Discussion

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flowers were observed in sectors with dense vegetation and intermediate ones; in August, unripe fruits prevailed whereas in September mostly ripe fruits with a good seed content were found. Abundant flowers and unripe fruits were counted also in the plots with thin vegetation, but during the September census, most of the ripe fruits with the seeds were already dispersed (Table 28, Fig. 44).

Only few reproductive units were found in July and August on acidic silicate and no seed output was observed in September (Table 28, Fig. 44).

5. DISCUSSION

The present studies reveal that *Biscutella levigata* is predominantly allogamous and highly self-incompatible. However, its theoretically possible wide gene exchange is apparently limited, at least in some alpine subpopulations. Biology of reproduction undoubtedly plays an important role in this process; factors limiting the gene flow apparently operate both at the pollination phase as well as during seed development and their subsequent dispersal.

It seems that the limited gene flow in *B. levigata* is influenced by spatial and/or temporal variation in floral supply as well as by the foraging behaviour of pollinators. Populations of *Biscutella levigata* are variable as to their density. In the study area, population density was very low in dolomite grassland, whereas dense clusters of rosettes were found on dolomite scree. On serpentine, a rather consistent pattern in density was observed.

On the whole, about 10% of the rosettes produced inflorescences. The general pattern of production of floral structures in *B. levigata* is similar to e.g. *Hieracium floribundum* (THOMAS and DALE 1975). However, some differences between the substrata studied were noted. On dolomite, reproducing rosettes of *B. levigata* most frequently represented less than 10%, but the corresponding proportion on serpentine was always higher than 10%. On the other hand, no pronounced differences between various sites within a given substratum were observed. The average number of flowers per inflorescence was about 15, on dolomite scree usually being higher than on dolomite grassland, whereas on serpentine no distinct differences between the niches occurred. It seems therefore that the density of floral structures in B. levigata results primarily from the distribution pattern of whole flowering shoots.

Spatial separation of male and female functions should considerably reduce the deposition of self-pollen and increase the amount of outgoing pollen (see e.g. WEBB and BAWA 1983, BAWA and OPLER 1975, BAWA and BEACH 1981, LLOYD and YATES 1982). However, as emphasized by BAWA et al. (1983), temporal separation of male and female functions is more important than spatial separation in achieving a high level of outcrossing. In B. levigata flowers develop successively, the flowering period usually lasting from the middle of July to the middle of August. Flowers within a given inflorescence also open in a certain sequence from bottom to top.

The number of flower buds and flowers decreased greatly throughout the flowering season, numerous reproductive units being aborted. Limiting of flower resources by grazing was also an important factor in Biscutella levigata, especially on dolomite grassland and in highest sites on dolomite. A reduced floral supply represents a factor influencing the seed output; in predominantly allogamous taxa it obviously contributes to a reduced gene pool. Our observations corroborate the previous data: e.g. KRÜSI (1981) found that cutting in June almost completely prevented sexual reproduction in Brachypodium pinnatum because all flowering inflorescences were removed. Also in Cardamine insueta growing in hay meadows, all the flower stalks were usually removed by cutting. The seed production in the triploid hybrid, already limited on account of unbalanced genetic structure, was therefore completely prevented (URBANSKA 1980).

Gene flow in and between populations is influenced by the number of individuals mating at random, defined as breeding unit or neighbourhood size (KERSTER 1964, WRIGHT 1943, 1946). It was assumed that neighbourhood size in bee-pollinated species does not change in colonies with different densities (LEVIN and KERSTER 1969). However, in Phlox that is principally pollinated by Lepidoptera, the neighbourhood size was reported to range from 75 to 282 individuals in colonies of different densities (LEVIN and KERSTER 1968). Also RICHARDS and IBRAHIM (1978) emphasized a density-dependent neighbourhood size in *Primula veris*. The much lower frequency of insect visits in areas of low plant density are likely to make neighbourhood size highly density-dependent and will not be compensated for by greater insect travel.

The neighbourhood size in *B. levigata* was not studied in detail and our observations have only an indicative value. In the alpine vegetation belt bees usually do not occur. During the four vegetation seasons of the present study, only few *Syrphidae* and *Lepidoptera* were observed as visitors to *Biscutella* flowers. According to KAY (1978) *Syrphidae* show a strong preference for yellow flowers. Their habit of remaining stationary in the air and suddenly flying distances over several meters at a very high speed makes their foraging pattern rather unpredictable. *Lepidoptera* move typically from a given plant to one of its near-neighbours; although long-distance flights are a part of their normal behaviour pattern, these proved to be rare events i.e. not exceeding 2% (LEVIN and KERSTER 1968). Precise behaviour of insects visiting *Biscutella levigata* remain to be investigated, but it is not excluded that differences in population density observable in various sectors may influence the foraging pattern of pollinators. HANDEL (1983) argued recently that the pollination biology of any species is not constant among populations, but may change with the nature and behaviour of the available pollinators. This aspect should also be taken into account in future investigations on *B. levigata*.

The sexual reproduction in *B. levigata* is greatly influenced not only by flower resources and pollinators but also by grazing intensity. Also at later post-mating stages grazers may eliminate some reproductive units. The amount of fruits per m^2 was very low in dolomite grassland and low in dolomite intermediate sectors. The seed output may therefore vary dramatically from site to site, especially on dolomite: for instance, in a highest sector on dolomite no fruits at all were produced for four years because all flowers or unripe fruits were grazed by *Capra ibex*.

Seed dispersal in *Biscutella levigata* most frequently involve the whole fruits (MÜLLER-SCHNEIDER 1977). Our field observations suggest that the dispersal pattern in *B. levigata* is rather complex. Strong gusts of wind can occasionally tear off ripe fruits and transport them over longer distances. The water running from melting snow can also transport fruits lying on the soil downhill to lower sites. Most frequently, however, the fruits fall to the ground and remain in the immediate vicinity of the mother plant. In case of early snowfall in autumn the inflorescences are pressed down with all the fruits on them. After the snow has melted, the whole group of seeds germinates forming a dense cluster (GASSER 1983). A similar pattern of local dispersal was observed in alpine populations of *Ranunculus montanus* s.l. by DICKENMANN (1982). MARCHAND and ROACH (1980) considered wind as the important agent of seed dispersal in *Arenaria groenlandica* and *Diapensia lapponica* in the alpine tundra; however, they noted that the seeds were usually not transported further than 0.5 m to 1 m. *Arenaria groenlandica* and *Diapensia lapponica* have no particular adaptations for seed dispersal by wind. *Senecio jacobaea* on the other hand, produce achenes with typical pappus morphology. Thea are adapted to dispersal by wind, but netherless 60% of all achenes produced remain close to the mother plants, only about 0.4% being distributed further than 4.6 m (POOLE and CAIRNS 1940).

The seed dispersal in *Biscutella levigata* often results in the formation of seedling cohorts representing siblings or half-siblings; the gene pool of a given population sector may thus be locally limited.

The germination capacity of *Biscutella levigata* on moist blotting paper in the climatic chamber consistently approached 100%. Contrary to this pattern, germination percentages in the field were variable and apparently influenced by alpine substrata; the greenhouse experiments also indicated influence of substratum on germinating behaviour. The present results corroborate the previous data of e.g. FOSSATI (1980) who found great influence of substratum on germination in alpine plants. Also SCHÜTZ and URBANSKA (1984) observed differential seed germination in agamospermous *Taraxacum alpinum* from carbonate and acidic silicate. The behaviour of *B. levigata* shows that germinating behaviour of alpine plants may reflect adaptation to various substrata. In this respect, our results do not support the opinion of some previous authors (e.g. ELLENBERG 1958, GIGON 1971) who argued that substratum influences later developmental phases, but not the germinating behaviour in plants.

Freshly germinated seeds of *B. levigata* were found in the wild during the whole vegetation period, but germination occurred mostly soon after the snow had melted. Our field experiments demonstrate that seeds of *B. levigata* remain viable for at least several years in alpine soils. Seed dormancy seems to be enforced and the persistent population of buried

seeds in alpine soils is apparently composed of various generations. In this respect, Biscutella levigata is similar to many other alpine species (see e.g. FOSSATI 1980, WEILENMANN 1981, ZUUR-ISLER 1982, SCHÜTZ 1983, and SCHÜTZ unpubl).
The pre-establishment mortality of Biscutella levigata was very high in the extreme environment of scree and most seedlings died after germination, the survivorship curve being of DEEVEY type III. Contrary to this pattern, the survival of seedlings in dense vegetation was surprisingly high; their survivorship curve was that of DEEVEY type II, the mortality risk being always more or less constant. The present results are in agreement with data of ZUUR-ISLER (1982) of alpine serpentine plants as well as with those of FOSSATI (1980) concerning taxa from carbonate and acidic silicate. On the other hand, MARCHAND (1984) found the greatest single cause of mortality in frost-heaving at the end of the growing season. Seedling mortality is often the result of soil drought and needle ice formation (BLISS 1985). It seems that soil water stress might have had an adverse effect on seedling development of Biscutella levigata especially on dolomite scree; however, drought often occurs for longer periods at high altitudes and cannot be considered as an isolated event in the life of alpine plants.
The present results suggest that the recruitment of new genets follows different pathways in various ecological niches of B. levigata and obviously influences the gene pool of given sectors.

Not only life history elements but also clonal growth limits the gene flow in Biscutella levigata. The young genets form additional rosettes rather rapidly; our field observations corroborate previous experimental data of MANTON (1934) and WEILENMANN (1981). Even under harsh alpine conditions the first additional rosettes were observed already in one-year-old genets. First additional rosettes appear close to the mother rosette, but in older plants, rosettes from new root suckers were developed also at some distance, up to approximately 1 m.
The ramets of B. levigata often grow very mosaic-like and no influence of the slope gradient on spatial pattern were observed. The behaviour of B. levigata is similar to that observed in Viola blanda, V. pallens, and V. incognita (SCHELLNER et al. 1982) as well as Cardamine rivularis, C. insueta, and C. schulzii (ZIMMERLI 1983). Unfortunately, it could not be decided with field methods whether all adjacent rosettes belong to the

same clone or represent different genets as *Biscutella levigata* has no morphological characters that could be used as markers. In this respect, *B. levigata* differs from *Trifolium repens* where CAHN and HARPER (1976) identified clones by leaf markers and found that various genets were intimately mixed. Genets of *Festuca rubra* could also have been identified by some morphological characters; in this taxon, however, genets grow mostly in neighbourship (HARBERD 1961).

Limited size of breeding units is a prerequisite for the formation of local races which is a first step in primary speciation (GRANT 1963, 1981, 1985). The present results bring mostly circumstantial evidence of gene flow limitations in *Biscutella levigata*. However, the alpine populations studied in the course of the present investigations exhibit clear adaptations to their substrata, not in morphological but in physiological characteristics, and therefore should be considered as edaphic races.

A further ecological differentiation in *Biscutella levigata* occurs on dolomite. It is influenced by particular niches and mostly reflected in demographic structure of population sectors. Depending on a given sector, competition and/or soil development lead to differences in size, density, and/or distribution of age-state variants; the present study corroborates our previous data (GASSER 1983). In the highest sites on dolomite and serpentine, seedlings were scarce and the limited gene pool in these sectors apparently remains rather stabilized. Growth pattern as well as absence of seedling cohorts in dolomite grassland strongly suggest that the population turnover is rather low and the gene pool very limited indeed; on the other hand, the subpopulations occurring on dolomite scree may have both a larger gene pool and higher turnover rates. Intermediate sectors on dolomite are also intermediary in their demographic parameters, between the extreme sites of grassland and scree; the differentiation pattern observed should therefore be considered as (eco)clinal rather than racial.

For the time being, it remains an open question what the input of particular genotypes into the gene pool of a given population sector of *B. levigata* might be. Both quantitative data on clonal growth and vegetative propagation as well as electrophoretic study of isoenzymes are indispensable for a precise assessment. The intricate pattern of sexual reproduction and vegetative propagation in *B. levigata* suggests that its behaviour may be comparable to e.g. Ranunculus repens (SARUKHAN and HARPER 1973) or Trifolium repens (BURDON 1983). Further studies in this respect should prove worthwile.

SUMMARY

Biscutella levigata from the alpine vegetation belt of Davos is predominantly allogamous and highly self-incompatible. However, neighbourhood size is apparently restricted by factors operating in the pollination phase, in seed development, and in seed dispersal. Clear adaptations to dolomite and serpentine were observed; germinating behaviour as well as mortality and development of young plants proved to be greatly dependent on substratum and origin in laboratory, greenhouse, and field trials.
B. levigata forms edaphic races on various alpine substrata. In addition, an (eco)clinal differentiation on dolomite was observed. The subpopulations occurring in dense dolomite grassland were small, had a very low density of ramets and seedlings were scarce. On the other hand, subpopulations inhabiting dolomite scree had a high density of ramets, and seedlings occurred frequently. The subpopulations of intermediate dolomite sites were intermediary. Contrary to the pattern found on dolomite, the demographic behaviour of B. levigata on serpentine was similar in all sites studied.
In conclusion, influence of neighbourhood size on microdifferentiation in plants is briefly discussed.

ZUSAMMENFASSUNG

Biscutella levigata aus der alpinen Stufe von Davos ist vorwiegend allogam und selbstinkompatibel. Der Genaustausch ist aber offensichtlich eingeschränkt durch Faktoren, die die Bestäubung, Samenentwicklung und Samenverbreitung beeinflussen. Dolomit- und Serpentinpflanzen weisen eine deutliche Adaptation an das jeweilige Substrat auf: Sowohl die Samenkeimung wie auch die Sterblichkeit und Entwicklung der Jungpflanzen war in der Klimakammer, im Gewächshaus und in Feldversuchen sehr stark vom Substrat und von der Herkunft beeinflusst.
Biscutella levigata bildet edaphische Rassen auf verschiedenen alpinen Substraten. Daneben wurde noch eine klinale Differenzierung auf Dolomit gefunden. Die Subpopulationen, die in dichtem Dolomitrasen vorkommen, sind klein, die klonalen Einheiten haben eine geringe Dichte, und Keimlinge sind selten. Andererseits sind die Subpopulationen auf Dolomitschutt weiter verbreitet, haben eine hohe Dichte von klonalen Einheiten, und Keimlinge sind häufig. Die Subpopulationen auf intermediären Dolomitflächen stehen dazwischen. Im Gegensatz zum Verbreitungsmuster auf Dolomit ist das demographische Verhalten von B. levigata in allen Serpentinflächen ähnlich, und gleicht demjenigen auf Dolomitschutt.
Zusammenfassend wird noch kurz der Einfluss der Stärke des Genflusses auf die Mikrodifferenzierung diskutiert.