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Artikel: Influence of gaps and neighbouring plants on seedling establishment in limestone grassland : experimental field studies in northern Switzerland = Einfluss von Kahlstellen und benachbarten Pflanzen auf die Keimlingsentwicklung in Trespen-Halbtrochenrasen : experimentelle Felduntersuchungen in der Nordschweiz

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4. DISCUSSION

4.1. NEIGHBOURHOOD EFFECTS ON GERMINATION

Germination is obviously not limited by the availability of open microsites in the grassland of the Gräte. Sowing of seeds resulted in higher seedling densities in all microsites than were observed in the natural vegetation, regardless of their cover. Moderate vegetation cover even enhanced the emergence resulting in a high number of seedlings in edges and moss-covered microsites. Limiting factors for the emergence of all species seem thus to be rather the availability of seeds and climatic conditions including soil water availability.
The delayed emergence under the vegetation cover had no influence on the number of seedlings and their establishment. The only species with an age-dependent mortality was *Primula*, whose time of emergence was not influenced by the vegetation cover.
It is plausible that vegetation cover did not inhibit recruitment, as the canopy is short in autumn and spring, i.e. at the time when germination occurs. As drought is frequent at that time, moderate vegetation cover may even enhance germination by preventing a rapid desiccation of the topsoil.

4.2. PATTERNS OF ESTABLISHMENT

Based on survival during the first growth period, three major patterns of establishment in relation to the influence of neighbouring plants could be distinguished among the six species studied.

- Low mortality in all microsites. The establishment of the seedlings was either slightly hampered by neighbouring plants or no clear effect could be detected (*Plantago lanceolata* and *Sanguisorba minor*).
- Low mortality in gaps, reduced survival under vegetation cover (*Linum catharticum*).
- High mortality in open microsites because of the harsh abiotic conditions. Survival was clearly improved in the shelter of the vegetation (*Arabis hirsuta* and *Primula veris* s.l.).

The pattern of establishmentary behaviour that a species shows, is influenced by the environmental conditions. The possible variation of this pattern from year to year could be seen in the establishment of *Medicago lupulina*. It had a high total survival in 1987, while in 1988 it suffered high mortality with slightly better survival under cover of *Onobrychis*.

4.2.1. Low mortality in all microsites

The species with a low mortality, *Plantago* and *Sanguisorba*, as well as *Medicago* in 1987, established well in all microsites. They were not much affected by the harsh climatic conditions in the open microsites, and competition by established vegetation did only slightly reduce their survival. Their growth was somewhat inhibited in tufts, but also here the plants appeared healthy. The good survival was not limited just to the first growth period, but was pronounced in the second year as well. These best surviving species were also the best growing ones among the species studied, and among the most abundant ones in the meadow.

Large seeds enable these species to expand their roots and leaves quickly. With their deep root system they can escape the dry conditions of the topsoil and the erect leaves obtain light also in closed vegetation. Large seeds and quick initial growth even in shade are important characteristics for establishment in closed turf (GRIME and JEFFREY 1965, GROSS 1984).

Causes of death were not easy to detect, as the seedlings mostly just vanished. Mortality occurred mainly during the growth period and was slightly higher in tufts, which indicates a reduced survival of the plants because of competition. Despite the smaller size most plants grew well in tufts, and competition itself may not prevent establishment. It rather increased the vulnerability of the seedlings to other factors such as desiccation, pathogens and herbivory. If the growth of the roots is inhibited by competition, drying out of the plants may be more likely. Plants growing in shady conditions are often susceptible to fungal diseases (GRIME 1965, GRIME and JEFFREY 1965). Microsites influenced the activity of animals, e.g. aphids were often observed in *Onobrychis* tufts and the holes of crickets (*Gryllus campestris*) only in gap-microsites. Worm heaps occurred also in tufts. Young plants of *Plantago* and *Sanguisorba* were however rather resistant towards burrowing because of their erect growth-form.

4.2.2. Low mortality in gaps, reduced survival under vegetation cover

Dense vegetation inhibited the establishment of *Linum*. On the other hand, mortality was higher in large gaps than in those of an intermediate size. This

is partly in accordance with previous studies on *Linum*, which found the best establishment of this species at intermediate vegetation densities (HILLIER 1984, SCHENKEVELD and VERKAAR 1984, KELLY 1989). However, the present work suggests that establishment is best in gaps of intermediate size rather than in sparse vegetation, as in the cited studies.
Seeds of *Linum* are small and form a large seed bank. Seedlings occur very abundantly in natural vegetation but have a rather high mortality. Fungal diseases seem to be an important cause of death for *Linum*. VAN TOOREN (1990) also reports this as an important mortality factor. A large number of seedlings with a high mortality together with the preference for rather open microsites fits well in the described character of *Linum* as stress-tolerant ruderal (GRIME et al. 1988) or spender (DURING et al. 1985).

4.2.3. High mortality in open microsites, improved establishment in vegetation

Arabis hirsuta and *Primula veris* s.l. could hardly establish at all in open microsites. In the shelter of vegetation they survived markedly better, although not quite as well as *Sanguisorba* and *Plantago*.
The main cause of mortality for *Arabis* and *Primula* was desiccation. Highest death rates of seedlings occurred after mowing when the vegetation was low and the topsoil dried up. *Arabis* suffered high mortality also in spring, when the seedlings in gap-microsites desiccated after uprooting by frost. The shelter of vegetation reduced the impact of climate thus enhancing establishment. Even a sparse moss cover improved the survival of *Arabis*.
Though *Arabis* is less abundant in the natural vegetation than the other species, it cannot be regarded as rare. Therefore its poor survival was rather surprising, especially the total failure to establish in gaps. This species is often described as a ruderal with a preference for open habitats. As the environmental conditions are so crucial for the establishment of *Arabis* it is likely to vary from year to year. Favourable years may be decisive for its existence on the Gräte. The study period was obviously unfavourable for this species. There was little snow in either winter, which increased the impact of frost-heave. Drought periods in spring and after mowing enhanced desiccation.
Microsites with higher nutrient levels might be important especially for the performance of *Arabis*, as it is one of the few plants in limestone grasslands without mycorrhiza (HARLEY and HARLEY 1986). Such microsites are e.g. colonies of voles with faecal deposits, in which the abundance of *Arabis* is in-

creased compared to vegetation without the influence of voles (LEUTERT 1983).

The vulnerability of the seedlings of *Primula* in open microsites may explain its habitat requirements. The subspecies *suaveolens*, to which the studied plants belong, is usually found in shady habitats such as open woodlands and its occurrence in an open meadow, as on the study site, is rather uncommon. In a meadow favourable microsites for its establishment are likely to be scarce. This is however influenced by the time of mowing, as the hardiness of the seedlings against desiccation increases with their age. Mowing in June every or every other year is harmful for *Primula* compared to a later or a less frequent mowing (KRÜSI 1981, MERZ 1986). In meadows near the study site mown end of June, *Primula* is almost extinguished (MERZ 1986). The meadow of the present study is mown in mid-July, and the occurrence of *Primula* here shows, that this difference of 2-3 weeks in the time of mowing is already decisive for establishment. Older seedlings are better able to withstand desiccation after the mowing and are more likely to find favourable microsites. Variation in phenological development may cause similar differences in establishment between the years.

Such subtleties may be important for the existence of a species in a community and should be considered when choosing management practices in nature conservation.

The behaviour of *Medicago* and *Linum* shows, that establishment of a species may greatly vary between the years and short-term studies give only an incomplete picture about the regeneration of a species. The variation in environmental conditions and occurrence of favourable years may be more limiting for the existence of these species than favourable microsites.

4.3. NEIGHBOURHOOD EFFECTS ON ESTABLISHMENT AND SUBSEQUENT SURVIVAL

4.3.1. Significance of competition

On the whole, competition by the established vegetation did not prevent the establishment of seedlings of most species on the study site. It reduced growth and may have caused a higher mortality risk, but survival of the seedlings was fairly high even in densely vegetated tuft-microsites. After one growth period, survival of emerged seedlings was mostly over 50% in these microsites. Lower survival in tufts occurred only when the mortality cause was drought or fungal disease, and in these cases vegetation cover either improved the survival or had no influence. Gaps may be important for the regeneration of short-lived species, as the behaviour of *Linum* indicates.

In small gaps, like the ones used in the present study, mainly the above-ground competition is reduced. Below-ground competition occurs also in these microsites because of the lateral growth of the roots of the neighbouring vegetation. The significance of microsites with no competition at all (e.g. large gaps) is however likely to be small in the community studied, as such microsites do not occur frequently.

This unimportance of competition for establishment results obviously from the low growth-rates of the whole vegetation in these nutrient poor habitats, and the yearly mowing. As above-ground productivity is low and growth after the mowing poor, competition for light is likely to be intense only during a short time of the year. Further, the mowing keeps the ground fairly open by removing the above-ground biomass periodically and preventing the accumulation of litter. The rather early mowing removes nutrients with the phytomass preventing the dominance of species, which would be able to accumulate the nutrients. Below-ground competition reduces the growth of the seedlings. Nevertheless they obtain enough nutrients to survive.

The results conflict with a common opinion, that regards competition as the main hazard for seedlings (e.g. FENNER 1985, WATKINSON 1986). That opinion is based on a vast number of studies under nutrient rich conditions, where the detrimental effects of competition by established vegetation on seedling establishment is clearly shown (CARUSO 1970, FOSTER 1964, GOLDBERG and WERNER 1983, GROSS 1980, GROSS and WERNER 1982, MCCONNAUGHAY and BAZZAZ 1987, NEWELL et al. 1981, PUTWAIN and HARPER 1970, ROBOCKER et al. 1953, ROSS and HARPER 1972, SHAW and ANTONOVICS 1986, SILVERTOWN and TREMLETT 1989, STERGIOS 1976, TURKINGTON et al. 1979). It is however often neglected, that these effects depend on the productivity of the habitat. The impact of competition on plant growth decreases with decreasing nutrient levels and increasing disturbance (CAMPBELL and GRIME subm.). The present work indicates this to be the case also for seedling establishment, and there is also supporting evidence in the literature. Fertilizer treatment often results in a poorer establishment of seedlings (FOSTER 1964, HOWE and SNAYDON 1986, KEDDY 1981, KELLY 1989, PEMADASA and LOWELL 1974, but see MILES 1973b, 1974). In nutrient-poor habitats gaps are not the most favourable microsites for establishment, although germination is often improved in them (SCHENKE-

VELD and VERKAAR 1984, SILVERTOWN 1981, SILVERTOWN and WILKIN 1983). The habitat-dependent variation of the significance of gaps on seedling establishment has been shown by HILLIER (1984) in chalk grasslands in Derbyshire. The regeneration by seed was strongly gap-dependent in north-facing slopes while in south-facing slopes the emergence of seedlings did not increase in gaps and survival was even enhanced by the presence of established vegetation. The north-facing slopes had a more luxuriant vegetation, where gaps were the only possibility for many species to escape competition in contrast to the more open south-facing slopes where drought was a more important factor. Also SHARITZ and MCCORMICK (1973) observed in case of two annuals in communities on granite outcrops in the southeastern United States, that with increasing environmental harshness the importance of competitive interactions between species decreases.

The effect of vegetation may be negative also on infertile soils, but the mechanism is not necessarily competition. MILES (1972, 1973a, 1974) found an improved establishment on experimentally bared soil in a southern English heath and in different sites in Scotland, mostly in rather species-poor *Callunetum* communities on podsolic or peaty soils. He produced the gaps by stripping the vegetation with a sharp spade disturbing also the litter on the soil surface and the other top-layers. The exposed mineral soil might thus have been responsible for the improved establishment rather than the reduced competition, as the physical properties of *Calluna* raw humus are unfavourable for seedling establishment (ELLENBERG 1986). MILES (1972) mentions drought as the main cause of mortality. It is also possible that the vegetation structure of a *Callunetum* might be unfavourable for seedlings. In winter however the mortality in vegetation was less than in bare plots, due to reduced frost heave (MILES 1973a).

The effect of established vegetation on seedlings consists of different mechanisms, e.g. above- and belowground competition, sheltering or influence on other organisms like herbivores or mycorrhiza. The relative importance of these mechanisms and the outcome of interaction depends on the environmental conditions. Considering the results of the present study and the evidence gained from the literature, one can say that competition by established vegetation surely reduces the growth of seedlings and may prevent their establishment, but in less productive habitats other factors gain in importance and may overweigh the effects of competition.

4.3.2. Shelter against adverse climate

Climatic factors, such as frost heave and drought, cause the high mortality of *Arabis* and *Primula*. The small size of their roots does not give enough support in the moving soil and does not allow water uptake in a dry top soil. The establishment is enhanced under vegetation cover, as the roots of neighbouring plants stabilize the soil and the canopy protects the topsoil effectively against desiccation. The sheltering effect of vegetation on micro-climate can be very pronounced, as the measurements of CERLETTI (1988) on the Gräte have shown. He measured the influence of vegetation on water-regime in topsoil. During sunny summer weather the topsoil dried fast in gaps of the size of 30x35 cm, and its wilting point was reached already two days after the last precipitation. After seven days the soil was completely dried out up to a depth of 3-4 cm. In sheltered microsites the topsoil never dried below the wilting-point, even not after the mowing, when the vegetation was very low. The exposure had a significant effect. South-facing edges of the vegetated patches dried out rapidly while the northern edge had a more favourable water-regime. Vegetation has a similar effect on the relative humidity of the air and on the soil surface temperature (VON GUNTEN 1987).
At the study site, gaps are created mainly by small mammals, voles and moles. Nutrient levels in the upheaved soil are lower than those in the topsoil under undisturbed vegetation (SCHÄPPI 1989), and the loose soil in the fairly large gaps desiccates quickly. All this reduces the significance of gaps for seedling recruitment. Seedlings are rarely observed in them and the slow recolonization occurs vegetatively from the surroundings (pers.obs.). The increase of some short-lived species, also *Arabis*, due to vole-activity in fertilized and unfertilized meadows, as observed by LEUTERT (1983) in same area as the present study, might be explained by the different importance of gaps in different habitats and in different years. Also the influence of enhanced nutrient levels by voles are important for many species, as already discussed in Chapter 4.3.1. LEUTERT (1983) did not establish, whether the increase of the short-lived species, as compared to the closed vegetation, occurs in the centre of the vole-gaps or in the more protected edges.
The significance of gaps on regeneration by seed is often emphasized, but sheltering effects are mostly considered to restrict themselves to habitats with extremely severe climatic conditions. The necessity of sheltering nurse-plants for seedling establishment is known e.g. in the Sonoran Desert (FRANCO and NOBEL 1988, 1989, NIERING et al. 1963, TURNER et al. 1966) and in subalpine

herb communities in Utah (ELLISON 1949). In these habitats seedlings are not able to survive on bare soil, as the temperature, desiccation, frost-heave or herbivory are too severe. Besides that, the soil nitrogen levels are higher under nurse-plants. Competition reduces the growth of the seedlings in patches of vegetation, but the overall effect is still positive for the seedlings. Slight differences in their position in the vegetation patches strongly influence the outcome of the interaction (FRANCO and NOBEL 1988, 1989).

Shelter plays a role in establishment also in more mesic habitats, if not always so obviously. Often the effects of competition are just outweighed. Apart from the work of HILLIER (1984, see Chapter 4.3.1), there is further evidence for sheltering effects in the literature. SCHENKEVELD and VERKAAR (1984) observed that in Dutch chalk grasslands the early survival of many short-lived species was better in dense than in open vegetation or in bare sites. In summer, when the vegetation cover was closing, this was however partly reversed. In a southern-English chalk grassland the emergence was enhanced in microsites with reduced cover (SILVERTOWN 1981, SILVERTOWN and WILKIN 1983), but there was no relationship between mortality and the cover of microsites. In a year of drought, seedling mortality was even lower in microsites with more cover (SILVERTOWN 1979). In a midsuccessional oldfield studied by GOLDBERG (1987) establishment in gaps and vegetated microsites differed only marginally as the positive effect of reduced competition in the gaps was outweighed by the desiccation of the topsoil.

In a dry Texas grassland FOWLER (1988) observed a better establishment of seedlings of the grasses *Aristida longiseta* and *Bouteloa rigidiseta* with neighbouring plants of the same species than without neighbours. She considered this phenomenon mainly as aggregation of seedlings on favourable microsites, perhaps also as some facilitation due to shading. In the greenhouse the establishment of these species was enhanced in microsites sheltered by litter or rocks, where the topsoil desiccated less (FOWLER 1986).

The positive effect of shelter, as observed in the present study, are thus more abundant than generally assumed. Apart from extreme habitats, where their significance is obvious, they are important also in more mesic habitats, especially during extreme years and for species, which are at the limit of their tolerance. Whether this positive influence of vegetation on establishment has a lasting effect on growth and reproduction may still be questioned. The two years of observation in the present study were too short a time to answer this because of the slow growth of the plants. The requirements of juvenile and adult plants may be different from those of seedlings (MORRIS and WOOD

1989, PARRISH and BAZZAZ 1985). In habitats with low production, vulnerability to climatic hazards seems to be more decisive than competitive ability in the early life stages such as germination and establishment. Positive effects of neighbours such as sheltering may thus be important. In later stages competitive effects may become more significant and determine the relative abundance of the species, as the work by MITCHLEY and GRUBB (1986) and MARTI (in prep.) suggests.

4.3.3. Effect of different species as neighbours

Species differ in their influence on the establishment and growth of seedlings in their neighbourhood. In the present study the performance of the seedlings was often better near *Onobrychis* than near *Bromus*. This results probably from the different growth form of the species, particularly from the different root morphology and also from differences in decomposition rates of their leaves (see also Chapter 3.2.1). Levels of available nutrients below the different species may also differ, particularly that of nitrogen, as *Onobrychis* has a symbiotic association with nitrogen-fixing organisms. There is a small-scale variation in the levels of nitrogen, phosphate or potassium in the soil of the study site (SCHÄPPI 1989), but no clear correlation with the vegetation cover, specially with *Onobrychis*, could be found. The importance of the effect of individual species on a microsite in natural vegetation might be too diffuse to be measured, as the individuals are tightly interwoven. Thus their effect on the establishment of seedlings may be less pronounced than in the monospecific patches in the experimental plots of the present work.
There was no combination of central plant and seedlings of the same species, and there is thus no information about possible differences in the intra- and interspecific interactions between seedlings and established vegetation. This is frequently observed in forests, where many tree species are able to regenerate better in the neighbourhood of other species than their own (FORCIER 1975, FOX 1977, SIMAK 1951, WOODS 1984).

4.4. FURTHER PERFORMANCE OF THE PLANTS AND CONSEQUENCES FOR SPECIES-RICHNESS

In the studied grassland many plants are able to survive for years as tiny plantlets. CHIPPINDALE (1948) and FENNER (1978) have previously observed this kind of arrested growth of seedlings during several months, but under nutrient-poor conditions seedlings are obviously able to remain in this state much longer. Whether their development to adulthood requires favourable years, some incidental events in the neighbourhood such as the excrements of animals or the dying of neighbouring plants, or just time, remains unanswered. For the regeneration of forest trees such dormant juvenile plants are important (HIBBS and FISCHER 1979, MAYER 1980, SERNANDER 1936, UHL et al. 1988), but in grasslands their significance is unknown. Mycorrhizal infection can be very important for the survival of such seedlings (GRIME et al. 1987). This might be the effect of assimilates exported from dominant species to seedlings over the mycorrhizal network (READ et al. 1985).

The observed slow growth and the ability of juvenile plants to survive for a long time in vegetation allow a high species density in a small scale. This confirms the significance of the low nutrient levels and mowing for the maintenance of the species richness and supports the models of GRIME (1979) and HUSTON (1979). They suggest, that high species densities are possible in high or intermediate levels of stress and disturbance, as the expression of competitive dominance is limited. In too extreme habitats the number of species declines, as only a few specialists are able to survive.

Because of slow growth and good survival, immigrated propagules and occasional favourable years for seed production or establishment also have long-lasting effects on species composition (SHMIDA and ELLNER 1984). Such effects may be particularly important for short-lived species, as gaps (GRUBB 1976, KELLY 1989, RUSCH 1988) and dry years momentarily reducing the cover of perennial species (LÜDI and ZOLLER 1949) are important for their regeneration even in nutrient poor habitats.

In the study site the annual species were rare even in open microsites. It is interesting, that the exceptions were *Rhinanthus alectorolophus, Rh. minor* and *Trifolium dubium*, species which are able to gain nutrients from other organisms either hemi-parasitically or symbiotically. Other interactions than competition might be decisive also for the establishment of annual species in this habitat.