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7. ENGLISCHE ZUSAMMENFASSUNGEN DER IM BERICHTS- JAHR 1994 ABGESCHLOSSENEN DISSERTATIONEN

(Summaries of Ph. D. Theses)

GILGEN René. Pflanzensoziologisch-ökologische Untersuchungen an Schlagfluren im schweizerischen Mittelland über Würmmoränen. Veröff. Geobot. Inst. ETH, Stiftung Rübel, Zürich 116, 127 S.

Plantsociological and Ecological Investigations in Woodland Clearings on Moraines of the Last Glacial Period in the Swiss Midlands.

The present study deals with ecological and phytosociological aspects of quite recent woodland clearings. For this purpose, 113 clearings, mostly located on moraines of the last glacial period in the northeastern and eastern part of the Swiss Midlands, were investigated from 1989 till 1992. The syndynamical and syntaxonomical changes of clearing communities were observed. Another main point of interest was the effect of clear cutting on the microclimate and soil characteristics. Furthermore, germinating experiments with soil samples from forests and woodland clearings were performed, in order to examine the seed banks of these stands and to establish their significance for the colonization of new clearings.

Following are the most important results:

- The impact of the clear cut on the microclimate and the characteristics of the soil generally corresponded with the results of earlier investigations. The improved soil conditions (mostly phosphorus and potassium) caused by the release of nutrients on the examined areas seem to last longer than the supposed two or three years. The released nutrients are taken up by well developed clearing vegetation. Parts of the nutrients returned back relatively fast by decomposition of the herbs in spring.

- Phytosociological classification: A separation of the *Epilobion* from the *Atropion* was possible with groups of typical acid soil indicators. The two variants of *Rubus*-communities were apposed to the *Sambuco-Salicion*. The clearing communities on eight sites were unique, characterized by special conditions.

The relevés of the *Epilobion* belong to a *Carex pilulifera*-clearing community (*Senecioni silvatici-Epilobietum angustifolii* Tx. 50), which occurred in three different variants.

Because of mostly optimal site conditions with little competition during colonization, the plant communities of the *Atropion* were usually very rich in species and strongly influenced by random colonization, as well as by the history of the stands. Therefore, on average sites a phytosociological distinction of the *Carex silvatica*-clearing community was difficult. Nevertheless several formations were described.

One of the *Rubus*-communities of the *Sambuco-Salicion* was close to the *Epilobion*, the other to the *Atropion*.

- Syndynamical evaluations were carried out for nine ecological groups and the number of species. They demonstrated the greatest species diversity already in the first or second year of succession.

Maintenance, such as cutting of shrubs and mowing, lead to a further increase in the number of plant species. The distribution pattern of the nine ecological groups was also altered. For the syndynamical interpretations, better results were obtained by the cover of the shrub layer, than by the actual age of the woodland clearings.

- Clearing communities are mostly very rich in species. On the 113 plots studied, 492 plant species were found. The average for the relevés of 50 m² was about 50 species. The whole clearing, with an average area of 2280 m², contained a mean of 81 species. The significance of the species pool in the surrounding areas for the species variety was established: Three times as many species from gardens came up in clearings near towns (Zürich, Bülach).
- The seed bank of the first 10 cm was distinctively different in quality and quantity, both within the plots and between different stands. The average seed pool of two forest soils contained 3'630 seeds per m² in a spruce forest, respectively 4250 seeds per m² in deciduous seedling forests. Four soil samples of woodland clearings, investigated by the same method, reached values between 6390 seeds per m² and about 10'000 seeds per m².
In the clearings, most of the species in the seed bank were also been found in the present vegetation. The seed pool of the clearing contained only a few additional plant species. On the other hand, at least half of the species in the seed bank did not occur in the actual vegetation of the mature forest.
These results indicate the importance of seed banks for the colonization of new stands.
- Woodland clearings are important for nature conservancy, especially in dark age-class forest. Many species with a great necessity for light have the possibility to come up and survive. But in order to improve their dispersal, forest stands with natural stocking should increase.

EGGER Brigitte. *Végétation et stations alpines sur serpentine près de Davos*.
Veröff. Geobot. Inst. ETH, Stiftung Rübel, Zürich, 117, 275 S.
Vegetation and Habitats on Alpine Serpentine near Davos.

This work describes vegetation and habitats of one of the barely studied serpentine outcrops of the Alps and discusses their connection with other serpentines. The 6 km² of augite serpentine of Davos, 47°N/10°E, lie to the east of the ophiolite wreath of the alpine arc. The studied alpine 3.5 km² between 2200 and 2600 m are marked by tourism. At 2400 m, the annual temperature is -2°C, during the 4 vegetation months +4°C, annual precipitations amount to 1200 mm with a maximum in summer. Covered by the pleistocene glaciations, the area has been recognized from 15'000 years on.

Vegetation.

Compared to the surroundings, vegetation is spare, the natural timber line lower, most of the area less than 1% covered, with sparse plants, on raw stony soils. The rare patches of turf lie in stable and fresh colluvial spots and the rare patches of dwarf shrubs on well exposed stable slopes, both on ± brownified alpine ranker. (At subalpine level there are mountain pine thicket and forest, on ± acid brown soil.) Physiognomically the vegetation on carbonates constitutes an intermediate state between those on serpentine and on silicates.

The serpentine shelters 128 vascular species (of which 100 frequent) from the 327 alpine of the region, the silicates 225 (127), the carbonates 187 (143): without own alpine species (but 1 subalpine) serpentine assembles an original combination of species from the region, i.e. 53 ubiquitous, 46 silicoles, 25 carbonaticoles, (4 preferential serpen-tinicoles). None of the proper alpine species of the region which grows well on silicates and on carbonates fails to grow on serpentine.

138 vegetation relevés, with 2 to 47 species, according to floristic differentiation, have been ordered along the great gradient of soil and vegetation development, and classified: (1) debris upper alpine; (2) snow-beds; (3) semi-lawn; (4) sunny debris lower alpine; (5) dwarf herbous heath; (6) heath; (7) lawn. There is a clear floristic and pedochemical threshold between units 1-4 with scattered and discontinuous vegetation and some remarkably constant species, and units 5-7 with developed vegetation, distinguished by the additional presence of the constant lawn, dwarf heath and heath species (units distribution according to topography).

Sparsely colonized spots, a little humid, on basic mineral soil, bear a rather carbonatophile flora; heath, lawn, wet spots with a humous or already acidified upper horizon bear a narrow association of basicophiles and of partly marked acidophiles (typical for serpentines). There is probably a specific rooting in the different horizons and fractions, differing in pH and N form.

The discerned vegetation units can not be assigned to any described phytosociological unit because the singular species which constitute them (there being no species unique to serpentine) find their principal distribution otherwise in associations diverging greatly in habitat and sociology. Given the local character of the relevés, creation of new associations is not proposed.

Davos belongs to the pole of the youngest vegetations on serpentine, from glaciated zones, with few or no taxons of their own or taxons of low-rank, and a visibly restricted biomass. The most related serpentine vegetations are first the alpine ones, e.g. of Oberhalbstein (nearly identical), then the one of Aosta, finally those of Scotland and Scandinavia.

Soils.

The soil sequence of serpentine, free from foreign influence and water saturation, ranges from widespread lithosols to a few \pm brownified alpine ranker. Compared to adjacent sites, pedogenesis is slow. All soils remain skeletal. It is suggested that the poverty in fine earth is due to discordance between the alterability of the rock and of its minerals in the more rapidly dissolved fine fraction. The basic alteration products curb acidification, desaturation remains weak, with Mg largely dominating exchangeable cations. Humification ranges from moder to mull. The sequence fits well in the more general brownification over ferromagnesian silicates rich in clay and poor in quartz, under mull, in cold and temperate climate.

Compared to adjacent silicates and carbonates, serpentine shows an own constellation of pedochemical characteristics at the level of fine earth: as much C N P; unusually high exchangeable Ni and Mg/Ca; as low Ca as on silicates, similar granulosesities; as low K and as high Mg as on carbonates, similar C/N and CEC; the other values either intermediate or as favorable as on one of the substrates.

Augite rock from Davos contains a little more Al and Ca, less Cr and Ni than average serpentine. Soil exchangeable Ca Mg K Ca/Mg fit well among those on serpentine in temperate climate. Relative values found in plants tend to confirm availability assessed in soils.

The great gradient along vegetation development is largely parallel to soil development, from raw to brownified soils, as it shows in the graphs of the similarities based on correspondence analysis of floristic, pedochemical and combined data. C N P K Ca Mg Ca/Mg Scat CEC h+ increase with soil development as well as with stability, colluviality, skeleton alteration, clay content, vegetation cover and number of species, whereas pH, V, skeleton and altitude decrease. With the process of development one witnesses accumulation, growing availability, an improving ratio between just those elements vital to plants that are absent or rare in the rock, partly thanks to effective mineralisation peculiar to mull. These tendencies in the development are almost found again from bottom to top in the soil profiles, which reveal a discreet differentiation of the horizons.

Chemical composition of whole plants.

Comparison between serpentine silicates, carbonates reveals that serpentine has its own status. Whereas N P K C/N and ash content hardly vary between substrates (contrarily to other serpentines) and are very specific to the species, chiefly K, the other elements reflect rather the substrate: on serpentine Ni Cr Co Fe are high (though lower than on other alpine serpentines), Ca/Mg far inferior to 1; on serpentine and silicates Ca and Mo are low, Si high; on serpentine and on carbonates Mg is high, Al P K are relatively low; the remaining microelements reflect the underlying rock. In regard to the rock it is K, then P, which plants on serpentine accumulate the most, whereas Ca and Ca/Mg improvement remains modest.

Silicoles, calcicoles and indifferent species on serpentine tend to differ: with Ca Mg Si, silicoles/calcicoles tend to behave as if they knew best how to limit the elements in excess on their usual substrate; for K P and micronutrients, they tend to recall the composition they have on their usual substrate, reflecting this parent-rock; indifferent species tend to tolerate in their tissues the most unfavourable contents, in excess or in deficiency, possibly through ecotypic adaptation.

Considered in regard to the rock, the alimentation of the studied silicoles/calcicoles seems primarily to turn around a certain necessary amount of K and P, even at the price of absorbing, in \pm forced accompaniment, high rates of Ca Mg Si, according to whichever of these elements predominates in the initial substrate.

Conclusions.

The original response of vegetation to (non-tropical) serpentine is conceived here as a strategy of stress-tolerance. Now the responses to different stresses, such as dryness, nutrient deficiency, heavy and toxic metals, alpine and arctic climate, converge toward a slowing down of life (and of pedogenesis). This multiplicity of stresses on serpentine, to mention only modesty in essential nutrients and excess in elements with toxic tendency, reinforces the vegetation response and leads to the great contrasts between vegetation (and soils) on serpentine and on other substrates. Contrasts, however, less extreme in Davos than on lower sites because of the common stress of alpine climate and of the post-glacial recolonization history. The various stress factors are considered as specific resistances leading to the slowing down of life; this slowing down is the energetic price for adaptations and tolerances, i.e. specializations (to only mention the inherent slow growing rate). Moreover, this slowing down corresponds to an extraordinary knowledge, a unique richness, hidden behind what is easily called the sterility of the serpentine.

RAMSEIER Dieter. Entwicklung und Beurteilung von Ansaatmischungen für Wanderbrachen. Veröff. Geobot. Inst. ETH, Stiftung Rübel, Zürich 118, 134 S.

Development and Assessment of Seed Mixtures for Wandering Fallows.

A "Wanderbrache" (wandering fallow) is a stripe of arable field, 6 to 8 m wide, which remains fallow. Each year, the fallow stripe is moved by half of its width. This system serves to protect rare plant species as well as animals. Wandering fallows also promote beneficial arthropods and improve soil quality. The aim of this thesis was to develop special mixtures of seeds to achieve a high diversity of flora and fauna in such stripes. The mixtures were sown on wandering fallows at 5 experimental sites with 4 replicates each in autumn and in

spring. Comparisons were made on these sown plots, plots without sowing, and plots sown with cut infructescences.

On the 5 wandering fallows (each 242 m² in area), 25 to 65 species grew spontaneously in the first year and 28 to 59 species in the second year (volunteers). 22 of the total 159 spontaneous species are endangered or vulnerable in the particular region according to the Red List of LANDOLT (1991). The number of sown species which established was weakly correlated with the number of spontaneous species.

The rates of establishment of *Agrostemma githago* and *Centaurea cyanus* was two to three times higher on fields sown in October than on fields sown in May, which is typical for segetal flora. However, *Legousia speculum-veneris* established four times better when sown in May than when sown in October.

Most biennial and perennial species established better after sowing in autumn as well. In particular *Pastinaca sativa* established to only 0.7% after spring-sowing but to 24% when sown in autumn. This species produced three times as many seeds per plant and more than 100 times as many seeds per area when sown in autumn compared to spring. Whereas *Achillea millefolium*, *Centaurea jacea* and *Tragopogon orientalis* established better when sown in spring. In general, most species developed more seeds per plant, as well as more seeds per m², when sown in autumn.

Most species have a low establishment rate when transferred by cut infructescences.

In the stripes which are two years old mostly ruderals and meadow species such as *Echium vulgare* and *Pastinaca sativa* were dominant. The rare, annual segetals *Bupleurum rotundifolium*, *Centaurea cyanus*, *Delphinium consolida*, *Legousia speculum-veneris* and *Papaver dubium* nearly disappeared, whereas *Papaver rhoeas* was the only annual with more plants per m² in the second year than in the first year. However, in the second year, *P. rhoeas* produced four times fewer flowers per plant, so that the final seed production per m² was lower in the second year.

Centaurea cyanus had a propagule multiplication factor of 1000, *Agrostemma githago* of 600. This indicates that the system of wandering fallows is a good method to introduce suitable species to arable lands, especially to segetal reserves.

The seed production of the naturally occurring weedy species like *Galium aparine*, *Capsella bursa-pastoris* and *Matricaria chamomilla* was reduced by sowing the developed seed mixture, but not completely suppressed. This competitive effect is stronger in the second year.

The total propagule-biomass produced was always higher when the initial seeds were sown in autumn than in spring: 58-320 g/m² (mean 220 g/m²) versus 28-90 g/m² (mean 69 g/m²) in the first year; and 180-560 g/m² (mean 440 g/m²) versus 96-340 g/m² (mean 180 g/m²) in the second year.

29'000-660'000 propagules m⁻² year⁻¹ were produced on average, though there were no significant differences among treatments or sites.

There was no influence of sowing upon the show area of the pollination units (projection of the biggest diameter to the plane) in the first year but in the second year the show area increased considerably in plots sown with the seed mixtures as compared to the unsown plots.

The evenness based on seed mass increased from the first to the second year. It was lower for sown species than for spontaneous species when the two were looked at separately. Plots with high propagule biomass (> 1000 g/m²) always had a low evenness; whereas plots with a low propagule biomass (< 200 g/m²) had evenness-values ranging from low values to values as high as 30%.

Finally, a seed mixture "o" is proposed which is not only good for wandering fallows but for stationary fallow stripes as well.

MARTI Karin. Zum Standort von *Magnocaricion*-Gesellschaften in der Schweiz (*Caricetum elatae*, *Caricetum paniculatae*, *Caricetum ripariae*, *Caricetum vesicariae*). Veröff. Geobot. Inst. ETH, Stiftung Rübel, Zürich 120, 97 S.

Site Conditions of Magnocaricion Associations in Switzerland (Caricetum elatae, Caricetum paniculatae, Caricetum ripariae, Caricetum vesicariae).

In the present study particular interest is focused on the site conditions of *Magnocaricion* associations which are dominated by *Carex elata*, *Carex paradoxa*, *Carex paniculata* and *Carex riparia*. The associations are: *Caricetum elatae typicum*; *Caricetum elatae comaretosum*, typical variant; *Caricetum elatae comaretosum, Carex paradoxa*-variant; *Caricetum paniculatae*; *Caricetum ripariae*; *Caricetum vesicariae*.

Most of the study sites are situated in Kanton Zürich. Further sites are at the border of the lake of the Reuss (Kanton Aargau), at the southern border of the lake of Neuenburg, and in the Jura.

The phytosociological relevés of the study sites were grouped, first, according to the characteristic and differential species and second, by multivariate analysis.

During the vegetation periods from 1986 to 1988 the ground-water table was monthly measured and water samples were chemically analysed (pH, electrical conductivity, ortho-PO₄, P-tot, NO₃, NH₄, Na, K, Ca, Mg). Soil samples were taken in autumn and chemical analyses were carried out for C_{org}, pH, ortho-PO₄, P-tot, NO₃, NH₄, Na, K, Ca, Mg. Furthermore, the above- and belowground tissue nutrient concentrations (N-tot, P-tot, C_{org}, K, Na, Ca, Mg, Mn, Fe, Cu) of the *Carex* species and their biomass were investigated. The exponential mean temperatures were measured.

A principal component analysis was carried out using the data of the site conditions. Their relation to the vegetation groups was investigated by discriminant and variant analyses.

The study sites show differences in the electrical conductivity and the phosphorus concentrations of the water, the total nitrogen and the organic carbon concentrations and the V-value of the soil. (All studied soils belong to the "Anmoor"-soils.) These differences do not clearly correlate to the vegetation groups.

The vegetation groups formed by multivariate analyses are better differentiated than the vegetation groups formed by characteristic species. In both cases the S-value of the soil is one of the most discriminant factors. Moreover the Mg-concentrations of the soil and the electrical conductivity of the water also play a differential role.

However, the occurrence of these *Magnocaricion* associations at a certain site is not explained by these factors. The uptake of nitrogen and phosphorus by the plants seems to be more important. This is influenced by the periodically high water levels and floodings. The uptake of phosphorus depends on the solubility in the soil, which is related to the water regime. The nitrogen uptake depends on the ability of the plants to use ammonium instead of nitrate. If the plants use only nitrate, the water flow is important. The nitrogen and phosphorus uptake cannot be demonstrated by the water and soil data, but can be seen by the nitrogen and phosphorus concentrations of the plants. *Carex paniculata* has higher average nitrogen and phosphorus concentrations and *Carex riparia* higher average phosphorus concentrations than *Carex elata* and *Carex paradoxa*. For these four *Carex* species the uptake of nitrogen and phosphorus in relation to the water regime is discussed.

The present study demonstrates that the nutrient concentrations of the *Carex* species as well as the site conditions of the studied associations do not differ significantly. Therefore it is proposed to categorise these six associations as one - *Magnocaricetum* - with the possible further sub-division of the dominating *Carex* species.

LEUTHOLD Barbara. Vegetations- und Standortsveränderungen auf von Hochwasser überschlickten Streuwiesen. Veröff. Geobot. Inst. ETH, Stiftung Rübel, Zürich 121, 83 S.

Changes in Vegetation and Site Conditions in Wet Meadows after a Flood.

This study deals with the secondary succession of wet meadows after a flood. The observations were carried out in the delta of the river Reuss in Central Switzerland, which was flooded in August 1987. This area had been examined before the flood for a landscape development plan. The flood deposited silt over the whole area, which was removed from some plots.

Floristic development was observed by means of relevés in permanent plots. In addition, the frequency of eight selected species was registered. Changes in site conditions were monitored by measurements of ground water levels and by chemical analyses of the ground water and the soil.

The main results were:

- The flood improved the situations for species with subterranean runners, i. e. *Phragmites communis*, *Equisetum palustre*, *Juncus articulatus*, *Agrostis gigantea*, and in areas with a medium layer of silt, *Eriophorum angustifolium*, and *Heleocharis uniglumis*. All sedges and orchids, as well as most of the dicotyledones, were repressed at first, but by the end of the field examinations most of these species were able to spread again. A few species, especially some of the orchids, disappeared after the flood. In exchange, other plants were brought in, but most of them couldn't persist.
- The survival of plant communities depended on the depth of the silt layer: The limit for the *Primulo-Schoenetum* was about 5 cm; for the *Ranunculo-Caricetum hostianae* and the *Caricetum davallianae*, about 10 cm; for the *Caricetum elatae* and the *Stachyo-Molinietum*, 10-15 cm; and for the *Valeriana-Filipenduletum*, 20-25 cm.
- Recuperation of the original vegetation was observed only in the plots where the silt layer had been removed, whereas, the original vegetation did not regenerate in the silt covered plots. In the plots with a thick silt layer, a pseudo-secondary-*Phragmitetum* came up.
- As expected, the ground water was on a lower level after the flood. In plots with thick silt layers, the amplitude of the ground water level was greater than in comparable plots with less silt.
- No correlation could be found between changes in vegetation and changes in chemistry of the ground water.
- The analyses showed that the flood did not cause a fertilization. It is assumed that the low content of humus in the silt layer and its low capacity to hold water are the most important factors causing changes in site conditions.

FISCHER Hagen S. Simulation der räumlichen Verteilung von Pflanzengesellschaften auf der Basis von Standortskarten. Dargestellt am Beispiel des MaB-Testgebiets Davos. Veröff. Geobot. Inst. ETH, Stiftung Rübel, Zürich 122, 143 S.

Simulation of the Spacial Distribution of Plant Communities Based on Maps of Site Factors. Investigated in the MaB Test Site Davos.

In order to make quantitative predictions of changes in vegetation on the basis of planned or anticipated changes in the habitat, it is necessary to formalize the dependencies of the vegetation on the habitat by means of a model. In the present work such a model is set up for an area of approx. 100 km² around Davos in the Swiss Alps.

An overview is provided of the climate, geology and the soils in the investigated area. A syntaxonomical overview of all vegetation units and a synoptical table of all phytosociological samples from the area published to date provide a picture of the simulated vegetation.

The available habitat variables in the form of digital grid maps with a resolution of 50 m x 50 m obtained from the Swiss MaB project are discussed in respect of their significance to the simulation of vegetation.

By means of the vegetation model based on a Bayes classifier, it was possible to simulate successfully the distribution of vegetation types in the landscape. The model enables diverse variable types and any distribution functions to be processed. The presumptions for the application of the model, the transferability, and methods for a priori and a posteriori selection of variables are discussed and investigated for the present data set. Vegetation mapping, prediction of scenarios (e.g. climatic warming), and probability maps for individual types of vegetation are introduced as possible applications of the model.

The ecological preference function, which quantitatively describes the ecological amplitude and the optima of the vegetation types, can be derived from the model parameters. The ecological preference function has the advantage that the ecological amplitude does not increase monotonously with the sample size and is not defined by the (untypical) extreme values.

In a second modelling approach, the Bayes classifier is linked with a canonical correspondence analysis. This model is based on metrical soil data and phytosociological samples. It represents a non-linear projection of the ecological space onto the floristic space. A multistage process makes possible the visual control of the simulation.

The data base and the display system developed for this study for representing digital maps on a μ -VAX graphic work station are described in the appendix.

GRAF Frank. Ecology and Sociology of Macromycetes in Snow-beds with *Salix herbacea* L. in the Alpine Valley of Radönt (Grisons, Switzerland). Diss. Bot. 235. J. Cramer, Berlin. 242 S.

Ökologie und Soziologie von Makromyceten in Schneetälchen mit Salix herbacea L. (Krautweide) aus dem alpinen Radönter Tal (Graubünden, Schweiz).

During a three year period (1988-90) macromycetes were investigated and mapped in 13 permanent plots of 50 m² each. The plots were situated in the Valley of Radönt (Grisons, Switzerland) between 2400 and 2500 m. Nine plots were located in snow-bed communities of which six in *Salicetum herbaceae* and three in *Polytrichetum sexangularis* associations. For comparison, one plot each was chosen in closely related plant communities, viz. *Eriophoretum scheuchzeri*, *Oxyrietum digynae*, *Caricetum curvulae* and *Loiseleurio-Cetrarietum*. The plant associations analysis of the 13 plots resulted in 63 phanerogams, 23 mosses, 39 lichens, and one pteridophyte. The evaluation of the weekly recorded field data (in 1988 occasionally also fortnightly) provided the source material for the elu-

cidation of the following mycoecological and mycosociological aspects:

- analysis of the influence of climatic (precipitation, maximum-minimum air temperatures) and edaphic parameters (physical and chemical soil properties) on carpophore phenology and productivity.
- abundance, frequency, dynamics, spatial distribution, and phenology of macromycetes in snow-beds on siliceous rock material, with focus on the species associated with *Salix herbacea*.
- relationships between snow-melting zones (isochiones) and spatial distribution of macromycetes, especially ectomycorrhizal partners associated with *S. herbacea*.
- to check the aptitude of the dwarf willow in connection with ectomycorrhizal partners regarding alpine restoration.

Besides the 35 field trips during winter time to check snow conditions, 47 collecting excursions to the 13 plots took place, lasting one to three days each. As a result, 94 fungal taxa were registered, represented by a total of 26'413 carpophores. Of those, 21'883 individuals were mapped in 10'497 records. The highest diversity was noticed for the Basidiomycetes which constituted 85 species (90%) followed by the Ascomycetes with 7 spp. (8%) and the Gastromycetes and the Myxomycetes with 1 sp. (1%) each. The ectomycorrhiza forming partners of *S. herbacea* were represented by 60 species (64%). The evaluation of the sampled data resulted in the following major characteristics for macromycetes in snow-beds with *S. herbacea*:

- dependence of the start of major carpophore production on a time sequence of minimum temperatures above zero and a slightly positive correlation between the productivity and precipitation.
- one single significant aspect of carpophore productivity with its maximum between the end of August and the beginning of September.
- overwhelming dominance of ectomycorrhizal species in the *Salicetum herbaceae* mostly belonging to the genera *Astrosprina*, *Cortinarius*, *Hebeloma*, *Inocybe*, *Laccaria* and *Russula*.
- absence of typical saprobic (parasitic macromycetes in the *Salicetum herbaceae* except for scattered occurrence of *Entoloma atropellitum* and *Hypholoma myosotidis* and of some moss specific species such as *Galerina* spp. and *Psilocybe* spp.
- relationships between snow (duration of permanent snow covering, melting process, and isochiones), fructification season of the macromycetes, and spatial distribution of selected ectomycorrhizal species.
- a check list of selected macromycetes with indicator function based on mapping cards of spatial distribution and results of soil analyses.

The study of pertinent literature about arctic and alpine macromycetes in Europe which are associated with *S. herbacea* proceeded in 296 species. The comparison with four mycoecological and mycosociological investigations carried out in the Alps resulted in 95 taxa reported from the *Salicetum herbaceae* association of which 60 species were also registered during the present study. As a result of this comparison, 19 species (16 ectomycorrhizal partners of *S. herbacea*) with a significantly higher frequency are proposed as characteristic taxa of the *Salicetum herbaceae*. Furthermore, interspecific association was tested between selected macromycetes resulting also in distinct negative co-occurrences with *Inocybe* spp. as one partner.

Three axenic cultures of potential ectomycorrhizal symbionts (*Cortinarius favrei*, *Hebeloma repandum*, *Hymenogaster saliciphilus*) of *S. herbacea* and sterile and non-sterile seedlings of the dwarf willow have been maintained. Furthermore, successful cutting experiments were carried out with *S. herbacea*. The ectomycorrhizal synthesis between *Hebeloma repandum* and *S. Herbacea* was successful for sterile seedlings and

sterile and non-sterile cuttings of the dwarf willow respectively.

Analysis and comparison between mapping cards of isochiones and ectomycorrhizal macrophytes and soil properties uncovered interesting relationships such as the restriction of *Entoloma alpicola* and *Inocybe lacera* to spots of shortest and longest snow covering, respectively. A selection of the most powerful ectomycorrhizal macromycetes regarding alpine restoration is proposed here. Depending on climatic and edaphic parameters these are the following combinations: *Salix herbacea* with *Cortinarius favrei*, *Entoloma alpicola*, *Hebeloma marginatum*, *H. repandum*, *Hymenogaster saliciphilus*, *Inocybe lacera*, *Laccaria montana*, and *Russula norvegica*.

Furthermore, during the present study two unknown macromycetes were discovered and described. In the case of *Hymenogaster saliciphilus*, it was the first time that in the alpine zone a hypogeous Basidiomycete had been registered associated with *S. herbacea*. *Sclerotinia glacialis* (Ascomycetes, Helotiales) was exclusively found in close association with *Ranunculus glacialis*.

MARTI Roland. Einfluss der Wurzelkonkurrenz auf die Koexistenz von seltenen mit häufigen Pflanzenarten in Trespen-Halbtrockenrasen. Veröff. Geobot. Inst. ETH, Stiftung Rübel, Zürich 123, 147 S.

The Influence of Root Competition on the Coexistence of Sparse and Common Perennials in Two Limestone Grasslands.

Why are so many plant species of low abundance in limestone grasslands, and remain so? What is the role of root competition? The influence of root competition on the diversity and coexistence of plant species was investigated in two limestone grasslands in northern Switzerland. The study sites (Gräte and Emmerberg) are mown meadows, rich in species. The Gräte site was poor in nutrients, while the Emmerberg site was slightly fertilized. The following eight perennial species were chosen for the experiments: *Bromus erectus*, *Dactylis glomerata*, *Salvia pratensis*, *Centaurea jacea*, *Scabiosa columbaria*, *Chrysanthemum leucanthemum*, *Anthyllis vulgaris*, *Primula columnae* (synonym: *Primula veris* ssp. *suaveolens*). Well established individuals of each species were chosen on both sites, 25 individuals as treatment plants and 25 neighbouring individuals as control plants. Additionally, some individuals were planted into nutrient rich soil in an experimental garden. The plants in a circumference of 12-25 cm around the treatment plants (target individuals) were removed to a depth of 2 cm (removal method). Root competition was excluded by a polyethylene-foil (trenching method). The plants were investigated for 3 years.

1. In the swards, the dominant species *Bromus erectus* represented 40% of the above-ground phytomass. *Salvia pratensis* was subdominant. The root/shoot-ratio was $\geq 3:1$ on the Gräte site, and 2:1 on the Emmerberg site. At least 80% of the roots were found in the upper 10 cm of soil. Half of the above-ground phytomass was between 0-10 cm. Thus, the influence of the above-ground competition was minor.
2. The fundamental as well as the realized niches were investigated for the eight species. Surprisingly, the rarely occurring species *Anthyllis vulgaris* and *Primula columnae* proved to be highly adapted to the site and were as competitive as the dominant species *Bromus erectus* and *Salvia pratensis*.
3. After removal of root competition, the increase in reproductive structures was larger than in vegetative ones. The extent of allocation correlated more with growth form

than with absence of competition. In contrast to weak competitors, the flowering-ratio of strong competitors was not affected by the treatment. The shoot density of strong competitors was increased by the treatment, but decreased for weak competitors. Possible reasons for the differences in competitiveness are discussed.

4. On the Gräte site, individuals of dominant species developed 2-5 times more shoots and 5-20 times more flowering units when root competition was prevented. Individuals of weak competitors had 4-17 times as many shoots and 10-770 times as many flowering units.
On the slightly fertilized Emmerberg site, the main differences were to be seen in the vegetative parameters. The individuals of strong competitors developed 4-5 times as many shoots as the control plants. In contrast, individuals of weak competitors had 7-28 times as many shoots in the absence of root competition.
These results show that several species in limestone grasslands are limited by root competition.
5. Climatic extremes influenced the competition of the species investigated. In addition the reaction of the treatment plants differed from that of the control plants. The effect of herbivory or parasitic fungi (e.g. *Epichloë typhina*) was stronger upon treatment than upon control plants though effect is minor compared with that of competition.
6. On the Gräte site, *Salvia pratensis* showed the highest half-life (45 years) and *Anthyllis vulgaris* (2.1 years) the lowest. The species composition is determined by the turnover of individuals.
The plants investigated on the Emmerberg site had half-lives of 4-7 years. Here the significance of root competition was altered since slight fertilization of the site enhances the ability to take up nutrients, whereas the capacity to store nutrients loses its importance.
7. The average number of individuals which die per year for each species was calculated from their half-lives. The results suggest a gap-turnover of only 3.3% of the total area per year on the Gräte site and 9.2% on the Emmerberg site.
8. On the Gräte site, only one out of 10'000-30'000 seeds produced each year of the dominant species or of the strong competitors has to reach the adult stage in order to preserve the species composition. The short-living species or the weak competitors need to bring up one individual out of 600-2'000 seeds.
9. Why do some species occur and remain sparse in the stand? The following description applies to the grasslands investigated: a set matrix of common tussock perennials dominate the site and rather sparse, short-lived gap colonizers occupy in between. Because of the occupation of space and nutrients by long-lived species the role of root competition is mostly passive.
10. In limestone grasslands, root competition is more important for the dominance of matrix species than abiotic site parameters. Dominant species are strong competitors, but competitiveness does not guarantee dominance. Root competition is only one of several influences upon the short-lived gap colonizers. As can be seen from points 1-9, the diversity of site factors is high, none of which is dominant within the stand. This fact as well as the very slow turnover of mature plants in these ecosystems are most crucial for the species diversity in limestone grasslands.
11. The direct vs. indirect and active vs. passive mechanisms of root competition are discussed in a table in chapter 5. The Matrix Model is set in the context of the Evolutionary Stable Strategy, the Mosaic Cycle Concept and the CSR-Model.
12. Causes for the sparseness of many species are discussed in relation to nature conservation. Possibilities for favouring certain species are discussed.

KEEL Andreas. Vegetationskundlich-ökologische Untersuchungen und Bewirtschaftungsexperimente in Halbtrockenwiesen (*Mesobromion*) auf dem Schaffhauser Randen. Veröff. Geobot. Inst. ETH, Stiftung Rübel, Zürich 124, 181 S.

Phytosociological and Ecological Investigations and Experimental Management in Mesobromion Limestone-grassland on the Randen, a Jurassic Mountain in Northern Switzerland.

The phytosociological complex of the Mesobromion limestone grassland (with transitions to the *Arrhenatherion* and the successional stages of both) on the Randen, a Jurassic mountain in the north of Switzerland (canton Schaffhausen), was investigated in this thesis. In the two subregions of Bargaen, Tannbüel, and Merishausen, Gräental, study areas were established and the vegetation patterns of microsites investigated by means of grid vegetation samples of 100 dm² / 1 m² each. These grid relevés served to determine the influence of cutting, burning and no management on the (other) site conditions and the vegetation.

1. The five types of *Mesobromion* described by ZOLLER (1954b) are based on his vegetation samples of 1947/48 and were essentially confirmed by the samples of 1976/77 for this study. The species composition of the vegetation indicated, in general, conditions with more nitrogen (nutrient indicators). It could not be decided if this increase in nitrogen stemmed from the atmosphere and/or if it was due to agriculture or methodical reasons. As a "new" type without management the (more) eutrophic *Mesobrometum*-type with *Inula conyza* was described.
2. Especially species on very oligotrophic areas of dry grassland, which is cut regularly but late in the year, are more threatened than in 1947/48. Species, such as *Crepis alpestris*, *Linum tenuifolium*, *Globularia elongata* and *Hieracium cymosum* as well as many orchids in former oligotrophic meadows showed a sharp decline.
3. Cutting, burning, and no management have different impacts on the vegetation and other site conditions. In this study, they were regarded as impulse donors that influence, together with other sporadically effective, irregular, or cyclic site conditions (dry seasons, disturbance by herbivores, etc.), the vectors of vegetation change on the varying *Mesobromion*-sites.
4. The immigration of copse plants was investigated as an example of a vegetation change easy to trace back. Corresponding to different soil types and conditions of the surrounding area, the comparison of the dynamics on two experimental plots revealed two completely different processes. On subdivisions of the area BG, Bargaen, Tannbüel, the species of pioneer wood appeared within a few years of no management, the most important copse species being *Pinus silvestris*, *Juniperus communis* and *Picea excelsa*. Subsequently, no additional copses, but a 'stabilised' grass stage developed between the wooded parts. On MG, Merishausen, Gräental, however, only a long-standing cover of brushwood developed, *Prunus spinosa* growing into the uncut meadow (which had no management and did not contain any copses) at a rate of about 30 cm/year.
5. When the investigation area BM was cut again, the nitrogen content of its soil did not differ from that of a second area that was still without management. On the burnt area, the nitrogen content available to plants increased slightly with a corresponding rise in the number of nutrient indicating species.

6. The fire temperatures in similar experiments in *Mesobrometum*-sites were largely confirmed. Maximum temperatures of up to 640°C were measured a few millimeters above the soil surface. Hot headwind fires nearly completely destroyed the green plant parts above ground. Fires in the wind direction entailed less high temperatures and the formation of a mosaic of damaged and undamaged living plant parts. Air-dried litter quantities of less than 100 g/m² could not be burnt.
7. The production of biomass varies depending on varying annual weather conditions and on the site. Areas without management "produced" the highest amount of biomass, cut areas contained little biomass; and burnt areas ranged inbetween. Despite the low productivity of the sites at the start, the regular annual cut in late summer resulted in a decrease of surface biomass formation.
8. On the investigation site BM, Barga, Tannbüel, the annual amount of nitrogen available to plants was supposed to be 1.5-3 g/m². The late summer cut withdrew about 1.55-3.55 g N/m² and 0.12-0.37 g P/m². On the other hand, when the area was burnt by means of medium and hot fires in the spring, the total amount of phosphor and about one third of the nitrogen remained in the ashes.
9. The grid vegetation samples involved a great deal of work; however, they provided a good short-term impression of the dispersal pattern of the species in an area and already gave indications of each species' behaviour and of vectors of vegetation fluctuations after a few years. In this thesis, 26 distribution patterns (three annual sequences each) of 22 species are shown by way of examples.
10. Homogeneity and stability of a vegetation are integrative qualities. Homogeneous and inhomogeneous, stable and unstable species distribution patterns superimposed each other.
11. The grid vegetation samples gave evidence that some species behave equally on all investigated, similar *Mesobrometum*-sites; other species, however, vary in their behaviour on these sites. The course of weather conditions, dry seasons in particular, essentially modify the conditions of a site. The litter layer, on the contrary, reduces the negative effects of dry periods and insolation. For example the new establishment of seedlings of many species was enhanced or reduced depending on the density of the litter layer.
12. A change in the management (from cutting to no management or vice versa) caused no short-term disappearance of species; neither was the establishment of new species, unknown to the investigation area, registered.
Cutting (especially at the end of the vegetation period) and no management induced little short-term changes to the composition of the vegetation on the investigated areas. Especially the very dry oligotrophic investigation areas ML und BL, which are exposed to strong insolation, reacted slowly. Faster changes were recorded on the mesic investigation area BS.
13. Burning had strong short-term effects on the composition of the vegetation. Particularly species with hibernating parts, which lie just below or above the soil surface, were concerned: especially the moss layer, seedlings, and young plants, as well as rosette-hemicryptophytes (except *Primula veris*). As a whole, there was not a considerable decline of species in the first years.
14. The relative high number of species in a *Mesobrometum* can be explained as follows: If site conditions vary and particularly if a differentiation into niches of a small size can be found, many species will establish. The restriction of dominance of any possible competitive (high-growing) plants by oligotrophy, dryness, cutting, etc. enables many stress-resistant individuals to hold out, particularly as long as they are small young plants that receive sufficient light, and to wait for conditions that favour

their growth and fructification. The (cyclic) variability and certain chance factors of some environmental influences makes it impossible for a plant to develop a best-adapted behaviour to all microsites and at all times.

JEKER Marianne. Taxonomische und phytochemische Untersuchungen in der Gattung *Betonica* L. Veröff. Geobot. Inst. ETH, Stiftung Rübel, Zürich. (In Vorbereitung).

Taxonomical and Phytochemical Investigations in the Genus Betonica L.

In the present study, taxonomical and phytochemical investigations were carried out on the European species *Betonica* L.

Plant material (43 populations) was collected in Russia, Greece, Albania, former Yugoslavia, Austria, Italy, France, Spain, and Switzerland and cultivated in Switzerland.

Botany

Of each of the 43 cultivated populations, 100 leaves, calyces, corollae, as well as nutlets were pressed and measured. The great amount of recorded data was evaluated statistically, whereby descriptive, uni- and multivariate statistics were applied. Five distinct groups can be separated by means of multivariate analysis: *B. officinalis* s.l., *B. alopecuros* s.l., *B. scardica*, *B. hirsuta*, and *B. grandiflora*.

The univariate analysis gives evidence for division of the taxon *B. officinalis* s.l. into *B. officinalis* s.str., *B. haussknechtii*, *B. serotina*, and *B. stricta*; and the taxon *B. alopecuros* s.l. into *B. alopecuros* s.str., *B. jacquinii*, and *B. divulsa*. Additional morphological investigations

of a great number of voucher specimens were useful for diagnosis and a synoptic key.

About 1400 crossing experiments were carried out with the morphologically well defined taxa, *B. alopecuros* s.l., *B. officinalis* s.str., *B. scardica*, and *B. hirsuta*. The results of the crossing experiments showed that the species investigated are crossable. Only 1% of the seeds have germinated so far.

Chemistry

The first section describes the isolation of compounds from Herba *Betonicae officinalis* by Craig distribution, gel-chromatography, and middle-pressure reversed-phase chromatography. The second section deals with the structure elucidation of the isolated compounds (UV/VIS-spectroscopy with Shift reagent, melting point, IR, FAB-MS, and NMR spectroscopy; 1D-experiments; ¹H- and ¹³C-NMR, 2D-experiments, ¹H-¹H-COSY and ¹H-¹³C-COSY).

The following compounds were new to literature:

- (1R*,4αR*,7αS*)-4-[(β-D-Allopyranosyl)oxy]-1-[(β-D-glucopyranosyl)oxy] 4α,6,7,7α -tetrahydrocyclopenta[c]pyran-5(1H)-one (allobetonoside, main compound)
- 6-O-acetylmioyroside,
- Veratroyl-O-β-D-apiofuranosyl(1''-6')-O-β-D-glucopyranoside

Other compounds isolated and elucidated by spectroscopic methods from Herba *Betonicae officinalis* for the first time are:

- the iridoids acetylharpagide and reptoside

The following compounds are new to the literature:

- (*1R*,4 α R*,7 α S**)-4-[(β -D-Allopyranosyl)oxy]-1-[(β -D-glucopyranosyl)oxy]-4 α ,6,7,7 α -tetrahydrocyclopenta[*c*]pyran-5(1H)-one (allobetonoside, main compound)
- 6-O-acetylmiospyroside,
- Veratroyl-O- β -D-apiofuranosyl(1''-6')-O- β -D-glucopyranoside

Other compounds isolated and elucidated by spectroscopic methods from Herba *Betonicae officinalis* for the first time are:

- the iridoids acetylharpagide and reptoside
- the phenylpropanoidglycosides forsythoside B and acteoside
- the amino acid L-tryptophane

According to our chemotaxonomical investigations, the group of *Betonica officinalis* shows a homogeneous, chromatographic pattern. In most of the species, the iridoids, allobetonoside, 6'-O-acetylmiosporoside, and acetylharpagide, and the cinnamoic acid derivatives forsythoside B and acteoside can be detected. For differentiation within the group of *Betonica* other criteria than chemical ones must be considered. The HPLC analyses however, show considerable chemical differences in the flavonoid and iridoid pattern to the *Stachys recta*-group.

Botanical tests

In conspicuous contrast to present days, the roots and shoots of *B. officinalis* L., once enjoyed a high medicinal reputation. In the last section of the present study, biological experiments are described which were carried out in order to characterize the biological activity of the crude extract. There was no sedative effect. A slight calcium-antagonistic activity and antibacterial effects, however, were detected.
