The measurement and analysis of competitive ability among populations of white clover and perennial ryegrass

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Summary. Analysis of the competitive interactions among a set of white clover and perennial ryegrass populations indicated that the intra-specific pressures exerted by the white clover plants upon themselves were significantly greater than the inter-specific pressures they exerted upon the perennial ryegrass. This partitioning of competitive effects could not be carried out on the ryegrass populations, however, because the data required the fitting of separate models to monocultures and duocultures. Although not significant at this stage of the experiment, trends were detected among some of the clover-ryegrass duocultures that could be related to their previous coexistence. The results are briefly discussed in relation to the problems surrounding the measurement of competitive effects among species that ideally require very different managements.

Key words: Inter-specific competition — Intra-specific competition — Co-existence — White clover — Perennial ryegrass

Introduction

Individuals living within a mixed community will be exposed to competition from like and unlike individuals whenever and wherever the demand for an essential resource exceeds its immediate supply. Experimental evidence indicates that the impact of competition between similar individuals is generally the greater (Connell 1983; Hill et al. 1987b), if only because such individuals will make comparable demands upon these resources. Clearly, the development of crop varieties destined for use in mixtures will require alternative breeding strategies, with the emphasis being placed upon mixture productivity rather than varietal performance per se. Putative mixture components should be brought together at an early stage of the breeding programme so that their "ecological combining ability" may be improved (Harper 1967; Hill and Michaelson-Yeates 1987b). It is in this context that co-adapted components may play a role. Indeed, the use of such components has been advocated as one way of improving the performance of the grass/legume pastures that are a feature of temperate grasslands (Evans et al. 1985), and as a means of increasing the productivity of the inter-cropping systems of agriculture practiced in many developing countries (Chirwa 1985).

The study of competition between two such contrasting competitors as white clover (Trifolium repens) and perennial ryegrass (Lolium perenne) over a period of time poses certain problems, however, because the former can fix atmospheric nitrogen symbiotically and convert it to plant protein. Moreover, within 2 years of establishment white clover changes from a tap root to a shallow fibrous rooting system (Burdon 1983), and releases the atmospheric nitrogen that it has fixed to the companion grass, following the decay of plant parts (Ball 1977). Ideally, therefore, experiments designed to study competition between white clover and perennial ryegrass should cover these events. The longer such experiments last, however, the greater the management problems are likely to be, particularly in relation to the application of nitrogenous fertilizer. Withholding nitrogenous fertilizer inevitably reduces the long term performance of ryegrass plants in monocultures compared to their performance in duocultures. To apply nitrogen, however, immediately places the clover populations at a competitive disadvantage, because ryegrass utilizes this source of nitrogen more efficiently (Frame and
Newbould 1984; Chestnutt and Lowe 1970), even though white clover will preferentially use mineral nitrogen rather than fix atmospheric nitrogen (Rys and Mytton 1985; Mytton and Rys 1985). Additional problems are created by the defoliation regime, with a cutting-only management expected to favour clover, whereas continuous grazing by sheep drastically reduces the white clover content of a pasture (Evans and Williams 1987). In view of these difficulties, it was decided to adopt a compromise and apply some nitrogenous fertilizer to the ryegrass monocultures, even though this will probably lead to a disparity in ryegrass performance between mono- and duocultures, and hence reduce the amount of information supplied by the experiment.

The present paper analyses the effects of competition upon white clover and perennial ryegrass populations, some of which have previously coexisted.

Materials and methods

Three white clover populations — Menna, Ac 3160 and S.100 — and three perennial ryegrass populations — Ajax, Ba 8625 and S.23 — supplied the experimental material. Of these the Menna/Ajax and Ac 3160/Ba 8625 combinations have a history of coexistence, the latter in Northern Italy, while the former is of indigenous origin. The experiment, which was based on the modified substitution design described by Mather et al. (1982), contained the six populations grown as monocultures and all nine clover-ryegrass duocultures. Its structure is illustrated below with reference to the Menna/Ajax combination, though the same densities and proportions obviously apply to all nine clover-ryegrass combinations.

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<tr>
<th>Proportion</th>
<th>Menna</th>
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A randomized complete block design with two replicates was used for this experiment, which was sown in May, 1985. In each replicate there were 51 experimental plots, of which 24 (6 x 4) were monocultures and 27 (9 x 3) were duocultures. Each plot measured 1.5 m square. The reference density, N (1.00) was 4.5 kg ha⁻¹ (0.45 g m⁻²) for clover and 15 kg ha⁻¹ (1.5 g m⁻²) for perennial ryegrass, subject to adjustment for germination differences. These seed rates were higher than those commonly used in agricultural practice. Manurial dressings were applied to the seedbed as follows: 5 t ha⁻¹ of ground limestone and 250 kg ha⁻¹ of both muriate of potash (60% K₂O) and superphosphate (21% P₂O₅). The potash and phosphate dressings were repeated annually. In addition, the ryegrass monocultures received 200 kg ha⁻¹ of nitrogen per annum, at which rate the annual yield of the ryegrass monocultures and the clover-ryegrass duocultures were expected to be comparable (Morrison et al. 1985). In this respect, therefore, the ryegrass monoculture plots were treated differently from the remaining experimental plots.

The experiment was established during the summer of 1985, with a clearing cut taken in August. Although some recordings were made during the autumn of 1985, the data presented here relate to 1986, the first full harvest year. During 1986 the experiment was cut five times between May and October, using an Allen autoscythe set to a cutting height of 3 cm. Before each harvest a 0.5 m border was cut from around each plot and discarded. After cutting a 100 g subsample of fresh material was collected from each plot and separated into its clover and grass fractions where necessary. These sub-samples were dried and weighed. Other characters were also recorded. Prior to each cut a longitudinal transect was placed down the middle of each plot and the height of the clover and/or grass canopy measured at 60 cm intervals along this transect. After each cut a diagonal transect was placed across all plots containing clover and the number of stolons crossing the transect was recorded. Approximately 10 days after each cut clover leaf number and/or ryegrass tiller number were recorded within four random quadrats per plot. Each quadrat covered 80 cm². Information was therefore obtained on clover dry weight, stolon number, leaf number and canopy height, and on ryegrass dry weight, tiller number and canopy height.

These data were analysed by the techniques devised by Mather and Caligari (1981), with the reference density (N) being 1.00 for this experiment, while x, the proportion of plants in an indicator population omitted from monocultures or substituted by an associate competitor in duocultures, had values of −0.25, −0.50 and −0.75. Full details of the analytical techniques employed here are given by Mather and Caligari (1981) and by Hill et al. (1987a). Briefly, however, regression analysis is used to quantify the relative strengths of intra- and inter-genotypic (specific) competition. If a single indicator genotype or species (A) is grown in a density series of monocultures and the character is defined in such a way that its mean expression shows a linear regression on density, the regression coefficient, $b_A$, provides a measure of the strength of intra-genotypic (specific) competition. Replacing those individuals omitted from the monocultures of A by the same number of individuals from a second or associate competitor (B) enables a further regression to be calculated, whose slope, $b_B$, measures the inter-genotypic (specific) competitive effect of B upon A in addition to the intra-genotypic (specific) competitive effect of A upon itself. Subtraction of $b_B$ from $b_A$ will therefore estimate the strength of the inter-genotypic (specific) competitive effect of the associate competitor B upon the indicator population A. The roles of the indicator and associate competitor (A and B) are, of course, reversible.

Analyses and results

Preliminary analyses revealed that, although the clover and grass canopies were taller in duocultures than in monocultures (see also Hill and Michaelson-Yeates 1987a), there were no further differences arising from the omission of plants in monocultures or the substitution by an associate competitor in duocultures. Attention was therefore focussed on the remaining three clover and two ryegrass characters in the ensuing analyses. Prior to these analyses, however, the data were converted to a 'per plant' basis. For this purpose the 25% point ($x = -0.75$) was used as the baseline.