Summary

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The Influence of Root Competition on the Coexistence of Sparse and Common Perennials in Two Limestone Grasslands

Why are so many plant species of low abundance in limestone grasslands, and remain so? What is the role of root competition? The influence of root competition on the diversity and coexistence of plant species was investigated in two limestone grasslands in northern Switzerland. The study sites (Gräte and Emmerberg) are mown meadows, rich in species. The Gräte site was poor in nutrients, while the Emmerberg site was slightly fertilized. The following eight perennial species were chosen for the experiments: *Bromus erectus*, *Dactylis glomerata*, *Salvia pratensis*, *Centaurea jacea*, *Scabiosa columbaria*, *Chrysanthemum leucanthemum*, *Anthyllis vulgaris*, *Primula columnae* (synonym: *Primula veris* ssp. *suaveolens*). Well established individuals of each species were chosen on both sites, 25 individuals as treatment plants and 25 neighbouring individuals as control plants. Additionally, some individuals were planted into nutrient rich soil in an experimental garden. The plants in a circumference of 12-25cm around the treatment plants (target individuals) were removed to a depth of 2cm (removal method). Root competition was excluded by a polyethylene-foil (trenching method). The plants were investigated for 3 years.

1. In the swards, the dominant species *Bromus erectus* represented 40% of the above-ground phytomass. *Salvia pratensis* was subdominant. The root/shoot-ratio was ≥ 3 : 1 on the Gräte site, and 2: 1 on the Emmerberg site. At least 80% of the roots were found in the upper 10cm of soil. Half of the above-ground phytomass was between 0-10cm. Thus, the influence of the above-ground competition was minor.

2. The fundamental as well as the realized niches were investigated for the eeight species. Surprisingly, the rarely occurring species *Anthyllis vulgaris* and *Primula columnae* proved to be highly adapted to the site and were as competitive as the dominant species *Bromus erectus* and *Salvia pratensis*.

3. After removal of root competition, the increase in reproductive structures was larger than in vegetative ones. The extent of allocation correlated more with growth form than with absence of competition. In contrast to weak competitors, the flowering-ratio of strong competitors was not affected by the treatment. The shoot density of strong competitors was increased by the treatment, but decreased for weak competitors. Possible reasons for the differences in competitiveness are discussed.

4. On the Gräte site, individuals of dominant species developed 2-5 times more shoots and 5-20 times more flowering units when root competition was prevented. Individuals of weak competitors had 4-17 times as many shoots and 10-770 times as many flowering units.
   On the slightly fertilized Emmerberg site, the differencse showed mainly in the vegetative parameters. The individuals of strong competitors developed 4-5 times as many shoots as the control plants. In contrast, individuals of weak competitors had 7-28 times as many shoots in the absence of root competition.
   These results show that several species in limestone grasslands are limited by root competition.

5. Climatic extremes influenced the competition of the species investigated. In addition the reaction of the treatment plants differed from that of the control plants. The effect of herbi-

vory or parasitic fungi (e.g. *Epichloë typhina*) was stronger upon treatment than upon control plants though effect is minor compared with that of competition.

6. On the Gräte site, *Salvia pratensis* showed the highest half-life (45 years) and *Anthyllis vulgaris* (2.1 years) the lowest. The species composition is determined by the turnover of individuals.
   The plants investigated on the Emmerberg site had half-lives of 4-7 years. Here the significance of root competition was altered since slight fertilization of the site enhances the ability to take up nutrients, whereas the capacity to store nutrients loses its importance.

7. The average number of individuals which die per year for each species was calculated from their half-lives. The results suggest a gap-turnover of only 3.3% of the total area per year on the Gräte site and 9.2% on the Emmerberg site.

8. On the Gräte site, only one out of 10'000-30'000 seeds produced each year of the dominant species or of the strong competitors has to reach the adult stage in order to preserve the species composition. The short-living species or the weak competitors need to bring up one individual out of 600-2'000 seeds.

9. Why do some species occur and remain sparse in the stand? The following description applies to the grasslands investigated: a set matrix of common tussock perennials dominate the site and rather sparse, short-lived gap colonizers occupy in between. Because of the occupation of space and nutrients by long-lived species the role of root competition is mostly passive.

10. In limestone grasslands, root competition is more important for the dominance of matrix species than abiotic site parameters. Dominant species are strong competitors, but competitiveness does not guarantee dominance. Root competition is only one of several influences upon the short-lived gap colonizers. As can be seen from points 1-9, the diversity of site factors is high, none of which is dominant within the stand. This fact as well as the very slow turnover of mature plants in these ecosystems are most crucial for the species diversity in limestone grasslands.

11. The direct vs. indirect and active vs. passive mechanisms of root competition are discussed in a table in chapter 5. The Matrix Model is set in the context of the Evolutionary Stable Strategy, the Mosaic Cycle Concept and the CSR-Model.

12. Causes for the sparseness of many species are discussed in relation to nature conservation. Possibilities for favouring certain species are discussed.