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INTERSPECIFIC RELATIONS AND THE BREEDING OF PASTURE PLANTS FOR SEMIARID REGIONS

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ABSTRACT

One hundred plants of NC-83-1 alfalfa (*Medicago sativa*) were vegetatively propagated and grown in a replicated spaced-plant selection nursery in association with Fairway crested wheatgrass (*Agropyron cristatum*), Oahe intermediate wheatgrass (*Thinopyrum intermedium*), RS-2 hybrid (*Elytrigia repens* x *Pseudoroegneria spicata*), Vinall Russian wildrye (*Psathyrostachys juncea*), and NC-83-1 alfalfa. Plants were spaced 0.5 m apart on a rectangular grid with eight associated species plants surrounding each centre alfalfa plant. Forage yield per plant was measured in four harvests each year during the second and third years following establishment. Alfalfa was the most competitive associated species. Rhizomatous grasses were more competitive than bunchgrasses. Potential yield gains were estimated according to four selection criteria. All criteria resulted in significant estimated gains but no criterion was distinctly superior. Selection based on total plot weight within each of the five associated species resulted in the greatest potential gain. Selection based on alfalfa plant weight averaged over all five of the associated species resulted in the lowest potential gain.

KEYWORDS

Alfalfa, competition, crested wheatgrass, grass, intermediate wheatgrass, legumes, range, Russian wildrye, *Agropyron cristatum*, *Elytrigia repens*, *Medicago falcata*, *Medicago sativa*, *Psathyrostachys juncea*, *Pseudoroegneria spicata*, *Thinopyrum intermedium*.

INTRODUCTION

In his classic review of competition among crop and pasture plants, Donald (1963) concluded that a mixture of two genotypes cannot fix more carbon than the more productive of the two genotypes fixes when grown in monoculture. However, after reviewing the published data on 344 varietal or interspecific mixtures, Trenbath (1974) concluded that legume-grass mixtures grown for forage have yield and quality advantages. He attributed the advantages to special nutrient interactions between the two types of components. Significant legume to grass nitrogen transfer is known to occur in such mixtures and the amount of nitrogen transferred is dependent upon the proportion of legume in the mixture (Brophy *et al.* 1984). Most of these studies were done in agronomic rather than rangeland environments.

Species mixtures for semiarid rangeland seeding

Grass species most often used in seeded rainfed pastures in semiarid and arid environments of the western United States are smooth bromegrass (*Bromus inermis* Leyss.), intermediate wheatgrass (*Thinpyrum intermedium* [Host] Barkworth & D.R. Dewey), and the crested wheatgrasses (*Agropyron cristatum* [L.] Gaertner s. lat., *A. desertorum* [Fisch. ex Link] Schultes, and *A. fragile* [Roth] Candargy). Bromegrass is best adapted to areas near the subhumid region and the crested wheatgrasses are most drought resistant. Legumes most often selected as the second component of binary mixtures are alfalfa (*Medicago sativa* L. and *M. falcata* L.) or sweetclover (*Melilotus alba* Desr. and *M. officinalis* [L.] Lam.) (Rumbaugh and Townsend 1985). Dubbs (1971, 1975), Kilcher *et al.* (1966), Kilcher and Heinrichs (1971), and Leyshon *et al.* (1981) intensively studied binary species mixtures of grasses and alfalfa in semiarid environments. Alfalfa plus crested wheatgrass and alfalfa plus intermediate wheatgrass yielded significantly (P 0.05) more forage than alfalfa plus either Russian wildrye (*Psathyrostachys juncea* [Fisch.] Nevski) or smooth bromegrass or than alfalfa alone. All of the legume-grass mixtures yielded more than grasses seeded in monocultures (cooperation). Alfalfa plants received more competition from other alfalfa plants than from grass plants. Russian wildrye was the most competitive grass associate with alfalfa and intermediate wheatgrass was the least competitive associate.

Cultivar and progeny yields in binary mixtures

Data from semiarid or arid rainfed experiments are not available. The following results were obtained in more humid environments. Wilsie (1949) and Van Keuren (1961) concluded that critical yield testing of grass-legume mixtures could not be replaced by pure stand yield trials. Casler and Drolsom (1984) suggested that forage grasses should be yield-tested in both pure stands and in mixtures with alfalfa if:

- A proposed cultivar is to be grown under both conditions.
- The genetic correlation between pure and mixed stands is low.

In their investigations of cool season grasses and alfalfa, mean seasonal forage yield ranks for pure and mixed stands were generally not correlated for cultivars of any species. Similarly, eight clover populations (*Trifolium repens* L.) were grown as monocultures and in mixtures with two cultivars of perennial ryegress (*Lolium perenne* L.) in a humid climate at the Welsh Plant Breeding Station (Rhodes and Mee 1982). The grass cultivars differed in aggressiveness and the ranking of the clover cultivars varied with the companion grass cultivar. Reich and Casler (1985) suggested that selection among smooth bromegrass progenies for forage quality might be aided by evaluating them in mixed stands with alfalfa.

Selection of spaced plants

Selection for productivity under spaced-plant conditions has been the major technique utilized to construct synthetic varieties of forage grasses in Europe (Cooper 1959, Hayward 1983) and in the U.S.A. (Burton 1974, 1985). Most often, spaced-plant selection nurseries and progeny trials consisting only of one species are used.

Four cultivars of alfalfa were evaluated as spaced plants and in broadcast and drilled plots, with and without a companion grass, at Aberystwyth (Davies and Reuch 1964). Widely spaced plants gave a misleading impression of the yield and drought resistance of some cultivars. In an irrigated test in Nevada, Stortz *et al.* (1984) measured yields of three alfalfa populations with plants positioned in honeycomb configurations at 30, 17.5 and 10 cm distances between plant centres. There was a complex interaction among per plot yield, per plant yield, density, and population, indicating the difficulty of phenotypic selection for yield in these environments. A similar evaluation has not been conducted at a nonirrigated, semiarid site, although Irvine and Jefferson (1984) evaluated ten alfalfa cultivars at a site receiving 360 mm of precipitation annually in southwestern Saskatchewan. Cultivars were in rows 30 cm and 90 cm apart. There was a significant cultivar by spacing interaction during the three-year experiment. Their data indicated that *Medicago falcata* cultivars better exploited the moisture available from reduced interplant competition in wide row spacings than did *M. sativa* cultivars.

Research objective

Since plant species and cultivars are known to interact in ways that either increase or decrease total and relative yields in grass-legume mixtures, plant breeders must consider whether clones of a species to be improved must be selected while growing in association with the species with which the resulting improved cultivar will ultimately be used. Our objective was to evaluate whether alfalfa clones respond differentially to association with five species commonly recommended for semiarid pasture plantings.

MATERIALS AND METHODS

One-hundred randomly chosen plants of the NC-83-1 alfalfa germplasm release (Kehr *et al.* 1975) were vegetatively propagated during the winter of 1982-83. Plants of five species to be grown in association with the 100 alfalfa clones were started from seed at the same time. Alfalfa was included as one of the associated species since breeders customarily select alfalfa plants and clones in nurseries where they are grown close to other plants of the same source population. Three of the grass cultivars, Fairway, Oahe, and Vinall, are widely grown in semiarid North America and often are grown with alfalfa. The fourth grass, 'RS-2', is a recently released germplasm (Asay and Dewey 1981) which may be widely used in some of the western states.

Rooted plants and propagules were transplanted to the field in May, 1983, and irrigated twice to ensure establishment. Each alfalfa propagule was surrounded by eight border plants of an associated species. All plants were spaced 0.5 m apart in a rectangular grid pattern. This plant density approximates that which occurs in the drier parts of the semiarid rangelands of the United States, and insured that the plants were close enough to interact. Range forage breeders often select plants from such nurseries on the basis of topgrowth biomass (Away *et al.* 1985a, 1985b). Plots consisting only of grasses were not included in the study because of limited experimental resources.

The experimental design was a two-replicate split-plot; whole plot treatments were the five associated species, and sub-plot treatments were the alfalfa cones. The experimental field is at 1,369 m elevation and receives an average of 440 mm precipitation annually. The soil is a coarse-silty caronatic mesic Typic Haploxeroll. Weeds were controlled manually throughout the experiment. All plants were clipped twice in 1983 and the forage discarded. Four individual plant harvests were made in 1984 and again in 1985. Harvests were initiated when alfalfa clones were at the one-tenth bloom stage. Clipping height was 2.5 to 5.0 cm. Forage was dried in a forced-air oven at 100 °C prior to weighing. Thirty-seven clones with less than perfect stands throughout the experiment were deleted from further consideration. Stand loss was attributed primarily to rodent damage during the winter. Average weight of the center alfalfa plant, eight associated border plants, and total plot weight were then calculated on a per year basis. The potential gains in forage yield based on the four criteria listed in Table 1 were computed for the remaining 63 clones to evaluate the relative effectiveness of the selection procedures. Data were analyzed by analysis of variance, correlation, and t-test procedures.

Table 1. **Identification codes for selection criteria used in the species association study.**

Identification code	Criterion
0	No selection
1	Fifteen percent of the population selected with alfalfa shoot weight (g/year) when grown with alfalfa as the associated species as the criterion.
2	Fifteen percent of the population selected with plot weight (g/year) averaged over all five associated species as the criterion.
3	Fifteen percent of the population selected with alfalfa shoot weight (g/year) within each of the five associated species as the criterion.
4	Fifteen percent of the population selected with plot weight (g/year) within each of the five associated species as the criterion.

RESULTS AND INTERPRETATION

Average forage weight per plot almost doubled when alfalfa was the associated species instead of any of the four grass species (Table 2). Plot weight with intermediate wheatgrass exceeded that of RS-2 hybrid wheatgrass and both of these grasses were superior to crested wheatgrass or Russian wildrye. Average weight of the center alfalfa plant was inversely related to average total plot weight, except when alfalfa was grown with crested wheatgrass or Russian wildrye. Based on average alfalfa clone weights, the ranking of the associated species in terms of their competitiveness with the alfalfa clones was alfalfa > intermediate wheatgrass >RS-2>Russian wildrye > crested wheatgrass. However, within each associated species, weight of the center alfalfa plant was positively correlated with total plot weight. The coefficients of correlation (r) were 0.89 within crested wheatgrass, 0.72 within intermediate wheatgrass, 0.78 within RS-2, 0.83 within Russian wildrye, and 0.66 within alfalfa.

The analysis of variance demonstrated that where alfalfa was the border species, both alfalfa clone shoot weight and total plot weight differed significantly ($P < 0.01$) from plots in which grasses were the border species. Intermediate wheatgrass plots differed significantly ($P < 0.01$) from RS-2 plots, and the average of the bunchgrasses differed significantly from that of the rhizomatous grasses for each of the two attributes. Total plot weights from crested wheatgrass and Russian wildrye plots were significantly different ($P < 0.05$) but weights of the alfalfa clones were similar ($P > 0.05$) when grown with these two bunchgrasses.

These results are quite different than those obtained by Kilcher *et al.* (1966) and by Dubbs (1971, 1975) in tests using row plantings. Dubbs found that alfalfa competing against alfalfa yielded less forage than alfalfa competing against grasses. Russian wildrye was the least competitive grass in our experiment but was the most competitive grass in the experiments conducted in Saskatchewan and Montana. The effects may be attributable to the plant materials, the planting pattern, the spatial density of the plants, or to environmental differences.

In our experiment, as in the experiments cited above, alfalfa competed more strongly against the 63 alfalfa clones than any of the grasses. The two grass species which spread by means of rhizomes competed against alfalfa more

Table 2. **Average dry shoot weight of an alfalfa plant and of 8 border plants per plot of an associated species when grown in Cache Valley, Utah in 1984 and 1985. Two replications, sixty-three alfalfa clones, and four harvests each year.**

Associated species	Component	Shoot weight (g/year) 1984	1985	Average
Crested wheatgrass	Alfalfa	563	341	452
	Border	392	247	319
	Plot total	955	587	771
Intermediate wheatgrass	Alfalfa	436	269	352
	Border	846	357	602
	Plot total	1,282	626	954
RS-2 hybrid	Alfalfa	485	309	397
	Border	656	224	440
	Plot total	1,141	534	837
Russian wildrye	Alfalfa	520	341	430
	Border	422	165	293
	Plot total	942	506	724
Alfalfa	Alfalfa	219	115	167
	Border	2,116	1,006	1,561
	Plot total	2,335	1,121	1,728
Mean	Alfalfa	445	275	360
	Border	886	400	643
	Plot total	1,331	675	1,003

vigorously than the two bunchgrasses, perhaps because the grass border invaded close to the center alfalfa plant. The border plants of crested wheatgrass produced more forage than those of Russian wildrye ($P<0.05$) but these two species were almost equally competitive with alfalfa. Although no data are available to document our interpretation, we believe that the competitive differences among the species in our study were due to root effects, since the harvests were made during the second and third years of stand life and the 0.5 m plant spacing permitted adequate light to reach all grass plants in the nursery at all harvests.

The differences in shoot weight among the 63 alfalfa clones and in total plot weight were significant ($P<0.01$). However, the clone by associated species interaction was not statistically significant ($P<0.05$). Thus, by this test, all of the five associated species ranked the 63 alfalfa clones in approximately the same way. If valid, this enormously simplifies the selection of alfalfa to be grown with a number of grass species on semiarid rangelands. Any synthetic cultivar developed from clones selected in a nursery containing only alfalfa would be expected to do as well in mixtures with any grass. This conclusion was partially supported by rank correlation of the clones among all possible pairs of the associated species. Each correlation was positive and differed significantly from zero ($P<0.01$), although the magnitude of the coefficient of association for the highest correlation was only $r^2 = 0.56$. The magnitudes of the coefficients of association were much lower when the clones were ranked within competition species on the basis of plot weights. The r^2 values ranged from 0.03 to 0.43. Thus, the possibility for selecting subsets of clones with differing competitive abilities is more likely when plot weight is the attribute upon which selection is based.

Selection was simulated according to the four criteria listed in Table 1. The ten superior clones selected on the basis of average alfalfa plant shoot weight (criterion 1) included six of those selected on the basis of total plot weight (criterion 2). This degree of commonality was exceeded only by four other pairs of the selection criteria variants shown in Table 3. Only five clones (19, 22, 30, 42, 68) appeared in six or more of the twelve sets of ten superior clones listed in that table. Many of the selection procedures significantly ($P<0.05$) increased potential total plot weight (Table 4). The lowest gains resulted when alfalfa was the associated species. The greatest potential relative gain

Table 3. Alfalfa clones (numbers are identification codes) included in sets of ten selected from sixty-three clones according to four selection criteria. Species are coded as Agcr = *Agropyron cristatum* Thin = *Thinopyrum intermedium*, RS-2 = *Elytrigia repens* x *Pseudoroegneria spicata*, Psju = *Psathyrostachys juncea*, and Mesa = *Medicago sativa*.

			Criterion									
			(3) Alfalfa weight (g/year)					(4) Plot weight (g/year)				
	(1) Alfalfa	(2) Plot	Associated species					Associated species				
Rank	weight (g/year)	weight (g/year)	Agcr	Thin	RS-2	Psju	Mesa	Agcr	Thin	RS-2	Psju	Mesa
1	42	19	19	22	22	68	42	62	2	68	19	7
2	30	2	62	46	68	19	30	65	19	5	22	1
3	22	22	22	19	30	22	22	19	18	30	38	32
4	68	52	42	38	19	30	68	22	1	65	30	42
5	32	30	68	99	46	62	60	2	54	22	68	2
6	19	42	8	42	38	38	32	52	3	93	18	54
7	36	65	2	36	93	86	19	8	9	53	39	52
8	11	9	65	39	53	93	36	68	60	23	11	9
9	78	68	36	44	79	39	11	42	30	46	86	44
10	46	46	78	18	23	72	78	53	52	14	72	81

Table 4. Mean plot dry weights (g/year) for sixty-three unselected alfalfa clones and for sets of the ten most superior clones selected according to four criteria. The potential gain (selection differential as a percent of the source population mean) is shown in parentheses.

Associated	Selection criterion				
species	0	1	2	3	4
Crested wheatgrass	771	875 (13)**	924 (20)*	943 (22)**	957 (24)**
Intermediate wheatgrass	954	1,010 (6)	1,070 (12)	1,040 (9)	1,115 (17)*
RS-2 hybrid	837	912 (9)	981 (17)*	968 (16)*	1,008 (20)*
Russian wildrye	724	833 (15) *	822 (14)*	880 (22)**	893 (23)**
Alfalfa	1,728	1,787 (3)	1,798 (4)	1,772 (3)	1,931 (12)
Mean	1,003	1,083 (8)*	1,119 (12)**	1,121 (14)**	1,181 (18)**

*, ** Selected set of 10 clones superior to the comparable value for the unselected population (criterion 0) at $P<0.05$ and $P<0.01$, respectively, when evaluated by a t test.

(selection differential), averaged across all selection criteria, was achieved when crested wheatgrass was the associated species (20%), but this gain was only slightly better than when Russian wildrye was the associated species (18%). Thus, more relative gain should be possible with the less competitive bunchgrasses as the associated species than with the more competitive alfalfa or the rhizomatous grasses.

Selection based on total plot weight within each of the five associated species (criterion 4) maximized the average potential gain, and the gain within each of the five associated species (Table 4). However, all four selection criteria resulted in clonal subsets which significantly exceed the average plot weight of the unselected source population. When evaluated by Student's t test procedures, none of the selection criteria was superior ($P < 0.05$) to any other of the selection criteria in average potential gain. All selection criteria were superior to no selection (criterion 0 in Table 4). The potential gains cited could not be achieved unless narrow sense heritabilities for all mixture components equalled 1. In our experiment, the parentage of the border plants was not controlled. The broad sense heritability of the center alfalfa clones computed from the analysis of variance was less than 1 ($H = 0.78$). Thus, the potential gains indicate relative rather than acutal potential for breeding progress.

We suggest that an ideal breeding programme to develop superior plant materials for semiarid rangelands would involve simultaneous selection of both grass and legume species. In the early stages of the selection programme, grass and legume plants could be interplanted so that every legume plant is associated with grass plants and every grass plant is associated with legume plants. Individual plant data would enable the selection of plants of both species on the basis of total plot weights, which consist of the center species plant and its associated border. In advanced stages of selection, the process would be repeated using propagules of a few highly selected clones. Appropriate designs have been suggested by Keller (1946), Hamblin *et al.* (1976), and possibly others.

CONCLUSION

Alfalfa breeders, and possibly grass breeders, selecting plant materials for mixed species pastures should select plants from nurseries or progeny trials where the species is grown in association with one or more of the species with which the improved cultivar will be seeded. Estimated gains when alfalfa was grown in association with grasses exceeded those when alfalfa was grown in association with alfalfa. Although yields from mixtures of alfalfa and rhizomatous grass species exceeded yields from mixtures of alfalfa and bunchgrass species, the greatest percentage gains in total plot weights might be achieved in mixtures with bunchgrasses. Greater gains may be achieved when selection is based on plot weight, including the weight of associated species, than when selection is based only on alfalfa plant weight.

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SYMPOSIUM DISCUSSION

Dr H.S. Easton, Grasslands Division, DSIR

The bar graphs of the lucerne clone growth and the growth of the associate plant side by side seem to show an inverse relationship between growth of the lucerne plant and growth of the associate plant. Lucerne as an associate fits that pattern as do the two bunch grasses and the two rhizome grasses. To what extent is the lucerne associate effect, as opposed to the grass associate effect, simply due to the fact that it is growing?

Rumbaugh

The growth on a per plant basis of the alfalfa border is slightly higher than the growth of the central alfalfa propagule. One reason for that is that it has a grass on the other side of it, rather than being totally surrounded on all sides by alfalfa, as is the case with the central propagule. I am sure there are also differences in rooting patterns between the species, and next summer we will be taking root cores.

Dr S.A. Menzies, Plant Diseases Division, DSIR

I presume that in designing your trials for competition between species, you arbitrarily chose .5 metre spacing and 3 harvests a year. How representative is that of what is natural in the field?

Rumbaugh

There is a lot of latitude there because the plant density in western ecosystem varies considerably. A spacing of 0.5 m is, however, a reasonable approximation of the stands in many of the ecosystems we are looking at, and it is convenient to lay out, and work with. If I were to do the experiment over again, I think that I would try to achieve a slightly higher population density rather than one that was lower. A space of 0.25 m between plants would be the minimum.