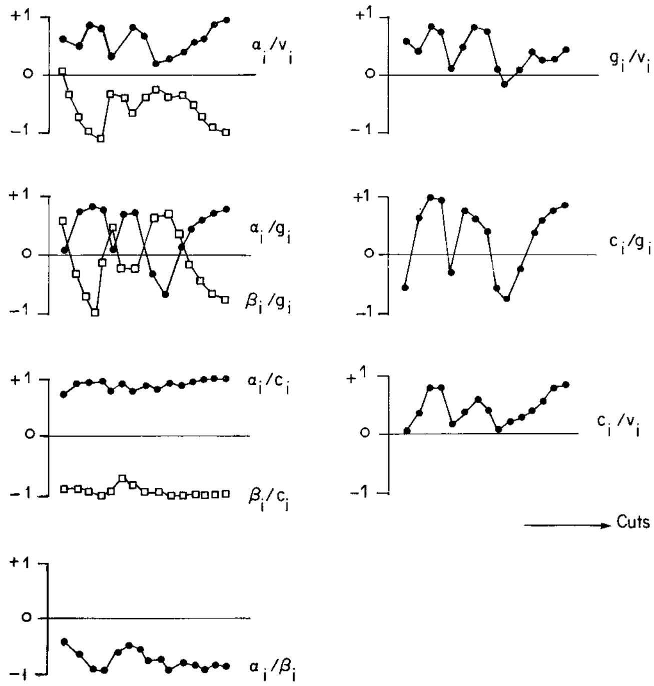

Figure 8

Variation in correlation coefficients between parameters (see fig. 7) during cuts.
In ordinate, correlation coefficient.
In abscissa, successive cuts.

Variation des coefficients de corrélation entre les paramètres (voir fig. 7) au cours des coupes.
En ordonnée le coefficient de corrélation.
En abscisse la succession des coupes.

of the correlation coefficients. It seems in fact that the nature of the interference effects demands to be studied cut by cut and for a sufficient number of cuts to demonstrate the alternation between the two species. The same conclusions on the nature of the interference effects could be reached by different methods and at different levels : at the level of each pair of partners by the plastic responses, at the level of each recurrent population by the linear parameters and at the level of the experiment taken as a whole by the correlation coefficient between the linear parameters. These three different levels of analysis are represented in the scheme of figure 9.

E. Prediction of association performance

Besides knowledge of the nature of interference effects, the breeder is interested in the prediction of association performance as a whole. In this case, the analysis of the average or the total harvested biomass becomes necessary.

A first rough prediction can be made by the observation of the ranking of monocultures, because in general the best associations are those involving the best monocultures. So, the simplest way of predicting

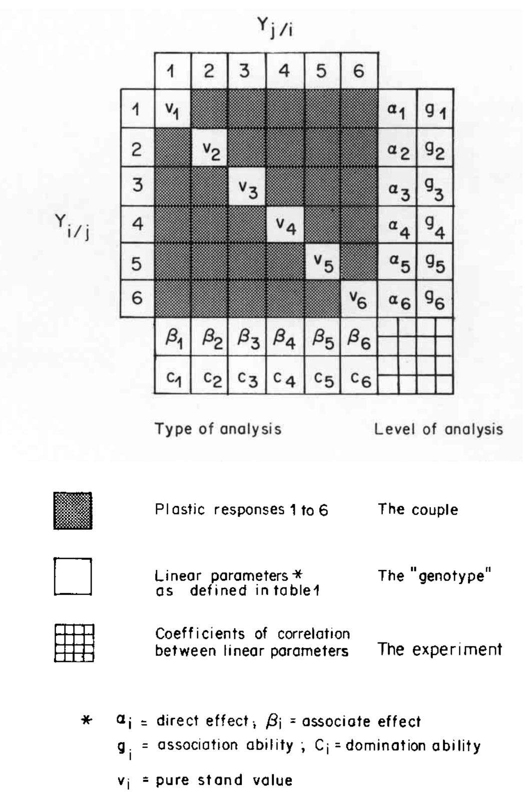

Figure 9

Types and levels of analysis of experimental data of binary associations.

Types et niveaux d'analyse des données expérimentales des associations binaires.

association performance is to take the average of every pair of monocultures. However, over-compensation effects can lead to underestimation. In fact, in our grass-legume association experiments, the average values of association biomass were always above the average of the corresponding monocultures, as a consequence of over-compensation effects cumulated through the cuts.

In figure 10, the average yields of the associations in experiments n.1, n.2 and n.3 are plotted against the average of every pair of monocultures. In the absence of interference effects, "theoretical" association performance would follow a line bisecting the field (line of slope b = 1). All the experimental points did seem to follow a regression line with a slope not too different from unity, but they were all displaced towards the upper part of the diagram ; in our opinion, this is the consequence of over-compensation effects, and a good prediction of association performance should be based on the knowledge of the over-compensation values.

Assuming that inter-specific interference effects were of the same nature as intra-specific ones, and that, in the intra-specific binary association, performance was well estimated by taking into account the ratio between them as well as the average of every pair of monocultures (ZANNONE, 1985), we applied the same tentative approach to the grass-lucerne experimental data. In fact, in this case also, the association yield appeared related to the ratio between the two corresponding monocultures (fig. 11) : when the ratio between the two partners of each association increased (i.e. the difference between the partners increased, and the heterogeneity of the association

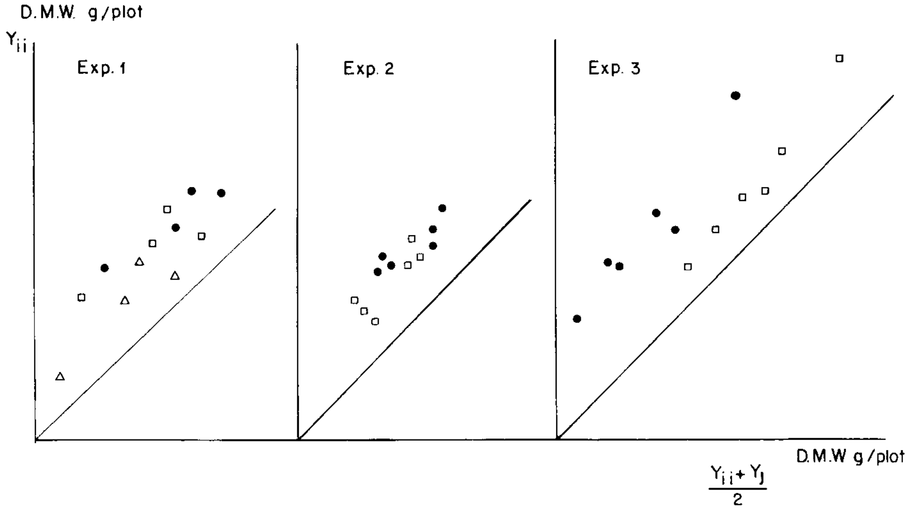

Figure 10

Relationship between the yield of binary associations (dry matter) and the average of every pair of monocultures.
In ordinate, association yield in g/plot.
In abscissa, average of every pair of monocultures.

Relation entre la performance des associations binaires (matière sèche) et la moyenne de chaque couple de cultures pures.
En ordonnée la performance des associations en g/parcelle.
En abscisse la moyenne de chaque couple de cultures pures.

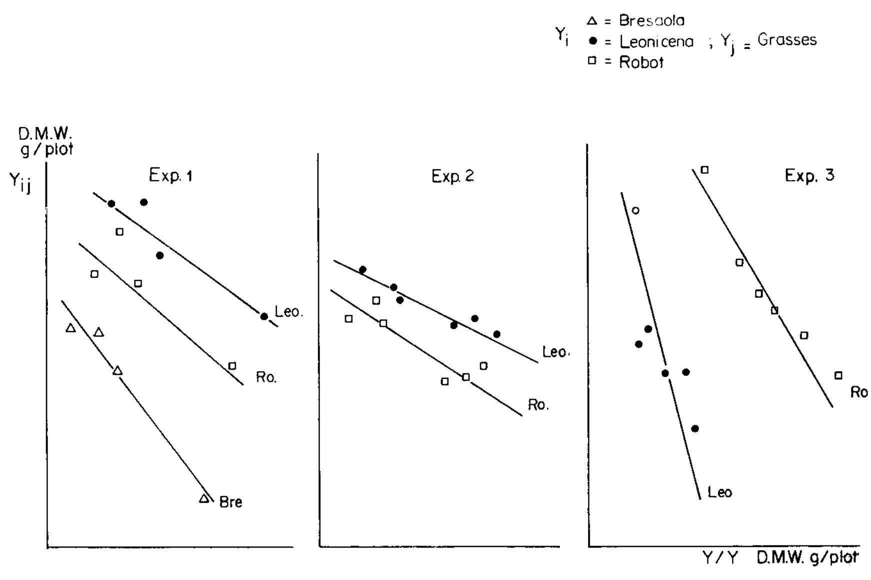

Figure 11

Relationship between the yield of binary associations (dry matter) and the ratio between the two monocultures.
In ordinate, association yield in g/plot.
In abscissa, ratio between the two monocultures.

Relation entre la performance des associations binaires (matière sèche) et le rapport entre les deux cultures pures correspondantes.
En ordonnée la performance des associations en g/parcelle.
En abscisse le rapport entre les deux cultures pures.

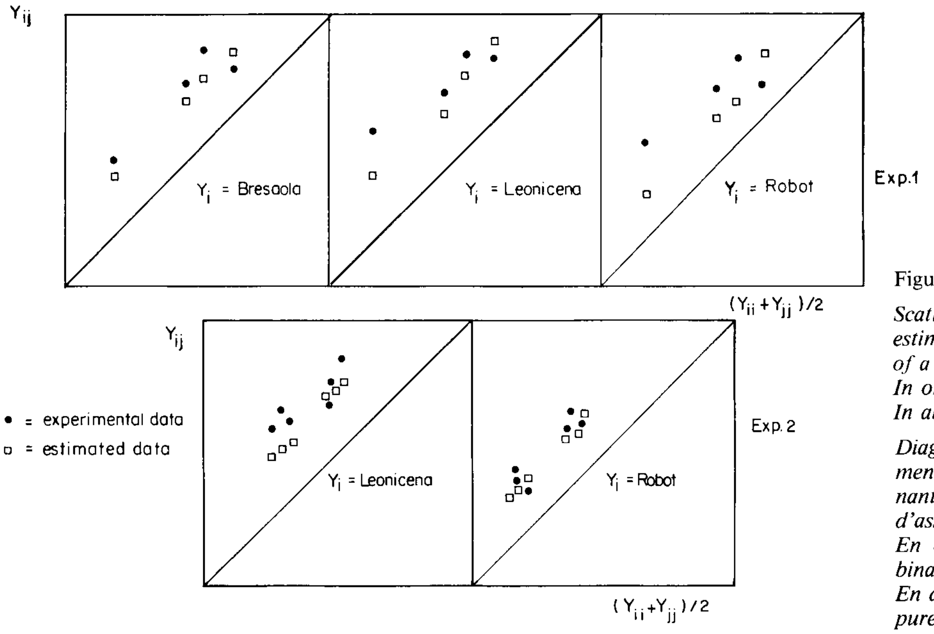

Figure 12

Scatter chart of the experimental (•) and estimated (*) data regarding dry matter per plot of a series of grass-lucerne binary associations. In ordinate, yield of binary associations. In abscissa, average of pairs of monocultures.

Diagramme de dispersion des données expérimentales (•) et des données estimées (*) concernant la matière sèche par parcelle d'une série d'associations binaires graminée + luzerne. En ordonnée la performance des associations binaires. En abscisse la moyenne des couples de cultures pures.

increased as a consequence), the yield of the association decreased. Here again, as in the intra-specific associations, the slope of the regression lines was related to the vigour of the population ; in the greenhouse experiments, cv. Leonicena appeared in fact more vigorous than cv. Robot, while in the field (exp. 3) the opposite was true. Despite the high value of the correlation coefficients (− 0.9), no statistical significance was found in experiment n.1, because of the small number of pairs in each set of associations.

It is worthwhile to recall that such a relationship is found only when the associations are considered set by set of recurrent populations. So, the tentative approach for the prediction was applied to every set of binary associations, by calculating the regression line of the ratio between two monocultures on the average of the same two monocultures :

$$Y_{ii}/Y_{jj} = a + b\frac{Y_{ii} + Y_{jj}}{2}. \qquad (A)$$

The simplest formula of prediction, based on the monoculture average only :

$$Y_{ij} = \frac{Y_{ii} + Y_{jj}}{2} \qquad (B)$$

is modified by adding to the second part of the formula the term

$$b \cdot \frac{Y_{ii} + Y_{jj}}{2}.$$

The estimation is thus made by the formula

$$Y_{ij} = \frac{Y_{ii} + Y_{jj}}{2} + b \cdot \frac{Y_{ii} + Y_{jj}}{2} \qquad (C)$$

This method, applied to experiments n.1 and n.2 gave the results shown in figure 12. In spite of the good correlation between the experimental and the estimated data (table 6), a portion of the overcompensation effect still remained underestimated.

TABLE 6

Correlation coefficients between the experimental values of grass-lucerne association performance and their estimation by formula (C).

Coefficients de corrélation entre les valeurs expérimentales d'associations graminée + luzerne et leur estimation à partir de la formule (C) (voir le texte).

Recurrent population	Correlation coefficient
LUCERNE	
Bresaola	0.916
Leonicena	0.939
Robot	0.810
COCKSFOOT	
Dora	0.991
Prairial	0.976
TALL FESCUE	
Manade	0.954
Penna	0.976

A further investigation would be necessary to calculate, on the basis of monoculture performance, the likely amount of overcompensation that will occur in different associations. Our empirical approach was simply suggested by the experimental data and by the striking uniformity of the intra- and inter-specific interference results.

IV. CONCLUSIONS

In a series of experiments on intra-specific (ZANNONE *et al.*, 1983) and inter-specific (PAOLETTI & LOCATELLI, 1982 ; ROTILI *et al.*, 1982 ; ZANNONE *et al.*, 1982) binary associations, the nature of interference effects was proved to be the same. They were characterized by the advantage of one partner and the disadvantage of the other (competition). In the binary associations of lucerne, red clover, tall fescue and cocksfoot the competition effect, as revealed by the plastic responses, were represented by two lines which diverged more and more over the course of the seasons, leading to the disappearance of the weaker partner. In contrast, in the grass-legume binary associations, the competition effects were alternatively in favour of either partner, and showed an over-compensation effect bringing the associations to produce more than the average of the two corresponding monocultures, and often more than the better of the two pure stands. In the binary associations of different grasses (cocksfoot, tall fescue) with lucerne, the over-compensation effect was greater when the lucerne populations were associated with early or semi-early grasses because the grass population was allowed to display its yield potential before the lucerne reached its maximum vigour.

The best grass-legume associations were those between the best monocultures, any increasing difference in vigour between the two partners causing a decrease in association yield. This is in agreement with ROTILI's statement on the relationship between homogeneity and yield capacity (ROTILI, 1979), already confirmed by the intra-specific association results (ZANNONE, 1984, 1985). The greater the heterogeneity for vigour of the components of a population, the larger will be the difference which develops between individuals over the seasons the to, advantage of the vigorous ones and to the detriment of the weaker ones. The final result of such a negative development in population structure will be high mortality and loss of yield and persistence. In fact, the best performing associations were also the most persistent.

Based on these results, a model is proposed for binary interspecific association of perennial grass and lucerne cultivars, suitable for intensive management systems like those of the Po Valley. In this model, earliness and vigour are considered side, be persistence and stability in yielding capacity. The slight displacement in earliness, which proved to be advantageous in our region, might not be advantageous in other regions, such as North Europe, Central Italy or the Nile delta. In fact, the type of plastic response was constant in all the interspecific interference experiments (i.e. competition with over-compensation) but the intensity of the response and even the direction (+ − or − +) could change according to environmental conditions or management techniques. When the characteristics of a given legume cultivar and the region of cultivation are defined, it is possible to make a fairly good prediction of the grass partner which would be most suitable for producing a high-performance binary association.

Correct estimation of association performance based on monoculture performance should take into due account not only the average of the monocultures but also the ratio between them. A further improvement of prediction would be achieved if it was possible to calculate the probable over-compensation effect attributable to each population.

Comparison among different methods of analysis showed that the nature of interference effects demands to be described cut by cut, and for a number of cuts sufficiently high to show the trend of population responses. Whatever the model of analysis should be, its application to the average of several cuts is liable to mislead because over-compensation effects are neglected.

The whole series of experiments on binary grass-legume associations carried out at the Forage Crops Institute of Lodi, confirms the conclusion drawn from the intra-specific interference experiments that, in order to breed cultivars suitable for association, it is not necessary to select in association. It is sufficient to select in monoculture, taking account of the appropriate environmental conditions and to associate the cultivars showing the best performance in these environments (ZANNONE *et al.*, 1985). The ratio in vigour between the two partners has to be as near as possible to unity, while earliness in flowering has to be in favour of the grass partner, to allow optimal exploitation of the yield potential of both species.

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