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Source: *Oikos*, Vol. 51, No. 1, (Jan., 1988), pp. 3-12

Published by: Blackwell Publishing on behalf of Nordic Society Oikos

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Accessed: 16/04/2008 12:04

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‘Pecking order’ of four plant species from pastures of different ages

Lonnie W. Aarssen

Aarssen, L. W. 1988. ‘Pecking order’ of four plant species from pastures of different ages. – *Oikos* 51: 3–12.

The rank order of competitive effects (‘pecking order’) was studied for four species collected as seeds from each of three different-aged pastures. Based on all pairwise comparisons of performance in mixtures, species rank order was linear for plants from each pasture but the position of species was not identical for each pasture. These rank orders showed no relationship to the rank orders of abundance in the field. Rank orders in four-species mixtures were similar, but not identical to those based on pairwise mixtures for plants from the two younger pastures. The extent to which one species was able to deny resources to another was generally independent of the age of the pasture from which the plants were collected. The extent to which the two components of a mixture made demands on the same resources decreased with increasing pasture age for two pairs of species. These results are contrasted with results from an earlier study involving the same four species collected as neighbouring clones, rather than as seeds. Rank order of suppressive effects on a given target differed depending on which species was the target and generally differed from rank orders based on all pairwise comparisons of performance in mixtures. ‘Constancy’ of rank order (with different targets) decreased with increasing age of the pasture from which plants were collected. The data suggest that a variable rank order of species against different targets may be a consequence of: 1) different degrees to which species make demands on the same resources when the target is changed, and/or 2) different degrees of beneficial effects on different targets, and/or 3) different relative competitive abilities against different targets.

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Introduction

Numerous descriptive studies and field experiments have established that competitive interaction is common in most natural vegetation (Braakhekke 1985). The structure of a plant community therefore, will often be determined to a large extent by the relative suppressive effects of species on each other. This rank order or “pecking order” (Harper 1977) may, for example, indicate a strong dominance hierarchy. Alternatively, most or all of the species in a community may be essentially equivalent in their suppressive effects on each other.

Two different approaches have been used to represent the rank order of competitive effects among species.

In the first case, a group of species are ranked according to their relative suppressive effects on different target species. An important consideration resulting from this approach is whether the order of species in the ranking changes as the target species is changed. Some studies have indicated a constant rank order, i.e. unaffected by target species (e.g., Welbank 1963, Borknamm 1961a,b – cited in Grubb 1977, Obeid 1965 – cited in Harper 1977). Other studies however, have found a significant change in rank order when different targets were tested (e.g., Caputa 1948 – cited in Grubb, Haizel and Harper 1973, Turkington and Harper 1979). The factors affecting whether these rank orders are constant or variable have never been explicitly investigated.

Accepted 7 July 1987

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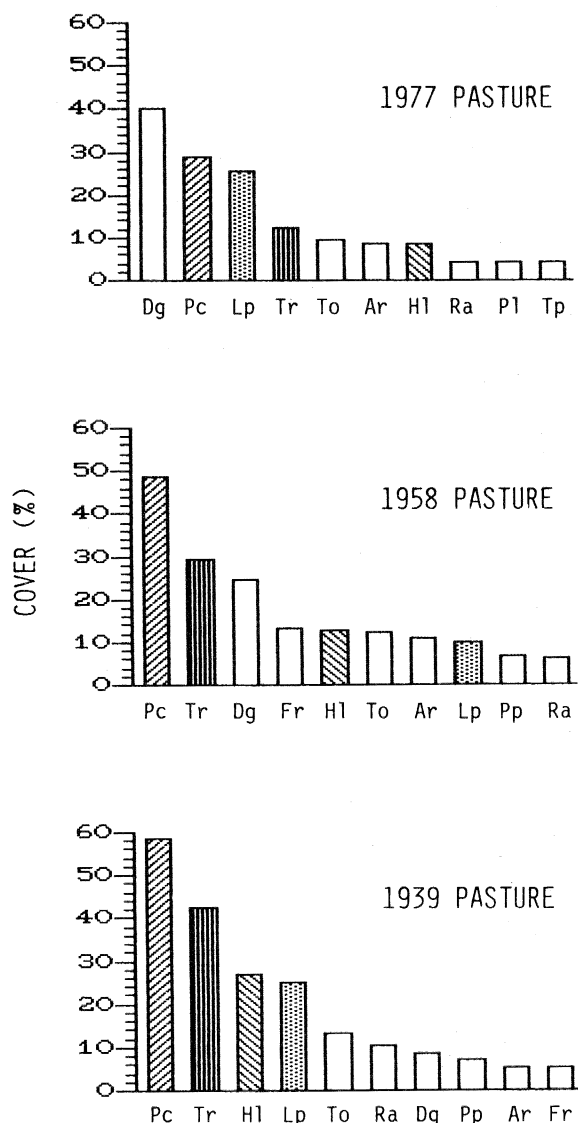


Fig. 1. Mean percentage cover (based on nine surveys between 1979 and 1982) for the ten most abundant species in each of three pastures in British Columbia. The four study species are indicated by cross-hatching. Ar, *Agropyron repens*; Dg, *Dactylis glomerata*; Fr, *Festuca rubra*; Hl, *Holcus lanatus*; Lp, *Lolium perenne*; Pp, *Phleum pratense*; Pl, *Plantago lanceolata*; Pc, *Poa compressa*; Ra, *Ranunculus acris*; To, *Taraxacum officinale*; Tp, *Trifolium pratense*; Tr, *Trifolium repens*. [from data in Aarssen and Turkington (1985a)].

In the second approach, rank order is represented by a competition matrix of coefficients which indicate, for all possible pairwise interactions, the extent to which one species is superior in its ability to suppress the other. The species may form a linear (transitive) hierarchy (e.g., $A > B > C$) or a more complex intransitive network where, for example, A is superior to B and B is superior to C but C is superior to A. This approach has been widely used to study over-growth interactions in sessile marine invertebrates where both transitive and

intransitive competitive relationships have been reported (see Buss 1986 for a recent review). Comparable studies for plants are scarce. Pemadasa and Lovell (1974) reported a linear rank order among one perennial and four dune annuals using this approach. Similarly, Fowler (1982) found a linear rank order among six species from a mown grassland and Roush and Radosovich (1985) found a linear rank order for four annual weeds.

How do these two different approaches correspond? Can the rank order of species based on relative performances in two-species mixtures be used to predict the rank order of suppressive effects on different targets? How does one interpret a variable rank order against different targets? These questions are addressed in the present paper which reports results of an experimental study using four species collected (as seed) from each of three different-aged pastures. A further objective was to compare the competitive relationships of the same species from pastures of different ages. The results are contrasted with those of an earlier study (Aarssen and Turkington 1985b) involving the same four species from the same pastures, but in which neighbouring clones were collected rather than seed.

Methods

The study site consisted of three different aged-pastures in the lower Fraser Valley of British Columbia, Canada. The pastures were last sown in 1977, 1958, and 1939 respectively and had since been used only for cattle grazing and occasional mowing for hay. All three pastures were sown with a mixture comprised of the same species and none of the fields had ever received any chemical fertilizers or pesticides. Further details of these pastures are given in Aarssen and Turkington (1985a).

Based on mean percent cover in nine surveys conducted over three years from June 1979 to March 1982, the four most abundant species in the 1939 pasture were *Poa compressa* L., *Trifolium repens* L., *Holcus lanatus* L. and *Lolium perenne* L. The abundances of these four species as well as other major species in each pasture over this survey period are illustrated in Fig. 1 (Aarssen and Turkington 1985a).

In the summer of 1982, the three fields were left free of grazing long enough to permit seed to ripen for the four species above. For each of these species in each pasture, 200 clones were selected randomly and two ripe inflorescences (containing mature seeds) were collected from each clone. The seeds of each species from a given pasture were threshed, mixed and stored at 4°C.

After eight months of storage, seeds were germinated in flats filled with sand. After three weeks, seedlings were selected randomly and planted into plastic pots (15 cm diam, 15 cm deep) filled with a standard potting mix of peat moss, sand and perlite (2:1:1). Seedlings were planted in the following arrangements for material from

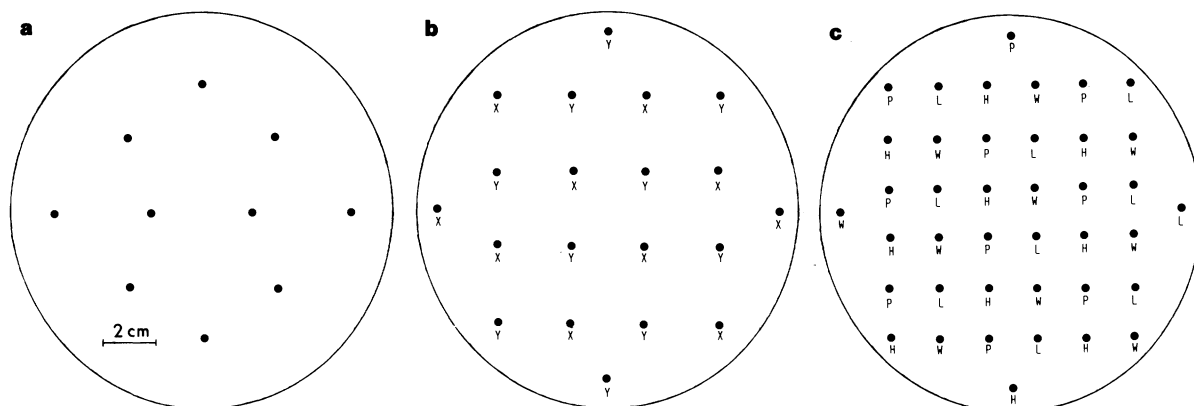


Fig. 2. Planting arrangements for a) monocultures with 10 plants per pot, b) monocultures and pairwise mixtures (of X and Y) with a total of 20 plants per pot, c) four-species mixture with a total of 40 plants per pot. H, *Holcus lanatus*; L, *Lolium perenne*; P, *Poa compressa*; W, *Trifolium repens*.

each pasture: monocultures at density 10 (Fig. 2a), monocultures at density 20, all two-species mixtures at total density 20 and component density 10 (Fig. 2b), and a four-species mixture at total density 40 and component density 10 (Fig. 2c). The monocultures were planted for each species from each pasture. Mixtures were comprised of plants originating from the same pasture. All planting arrangements were replicated five times.

Pots were arranged randomly in a heated glasshouse with 15 h day and 9 h night and were rearranged randomly every two weeks. Four weeks after planting, each pot received 100 ml of a 2 g per liter solution of 20:20:20 NPK fertilizer with trace elements. Sixteen weeks after planting, pots were harvested by clipping all plants at ground level and separating above ground material according to species (for mixtures). Harvested material was oven dried at 100°C to constant dry weight and dry weight biomass was recorded.

Data analyses

Analyses of variance were performed to compare, for each density, monoculture yields across pasture age. Differences in monoculture yields at densities 10 versus 20 plants per pot were determined from t-tests.

The rank order of relative suppressive effects of species on each other was determined in two ways:

a) *Based on all pairwise comparisons of performance in mixtures.* For each mixture, a Yield Suppression Coefficient ($S_{(ij)}$) (Aarssen 1985) was calculated for each component species (i) as follows:

$$S_{(ij)} = Y_{ij}/\bar{Y}_i \quad (1)$$

where Y_{ij} is the yield of species i in equiproportioned mixture with species j at total density 20, and \bar{Y}_i is the mean ($n=5$) yield of species i in monoculture at density 10. $S_{(ij)}$ may range from 0 (maximum suppression) to 1.0

where i is unaffected by j. ($S_{(ij)}$ may exceed 1.0 but only if the suppressive effects of j on i are outweighed by beneficial effects of j on i). A value of $S_{(ij)} = 0.4$ for example, would indicate that species i in mixture with j is suppressed to 40% of its mean yield in monoculture (\bar{Y}_i) at the same component density. Mean Yield Suppression Coefficients for the two components of each mixture were compared using a t-test and used to identify a rank order of species for each pasture.

b) *Based on relative suppressive effects on different targets.* For each species regarded as a 'target' (i), the rank order of suppressive effects of the four associate species on the target was determined by analysis of variance of $S_{(ij)}$ (Eq. 1). The suppressive effect of species i on itself was calculated as:

$$S_{(ii)} = (Y_{ii}/2)/\bar{Y}_i \quad (2)$$

where Y_{ii} is the yield of species i in monoculture at density 20. \bar{Y}_i is defined as for Eq. (1). Multiple comparisons of the suppressive effects among the four associates on each target were analyzed by Tukey's HSD (Sokal and Rohlf 1981: 245) and used to identify a rank order.

The constancy of rank order (C), or the degree to which rank order was unaffected by the target species, was calculated as:

$$C = \sum_i \sum_j [(P_{i>j})^2 + (P_{j>i})^2 + (P_{i=j})^2]/(n^2-n)/2 \quad (3)$$

where n is the number of possible target species (i.e. 4 in the present case) and hence the number of rank orders determined. $(n^2-n)/2$ is the total number of possible pairs of n species. $P_{i>j}$ is the proportion of rank orders in which the suppressive effect of i on the target is greater than the suppressive effect of j. $P_{j>i}$ and $P_{i=j}$ are similarly defined. C ranges from 0.376 (for $n=4$) to 1.0, the latter representing a perfectly constant rank order of species regardless of which species is the target.

Tab. 1. Mean monoculture yields (and one standard deviation, n=5) at densities 10 and 20 plants per pot for plants collected from pastures sown in 1977, 1958 and 1939. P-values are indicated from t-tests of differences between means at densities 10 versus 20 plants per pot for each species from each pasture, and also from ANOVA for mean yields across pasture age for each density. Means with the same superscript letter for a given density do not differ significantly ($P>0.05$) (across pasture age) according to Tukey's HSD.

		Pasture			ANOVA
		1977	1958	1939	
a) <i>Holcus lanatus</i>					
Density	10	14.72 ^a (0.71)	13.87 ^a (2.41)	12.78 ^a (2.81)	P = 0.394
	20	10.83 ^a (1.27)	11.84 ^a (2.22)	11.82 ^a (2.20)	P = 0.652
		P<0.001***	P=0.200	P=0.563	
b) <i>Lolium perenne</i>					
Density	10	10.86 ^a (1.78)	10.79 ^a (1.11)	10.03 ^a (2.87)	P = 0.779
	20	11.64 ^a (1.01)	10.37 ^{ab} (0.77)	8.62 ^b (1.88)	P = 0.011*
		P=0.418	P=0.501	P=0.387	
c) <i>Poa compressa</i>					
Density	10	12.24 ^a (1.14)	13.17 ^a (1.23)	11.36 ^a (1.42)	P = 0.120
	20	12.45 ^a (2.75)	10.74 ^a (0.97)	9.87 ^a (2.25)	P = 0.190
		P=0.879	P=0.009**	P=0.244	
d) <i>Trifolium repens</i>					
Density	10	25.89 ^a (4.80)	27.55 ^a (5.94)	17.31 ^b (3.16)	P = 0.012*
	20	30.49 ^a (4.40)	28.73 ^a (4.33)	22.40 ^b (3.94)	P = 0.025*
		P=0.153	P=0.728	P=0.055	

* $P\leq 0.05$, ** $P\leq 0.01$, *** $P\leq 0.001$.

Yield Suppression Coefficients for each species (i) in four-species mixtures with j, k and l were calculated as follows:

$$S_{i(jkl)} = Y_{i(jkl)} / \bar{Y}_i \quad (4)$$

where $Y_{i(jkl)}$ is the yield of species i in mixture with species j, k and l at total density 40 and component density 10, and \bar{Y}_i is defined as for Eq. (1). Means of $S_{i(jkl)}$ for each species were compared across pasture age by analysis of variance. Multiple comparisons of mean $S_{i(jkl)}$ among the four species from a given pasture were analyzed by Tukey's HSD and used to identify a rank order based on four-species mixtures.

For each pairwise mixture, a Yield Suppression Ratio (YSR_{ij}) (Aarssen 1985) was calculated as follows:

$$YSR_{ij} = S_{i(j)} / S_{j(i)}, \quad S_{i(j)} < S_{j(i)} \quad (5)$$

where $S_{i(j)}$ is defined as for Eq. (1) and $S_{j(i)}$ is similarly defined. YSR_{ij} ranges from 0 to a maximum of 1.0 which indicates that species i and j are equivalent in their abilities to deny contested resources to each other (i.e. competitive abilities). A value closer to zero indicates greater dissimilarity in competitive ability. Means of YSR_{ij} for a given species pair were compared across pasture age by analysis of variance.

For each pairwise mixture, a Relative Yield Total (RYT_{ij}) (de Wit and van den Bergh 1965) was calculated as follows:

$$RYT_{ij} = (Y_{i(j)} / \bar{Y}_{ii}) + (Y_{j(i)} / \bar{Y}_{jj}) \quad (6)$$

where $Y_{i(j)}$ and $Y_{j(i)}$ are defined as for Eq. (1) and \bar{Y}_{ii} and \bar{Y}_{jj} are the mean (n=5) yields of species i and j respectively in monoculture at density 20. Means of RYT_{ij} for a given species pair were compared across pasture age by analysis of variance. All analyses were based on log

Tab. 2. Mean Yield Suppression Coefficients ($S_{i(j)}$, Eq. 1) (and one standard deviation, $n=5$) for targets (i) growing with associates (j) involving plants collected from a) 1977 pasture, b) 1958 pasture, and c) 1939 pasture. Asterisks indicate targets (i) with significantly greater $S_{i(j)}$ (i.e. greater competitive ability) than their interspecific associates (j) based on t-tests; * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$. The rank order of competitive abilities based on these pair-wise interactions is indicated for plants from each pasture. Species connected by underlining do not differ significantly in $S_{i(j)}$. H = *Holcus lanatus*, L = *Lolium perenne*, P = *Poa compressa*, T = *Trifolium repens*.

		Associate (j)				Rank order
		H	L	P	T	
a) 1977 pasture						<u>T>H</u> > <u>P>L</u>
Target (i)	H	0.368 (0.043)	0.534* (0.168)	0.593* (0.217)	0.550 (0.091)	
	L	0.279 (0.081)	0.536 (0.467)	0.483 (0.145)	0.440 (0.126)	
	P	0.301 (0.061)	0.517 (0.158)	0.509 (0.112)	0.408 (0.061)	
	T	0.683 (0.179)	0.783* (0.243)	0.801* (0.193)	0.589 (0.085)	
b) 1958 pasture						<u>T>H</u> > <u>P>L</u>
Target (i)	H	0.427 (0.080)	0.672*** (0.144)	0.538*** (0.104)	0.497 (0.254)	
	L	0.243 (0.102)	0.480 (0.036)	0.286 (0.198)	0.388 (0.129)	
	P	0.210 (0.040)	0.434 (0.105)	0.408 (0.037)	0.420 (0.118)	
	T	0.733 (0.220)	0.637* (0.130)	0.741** (0.099)	0.521 (0.079)	
c) 1939 pasture						H>T > <u>P>L</u>
Target (i)	H	0.462 (0.086)	0.827*** (0.104)	0.672* (0.219)	0.847** (0.274)	
	L	0.241 (0.062)	0.430 (0.094)	0.335 (0.125)	0.620 (0.148)	
	P	0.382 (0.092)	0.536 (0.203)	0.434 (0.099)	0.679 (0.059)	
	T	0.267 (0.167)	0.857* (0.153)	0.946*** (0.074)	0.647 (0.114)	

transformed data where variances were non-homogeneous.

Results

Total monoculture yields (per pot) at densities 10 versus 20 plants per pot did not differ significantly ($P > 0.05$) in most cases (Tab. 1). The only exceptions were *H. lanatus* from the 1977 pasture and *P. compressa* from the 1958 pasture which had significantly lower yields at higher density. For all species from all pastures therefore, harvested plants at density 10 were able to use all of the resources available to them. Consequently, in mixtures of 10 plants of each species, the yield of neither species could be said to reflect the use of any resources available in excess to the other. This is a necessary condition in order to meaningfully compare the relative performance of the two components of a mixture (Aarssen 1985).

Differences in monoculture yields of a given species from different aged pastures were significant ($P < 0.05$) for *L. perenne* at density 20 and for *T. repens* at both densities, where yields declined with increasing pasture age (Tab. 1).

Comparisons of Mean Yield Suppression Coefficients ($S_{i(j)}$) for components of a mixture indicated a linear rank order of relative competitive abilities among species for plants from each pasture (Tab. 2). The position of species in the rank order was the same for plants from the 1977 and 1958 pastures with T>H > P>L but for the 1939 pasture, the order was H>T > P>L. This indicates that *H. lanatus* and *T. repens* did not differ in competitive ability in the 1977 and 1958 pastures and both had greater competitive ability than *P. compressa* and *L. perenne*. In the 1939 pasture however, *H. lanatus* had significantly ($P < 0.05$) greater competitive ability than any other species.

The rank order of species was different based on the four-species mixtures (Tab. 3). In this case, for both the 1977 and 1958 pastures, *T. repens* had significantly ($P < 0.05$) greater competitive ability than any of the other three species (which were not significantly different). In the 1939 pasture however, the rank order was identical to that identified on the basis of pairwise mixtures (Tab. 3).

The performance of *H. lanatus* in mixture increased ($P < 0.001$) with increasing pasture age based on mean Yield Suppression Coefficients in four species mixtures

Tab. 3. Mean Yield Suppression Coefficients ($S_{i(jkl)}$, Eq. 4) (and one standard deviation, $n=5$) for targets (i) growing with associates) (j, k and l) in four-species mixtures involving plants collected from pastures sown in 1977, 1958 and 1939. P-values below each column are from analysis of variance of $S_{i(jkl)}$ across pasture age. Values for species within a given pasture which do not share the same superscript letter are significantly different ($P \leq 0.05$) according to Tukey's HSD. The corresponding rank order of competitive abilities is indicated for species from each pasture. Species connected by underlining do not differ significantly ($P > 0.05$).

Pasture	Target (i)				Rank order
	<i>Holcus lanatus</i> (H)	<i>Lolium perenne</i> (L)	<i>Poa compressa</i> (P)	<i>Trifolium repens</i> (T)	
1977	0.157 ^a (0.047)	0.149 ^a (0.040)	0.133 ^a (0.041)	0.556 ^b (0.162)	T>H>L>P
1958	0.222 ^a (0.048)	0.175 ^a (0.064)	0.213 ^a (0.112)	0.410 ^b (0.094)	T>H>P>L
1939	0.608 ^a (0.117)	0.115 ^b (0.035)	0.117 ^b (0.024)	0.258 ^c (0.182)	H>T>P>L
	P<0.001	P=0.187	P=0.077	P=0.007	

(Tab. 3) as well as in two species mixtures (for all associate species averaged) (Tab. 4). *T. repens* however, showed a decrease in mean Yield Suppression Coefficient with increasing pasture age, although this was statistically significant ($P=0.007$) in four-species mixtures only (Tab. 3). *P. compressa* had a significantly ($P<0.05$) greater mean Yield Suppression Coefficient for the 1939 pasture than for the 1958 pasture based on two-species mixtures (Tab. 4) but showed the opposite trend based on four-species mixtures (Tab. 3). Mean Yield Suppression Coefficients for *L. perenne* did not differ significantly across pasture age for either two-species or four-species mixtures (Tabs 3 and 4).

Mean Yield Suppression Ratios (YSR) for *H. lanatus* – *T. repens* mixtures decreased with increasing pasture age although this trend was not highly significant ($P=0.091$) (Tab. 5). This reflects the increasing competitive ability of *H. lanatus* relative to *T. repens* with increasing pasture age discussed above (Tab. 2). Mean YSR for other species pairs did not differ significantly ($P>0.05$) with increasing pasture age. The Mean Relative Yield Total (RYT) increased significantly with increasing pasture age for mixtures of *L. perenne* and *T. repens* ($P=0.03$) and for mixtures of *P. compressa* and *T. repens* ($P=0.0002$) (Tab. 6).

The rank orders of suppressive effects of the four species on each species considered as a target differed depending on which species was the target (Tab. 7). The constancy of rank order however was greatest ($C=0.792$) for plants from the 1977 pasture. Rank order was progressively less constant in the 1958 ($C=0.688$) and 1939 ($C=0.605$) pastures. Relative Yield Total was not significantly different for any target/associate combinations in the rank orders for the 1977 pasture (Tab. 7). However, for both the 1958 and 1939 pastures, RYT differed significantly among species combinations in three of the four rank orders. For the 1939 pasture, a lower position in the rank order was associated with a significantly higher RYT for each of the three rank orders involving *L. perenne*, *P. com-*

pressa and *T. repens* as targets. For the 1958 pasture, only the rank order for the target *T. repens* showed this relationship with RYT (Tab. 7).

Discussion

Interpretation of species 'pecking order'

Two approaches for representing the rank order of competitive effects among species were examined in this study. In one case, rank orders were based on the relative suppressive effects of species on a given target species, where each species was considered, in turn, as the 'target'. 'Constancy' of rank order (when the target species was changed) decreased with increasing age of the pasture from which plants were collected ($r = -0.998$, $P<0.05$). The more variable rank order for plants from the oldest pasture appears to be a consequence of the fact that, for some species, the extent to which they and the target make demands on the same

Tab. 4. Mean Yield Suppression Coefficients ($S_{i.}$) (and one standard deviation, $n=20$) for target species (i) growing with all associate species in pairwise mixtures involving plants collected from pastures sown in 1977, 1958 and 1939. P-values below each column are from analysis of variance of $S_{i.}$ across pasture age. Values within a column (for a given species) which do not share the same superscript letter are significantly different ($P<0.05$) according to Tukey's HSD.

Pasture	Target (i)			
	<i>Holcus lanatus</i>	<i>Lolium perenne</i>	<i>Poa pratensis</i>	<i>Trifolium repens</i>
1977	0.509 ^a (0.163)	0.437 ^a (0.146)	0.434 ^{ab} (0.140)	0.721 ^a (0.196)
1958	0.538 ^a (0.180)	0.355 ^a (0.153)	0.365 ^a (0.122)	0.663 ^a (0.164)
1939	0.710 ^b (0.238)	0.411 ^a (0.179)	0.508 ^b (0.161)	0.681 ^a (0.292)
	P=0.004	P=0.273	P=0.011	P=0.484

Tab. 5. Mean Yield Suppression Ratio (YSR_{ij}, Eq. 5) (and one standard deviation, n=5) for all possible pairwise mixtures of species i and j involving plants collected from pastures sown in 1977, 1958 and 1939. Probability levels are given from analysis of variance for YSR_{ij} across pasture age for each species pair. H = *Holcus lanatus*, L = *Lolium perenne*, P = *Poa compressa*, T = *Trifolium repens*.

Pasture	Species pair					
	H – L	H – P	H – T	L – P	L – T	P – T
1977	0.59 (0.31)	0.55 (0.20)	0.87 (0.36)	1.00 (0.35)	0.62 (0.29)	0.53 (0.18)
1958	0.35 (0.10)	0.40 (0.06)	0.77 (0.50)	0.77 (0.74)	0.64 (0.28)	0.59 (0.22)
1939	0.30 (0.09)	0.60 (0.21)	0.32 (0.16)	0.63 (0.12)	0.73 (0.13)	0.72 (0.11)
	P=0.097	P=0.174	P=0.091	P=0.324	P=0.762	P=0.254

resources (reflected by RYT) is different with different targets. In three of the rank orders for plants from the 1939 pasture, the lowest-ranking species had a significantly higher RYT with the target than did the higher ranking species (Tab. 7c). This indicates that, for plants from the oldest pasture, the species at the lowest position in the rank order had the least suppressive effect on the target at least partially because they were generally the least similar to the target in demands made on available resources (or had the most beneficial interaction with the target). This apparently accounts for rank order of species in the 1958 pasture to a lesser extent (i.e. for the target *T. repens* only) (Tab. 7b), but not at all for plants from the 1977 pasture (Tab. 7a).

These results suggest that at least two distinct components can be recognized in the interpretation of species rank order based on relative target suppression. The extent to which a target is suppressed by an associate will increase with: 1) an increase in the extent to which the target and associate make demands on the same resources (which might be loosely referred to as the amount of 'niche' overlap) and/or 2) an increase in the relative ability of the associate to deny these contested

resources to the target (i.e. relative competitive ability). A third factor cannot be overlooked; the extent of target suppression may also be affected by the degree to which the associate confers some benefit to the target.

The species were also ranked according to their relative performances in all pairwise combinations. The rank order of species here was not identical for plants from each pasture (Tab. 2). *H. lanatus* from the 1939 pasture had a greater competitive ability (under the conditions of this experiment) than any of the other three species from this pasture. For plants from the two younger pastures however, *H. lanatus* and *T. repens* did not differ significantly in their competitive ability against each other (Tab. 2). The general superiority of *H. lanatus*, as indicated in this experiment, is consistent with it showing the most striking increase in abundance with increasing pasture age, from the seventh most abundant species in the 1977 pasture to the fifth and third most abundant in the 1958 and 1939 pastures respectively (Fig. 1). In the 1939 pasture however, the abundance of *H. lanatus* did not differ from that of *L. perenne* and both were significantly ($P<0.05$) lower in abundance than either *Poa compressa* or *T. repens*

Tab. 6. Mean Relative Yield Total (RYT_{ij}, Eq. 6) (and one standard deviation, n = 5) for all possible pairwise mixtures of species i and j involving plants collected from pastures sown in 1977, 1958 and 1939. Probability levels are given from analysis of variance for RYT_{ij} across pasture age for each species pair. Values within a column (for a given species pair) which do not share the same superscript letter are significantly different ($P<0.05$) according to Tukey's HSD. H = *Holcus lanatus*, L = *Lolium perenne*, P = *Poa compressa*, T = *Trifolium repens*.

Pasture	Species pair					
	H – L	H – P	H – T	L – P	L – T	P – T
1977	0.99 ^a (0.21)	1.10 ^a (0.32)	1.29 ^a (0.23)	0.96 ^a (0.21)	1.08 ^a (0.18)	1.08 ^a (0.16)
1958	1.04 ^a (0.26)	0.89 ^a (0.16)	1.21 ^a (0.13)	0.84 ^a (0.16)	1.01 ^a (0.15)	1.23 ^a (0.11)
1939	1.18 ^a (0.08)	1.17 ^a (0.29)	1.12 ^a (0.36)	1.01 ^a (0.37)	1.38 ^b (0.26)	1.51 ^b (0.05)
	P=0.332	P=0.258	P=0.658	P=0.637	P=0.030	P=0.0002

Tab. 7. Rank order of suppressive effect of four species on each other (based on $S_{(ij)}$ from Tab. 2) for plants collected from a) 1977 pasture, b) 1958 pasture, c) 1939 pasture; H = *Holcus lanatus*, L = *Lolium perenne*, P = *Poa compressa*, T = *Trifolium repens*. Species connected by underlining do not differ significantly ($P > 0.05$) in their suppressive effects on the target according to Tukey's HSD. The Relative Yield Total (RYT) is indicated for each combination of target and associate in each rank order. RYT values with the same superscript letter in a given rank order do not differ significantly ($P > 0.05$) according to Tukey's HSD. Constancy of rank order (C, Eq. 3) among species is given for each pasture.

		Relative suppressive effect of associates on target (and RYT's)						
a) 1977 pasture		(C = 0.792)						
Target species	H	H	>	L	>	T	>	P
		1.00 ^a		0.99 ^a		1.29 ^a		1.10 ^a
	L	H	>	T	>	P	>	L
		0.99 ^a		1.08 ^a		0.96 ^a		1.00 ^a
	P	H	>	T	>	P	>	L
		1.10 ^a		1.08 ^a		1.00 ^a		0.96 ^a
Target species	T	T	>	H	>	L	>	P
		1.00 ^a		1.29 ^a		1.08 ^a		1.08 ^a
b) 1958 pasture		(C = 0.688)						
Target species	H	H	>	T	>	P	>	L
		1.00 ^{ab}		1.21 ^a		0.89 ^b		1.04 ^{ab}
	L	H	>	P	>	T	>	L
		1.04 ^a		0.84 ^a		1.01 ^a		1.00 ^a
	P	H	>	P	>	T	>	L
		0.89 ^a		1.00 ^a		1.23 ^b		0.84 ^a
Target species	T	T	>	L	>	H	>	P
		1.00 ^a		1.01 ^a		1.21 ^b		1.23 ^b
c) 1939 pasture		(C = 0.605)						
Target species	H	H	>	P	>	L	>	T
		1.00 ^a		1.17 ^a		1.18 ^a		1.12 ^a
	L	H	>	P	>	L	>	T
		1.18 ^a		1.01 ^a		1.00 ^a		1.38 ^b
	P	H	>	P	>	L	>	T
		1.17 ^a		1.00 ^a		1.01 ^a		1.51 ^b
Target species	T	H	>	T	>	L	>	P
		1.12 ^{ab}		1.00 ^a		1.38 ^{bc}		1.51 ^c

(Fig. 1). Clearly the rank order of species as determined in the present study bears no relation to their rank order of abundance in the field.

Rank orders based on all pairwise comparisons of performance in mixtures reflect the relative abilities of

species to deny to each other, those resources on which they both make demands. The degree to which demands are made on the same resources may differ for different species pairs, particularly for plants from the oldest pasture (Tab. 6), but this did not affect the transitivity of species; rank orders based on pair-wise interactions were linear for plants from all three pastures. Note that the relative position in such a rank order need not be the same as in a rank order based on relative target suppression. For example, for plants from the 1939 pasture, *T. repens* > *L. perenne* based on pairwise interaction (Tab. 2c) but *L. perenne* > *T. repens* in its suppressive effect on *L. perenne* (Tab. 7c). The latter appears to be a consequence of a greater Relative Yield Total for the mixture of *L. perenne* and *T. repens* (implying less 'niche' overlap or more beneficence) than for *L. perenne* growing with *L. perenne* (where RYT = 1.0 by definition) (Tab. 7c). Nevertheless, for those niche requirements of *L. perenne* and *T. repens* which do overlap, *T. repens* is the superior of the two in its ability to deny these contested resources to the other (under the conditions of this experiment) (Tab. 2c).

Although rank orders based on relative performances in mixtures were linear (i.e. transitive) in this study (Tab. 2), there is no reason to expect that this should be generally true. Plants may compete in several ways involving many different attributes (Aarssen 1983, 1984) which may define several opportunities for intransitive competitive relationships under natural conditions in plant communities. Given sufficient genetic variability, the most meaningful scale of intransitivity may even occur at the individual genotype level. These hypotheses remain virtually unexplored.

Further studies are needed to determine the extent to which a variable rank order of species or genotypes against different targets is a consequence of 1) different degrees of niche overlap with different targets, versus 2) different degrees of beneficial effects on different targets, versus 3) different relative competitive abilities against different targets. The present study cannot distinguish between 1) and 2) but the results suggest that the relative importance of these three factors may vary independently. If competitive abilities formed an intransitive network, the third factor would be expected to play a more significant role. Under natural field conditions there may also be higher-order interactions. In the present study, for example, rank orders based on four-species mixture (Tab. 3) were not the same as rank orders based on pairwise interactions (Tab. 2). For plants from the 1977 and 1958 pastures in four-species mixtures, *T. repens* was superior to all of the other species (which did not differ among themselves), but *H. lanatus* and *T. repens* were equally superior to the other two based on two-species interaction. Under natural field conditions, additional factors will be important, e.g. interactions with other species not included in the present study, spatial and temporal heterogeneity affecting relative competitive abilities and opportunities

for niche differentiation. Fowler (1982), for example, found that species rank order changed when soil water and nutrient levels were varied.

Differences among pastures: collecting seeds versus ramets

In a study similar to the present study, using the same pastures, Aarssen and Turkington (1985b) investigated the competitive relations among the same four species. They collected all possible pairs of the four species as neighbouring plants in physical contact in the field. Ramets propagated from these clones were planted with ramets from their natural neighbours in small plots in an out-door experimental garden. The results of the present study and this earlier study differ in two major respects. Firstly, in the present study, the extent to which one species was able to deny resources to another (reflected by YSR, Tab. 5) was generally independent of the age of the pasture from which the plants (as seed) were collected. Aarssen and Turkington (1985b) however, reported that in four out of these six possible species pairs, the difference in performance of the two mixture components significantly decreased with increasing pasture age. This suggested that neighbouring species in the oldest pasture were generally more similar in their competitive abilities than in the younger pastures. Secondly, the extent to which the two components of a mixture made demands on the same resources (indicated by RYT, Tab. 6), decreased with increasing pasture age for two species pairs (*L. perenne* – *T. repens* and *P. compressa* – *T. repens*) in the present study. (An increasing RYT may alternatively imply an increasing beneficial interaction). In the study by Aarssen and Turkington (1985b) however, none of these six species pairs showed any indication of such a relationship.

The plants used in the present study were derived from seed collected randomly from mature inflorescences in the field and therefore consisted of genotypes untested for their abilities to evade forces of natural selection that are imposed during and subsequent to germination under field conditions. The neighbouring clones used by Aarssen and Turkington (1985b) however can be regarded as 'proven survivors' in the sense that the zygote that each individual was derived from had successfully developed beyond the juvenile phase, despite close proximity to the other. The relative abundance of species in the field (Fig. 1) will reflect the outcome of interactions between 'proven survivors' and in the case of *P. compressa* and *T. repens* these may involve genotypes whose fitness are augmented by an enormous potential for clonal propagation. The contrasting results of Aarssen and Turkington (1985b) and the present study may, therefore, be a consequence of using plants derived from collected seeds and combined randomly in mixtures (in the present study) versus plants derived clonally from 'proven survivors' and combined in mixtures involving only clones that had been neighbours in the field (Aarssen and Turkington

1985b). Different results may also be a consequence of different experimental conditions. In the study by Aarssen and Turkington (1985b), the plants were clipped periodically which more closely resembled the conditions in the field imposed by grazing.

In the present study, both *L. perenne* and *T. repens* showed a significant decrease in monoculture yields with increasing pasture age (Tab. 1). Aarssen and Turkington (1985c) found the same trend of decreasing biomass for individual ramets of these species collected from these same three pastures. Aarssen and Turkington (1985c) suggested that this trend may be accounted for by differences in the length of time that these pastures had been grazed and hence represents the accumulation of selection pressures favouring small size. The comparable results of the present study indicate that these size differences are inherited by sexually produced offspring and are not merely a reflection of physiological changes in long-lived clones.

Acknowledgements – This research was supported by the Natural Sciences and Engineering Research Council of Canada and by the Advisory Research Council of Queen's University. Technical assistance was provided by B. Aarssen, G. Epp and S. Morgan. B. Aarssen, D. Goldberg and D. Taylor provided helpful comments on the manuscript.

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