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Effects of competition between alfalfa (*Medicago sativa* L.) hybrid and inbred plants on their seed and forage yield (1)

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SUMMARY

A study was conducted at Perugia (Italy) in 1981/1982 to evaluate the importance of competition in alfalfa (*Medicago sativa* L.) and to investigate the consequence of different percentages of inbred seeds on seed and forage yield. Three mixtures having ratios of inbred seed to hybrid seed (S_1/F_1) of 1/9, 1/2.33, 1/1 were sown, seed by seed, in micro-plots (50 × 30 cm) at a seeding rate of 1 600 seeds/m².

In 1981 data were collected on : establishment ; green matter yield per plant and dry matter yield/m² at 1st, 2nd and 3rd cut ; number of plants alive in the fall. In 1982 data were collected on : number of plants alive in the spring ; green matter yield per plant and dry matter yield/m² at 1st and 3rd cut ; seed yield per plant at 2nd cut ; height per plant at 1st cut.

The results can be summarized as follows : 1) forage yield of S_1 was much lower than that of F_1 plants in each of the 3 mixtures ; 2) since no differences were observed in dry matter yield/m² among mixtures, differences in S_1 seed percentage would not seem important to productivity of alfalfa ; 3) selective elimination of S_1 plants was present and particularly strong during the seeding year. One year after seeding only few S_1 plants survived ; 4) only 2 % of the seed produced in the 2nd year came from S_1 plants.

RÉSUMÉ

Effets de la compétition entre plantes de luzerne issues d'hybridation et d'autofécondation sur la production des semences et du fourrage.

En 1981-82, une recherche implantée à Pérouse (Italie) a eu pour but l'évaluation des conséquences que peuvent avoir différents pourcentages de semences obtenues par autofécondation sur la production de semences et de fourrage chez la luzerne (*Medicago sativa* L.). Trois mélanges, ayant une proportion entre semences obtenues par autofécondation et semences hybrides (S_1/F_1) respectivement de 1/9, 1/2,33, 1/1, ont été semés, graine par graine, sur des microparcelles (de 50 × 30 cm) ayant une densité de 1 600 graines par m².

En 1981 ont été relevées les données relatives à l'implantation, à la production de matière verte par plante et de matière sèche par m² à la 1^{re}, 2^e et 3^e coupe, au nombre de plantes vivantes en automne. En 1982 ont été relevées les données relatives au nombre de plantes vivantes au printemps, à la production de substance verte par plante et de substance sèche par m² à la 1^{re} et 3^e coupe, à la hauteur des plantes à la 1^{re} coupe, à la production de semences par plante à la 2^e coupe.

Les résultats peuvent être ainsi synthétisés : 1) dans les 3 mélanges, les plantes S_1 ont donné une production de fourrage beaucoup plus faible que celle des plantes F_1 ; 2) étant donné qu'il n'y a pas de différences significatives entre les mélanges pour la production de matière sèche par m², de grandes différences dans la proportion de semences issues l'autofécondation dans les lots de départ ne semblent pas influencer de façon significative la production fourragère de la luzerne ; 3) il y a eu une sélection des plantes S_1 particulièrement forte pendant l'année d'implantation. Après une année, le nombre des plantes S_1 survivantes a été très limité ; 4) les plantes S_1 ont contribué seulement dans la mesure de 2 % à la production de semences de l'année 1982.

I. INTRODUCTION

Genetic improvement of perennial forage species, such as alfalfa (*Medicago sativa* L.) is usually carried out under non-competitive conditions which are very

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different from those of commercial production (SCHAAF, 1976 ; LORENZETTI & PORCEDDU, 1977). The value of data collected on spaced plants depends on the significance of the correlation between the behaviour of the plants in breeding environment and in production trials. In alfalfa, selection based on plants grown at wide spacing is quite effective for highly heritable traits, such as disease resistance and maturity (CHRISTIE & KEOGHAN, 1979), but is not

effective for herbage yield and other important quantitative characters distinctly affected by competition where strong genotype per density interaction is present (TYSDAL & KIESSELBACH, 1944; PEARSON & ELLING, 1961; PANELLA & LORENZETTI, 1968; BUSBICE *et al.*, 1972). Therefore, as already stressed by ROTILI (1979), selection for alfalfa forage yield should be carried out under dense stand conditions. In this context, the study of competition between hybrid and inbred plants holds a high interest in understanding both the structure of the populations to be improved and the kind of varieties (hybrids or synthetics) to be produced. A strong selective pressure is present in alfalfa stands and the number of plants surviving the first year after seeding is generally in the range of 20-30 % of the seed sown (VIVENZA, 1914; HAUSSMAN, 1955; BROWN *et al.*, 1960; PANELLA, 1960; DEMARLY *et al.*, 1964; TESAR & JACOBS, 1972); this percentage further decreases in subsequent years to reach values around 10 % of seed sown at the end of the third year (VERONESI *et al.*, 1982).

A natural alfalfa population can be assumed as a mixture of inbred and hybrid plants, the percentage of selfing (largely dependent on environmental conditions) falling between 15 % (LESINS, 1961) and more than 40 % (VERONESI & LORENZETTI, 1982).

With the aim of evaluating the consequences of different percentages of inbred and hybrid plants on forage and seed yield in alfalfa, a study started at Perugia (Italy) in 1981 in which three seed mixtures having different ratios of inbred and hybrid seed were sown and evaluated under dense stand conditions.

II. MATERIALS AND METHODS

During the two year period 1981-1982 an alfalfa trial was conducted at Perugia (Italy) using three seed mixtures having ratios of inbred seed to hybrid seed (S_1/F_1) of 1/9, 1/2.33 and 1/1. Seeds were sown in micro-plots (50 × 30 cm) at a seeding rate of 1 600 seeds/m² (32 kg/ha). This seed density is normally used in Italian alfalfa stands. The three mixtures will be referred as mixture A (10 % S_1), B (30 % S_1) and C (50 % S_1). The S_1 and F_1 seeds were produced from 30 highly vigorous plants chosen in a three-year old stand of the Italian ecotype « S. Apollinare » and space transplanted. The experiment was based on the hypothesis that in a three-year old stand only vigorous plants derived from crossing should be present (KEHR, 1976; LORENZETTI, 1978). Self-pollination was obtained by manipulating bagged racemes while cross-pollination was obtained by tripping non-emasculated flowers of each one of the 30 plants with folded papers on which a large amount of pollen random collected from the other plants was present. In this way, self-fertilization is reduced to a minimum (BONCIARELLI, 1960). On the whole 100 flowers per plant were selfed and 100 were crossed. The F_1 initial seed lot was constructed bulking equal numbers of seed from each maternal parent; the S_1 initial seed lot was arranged the same way.

The seeds were scarified and each seed was sown 2.5 cm deep in the center of a square space (2.5 × 2.5 cm)

defined by the mesh of a plastic fence which was placed on each micro-plot surface and held in place with 30 cm nails. F_1 and S_1 seeds were randomly sown in each micro-plot, which had 240 seeds arranged in 20 cm rows with 12 seeds per row. Utilizing 2 rows around the perimeter as border it was possible to sow 16 rows of 8 seeds of experimental materials for each micro-plot (1 536 seeds in total). A complete randomized block design with four replications was employed. In 1981 data were collected on:

- establishment (number of plants alive 30 days after seeding);

- green matter yield (g/plant) and dry matter yield (g/m²) at 1st (June 15), 2nd (July 21) and 3rd cut (August 31);

- number of plants alive in the fall (October 30).

In 1982 data were collected on:

- number of plants alive in the spring (March 15);

- green matter yield (g/plant) and dry matter yield (g/m²) at 1st (June 2) and 3rd cut (October 13);

- height per plant (cm) at 1st cut (June 2);

- seed yield (g/plant and g/m²) at the 2nd cut (August 17).

Green matter yield per plant and height data were transformed before analysis using the log transformation due to the skewness of the original data. Arcsin transformation was used on survival percentage data. Data are presented in actual units.

III. RESULTS AND DISCUSSION

Means of annual green matter yield per plant and dry matter yield per m² in 1981 and 1982 are reported in table 1. In 1981, S_1 plants yielded 47 % less than F_1 in mixture A (1.18 vs 2.23 g/plant), 65 % less in B (1.03 vs 2.98 g/plant) and 60 % less in C (1.31 vs 3.25 g/plant); in 1982, S_1 plants yielded 56 % less in mixture A (2.13 vs 4.92 g/plant), 65 % less in B (2.23 vs 6.51 g/plant) and 72 % less in C (2.21 vs 7.91 g/plant). The results indicate a strong inbreeding effect which tends to increase over time and is higher than that normally shown in spaced plant trials, where S_1 plants produce approximately 30 % less than F_1 plants (PANELLA & LORENZETTI, 1966; LORENZETTI & PORCEDDU, 1968). Both in the 1st and in the 2nd year, different S_1 percentages did not significantly affect average green matter yield per plant or dry matter yield per m² of the three mixtures (table 1).

With respect to classes of progeny, S_1 plants never showed significant average green matter yield differences among mixtures. On the contrary, F_1 plants in mixtures A, B and C were all significantly different for this character in 1982. F_1 plants showed the lowest mean yield per plant in mixture A (2.23 g/plant in 1981 and 4.92 g/plant in 1982), where the lowest number of S_1 plants was present, and the highest mean value in mixture C (3.25 g/plant in 1981 and 7.91 g/plant in 1982), where the highest number of S_1 plants occurred (table 1).

Therefore, in accordance with CARNAHAN & PADEN (1967) it seems that, in dense plantings containing genotypes varying in yield potential, the more vigorous plants will compensate for the lower

TABLE 1

Annual green matter yield per plant and dry matter yield per m² in 1981 and 1982.
 Production annuelle de matière verte par plante et production de matière sèche par m² en 1981 et 1982.

Mixtures	1981			Dry matter yield (g/m ²) mixture	1982			Dry matter yield (g/m ²) mixture
	green matter yield (g/plant)				green matter yield (g/plant)			
	S ₁	F ₁	Mixture		S ₁	F ₁	Mixture	
A (10 % S ₁)	1.18 a*	2.23 a	2.16 a	825 a	2.13 a	4.92 a	4.89 a	955 a
B (30 % S ₁)	1.03 a	2.98 a	2.57 a	905 a	2.23 a	6.51 b	6.28 b	1 082 a
C (50 % S ₁)	1.31 a	3.25 a	2.55 a	779 a	2.21 a	7.91 c	6.89 b	1 049 a

* Means within a column followed by the same letter not significantly different at 1 % level.

yielding component of the population. Plant survival percentages of seeds sown are reported in figure 1. Survival percentages for all plants in the three mixtures were never significantly different at any one observation time and varied between 55 % (mixture C) and 64 % (mixture A) at the end of the seeding year and between 37 % (mixture A) and 27 % (mixture C) at the end of the second year. These survival percentages are close enough to those reported by DEMARLY *et al.* (1964), TESAR & JACKOBS (1972) and VERONESI *et al.* (1982) for alfalfa stands.

With respect to classes of progeny, percentages of F₁ plants alive in fall 1982 ranged between 41 % (mixture A) and 45 % (mixture C), whereas survival percentages of S₁ plants ranged between 1 % (mixture B) and 10 % (mixture C). The results of χ^2 tests on number of plants alive at any one observation time *versus* number expected if there were no differences in survival between S₁ and F₁ plants in A, B and C mixtures are reported in table 2. At the first observation time, we did not find evidence to reject the null hypothesis and this indicates that seedling elimination during establishment was not selective against S₁ genotypes. Selective elimination of S₁ plants started straight after, as soon as the struggle for light, water and nutrients began. In the process of competition plants with superior competitive ability obtain precedence and can attain more vigorous growth at the expense of weaker genotypes (YAMADA & HORIUCHI, 1960). In general, the greater the frequency of weaker phenotypes in a population, the stronger is the action of intraspecific competition against them. Probably for this reason, the different survivals of S₁ and F₁ plants became significant at the second observation time in mixture C and at the fourth observation time in mixture A and B. The χ^2 values increased over time showing a 1 % level of significance starting from the 3rd (7/21/1981), the 4th (8/31/1981) and the 6th (3/15/1982) observation times for mixtures C, B and A, respectively (table 2).

Numbers of plants alive and, in brackets, number of plants which produced seed at 1982 second cut (August 17) are reported in table 3. None of the 4 S₁ plants alive in mixture A produced seed. The percentages of S₁ plants which produced seed were between 0 % (mixture A) and 2.7 % (mixture C) of the seed sown. The same percentages relative to F₁

Figure 1

Plant survival percentages (100 % = number of seeds sown) in A (10 % S₁), B (30 % S₁) and C (50 % S₁) mixtures. (S. = seeding, 4/5/1981; E. = establishment, 5/5/1981; 1 = 1st cut, 6/15/1981; 2 = 2nd cut, 7/21/81; 3 = 3rd cut, 8/13/1981; F.S. = fall survival, 10/31/1981; S.R. = spring regrowth, 3/15/1982; 1 = 1st cut, 6/2/1982; 2 = 2nd cut, 8/17/1982; 3 = 3rd cut, 10/13/1982).

— F₁ + S₁; --- F₁; S₁.

Pourcentage des plantes vivantes (100 % = nombre des semences semées) dans les mélanges A (10 % S₁), B (30 % S₁) et C (50 % S₁). (S. = ensemencement, 5/4/1981; E. = implantation, 5/5/1981; 1 = 1^{re} coupe, 15/6/1981; 2 = 2^e coupe, 21/7/1981; 3 = 3^e coupe, 13/8/1981; F.S. = chute de la survivance, 31/10/1981; S.R. = repousse de printemps; 15/3/1982; 1 = 1^{re} coupe, 2/6/1982; 2 = 2^e coupe, 17/8/1982; 3 = 3^e coupe, 13/10/1982).

TABLE 2

Results of χ^2 tests on number of plants alive in mixtures A, B and C at the following observation times : 5/5/1981 (establishment), 6/15/1981 (1st cut), 7/21/1981 (2nd cut), 8/31/1981 (3rd cut), 10/30/1981 (fall survival), 3/15/1982 (spring regrowth), 6/2/1982 (1st cut), 8/17/1982 (2nd cut), 10/13/1982 (3rd cut). H_0 hypothesis : no differences in survival between S_1 and F_1 plants in A, B and C.

Résultats des tests χ^2 sur les plantes vivantes dans les mélanges A, B et C aux dates d'observation suivantes : 5/5/1981 (implantation), 15/6/1981 (1^{re} coupe), 21/7/1981 (2^e coupe), 31/8/1981 (3^e coupe), 30/10/1981 (chute de la survivance), 15/3/1982 (repousse de printemps), 2/6/1982 (1^{re} coupe), 17/8/1982 (2^e coupe), 13/10/1982 (3^e coupe). Hypothèse H_0 : il n'y a aucune différence dans la survivance entre plantes S_1 et F_1 dans les mélanges A, B, C.

Mixtures		Seeds sown	1981					1982			
			5/5	6/15	7/21	8/31	10/30	3/15	6/2	8/17	10/13
			pp alive	pp alive	pp alive	pp alive	pp alive	pp alive	pp alive	pp alive	pp alive
A	S ₁ (10 %)	52	44	43	32	23	20	12	9	4	2
	F ₁ (90 %)	460	404	393	320	320	309	286	242	208	190
	χ ²	—	n.s.	n.s.	n.s.	*	*	***	***	***	***
B	S ₁ (30 %)	152	134	113	93	67	61	39	33	12	2
	F ₁ (70 %)	360	300	295	273	251	242	224	200	167	159
	χ ²	—	n.s.	n.s.	n.s.	***	***	***	***	***	***
C	S ₁ (50 %)	256	196	175	137	105	95	74	58	31	25
	F ₁ (50 %)	256	229	222	200	188	186	169	158	127	115
	χ ²	—	n.s.	*	***	***	***	***	***	***	***

n.s. = not significant ; * = significant at 5 % level ; *** = significant at 1 % level.

TABLE 3

Number of plants alive and, in brackets, number of plants which produced seed in 1982 second cut (August 17).
Nombre de plantes vivantes et, entre parenthèses, nombre de plantes qui ont produit des semences à la 2^e coupe de l'année 1982 (17 Août).

Mixtures	Number of plants alive		
	S_1	F_1	Total
A (10 % S_1)	4 (—)	208 (88)	212 (88)
B (30 % S_1)	12 (4)	167 (89)	179 (93)
C (50 % S_1)	31 (7)	127 (70)	158 (77)

plants were between 27.3 % (mixture C) and 19.1 % (mixture A). Only 17 %, 18 % and 15 % of the total seed sown in mixtures A, B and C gave plants which, in turn, produced seed.

Means of seed yield per plant and per m^2 are

reported in table 4. S_1 plants yielded 0.18 g/plant in mixture B and 0.15 g/plant in mixture C ; F_1 plants yielded 0.28 g/plant in mixture A, 0.38 g/plant in mixture B and 0.43 g/plant in mixture C. Also these results indicate a clear inbreeding effect ; S_1 plants yielded 53 % less than F_1 in B mixture and 65 % less in C. S_1 plants produced no seeds in A mixture, 0.6 % of the total seed yield in B and 1 % in C.

With respect to classes of progeny, S_1 plants did not express significant average seed yield differences between B and C mixtures but the average seed yield of F_1 plants in mixture A (0.28 g/plant) was significantly lower than those of B (0.38 g/plant) and C (0.43 g/plant) which did not differ from each other. The average seed yield per plant of the three mixtures was affected by the different S_1 percentages, and mixture A showed a value (0.28 g/plant) significantly lower than those of B (0.38 g/plant) and C (0.40 g/plant). On the contrary, different S_1 percentages in the initial seed lots did not seem to effect average seed yield per m^2 of the three mixtures (tabl. 4).

TABLE 4
Seed yield per plant and per m^2 in 1982.
Production de semences par plante et par m^2 en 1982.

Mixtures	Seed yield					
	g/plant			g/ m^2		
	S_1	F_1	Mixture	S_1	F_1	Mixture
A (10 % S_1)	—	0.28 a	0.28 a	—	77 a	77.0 a
B (30 % S_1)	0.18 a*	0.38 b	0.38 b	0.7 a	106 a	106.7 a
C (50 % S_1)	0.15 a	0.43 b	0.40 b	1.0 a	94 a	95.0 a

* Means within a column followed by the same letter not significantly different at 1 % level.

Height at the 1st 1982 cut and total green matter yield per m² (1981 + 1982) are reported in table 5. Seed producer plants were characterized by average heights close together and twice those of non seed producer plants (62.64 cm vs 35.56 cm in mixture A, 65.05 cm vs 31.40 cm in B and 67.01 cm vs 31.19 cm in C). For what total green matter yield per m² is concerned, seed producer plants yielded 65 %, 76 % and 73 % of the total in mixtures A, B and C respectively. These results confirm that, under dense stand conditions, plants superior in height, which is one of the most powerful characters governing competitive ability (ROTILI & ZANNONE, 1974, 1975 ; YAMADA & HORIUCHI, 1960) are the most productive both in forage and in seed.

IV. CONCLUSIONS

The present research suggests the possibility of studying alfalfa populations under competitive conditions similar to those of a normal stand. Under these conditions, forage yield of S₁ plants is much lower than that of F₁ plants in a mixture, and this inbreeding effect tends to increase over time. As already shown in our preliminary results (VERONESI & LORENZETTI, 1983), average S₁ green matter yield is confirmed to be not significantly affected by their percentage in the mixture. The constant low yield of inbred plants seems to be associated with their inbred condition rather than with the presence of a lower or higher number of high competitive phenotypes. On the contrary, F₁ plants tend to increase their average yield as the percentage of S₁ plants in the mixture increases, showing high competitive effects. As a consequence, no differences were observed in dry matter yield/m² among mixtures and, in accordance with the results of TYSDAL & KIESSELBACH (1944) and PARRINI (1963), an increase or decrease of S₁ seed percentage in the initial seed lot would not seem very important with respect to productivity of an alfalfa stand both in the seeding and in the second year. Selective elimination of S₁ plants was very strong and, one year after seeding, only few S₁ plants survived, irrespective of their percentage in the initial seed lot.

TABLE 5

Height per plant at the first 1982 cut (cm) and total green matter yield per m² (1981 + 1982) of non seed producer and seed producer plants, respectively.

Hauteur des plantes à la 1^{re} coupe de 1982 (en cm) et production totale de matière verte par m² (1981 + 1982) respectivement des plantes non productrices et des plantes productrices de semences.

Mixtures		Characters	
		Height (3/15/1982) (cm)	Total green matter yield (g/m ²)
A	Non seed producers	35.56	2 091
	Seed producers	62.64	3 849
	Total	48.19	5 940
B	Non seed producers	31.40	1 556
	Seed producers	65.05	5 074
	Total	50.84	6 630
C	Non seed producers	31.19	1 666
	Seed producers	67.01	4 434
	Total	50.89	6 100

Only 0 %, 0.6 % and 1 % of the seed produced in the second year came from S₁ plants in A, B and C mixtures, respectively. Therefore, in alfalfa stands which have undergone competition, it seems likely that S₁ plants do not significantly contribute to seed yield. For this reason, it seems almost impossible that, in an alfalfa stands, plants derived from more than one cycle of selfing are present. The highest yielding phenotypes, which produced 60-70 % of the total forage yield and 100 % of the seed yield, were almost all F₁ plants coming from 15-20 % of the seed sown and were characterized by an average height twice the others ; this indicates that, as already shown by LORENZETTI (1981), in a leguminous forage species such as alfalfa forage yield selection is not incompatible with seed yield selection and can be done under dense stand conditions.

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