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Interference effects in white clover genotypes grown as pure stands and binary mixtures with different grass species and varieties

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Abstract Six white clover genotypes and eight grass varieties belonging to four different species were grown both in monoculture and as grass-legume binary mixtures in dense swards for two years under a mowing regime and a management including N fertilization. Dry matter yield and yield-related traits were recorded to investigate some aspects of inter-specific interference in white clover-based mixtures and to define a methodology for selecting genotypes of this clover suited to conditions of association. Clover was at a competitive disadvantage in most mixtures. Differences among grasses for aggressiveness were related more to variety vigour than to species. Clover compatibility proved specific only in relation to grass vigour. Variation among clovers for tolerance to competitive stress involved significant cross-over interactions passing from monoculture to severe stress conditions for clover yield and other traits, and was related positively to stolon density and negatively to yield and leaf gigantism traits recorded in monoculture. Clover selection for high levels of competitive stress seems possible either by genotype assessment in stress conditions or by a combination of high yield and stolon density assessed in monoculture.

Key words Compatibility · Competition · Inter-specific interference · Selection · *Trifolium repens*

Introduction

White clover (*Trifolium repens* L.) is a forage legume almost invariably grown in association with grass (Frame and Newbould 1986). In evaluating white clover genotypes for breeding purposes, different authors (Atwood and Garber 1942; Davies and Tyler 1961; Dijkstra and De Vos 1972) reported rather low correlations between performance as spaced plants and as plants in a dense, mixed sward, and concluded that a thorough evaluation could only be carried out in the latter condition. Annicchiarico and Piano (1993), assessing the yield of white clover genotypes in density conditions as pure stands and in binary mixtures with two ryegrass varieties, found relevant interaction effects between monoculture and association with one of the grasses. Positive interaction effects were observed in white clover-grass binary mixtures which had previously coexisted (Hill 1990; Lüscher and Jacquard 1991; Lüscher et al. 1992) as well as in some mixtures with no history of coexistence (Collins and Rhodes 1990). Emphasis has recently been placed on an interest in identifying traits related to general compatibility and usable as selection criteria in the breeding of this clover (Hill and Michaelson-Yeates 1987a; Collins and Rhodes 1990; Hill 1990).

In the present study, white clover genotypes, mostly of the Ladino type, were evaluated in dense swards together with grass varieties belonging to different species and with which no coexistence had previously taken place. Information was generated on the occurrence and extent of inter-specific interference effects on yield and some yield-related traits and on the relation between these effects and the traits recorded in monoculture, in order: (1) to gain a better understanding of some aspects of inter-specific interference in white clover-based mixtures and (2) to define for this clover a methodology of genotype evaluation suited to breeding for conditions of association.

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Materials and methods

About 30 white clover genotypes were randomly collected from experiment plots of Ladino ecotypes and from medium-to-large leaved varieties and, after vegetative multiplication, were evaluated in replicated pots and density conditions for canopy height, leaf size and stolon density and thickness. Six genotypes which seemed to adequately represent the range of variation available for the given traits were chosen for inclusion in the experiment, namely '17', '22' and '28', singled out from different Ladino farm ecotypes, '13.1' and '4', from two Ladino natural populations, and 'ME' from the variety 'Merwi'. Eight grass varieties belonging to four species (Table 1) were also included in the trial. Within the cocksfoot and the tall fescue groups, the varieties were chosen as contrasting for earliness, growth rhythm, and/or vigour.

After vegetative multiplication of the clovers and sowing of the grasses in Petri dishes, the materials were grown in jiffi pots for about 6 weeks before transplanting in the field, which took place in Lodi (Northern Italy) on a sandy-loam soil at the end of May 1990. The experiment lasted 2 years and was designed as a split-plot with four replications holding all the possible grass-legume binary mixtures, the monocultures of clover and those of grass on the main plots. Alternate clover and grass rows in the mixtures, and clover or grass rows in the pure stands of each component, were 10 cm apart in 80 × 40 cm plots. In the rows, grass seedlings were spaced 3 cm apart while clover clonal propagules, about 6 cm long, were 6 cm spaced. All received 40 kg ha^{-1} of N, 200 kg ha^{-1} of P_2O_5 and 250 kg ha^{-1} of K_2O prior to transplanting. In addition, the mixtures were given 40 and 70 kg ha^{-1} of N during the first and the second year's crop cycle respectively, while the grass monocultures were given a double amount of these rates, according to the ordinary, relatively intensive crop management in the region. The trial was regularly irrigated during summer and was mowed on July 5, August 7 and September 10 in 1990 and on May 3, June 20 and August 4 in 1991.

The occurrence of interference effects was assessed on the following traits: clover (CY), grass (GY) and total (TY) dry matter (D.M.) yield and clover percent (CP), computed over the second to the sixth cut on a 66 × 20 cm plot harvest area; canopy height of clovers (CH) and grasses (GH), measured at the fourth and the sixth cut; and clover stolon density (SD), determined at the end of the trial as the number of stolons transecting a 30 cm line. Some other traits were recorded only on the pure stands in order to characterize the materials, namely: clover size (length × width) of the central leaflet (LS) and stolon thickness (ST), measured at the fourth and the sixth cut on four random leaves and stolons; clover Spring growth, expressed as the ratio between Spring (fourth cut) and Summer (second, fifth and sixth cut) D.M. yield; and grass earliness (GE), observed prior to the fourth cut and expressed as early, medium, or late if heading of 10% of plants occurred respectively by the end of April, by May 6, or later. The average value of the observations was retained for statistical analysis for those traits recorded twice in the time. The relative yield total (RYT) (de Wit and Van den Bergh 1965) of each mixture was also computed and individually tested for difference to unity by a t test to assess the association advantage over the monocultures.

Following the experimental lay-out, interference effects between mixtures were depicted by a factorial analysis of variance (ANOVA) including the factors "clover" and "grass", whereas those between the monoculture and the association conditions were assessed separately for clovers and grasses by ANOVAs including, besides "clover" or "grass", the factor "condition" with the levels of monoculture and the average of mixtures (see Table 2). In these latter analyses, the variables CY, GY and SD were reported to a comparable unit area for the two conditions by retaining half of the value for the pure stands. For each clover trait, the monoculture and association information was then combined by a joint regression analysis (Finlay and Wilkinson 1963; Jacquard and Caputa 1970; Breese and Hill 1973) in which the clover mean values in the condition of monoculture and of association with each of the companion grasses were regressed on the condition mean value. Heterogeneity of "regressions" was tested on the term "deviations" from regression. Homogeneity of the error variances referring to each condition was preliminarily verified by Hartley's test. The occurrence of significant cross-over interactions was assessed by a t test comparison of the estimates of genotype regressions at certain condition mean values. The same assessment was carried out by the Gail and Simon (1985) test for GY between the conditions of monoculture and the average of mixtures. The characters recorded only on the pure stands were analyzed by a one-factor ANOVA. Relationships between traits were investigated by simple correlation analysis. All statistical analyses were performed by the SAS computer package.

Table 1 Grass variety, species, code, earliness (GE), mean and mean separation of the highest (a) and lowest (b) values of D.M. yield in t ha^{-1} (GY) recorded in monoculture

Variety	Species	Code	GE[a]	GY[b]
Cambria	Cocksfoot	CA	l	20.9 b
Dama	Cocksfoot	DA	m	14.6 b
Dora	Cocksfoot	DO	m	31.1 a
Festorina	Tall fescue	FE	l	29.4 a
Magno	Tall fescue	MA	e	29.7 a
Maris Kasba	Tall fescue	MK	l	20.3 b
Crema	Italian ryegrass	CM	l	27.7 a
Pamir	Perennial ryegrass	PA	e	23.4

[a] e = early, m = medium, l = late
[b] Values with different letters differ at $P \leq 0.05$ according to the Newman and Keuls test

Results

The RYT mean value was 1.45 indicating that mixtures yielded, on average, 45% more than the corresponding monocultures. Among mixtures, RYT ranged between 1.84 and 1.01 and proved significantly ($P \leq 0.05$) higher than the unity value in 31 associations out of 48.

Variation for yield traits among mixtures (Table 2) was attributable to both grass and clover mean effect for CY, TY and CP, but only to grass for GY. Mean values of CY and GY for each component are plotted in Fig. 1. As suggested by the ANOVA results also, clovers differed for general compatibility since a higher CY did not involve a lower GY. For the grasses, increasing clover percent was clearly associated with lower total yield, while no difference was observed for general compatibility expressed as a relevant deviation from the inverse relationship between CY and GY. Grass differences for the level of aggressiveness to clover were little relatable to species, as shown by the contrasting response of the cocksfoot varieties. Clover was at a competitive disadvantage with all grasses except 'Dama' (Fig. 1). 'Pamir' and 'Crema' roughly identified the limits of vigour of a range of grasses, including 'Cambria', 'Festorina' and 'Magno', which was interesting from an agronomic point of view. The use of these grasses allowed a reasonable compromise between a high total yield and a clover percent still acceptable according to Hill and Michaelson-Yeates (1987a) and Thomas (1992) since it was not lower than 20% for the mixture including the best yielding clover. Significant "clover × grass" interaction was found only for CY and CP (Table 2) indicating that compatibility effects related to specific clover-grass mixtures only occurred for clover yield. According to the partitioning of interaction results, these effects were related more to grass variety than to species. For CY, the interaction term was also significant between monoculture and association.

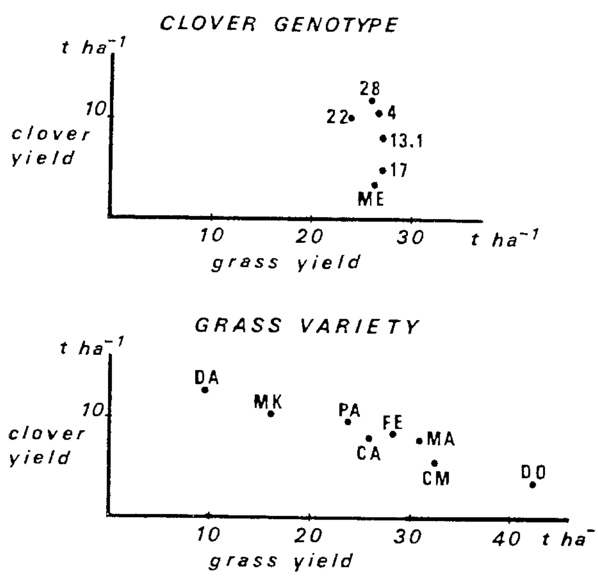
In the regression analysis of CY, regressions differed significantly (Table 2) and accounted for 56% of the

Table 2 F test results for (a) the factorial ANOVAs of six white clover genotypes and eight grass varieties (1) in binary mixtures and (2) in conditions of monoculture and association, and (b) the joint regression analysis of six white clover genotypes in conditions of monoculture and binary mixtures with eight grass varieties, for clover D.M. yield (CY), height (CH) and stolon density (SD), grass D.M. yield (GY) and height (GH), and total D.M. yield (TY) and clover percent (CP). (ns, *, **, ***: not significant, and significant at $P \leq 0.05$, 0.01 and 0.001, respectively)

Source of variation	*df*	CY	CH	SD	GY	GH	TY	CP
(a1) Clover (C)	5	***	***	***	ns	*	*	***
Grass (G)	7	***	***	***	***	***	***	***
– Among species	3	***	**	***	***	***	ns	***
– Within species	4	***	**	***	***	***	***	***
C × G	35	***	ns	ns	ns	ns	ns	**
– C × (among species)	15	*	ns	ns	ns	ns	ns	*
– C × (within species)	20	**	ns	ns	ns	ns	ns	**
(a2) Clover	5	***	***	***				
Condition	1	*	***	ns				
Clover × Condition	5	*	*	*				
Grass	7				***	***		
Condition	1				***	*		
Grass × Condition	7				**	ns		
(b) Regressions	5	***	**	**				
Deviations	35	ns	ns	ns				

interaction sum of squares whereas no significant deviation from regression was detected. Clover compatibility, therefore, appeared specific in relation to the level of competitive stress, i.e., vigour of the grass, but not in relation to variation for factors such as grass species or grass variety earliness (Table 1). The interaction effects mainly concerned the top-ranking '22' and '4' (Fig. 2). These genotypes and the stable and high-yielding '28' were compared (Table 3) in terms of slope, interpretable as an indicator of sensitivity to competitive stress, and estimates of regressions at the levels of monoculture and association with 'Pamir' and 'Crema'. The slopes differed significantly while significant cross-over interactions took place within the given range of conditions.

Fig. 1 Plot of the mean clover and grass D.M. yields of six white clover genotypes and eight grass varieties in binary mixtures



The clovers assessed as pure stands differed significantly for all traits except Spring growth. Genotype '22' was characterized by the highest values of CH, LS and ST and the lowest SD, while 'ME' showed almost oppo-

Fig. 2 Regression of the individual clover D.M. yield (*CY*) value on the condition mean value for six white clover genotypes in conditions of monoculture and binary mixtures with eight grass varieties

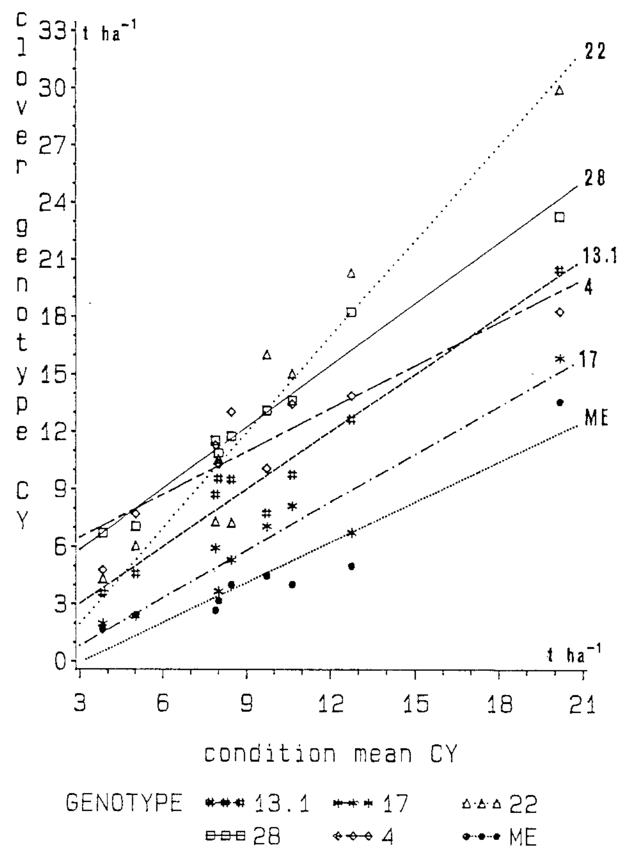


Table 3 Slopes and estimates of regressions of three white clover genotypes at abscissa values corresponding to certain conditions of association, for clover D. M. yield in t ha^{-1} (CY), height in cm (CH), number of stolons per metre (SD) and ratio between clover yield and number of stolons (CY/SD)

Trait[a]	Genotype		
	22	28	4
b_{cy}	1.66 a	1.07 b	0.75 c
CY at monoculture	30.6 a	24.2 b	19.3 c
CY at 'Pamir'	13.1 a	13.0 a	11.5 a
CY at 'Crema'	5.4 b	8.1 a	8.1 a
b_{ch}	0.52 b	1.33 a	1.29 a
CH at monoculture	22.0 a	20.5 ab	19.0 b
CH at 'Crema'	25.3 c	28.9 a	27.3 b
b_{sd}	0.53 b	0.88 b	1.19 a
SD at monoculture	27.9 c	42.2 b	56.3 a
SD at 'Crema'	13.4 b	17.7 b	29.2 a
$b_{cy/sd}$	4.42 a	0.01 b	0.39 b
CY/SD at monoculture	1.11 a	0.53 b	0.32 c
CY/SD at 'Crema'	0.43 ab	0.53 a	0.26 b

[a] Values with different letters differ at $P \leq 0.05$ for slopes and at $P \leq 0.01$ for estimates of regressions, following comparison by a t test

Table 4 Simple correlation coefficients for clover D.M. yield (CM_m), height (CH), stolon density (SD), central leaflet size (LS) and stolon thickness (ST) in monoculture, sensitivity to competitive stress (b_{cy}) and average clover (CY_a) and total (TY) D.M. yield in association for six white clover genotypes. (@, **: different from zero at $P \leq 0.10$ and 0.01, respectively)

Trait	CY_m	CY_a	b_{cy}	TY
CY_m	–	0.67	0.95**	0.10
CH	0.89**	0.80@	0.74@	0.38
SD	−0.54	0.15	−0.73@	0.58
LS	0.77@	0.31	0.83**	−0.17
ST	0.34	0.19	0.33	−0.06

site features. Both '28' and '17' had rather high LS and ST values, but the former was taller and produced more stolons. The clones '4' and '13.1' had relatively low values of LS and ST and high values of SD, but the former showed a taller canopy.

Clover in association, compared to monoculture, was on average significantly (Table 2) taller (+36%) and with a higher stolon density (+21%). For both traits, "clover × condition" from monoculture to association was significant while "clover × grass", though not significant, reached a P level ≤ 0.10. The interaction effects could be effectively described in terms of heterogeneity of genotype regressions whereas no significant deviation from regression was detected (Table 2). Slopes and estimates of regressions of '22', '4' and '28' at monoculture and 'Crema' conditions are given in Table 3 for these same traits. The former genotype, particularly sensitive to competitive stress, responded to increased levels of stress by a lower increase of plant stature and a decrease of stolon number relative to the others.

The ST values recorded for '22', '28' and '4' in monoculture, respectively 3.3, 2.9 and 2.5 mm, suggest that the differences among these clovers for stolon biomass production in that condition were much lower than those recorded for stolon density. Although stolon D.M. yield was not assessed in the experiment, the CY/SD ratio was computed to provide an indication of the variation of the ratio between aerial- and stolon-biomass of the genotypes across conditions. The joint regression analysis of this ratio, in which the "regression" term was significant at $P \leq 0.01$, provided the estimates reported in Table 3 for the three top-ranking genotypes. Passing from monoculture to the 'Crema' condition, '22' had a greatly reduced CY/SD ratio up to a value comparable to that of '28' which, by contrast, kept a constant ratio. The coefficient of the correlation between the genotype slope value for CY and those for CH (−0.63), SD (−0.83) and the CY/SD ratio (0.79), and that between b_{ch} and $b_{cy/sd}$ values (−0.86), confirmed the fairly close relationship between the genotype responses for these traits. While b_{sd} was highly correlated to SD in monoculture (r = 0.89), b_{ch} was not related to CH in that condition (r = −0.09).

Table 4 reports the correlation coefficients of each trait recorded in monoculture with sensitivity to competitive stress (b_{cy}) and average clover (CY_a) and total D.M. yield of the six genotypes. The latter two variables refer only to mixtures including those five grasses previously considered as agronomically interesting for association. Clover yields in monoculture and averaged over associations were only moderately correlated, confirming that an accurate assessment of a genotype performance in those mixed sward conditions could hardly be provided by its monoculture. Sensitivity to competitive stress was related positively to CY, LS and CH, and negatively to SD, assessed on the pure stands (Table 4). The latter trait also tended to a positive correlation with average total yield, while CH was generally related to high CY in all conditions.

The grass yield in pure stand is reported in Table 1. Although significant "grass × condition" interaction was detected for GY from monoculture to association (Table 2), no significant crossover interaction between these conditions was found even at $P \leq 0.20$. Plant height of grasses was significantly (Table 2) increased by association (+16% than in monoculture) reaching, on average, 48 cm. Within that condition, GH tended to be higher in those mixtures with higher-yielding clovers. Among grasses, the variation for GH and that for GY were strictly related. High GH in monoculture was associated with high GY in monoculture (r = 0.84) as well as to a further GY advantage in association expressed as the average GY interaction effect passing from monoculture to mixed sward condition (r = 0.85).

Discussion

As usual in forage grass-legume associations (Zannone et al. 1986), mixtures mostly outyielded the corresponding pure stands. The rather large extent of this interference effect seems attributable not only to complementary growth patterns of the components but also to the contribution of nitrogen fixed by the legume. In white clover, nitrogen is rather readily available from leaf and stolon decay (Harris 1987) and its below-ground transfer to the grass in a mixed sward can amount to about 70 kg/ha per year (Ledgard 1991). This transfer could also explain the lack of GY decrease in those mixtures including the best general compatible clovers. Hill and Michaelson-Yeates (1987a) and Evans et al. (1989) found a somewhat similar feature in ryegrass-white clover binary mixtures where differences in clover percent were only due to a clover effect.

A positive relation between total yield and grass aggressiveness has already been observed in white clover-based mixtures (Harris 1987). The high vigour of most grasses, combined with the effect of N fertilization, could explain (Frame and Newbould 1986) the strong competitive disadvantage of the clover in most mixtures. The differing aggressiveness showed by the cocksfoot varieties supports the hypothesis that the suppressing effect on white clover, often reported for this species, could be, at least under a cutting management, simply related to the involvement of vigorous varieties (Harris 1987).

Genotype assessment of forage crops is usually carried out in monoculture not only for reasons of cost limitation but also for evaluating, beside D.M. yield, other important characters such as seed yield components. As white clover is the component of higher value in a mixture, compatibility effects of practical interest in the breeding of this clover are those referring to genotypes whose mixtures have higher clover yields for a given total yield level and which cannot be predicted from the yield of monocultures. In this study, compatibility proved partly specific in relation to variation among clovers for tolerance to competitive stress. In intensive management conditions like ours, where the agronomically interesting mixtures were those in which clover experienced a severe competitive stress, this information proved particularly valuable since it was related to the occurrence of cross-over interactions between the monoculture and mixed sward conditions and these interactions, unlike those observed by Dijkstra and De Vos (1972), concerned the top-ranking genotypes.

Under our experimental conditions, relatively favourable with respect to water and nutrients, inter-specific competition mainly occurred for light (Austin 1990). Canopy height has been advocated as a fundamental trait for better withstanding this type of competition both for white clover (Harris 1987) and for other species (Keddy 1990). In our case, this was true only as far as the grasses were concerned. Grasses differed for yield responsiveness from pure stand to association but, because of the close relation between responsiveness, plant stature and yield in monoculture, the differences among grasses in association were greater but substantially consistent with those recorded on the pure stands. This finding is in agreement with those of Rotili (1985) and Zannone et al. (1986) concerning grass-legume binary mixtures of different non-stoloniferous forage species. In white clover, our results suggest that rather large inconsistencies may take place particularly between monoculture and severe competitive stress conditions. Hill and Michaelson-Yeates (1987a), studying white clover families in monoculture and two mixed sward conditions in which clover was not at competitive disadvantage, did not find significant "clover × condition" interaction for D.M. yield and indeed the correlation that we computed for the published clover yields between monoculture and the average of the associations was very high ($r = 0.99$). Annicchiarico and Piano (1993), considering a larger set of genotypes, found coefficients of 0.89 and 0.69 for the correlation of clover yields in pure stand with those in association with the grasses 'Pamir' and 'Crema', respectively. Competitive stress exerted by the latter, more vigorous, ryegrass was severe and clover sensitivity to it was still related negatively to stolon density and positively to leaflet size, but not to canopy height and clover yield, assessed on monocultures. The whole of our findings suggests a relation between the rather wide variation for sensitivity to competition that we found in white clover and its peculiar, stoloniferous growth habit. Higher stolon density could confer higher tolerance to competition exerted by vigorous grasses, whose stature is much greater than that of any white clover, by allowing the clover to better reach and exploit those spots in the canopy where light is still sufficient for good growth and progressively adapt to variation in the position of these spots. The importance of this feature seems confirmed by the fact that clovers increased average stolon density in association while genotype '22', the lowest stolon producer in monoculture, increased that production more than the others at increasing competitive stress, though this was associated to a cost in terms of canopy height. The differences in capability to respond to changes in grass canopy height by petiole elongation, which has been referred to as petiole plasticity and related to a higher general compatibility in white clover by Hill (1980) and Hill and Michaelson-Yeates (1987b), was also relatable to some extent to clover tolerance to competitive stress; but it could be viewed as a cause as well as an effect of that tolerance in our study. In favour of the latter hypothesis, Turkington and Harper (1979) observed that white clover genotypes responded to very high levels of competition by decreasing canopy height, whilst in the present work no further increase in average clover height was observed over the competition level (Fig. 1) corresponding to the association with 'Cambria', a grass with intermediate values of vigour and plant height. The influence of stolon density on tolerance to competitive stress is also supported by some observations of Atwood and Garber (1942) and Dijkstra and De Vos (1972).

Following on from our results, it is clear that compatibility can be a valuable objective in white clover breeding but needs to roughly define a target level of competitive stress to breed for. Preliminary genotype evaluation seems worthwhile in a pure stand condition. Then, if breeding is intended for high levels of grass competition, genotypes could be further assessed either in association with one or two vigorous grasses, or by a selection criterion referring to monoculture information to combine high values of yield and stolon density and giving to the latter trait a weight proportional to the target level of competitive stress. Further emphasis on high stolon density is justified when general persistence and/or tolerance to continuous grazing are important breeding objectives (Williams 1987; Rhodes 1991).

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