ABOVEGROUND AND BELOWGROUND COMPETITION AMONG PASTURE SPECIES

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Abstract

Eight pasture species were studied to determine the grown responses of seedlings recruiting into gaps in established swards of phalaris, with various degrees and combinations of competition aboveground and belowground. Species varied in their relative sensitivity to shoot or root competition, but there were strong interaction effects with shoot and root competition. Evidence was obtained that three of the species were more competitive for nutrients than phalaris. Root competition was important even though there were high levels of nutrients and water in the soil. This may be explained by the creation of local resource depletion zones around individual roots. Further work focussing on the mechanisms of competition, particularly by roots is needed.

Key words: Gaps, light, nutrients, root, shoot, water.

Competition from established vegetation is a major factor limiting the successful recruitment of seed-lings into gaps in pasture swards. A common assumption about productive vegetation on fertile soil (*ie.* agroecosystems) is that competition is mainly for light, with little competition for nutrients. However, Wilson (4) reviewed 23 studies that investigated root and shoot competition and found that root competition usually affected the balance between competing species more than shoot competition Grime (2) stated that "the terminal role of shading in competition on fertile soils should not be allowed to obscure the fact that in such circumstances competition for nutrients is severe and may be of critical importance". The classic experiment of Donald (1) in which the competitive superiority of *Lolium perenne* over *Phalaris aquatica*, in conditions of high soil fertility, was pronounced only in treatments which allowed root competition supports this view. The mechanisms that facilitate successful recruitment and the relative importance of competition aboveground (for light) and belowground (for nutrients or water) are poorly understood. Such understanding is needed to manage, predict and model changes in pasture species composition over time.

Methods

Eight pasture species were studied to determine the growth responses of seedlings recruiting into four gap treatments in phalaris (*Phalaris aquatica*) swards main-tained at a high (10 to 20 cm) or low (3 to 5 cm) height. The recruiting species included four annual grasses: barleygrass (*Hordeum leporinum*), soft brome (*Bromus mollis*), annual ryegrass (*Lolium rigidum*) and vulpia (*Vulpia bromoides*); one perennial grass, dan-thonia (*Danthonia richardsonii*); two legumes: cluster clover (*Trifolium glomeratum*) and subterraneum clover (*Trifolium subterraneum*); and one non-leguminous herb, capeweed (*Arctotheca calendula*). These treatments allowed assessment of recruitment for various pasture species into established swards of phalaris with various degrees and combinations of competition aboveground and belowground in a glasshouse experiment.

The two sward-height treatments were maintained by keeping swards clipped frequently to a 3 or 10 cm height.? In the low swards the light reaching the soil surface in the center of the gaps (on a daily basis) was 100% of full light, while in the high swards the amount of light in the gaps averaged 46% of full light. Within each sward height and recruiting species combination, the four gap, belowground competition treatments were:

• root exclusion tube and soil replacement (RE) no root competition;

• soil disturbance and replacement (GR) partial root competition;

• soil disturbance but no replacement (GC) partial root competition; and,

• no soil disturbance or replacement (UD)full root competition.

The gaps were open circular spaces on the soil surface, 75 mm diameter, and were maintained against aboveground encroachment by the phalaris sward with 4-cm long PVC cylinders pushed 1 cm into the soil. In gap treatment GC, the soil core beneath the gap was removed and replaced, causing some soil disturbance and severing all phalaris roots. In gap treatment GR, a soil core was removed and replaced with new soil (resource provision). Gap treatment RE was similar to treatment GR, but a PVC tube was used to isolate the roots.

The soil used was a compost mix with nutrients added. At the initiation of the experiment, the existing soil beneath the gaps had 16 mg/kg mineral N and the new soil had 30 mg/kg mineral N. Swards were watered daily to maintain soil water content at or near field capacity throughout the experiment. A total of 48 swards grown in large plastic bins (580 x 370 x 360 mm; 77 litres) represented the 2 sward height x 8 gap species x 3 replicate combinations. The 4 gap treatments were contained within each sward.

A number of seeds of the appropriate species were sown into each gap treatment. As the seedlings emerged and grew they were thinned gradually to one per gap treatment. The recruiting seedlings were allowed to grow for 7 weeks. At that time the shoots were harvested and their dry weight determined as an integrated measure of shoot and/or root competition. The plant dry weights were normalised relative to the dry weight for the low sward RE treatment (which served as the no competition control) for each species. Normalising the data facilitated comparison of competitive effects across species.

Results and discussion

Shoot competition without root competition was assessed by comparing seedling growth in high and low swards in the RE gap treatment. The effect of shoot competition on growth, expressed relative to the no competition control, ranged from 35% for danthonia to 150% for subterranean clover (Fig. 1). Root competition without shoot competition was assessed by comparing growth in RE with the other 3 gap treatments in the low swards. The effect of root competition on growth ranged from 42% for danthonia to 205% for barleygrass. The species differed in their relative response to shoot and root competition. In general, species could be grouped as being sensitive to shoot competition (capeweed and barleygrass), sensitive to root competition (subterranean and cluster clovers), sensitive to either shoot or root competition (danthonia, soft brome and vulpia) or sensitive to neither shoot nor root competition (annual ryegrass).

There were significant interactions between shoot and root competition for all species except soft brome (Fig. 1). Growth in the high swards with the most severe root competition (either the UD or GC gap treatment) was greatly reduced from the no competition control, and ranged from 6% for danthonia to 43% for soft brome.

In five of the species (danthonia, annual ryegrass, cluster clover, subterranean clover and vulpia) the best growth was obtained in the gap treatments with resource provision (RE and/or GR). However, for three species (barleygrass, soft brome and capeweed) the best growth was obtained outside the RE treatment, intended to eliminate root competition. In these cases the best grow-th was generally in the GR treatment. These results may be explained as assessing the ability of the recruiting seedlings to compete with the phalaris sward for nutrients. Where phalaris is the more competitive species, the recruiting plants did best in the RE and GR treatments. Conversely, species more competitive for nutrients than phalaris did best outside of the RE gap treatment. Here they had to compete with phalaris for nutrients, but also had a greater volume of soil to explore than when confined to the 2 litres of soil in the RE tubes.

In these results there were many interactions between shoot and root competition, and their relative effects on growth varied among species. Donald (1) demonstrated positive interactions between shoot and root competi-tion and suggested that it would occur generally. However, in reviewing the literature, Wilson (4) found no strong evidence for a positive interaction between shoot and root competition.

In grazed pastures, competition for light is generally slight to moderate (as in this experiment), rather than severe. When competition for light becomes severe, then the balance between the species becomes very asymmetrical due to a positive feedback mechanism causing "snowball" cumulation to occur (5). This results from the fact that light is generally a directional resource, so a plant which overtops another plant has a great advantage.

It is less easy to imagine a mechanism that would lead to snowball cumulation with nutrient competition, and experiments attempting to show it have failed to do so (5). Root competition was important in this experiment despite high levels of nutrients and water in the soil.? Competition does not uniformly lower the resource supply either above or belowground. Instead there can be a local depletion of resource in the immediate vicinity of individual roots. The ability to create depletion zones around roots depends on the resource supply in the soil, its transport rate through the soil, and the rate of uptake by the root (3). To compete for a resource, a plant must be able to deplete the amount available to its neighbours.? Either a high rate of resource supply to the available soil pool or a limited rate of diffusion through the soil may prevent a plant from strongly influencing the level of resource available to its neighbours. Thus, competition is a very dynamic process. This study has quantified the relative effects of shoot and root competition and their interaction on the growth of a number of pasture species.? Further work is needed to elucidate the mechanisms of competition, particularly by roots for nutrients and/or water.

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