Discussion

Objekttyp: **Chapter**

Zeitschrift: **Veröffentlichungen des Geobotanischen Institutes der Eidg. Tech. Hochschule, Stiftung Rübel, in Zürich**

Band (Jahr): **75 (1981)**

PDF erstellt am: **19.05.2024**

5. Discussion

Based upon short-term phenological data, predictions concerning the future development of a particular species under given conditions are not infallible; the present study shows no consistent behaviour pattern emerging from observations collected through only one growing season. For instance, elimination of the generative phase in *Bromus erectus* and *Buphthalmum salicifolium* turned out to be unfavourable solely for the latter species, the former species remaining apparently undamaged. On the other hand, reproduction by seed in *Aster amellus* and *Pimpinella saxifraga* did not coincide with cutting in mid June but the performance of the former species weakened towards extinction, whereas the latter was not influenced to any great extent by this treatment. Burning in March did not affect any actual aspect of sexual reproduction in *Brachypodium pinnatum* yet proved to be of competitive advantage for this species. The uncertain indicative value of short-term phenological records undoubtedly results from an insufficient knowledge of the competitive abilities of given species as well as their reproductive strategies, balance between sexual and vegetative reproduction being of particular importance. Relationships between life strategies of some species inhabiting calcareous grassland, the communities in which they occur and the way in which the present grazing intensity influences the survival of populations were recently studied in Great Britain by BRADSHAW and DOODY (1978). Some species were found to reproduce solely by seed (e.g. *Draba incana, Polygala amarella, Viola rupestris, Potentilla crantzii, Primula farinosa*), others by seed and vegetative means (e.g. *Viola riviniana*) whereas some species reproduced only vegetatively (e.g. *Carex ericetorum, Gentiana rupestris, Viola rupestris x riviniana*). From the great variety of life strategies exhibited by these species, BRADSHAW and DOODY (1978) concluded that no single overall management would ensure the survival of them all; our present results corroborate these conclusions. The variable behavioural pattern noticed in calcareous grassland apparently also occurs in other ecosystems. Species growing in the herb layer of deciduous woodland reproduce in general by vegetative means (KNIGHT 1964, MORGAN 1971, WIGHAM 1974, PERSSON 1975, HUTCHINS and BARKHAM 1976); however, sexual reproduction was found to be much more important than vegetative reproduction to the success of *Allium ursinum* (ERNST 1979). According to BRAUN-BLANQUET (1964, p. 509), reproduction phenomena such as blossom formation and ripening or fruit are much less important for competition than germination, sprouting, shoot formation, duration of foliage, falling of foliage and regeneration of roots.

The present results support the opinion that sexual vigour and competitive ability are not interdependent (e.g. SUKATSCHEV 1928, SAKAI 1961, 1965, SAKAI and GOTOH 1955, SOLBRIG and SIMPSON 1974). On the other hand, they point out the importance of studies dealing with the reproductive strategies of higher plants (e.g. HARPER and OGDEN 1970, OGDEN 1974, BARKHAM 1980a, b, URBANSKA-WORYTKIEWICS 1980, URBANSKA in press) as well as their regeneration niche (GRUBB 1977).

As long as little is known about the factors controlling the rank of an individual species in a plant community, mid-term phenological records seem to be a promising way of revealing developmental trends as reliably but earlier than traditional relevés. Observations on flowering intensity appear to be of particular interest. The predictive value of our conclusions drawn from mid-term phenological observations obviously could not have been verified directly, the study having been carried out for an insufficient period of time. However, some of the predictions could be partly confirmed by comparing different successional stages of *Mesobrometum* grassland. Mid-term phenological data indicated no management to be a less favourable treatment than cutting in mid June for *Bromus erectus* and *Ranunculus bulbosus*. These conclusions were corroborated by the fact that the above mentioned species either did not occur in later successional stages of the investigated communities or were present there to a much lesser degree than in regularly cut areas.

Evidence that mid-term observations of phenological phenomena are in the long term quite good indicators of habitat alterations also comes from the long-range observations of other authors. Within populations of *Primula veris* monitored over a period of twenty-eight years, TAMM (1972) found the frequency of flowering sharply declining about ten years earlier than the number of plants and thus the cover, due to changing conditions leading to increasing shade and leaf litter fall. WELLS (1972) described a population of *Pulsatilla* *vulgaris* where the percentage of flowering plants decreased quite remarkably after grazing stopped, the most drastic differences (65 vs. 9.3 per cent) appearing in the two first years.

The mid-term development of cover due to changing habitat conditions may sometimes be misleading in the long term. This phenomenon was observed in the course of the present study in *Bromus erectus*, a remarkable increase of cover being recorded in the three years following cessation of cutting; however, observations on communities representing more advanced successional stages showed a decline of cover appearing in the long term. A similar development was reported by WELLS (1972) in his study on the response of a population of *Pulsatilla vulgaris* towards the cessation of grazing: the number of plants increased notably during the first four years after grazing had stopped (90 vs. 849 plants) and decreased only later. However, the long-range development of both species referred to was indicated by a sharp decline in flowering intensity in the first two years following cessation of management.

Evidence that reproductive efficiency may be strongly influenced by stress conditions, has been shown by several authors both by field and laboratory observations. KICKUTH (personal communication 1980), observed in *Phragmites communis* a remarkable negative correlation between nutrient stress and flowering intensity as well as flowering time. LANDOLT et al. (1975) reported a strong positive influence of available nitrogen on the number of flower-heads with *Scabiosa columbaria* and *Scabiosa gramuntia*; at high nitrogen treatments the flowering began on average four to eight days earlier than at low treatments. In *Narcissus pseudonarcissus*, BARKHAM (1980a) found the percentage of shoots producing flowers to be strongly related to growing space. In *Trifolium repens*, stress due to interspecific competition resulted in remarkably reduced productivity and vigour (TURKINGTON et al. 1979). HARPER and OGDEN (1970) reported that plants of *Senecio vulgaris* grown within a limited pot space allocated less of their gross energy budget to seeds than individuals of the same species cultivated in favourable conditions. These few selected examples underline the importance of auto-phenological data in giving a better understanding of relations between plants and their biotic as well as abiotic environment.

The loss of the ability to reproduce by seed, however, does not mean that a population inevitably moves towards extinction. Some plants exhibit an astonishing ability to persist in unfavourable habitats where the conditions seem to be completely unsuitable for the development of seed and seedling establishment but apparently are not severe enough to eradicate the population entirely. This phenomenon has been observed e.g. by AUER (1923) in *Phragmites communis* and more recently by GORHAM (1957) in mire-inhabiting species. SUMMERFIELD (1972) described a population of *Narthecium ossifragum* which persisted in a particular mire site in Cheshire, Great Britain, without seedlings or any flowering individual over a period of at least 70 years. WELLS (1968) observed *Pulsatilla vulgaris* surviving in a no longer grazed, dense *Bromus erectus* sward for 30 years although plants became etiolated and did not flower; they subsequently flowered when the surface was grazed again. The survival ability is apparently related to the clonal growth, a condition that is often found in perennial Angiosperms combined in various proportions with reproduction by seed.

Nevertheless, the lack of sexual reproduction represents a serious handicap from a genetic point of view. Without sexual reproduction, no recombination is generated in a population and changing environmental conditions may lead in the long term to a genetic death preceding the actual disappearance of unfit individuals (GRANT 1963, 1975, URBANSKA in press).

Not only the phenological behaviour of individual species but also that of whole communities was found to be a good indicator of transformations taking place in the environment. The phenological response of whole communities towards habitat alterations proved to be rapid and very marked and to precede by far actual physical changes in the floristic composition of a given vegetation. In the second growing season following cessation of cutting, no actual change of the floristic composition was recognizable, but the June peak value of the number of flowering species had already fallen by about 50 per cent indicating a future physical decline of the small-scale homogeneity of the stand; this suggestion was confirmed by investigating the homogeneity in communities representing various successional stages. The synthetic colour diagrams were found to be clearly distinct from each other in the differently treated plots already in the third year of experimental management; previously they were quite uniform for all surfaces within the separate study areas. Changes in phenological behaviour of whole communities as described above could reasonably be expected; it is highly probable that the phenological rhythm of the whole community changes as well when the phenological behaviour of its individual components is changing.

Different plant communities have repeatedly been observed to show different phenological rhythms (e.g. MARCELLO 1962, TüXEN 1962, BALÁTOVÁ-TULÁČKOVÁ 1971, BOTTLÍKOVÁ 1973, FALIŃSKA 1972, 1973a, b, 1976, NEUHäUSL and NEUHäUSLOVA 1977, KRüSI 1980). For this reason, some authors have used phenological behaviour as a criterion for delimitation of phytosociological units (e.g. ZOLLER 1954, FALIŃSKA 1973a, b, HEJNÝ 1978). Very little work has been done so far using synthetic colour diagrams in the field of vegetation science. Instructive examples were furnished by the studies of FüLLEKRUG (1967, 1969) on three subassociations of the *Melico-Fagetum*, *Arrhenatheretum* and *Gentiano-Koelerietum*. FüLLEKRUG (1969) observed in a regularly cut *Arrhenatheretum* a colour peak occurring in late May whereas in an unused or only irregularly used *Gentiano-Koelerietum* a colour peak appeared in late August; these observations correspond quite well with our results obtained in managed and unmanaged surfaces of *Mesobrometum* communities studied in the present work. Synthetic colour diagrams were also worked out by BALÁTOVÁ-TULÁČKOVÁ (1971) for alluvial meadows in Silesia, by FALIŃSKA (1976) for ten forest communities in the Białowieża National Park and by NEUHäUSL and NEUHäUSLOVA (1977) for *Querco-Populetum* and *Galio-Carpinetum*. Unfortunately, all these authors did not estimate the percentage covered by the flowers but that covered by the whole plants, or referred to another unit, for example the 'degree of flowering of species' (FALIŃSKA 1976). A comparison of their results with the present data was therefore not very conclusive, colour diagrams based upon cover records and not upon phenological ones being of no particular predictive value.

It goes without saying that phenological methods have their limitations. One of the factors influencing the predictive value of phenological phenomena is their rather high sensitivity towards fluctuations in the environment. Even if a plant community is in 'equilibrium' this equilibrium is highly dynamic (RABOTNOV 1974, GRUBB 1977). Side by side with successional (i.e.

directional) changes there are fluctuational ones (e.g. BORNKAMM 1961, 1974, RABOTNOV 1974, BYKOV 1974, KNAPP 1974, KRÜSI 1978), caused by weather conditions and/or due to the intrinsic behaviour pattern of individual species. A good example of annual fluctuations in flowering intensity apparently influenced by meteorological conditions is represented by *Ranunculus bulbosus* studied in the course of the present work. Further information in this subject is provided e.g. by WELLS (1967, 1972) for *Spiranthes spiralis*, by ERNST (1979) for *Allium ursinum* or by BARKHAM (1980b) for *Narcissus pseudonarcissus*. Control plots are thus exceedingly important when using phenological methods, especially in a mid-term study; however, they can obviously fulfil their purpose only as long as the fundamental environmental conditions of the respective sites are fairly comparable. For example, BARKHAM (1980b) reports a negative population response of *Narcissus pseudonarcissus* L. in open sites and a positive response in shaded sites towards mean daily hours of sunshine for the period March - September. Individuals of a given species may apparently respond quite differently to weather variation within two adjacent but contrasting habitats.

In addition, the indicator value of phenological phenomena may be limited by microdifferentiation leading to a possible development of local races. Genetic differentiation within species influenced by various abiotic and biotic factors has been repeatedly observed. It seems that in some cases development of local races may occur over short distances and arise rather rapidly, as exemplified by the few selected data.

Investigating the *Ranunculus montanus* group in the alpine zone of Davos, DICKENMANN (1980) found that on an uniform siliceous substrate a microdifferentiation pattern emerged where diploid *R. grenerianus* (2n = 16) alternated with tetraploid *R. montanus* s.str. (2n = 32) within distances of about 5 to 10 m, exactly following the pattern of local relief. TURKINGTON and HARPER (1979) report microevolution in *Trifolium repens*; in response to diversifying selection pressures exerted by the neighbourhood of different species of grass with quite different seasonal rhythms of growth (*Lolium perenne, Holcus lanatus, Cynosurus cristatus, Agrostis tenuis*) *T. repens* developed four different types. SNAYDON (cited by BRADSHAW et al. 1965) found plants of *Agrostis canina* and *Festuca ovina* growing immediately below a zinc coated fence to be significantly more tolerant to zinc than the plants a few inches away on both sides of the fence.

That microdifferentiation really can occur over a short period of time, was elegantly demonstrated by ANTONOVICS (1978). He found with *Plantago lanceolata* that adaptation can take place within a single generation by screening appropriate individuals from a genetically variable seed pool.

According to MATHER (1953, 1955), development of local races is influenced by disruptive selection. If microdifferentiation occurs in a particular species, the extinction of a given population may be prevented; phenological phenomena may accordingly turn out to be misleading at the species level - at the race level, however, they hold true.

In conclusion, phenological observations can be considered to contribute more information on the structure and function of communities than traditional phytosociological methods. They also indicate transformations taking place in plant communities earlier than traditional relevés, this aspect being particularly important not only in studies on succession or the effect of different treatments but also in conservation management of communities containing threatened rare species. Owing to economic or technical factors, it is not always possible to continue the management by which the communities to be preserved have been created within a reserve of man-made ecosystems. Under such circumstances, early indicators revealing the effect of active conservation management are greatly needed; should the treatment used prove unsuitable for a threatened species, it may be possible to change the management plan in time.

Thus, phenological methods turned out to be a rather promising way to reveal developmental trends in plant communities. They are worthy of promotion.