The horizontal distribution of root biomass in a South African winter-rainfall desert community

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We address the question of whether the spatial distribution of root biomass mirrors the highly clumped distribution of shoot biomass in two desert plant communities (short and medium strandveld) on the west coast of South Africa. Results indicate that this is generally not the case. In both communities, there was no significant difference between the fine root (<2mm diameter) biomass under clumps compared with gaps between clumps. In the short strandveld, this was also the case for structural root mass. The only exception to this general trend was in the case of structural roots in the medium strandveld where there was more biomass under vegetation clumps. These patterns suggest that strandveld plants are shaped by the trade off between advantages of clumping and the inevitable competition for water that this association brings. In these communities, the competitive disadvantages of clumping aboveground may be offset by root foraging between clumps. Fertile islands do not seem to be a feature of these communities.

Introduction

As is the case for many arid systems (Aguiar and Sala 1999), an overwhelming above-ground structural feature of plant communities in the arid west coast strandveld (part of the winter rainfall Succulent Karoo biome) of South Africa is that most perennial plants (which constitute the bulk of shoot biomass) are concentrated into multi-species vegetation clumps (Eccles *et al.* 1999, Eccles *et al.* 2001, Eccles *et al.* 2002). It has been suggested that this arrangement provides individuals with substantial protection against damage by wind or animals and that this offsets any competitive disadvantage that they may experience (Eccles *et al.* 2001, Eccles *et al.* 2002). An inevitable question that emerges is what about the roots? This is particularly relevant in desert systems such as the strandveld where resources that are likely to be most limiting (water and, as a result, nutrients) are below-ground resources (Fowler 1986, Casper and Jackson 1997). For this reason one might expect the spatial arrangement of roots to differ fundamentally from the shoots. It is for this reason that root studies have a long history in desert systems (e.g. Scott and Van Breda 1937, Phillips and MacMahon 1981, Heitschmidt *et al.* 1988, Briones *et al.* 1996).

A variety of patterns of vertical root distributions have been reported in arid systems. Theoretically much attention has been paid to the possibility that different species may partition the soil profile in such a way as to minimise competition (e.g. Cody 1986, Briones *et al.* 1996). This is supported to some extent by evidence from broad scale surveys that certain species do occasionally specialise in resource acquisition across a range of depths (Sun *et al.* 1997). However, most empirical studies indicate that the bulk of root biomass in arid systems is confined to the upper 30cm of soil (Heitschmidt *et al.* 1988, Briones *et al.* 1996, Schultze *et al.* 1996, Nobel and Linton 1997, Sun *et al.* 1997) and it is difficult to see how such limited vertical space might be partitioned. The predominance of shallow rooting certainly appears to be the case in the Namaqualand communities of the Succulent Karoo biome (Esler and Rundel 1999). In two strandveld communities (short and medium strandveld), the available rooting depth is constrained by impenetrable subsoils between 0.6m and 2m. Despite this potentially available soil profile, observations from several soil pits indicate that in the short strandveld more than 90% of the root biomass is found in the top 30cm. In the medium strandveld at least 60% of root material is found in the top 30cm. In the context of Namaqualand, this vertical distribution of roots makes sense. Rainfall events are small but fairly regular and dew and fog may contribute significantly to total precipitation (Desmet and Cowling 1999, Esler and Rundel 1999). The result of this precipitation regime is that deep wetting of soil profiles is infrequent. A similar argument is echoed by Breshears *et al.* (1998) in another arid system.

An interesting aspect of root patterns in strandveld com-

munities is whether the below-ground distribution of biomass mirrors the highly clumped above-ground pattern horizontally. The balance of evidence in the literature suggests that in arid systems lateral roots may extend a great deal beyond the crowns of individuals, which, in turn, suggests that roots should fill the gaps (Phillips and MacMahon 1981, Heitschmidt *et al.* 1988, Beukman 1991, Brisson and Reynolds 1994). In contrast, Hook *et al.* (1994) have reported some evidence suggesting that root biomass declines in gaps in arid grasslands and they argue that these horizontal root gaps may be very important for establishment. In the case of the Namaqualand strandveld communities, circumstantial evidence does not support this gap recruitment hypothesis as the bulk of recruitment of perennial species occurs under or at the edge of vegetation clumps rather than in gaps (Yeaton and Esler 1990, Milton 1994, Milton and Dean 1995, Eccles 2000). From a theoretical perspective Schlesinger *et al.* (1990) have emphasised the importance of nutrients in certain arid systems, and have suggested that vegetation clumps may play a central role in concentrating these nutrients. If this model holds then one might expect to find that below-ground, root patterns do in fact mirror above-ground clumping patterns.

Given the implications that either of these two situations have for our understanding of plant resource acquisition strategies, especially in terms of resource heterogeneity, we set out to explore horizontal root distribution in representative examples of the short and medium strandveld communities. Our focus was on root biomass in general, rather than on species-specific patterns. There are two reasons for this. Firstly, the large element of chance in species associations in clumps does not suggest that rigid clump assembly rules are common (Eccles 2000), and without evidence for these it is difficult to visualise how species-specific niche differentiation could be at work. Secondly, the fact that there is fairly limited vertical distribution of roots once again suggests little scope for niche differentiation.

Materials and Methods

The study area is located near the mouth of the Groen River on the west coast of South Africa, Namaqualand (30°51'S, 17°34'E) and is part of the Succulent Karoo biome. The area receives an estimated annual average rainfall of 140mm, most of which falls in winter. As already mentioned, fog and dew are regular occurrences and may contribute significantly to the total precipitation. Temperatures in the area are generally moderate. The average maximum temperature in January (the hottest month) is about 20°C while the average minimum temperature in June (the coolest month) is about 9°C. Frosts do not occur. Wind is an important feature of the climatic regime (Desmet and Cowling 1999), causing high evaporative demands (particularly during hot föhn-like bergwind events); and even resulting in physical damage to plants directly or through sand blasting. Wind may also have profound effects on dispersal phases (particularly seeds). The soils are red aeolian sands overlying an impenetrable hardpan of impervious dorbank about 10cm thick at about 2m.

Two communities, short and medium strandveld (Boucher

and Le Roux 1989), dominate the vegetation in the area. Medium-lived (5–15 years, Jürgens *et al.* 1999) shrubs, particularly from the Asteraceae and Aizoaceae (incl. Mesembryanthemaceae) dominate both communities. In the short strandveld, these seldom exceed 50cm tall. In contrast, in the medium strandveld, shrubs may reach 2m tall in places.

In both communities we sampled 20 soil cores (7.5cm diameter x 30cm deep) each from under clump canopies and in the centre of gaps. To avoid biases in locating these cores we sampled consecutive clumps and gaps along randomly positioned transects. We did however restrict gap-coring to gaps with a width of at least 1m in the short strandveld and at least 2m in the medium strandveld. These gaps represent the upper 50% gap size category. Mean diameter of clumps in short strandveld was 2.5m (sem = 0.11, N = 20 clumps) and in medium strandveld, 5.17m (sem = 0.34, N = 20). Before taking cores, the first centimetre or so of soil was scraped away until the shallowest roots were exposed. The cores therefore represent the 1–31cm rooting zone that contains the bulk of root biomass in both communities. Root biomass was separated from the soil using a combination of sieving and manual methods. Roots with a diameter greater than 2mm (considered structural) were separated from the finer material. All root material was oven dried at 60°C for 48h and then weighed. Since we were specifically interested in the within-community distribution of root biomass rather than in between community comparisons, we analysed the data from the two communities (clump vs open) separately by means of t-tests.

Results

In the medium strandveld, there was no significant difference between the fine root biomass under clumps and in the open (P=0.372). In contrast, the coarse (or structural) root biomass was significantly greater under clumps than in the open (P=0.028, Figure 1). In the short strandveld the probability that the fine root biomass at the two positions was not significantly different fell just outside the 5% threshold (P=0.053) with the mean fine root biomass in the open being slightly greater than under clumps (Figure 1). There was however no evidence to suggest that the coarse root mass differed with position (P=0.419).

Discussion

Results indicate that below-ground biomass in these communities is more regularly distributed than above-ground biomass. The only exception to this is the case of structural roots in the medium strandveld community, and even here, the clear two-phase mosaic that has been described above-ground is not apparent (Eccles 2000). Interpreted in the most traditional sense, regular spatial patterns have usually been used to infer the existence of competition (Ludwig and Reynolds 1988), and we believe this to be a likely explanation in the strandveld communities. This competition-based interpretation is supported, in the case of the medium strandveld at least, by the results of another study where plants of several important species that were isolated from their clumps exhibited higher (more positive) water poten-
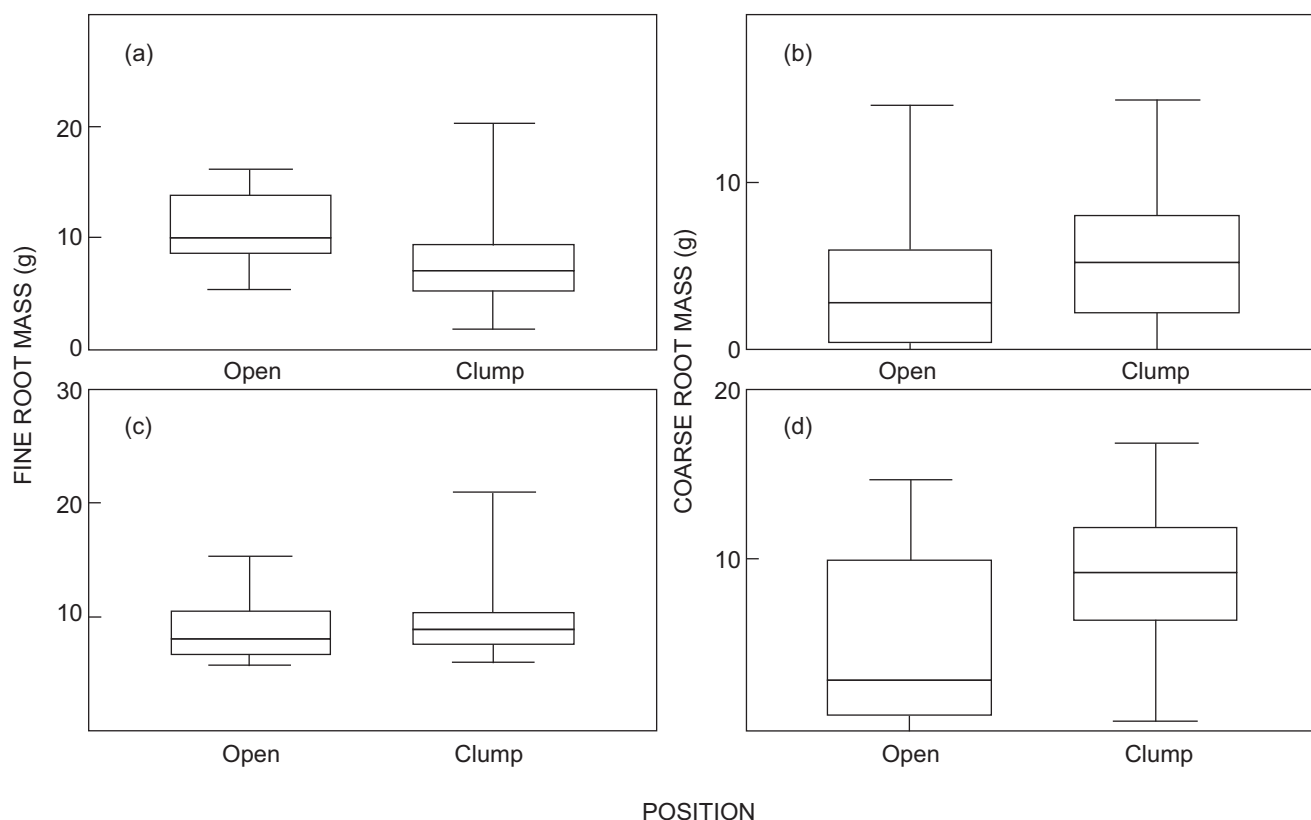
Figure 1: Box and whisker plots of biomass under clumps and in the open. Figures (a) and (b) are the fine and coarse biomass components respectively in the short strandveld community while (c) and (d) are the fine and coarse biomass components respectively in the medium strandveld community

tials than equivalent individuals in clumps (Eccles *et al.* 2001, Eccles *et al.* 2002). It would also appear that these species are able to osmotically adjust in order to mitigate this competitive effect (Eccles *et al.* 2001, Eccles *et al*. 2002), and we suggest that the regular spatial arrangement of roots reflects yet another strategy to minimise the effects of competition for water. From this perspective the plants in these communities appear to exhibit at least partial 'compensatory root growth' (Brisson and Reynolds 1994). The evidence once again points to the fact that plants in these communities are shaped by the trade off between the advantages of clumping and the inevitable competition for water that this association brings.

In addition, the apparently regular distribution of root biomass compliments the findings of Stock *et al.* (1999) who suggest that fertile islands associated with vegetation clumps are of little consequence in these communities. Even if there was nutritional enrichment under clumps, our results suggest that plants do not appear to respond to this. In fact, in the case of the short strandveld, it would appear that plants might even favour having their roots in the open. From this perspective, these communities seem to differ fundamentally from several other arid systems (Schlesinger *et al.* 1990). One possible explanation for this difference is that the rapid turnover of plants that has been reported in Namaqualand succulent communities (Cowling *et al.* 1999,

Jürgens *et al*. 1999) precludes the development of foci of enrichment (Stock *et al.* 1999). A further possible explanation is that good infiltration into sandy soils may prevent horizontal heterogeneity of soil water resources, thereby favouring homogenous distribution of roots.

What our results do not illuminate is whether there is any evidence for below-ground niche differentiation. As we have argued, circumstantial evidence in terms of the species make-up of clumps (Eccles *et al.* 1999) and the results reported here on rooting depths suggests that this may not be the case. However, this remains to be convincingly supported by detailed below-ground excavations.

To conclude, the fact that the spatial distribution of roots in these two strandveld communities appears to be far more regular than the highly clumped shoot distribution suggests that the below-ground growth behaviour is shaped by competition rather than facilitation. This result together with previous findings based on above-ground patterns (Eccles *et al.* 2001), clearly points to the importance of the trade-off between positive and negative interactions in shaping these desert plant communities.

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