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Summary

Comparison of alpine meadows on siliceous and on calcareous soils; competition experiments and ecological investigations in the *Nardetum* and the *Seslerietum* near Davos, Switzerland

From 1966 to 1970 alpine meadows on siliceous and on calcareous soils were compared ecologically in the region of Davos. On the Strelaberg (2355 m) near Davos and at Birmensdorf near Zurich germination, transplant and competition experiments were carried out with Nardus stricta, Sesleria coerulea, Carex sempervirens, Sieversia montana, Scabiosa lucida, Gentiana kochiana, G. clusii and some others.

In the chapter "Grundlagen" (p. 12) the terms "decisive" and "independent environmental factors" as well as "environmental factor immediately effective on the plant" are discussed. Competition and the design and interpretation of competition experiments are dealt with on p. 16 to p. 24. It is suggested that a clear distinction be made between the competition factor (= one of the biotic environmental factors) and the competition relationship (= one of the relationships that can exist between organisms or groups of organisms).

In the appendix analogies between organisms and biocoenoses (not phytocoenoses) are mentioned. In the biocoenoses the functional groups of species are considered analogous to the organs in an organism. (p. 139-144).

The comparison between the vegetation on siliceous soil and that on calcareous soil was carried out on 13 pairs of plots having environments as identical as possible. On the siliceous soil homogenous meadows of Nardetum alpigenum and Festucetum halleri (called together Nardetum in this paper) occur, which cover 90% of the soil and which are 5 to 10 cm high. On the calcareous soil the terraced meadows of the Seslerio-Caricetum sempervirentis (Seslerietum) were examined, which on the average cover only 30% of the soil and are 10 to 15 cm high. In this type the vegetation is limited almost exclusively to the frontal surfaces of the terraces, which are covered to 95%. The Nardetum grows in general on an alpine meadow brown-earth (parent rock: gneiss or acid schists), the Seslerietum on a shallow calcareous or dolomitic rendzina.

Results:

- 1. On and in unvegetated calcareous soil the temperature maxima and the exponential mean temperatures (eT) are considerably higher than in the corresponding siliceous soil, the difference in the water content being responsible for this. At the places that are covered with vegetation, however, the maxima and eT are lower in the calcareous than in the siliceous soil, because, where it occurs, vegetation is taller and denser on calcareous soil (p. 56-66).
- 2. The water content is in general considerably higher in the siliceous than in the calcareous soil. The water potential curves of samples of the fine soil fraction taken under vegetation do not differ significantly between soil types. Nevertheless, because of its high stone content, shallowness and greater permeability the calcareous soil is more xeric than the siliceous soil (p. 66-71).
- 3. Figures 8 and 9 give a survey of some soil chemical properties. The following points are noteworthy:
- a. The carbonate content of the Seslerietum-soils is between 2 and 70%. Apparently carbonate plays no important and probably only an indirect role for the formation of the Seslerietum, if the content in the soil is above a certain minimum level (p. 72).

- b. The pH(H₂O) of the calcareous soils is between 6.8 and 7.5, that of siliceous between 4.7 and 5.6. Thus these are not so acid that only strictly "acidophilous" species can grow on them (e.g. no aluminium toxicity) (p. 73 and 80).
- c. The content of readily available phosphate is approximately the same in the two soil types (p. 78).
- d. The content of readily available and reserve potassium are about twice as high in the siliceous than in the calcareous soils (p. 79).
- e. Slight but statistically significant differences exist between the two soil types in the contents of exchangeable potassium and sodium. In the calcareous soils the exchangeable calcium content is 10 to 20 times higher and the exchangeable magnesium content 5 to 10 times higher than in the siliceous soils. The cation exchange capacity is about 1.5 times higher (p. 79).
- f. The base saturation of the siliceous soils is 2 to 18% and that of the calcareous soils 71 to 100% (p. 80).
- 4. In the siliceous soils the nitrogen cycle produces mainly ammonium (\sim 10 kg/ha·year), while in the calcareous soils nitrate is produced exclusively (\sim 20 kg/ha·year). Experiments with 7 species fertilized with ammonium or nitrate showed no clear effect of the nitrogen form on growth (p. 78 and p. 121).
- 5. Germination experiments performed with 15 species in the laboratory and in pots in the field showed no substantial difference between the germination rates on siliceous and on calcareous soil; however, such differences probably exist in the natural environment (drought, solifluction). In the development of young plants considerable differences were noted between the two soils (p. 86-91).
- 6. Transplant experiments in nature showed that Nardus stricta survived on calcareous soil after a period of three years without competition from the Seslerietum-species, but with reduced vitality and without flowering. Sesleria coerulea grew \pm normally on Nardetum-soil without competition, and 50% of the transplanted individuals flowered in the third year (p. 91).
- 7. Cultivation experiments on siliceous and on calcareous soils show that the Nardetum-species Gentiana kochiana can not grow on calcareous soil and that the Seslerietum-species G.clusii grows poorly on siliceous soil. The Seslerietum-species Minuartia verna and Erica carnea (garden form) grow \pm normally on both soils (p. 119-121).
- 8. Carex sempervirens is an important species in both plant communities studied. Cultivation experiments indicate that there is an ecotypic edaphic differentiation (p. 116).
- 9. Four important species were cultivated in monoculture and in mixed culture on siliceous and on calcareous soils fertilized with ammonium or nitrate (see point 4). It is shown that in monoculture the Seslerietum-species Sesleria coerulea and Scabiosa lucida can grow on both soils. The Nardetum-species Nardus stricta and Sieversia montana grow poorly on calcareous soil and eventually die. In mixed culture on siliceous soil Sesleria is eliminated rapidly by Nardus and Scabiosa is eliminated by Sieversia, owing to the competition factor. This is shown by the replacement diagrams and by the relative crowding coefficients of DE WIT (p. 93-115 and fig. 11-22).
- 10. On the basis of these experiments, observations in nature, and published data, the species which in the vegetation table (table 6) have a constancy of $\geq 11\%$ were grouped as follows:

69 species grow in the Nardetum:

- 23 of these cannot grow on calcareous soil; the reasons for this are probably the chemical nature of the soil and the water supply.
- 7 other species grow on calcareous soil as well but not in the *Seslerietum*, the main reason for this is probably the competition factor. At least 4 of these species are polymorphic.

66 species grow in the Seslerietum:

- 7 of these cannot grow on siliceous soil; the reason for this is the chemical nature of the soil. All these species have their distribution center in the *Caricetum firmae*.
- 22 other species grow on siliceous soil as well but not in the *Nardetum*; the main reason for this is the competition factor. At least 3 of these species are polymorphic.

30 of the species mentioned grow both in the *Nardetum* and in the *Seslerietum*. At least 10 of these species are polymorphic.

Some of the 17 polymorphic species have different edaphic ecotypes on the two substrats (p. 131-135).

11. An ecological survey shows that the calcareous soil should be considered a widely distributed extreme habitat.

An explanation is provided for the greater productivity of the Seslerietum than of the Nardetum.

Figure 24 shows the decisive independent environmental factors, factors immediately effective on the plant, the web of interrelationships between these two kinds of factors, and the dependent biotic factors of the *Nardetum* and the *Seslerietum* (p. 126-131).

12. The question: "Which is the main reason for the floristic difference between the *Nardetum* and the *Seslerietum*?" is answered as follows:

The unbalanced ratio between the different ions in the calcareous soil is the combination of factors which, alone or in combination with other factors is responsible for the absence of the greatest number of *Nardetum*-species from the *Seslerietum*.

The competition from the *Nardetum*-species is the factor, always dependent upon other factors, which is responsible for the absence of the greatest number of *Seslerietum*-species from the *Nardetum* (p. 135–138).