

Introduction

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1. INTRODUCTION

Variation in plants is an expression of adaptation to particular environmental conditions. Differences in gene pool of the population, controlled not only by external but also by physiological isolation mechanisms (e.g. GRANT 1981, WHITE 1978), may represent various degrees of evolutionary divergence.

Speciation in plants is very complex and comprises numerous processes; its course may also vary from one group to another. VALENTINE (1962) distinguished principally between progressive and abrupt speciation; progressive or gradual speciation was defined as a differentiation process taking place by degrees, whereas abrupt speciation was characterised by a sudden change in number or structure of chromosomes. On the other hand, GRANT (1981) distinguished between primary speciation and hybrid speciation, emphasizing the degree of evolutionary divergence rather than the actual speed of evolution. The starting point of the primary speciation is a single genetically polymorphic population, whereas hybrid speciation is preceded by hybridization of two different taxa. Primary speciation is further subdivided into (i) geographical, (ii) quantum, and (iii) sympatric speciation.

The geographical speciation is the best known form of primary speciation. The first step in this process is the formation of local races. The increasing spatial isolation of populations may lead to the formation of geographical races. The beginning of reproductive isolation sets in at this stage. Reproductive isolation mechanisms which develop during the period of spatial isolation of two or more populations enable them to coexist without interbreeding even if they are brought together again. Formation of semi-species and species can be considered as an extension of these processes.

Quantum speciation leads from a local race to a new species, the intermediate stage being a small isolated or semi-isolated peripheral population. The variation-fixing forces in the process are selection and genetic drift, resulting in essential alternations of the genome. Quantum speciation is frequently accompanied by a drastic reduction in the size of the population.

Sympatric speciation so far remains a theoretical possibility (GRANT

1981). It postulates a short pathway from polymorphism to species within one single population by way of disruptive selection, no intermediate stage of racial differentiation being involved. In an ecologically very heterogeneous environment of high selective value, divergence to the species level might take place, especially if a small neighbourhood and/or partly asexual reproduction limit the gene-pool of a given sector of the population.

The genetical polymorphism in plant populations is influenced by various factors, reproductive behaviour and selection being of particular importance. Genetic variability is promoted by an open recombination system and reinforced by a wide dispersal of pollen and seed, but it decreases when selective pressures are strong. Pronounced differences in ecological conditions can lead to a strong differentiation even within a limited area (e.g. ANTONOVICS 1971) and races may be formed rapidly (e.g. WU and ANTONOVICS 1976).

Natural selection is a demographic process. Adaptation may thus be operationally definable in terms of mortality and fecundity, because particular individuals in a given population may show differences in survival and reproduction (ANTONOVICS 1976). Demographic parameters such as e.g. population size, density, and age structure seem to be useful in assessment of ecological and/or genetical differences between as well as within populations.

Plant demography is a rather young discipline issued from zoology; however, there are important differences in demographic behaviour between animals and plants. On account of their sedentary life, populations of plants may in some aspects be easier to study (HARPER 1977). On the other hand, plants may vary enormously in form and size. In plants with extensive clonal growth, identification of genotypes (genets) is sometimes virtually impossible because the clonal units (ramets) may be connected below ground. The seed dormancy may also make the demographic studies quite difficult. The specific aspects of plant life were taken into consideration in some concepts recently proposed in plant demography. For instance, HARPER and WHITE (1974) introduced the term of metapopulation considered as a sum of modules viz. buds, shoots, or leaves; in our opinion, ramets could also be treated as modules.

A correct assessment of age is rather difficult in many plants, herbs being a particularly complex material. Precise life tables have been

established so far only for a few perennial herbs (KERSTER 1968, LEVIN 1973). To deal with these difficulties RABOTNOV (1978) proposed the term of "coenopopulation". RABOTNOV who developed the original idea of PETROVSKII (1961) determined coenopopulation as a sum of specimens representing various age groups per unit area, the buried seeds included.

The classification of RABOTNOV (1978) relates to age-state rather than to the actual chronological age; it is based on four main periods in the life of plants reproducing by seeds:

- 1) The period of primary dormancy when individuals exist as viable seeds under natural conditions.
- 2) The virginal period lasting from germination to flowering.
- 3) The generative period - reproduction by seeds.
- 4) The senile period.

Demographic investigations are usually carried out in permanent plots; however, the methods used are, for the time being, far from being coordinated. For instance, SARUKHAN and HARPER (1973) adapted a pantograph to produce plant distribution maps on the scale of 1:5. TAMM (e.g. 1948, 1972 a,b) used for the same purpose a wire screen of 50 cm by 50 cm. DICKENMANN (1982) located the place of each individual of two Ranunculus taxa in a coordinate grid system. URBANSKA and LANDOLT (1978) showed the distribution pattern of reproducing plants in Cardamine spp. in form of a simplified raster map. The fidelity of such investigations depends e.g. on the size of the fine wire squares or exactness of the pantograph. Frequent controls are necessary in order to recognize all the specimens in the plot studied.

The raw census data serve to calculate recruitment of new plants, deaths, survivorship curves, and depletion curves. Also half lives and mean life expectancy can be estimated (e.g. DEEVEY 1947, HARPER 1967, 1977, 1978). The fate of plants can be followed directly in long-term studies (e.g. TAMM 1948-1972).

Demographic studies in high-altitude ecosystems have not been carried out to date. On account of the extreme life conditions and strong selective pressures occurring in the alpine vegetation belt, an area above the timberline was chosen for the present study.

Development of alpine soils frequently being not much advanced, edaphic factors may promote formation of local races (see e.g. LANDOLT 1971,

URBANSKA and SCHWANK 1980, DICKENMANN 1982). Taxa occurring on various alpine substrata are thus particularly interesting for study of a possible racial differentiation. Biscutella levigata s.str. chosen for the present study, grows in the Swiss Alps on carbonate, serpentine, and sometimes also on acidic silicate. Another reason for choosing Biscutella levigata was its complex reproductive strategy. B. levigata reproduces sexually and also forms ramets from adventitious root buds; the specialized form of clonal growth has a potential for vegetative multiplication, clone fragmentation being enhanced by alpine soil movements.

The classical studies of MANTON (1934, 1937) revealed the existence of diploid, tetraploid, and hexaploid races. The hexaploid race is known from only one locality in Spain. The tetraploid B. levigata s. str. has a continuous distribution throughout the Alps. The diploids form a series of disjunct populations in the lowlands north, east, and south of the Alps and occur as well in the Bernese Oberland (HESS et al. 1977). The geographical and ecological distribution of the diploids and tetraploids, when compared to the geological past of the area, suggests that the lowland diploid populations are relicts of an interglacial flora. The alpine tetraploid B. levigata, on the other hand, occurs in an area that was covered by ice during the last glacial period, and therefore appears to be a post-glacial immigrant (MANTON 1934).

Our preliminary observations (GASSER 1981) revealed that the demographic behaviour of Biscutella levigata occurring in high altitude sites on dolomite and serpentine followed two different patterns. In dolomite grassland the taxon occurred in a low density; on the other hand, a relatively high density was observed on dolomite scree slopes and in open serpentine vegetation (GASSER 1983). Racial differentiation in B. levigata was reflected in the germinating behaviour and in the pattern of seedling establishment, although no differences were observed in the morphological or cytological characteristics (GASSER 1981). The present study deals with further aspects of microdifferentiation and demography in alpine populations on the two substrata.

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