

Summaries of diploma and PhD theses (1997)

Objekttyp: **Group**

Zeitschrift: **Bulletin of the Geobotanical Institute ETH**

Band (Jahr): **64 (1998)**

PDF erstellt am: **21.05.2024**

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Summaries of diploma and PhD theses (1997)

Diploma theses (19)

Genetic variation in tissue density, growth-rate and turnover of *Dactylis glomerata* L. ecotypes

Genetische Variabilität von Gewebedichte, Wachstumsrate, und Turnover bei Dactylis glomerata L. Oekotypen; 32 pp.

URS AESCHLIMANN

1 Species from nutrient-rich habitats with a high maximal relative growth rate (*RGR*) have a low tissue density which helps to maximise resource acquisition. Slow growing species from low-productive habitats have a higher tissue density resulting in longer organ life-spans and reduced loss rates. These results have been obtained from interspecific comparisons among ecologically contrasting species. In the present study the relationships between tissue density, *RGR* and turnover were investigated with respect to ecotypic variation within one species. The aim was to assess whether tissue density shows a similar association with *RGR* and turnover in a microevolutionary context as it does in interspecific comparisons.

2 A growth analysis of 22 European ecotypes of *Dactylis glomerata* was conducted in growth chambers; for each ecotype *RGR* and tissue

density were investigated. Turnover was determined in a garden experiment.

3 Ecotypes differed in *RGR* and tissue density. There was a negative correlation between leaf tissue density and *RGR*. Relative growth rate was also negatively correlated with stem tissue density, and with root tissue density when the proportion of coarse roots was included. Ecotypes with a dense tissue had a lower specific root length. Northern ecotypes had a lower tissue density and higher *RGR* than the southern ones.

4 Due to pathogens and mortality in winter the results of the turnover-experiment were not conclusive.

5 The role of tissue density in determining the capacity for resource acquisition and *RGR* is confirmed by the present study. Low tissue density leads to high *RGR* not only in an interspecific comparison but also among ecotypes within a species.

Investigations on *Trollius*-*Chiastocheta* interaction in small and isolated plant populations

Untersuchungen zur Trollius-Chiastocheta-Interaktion in kleinen, isolierten Pflanzenpopulationen; 37 pp.

MARTIN BRATTELER

1 *Trollius europaeus* L. (Ranunculaceae) is exclusively pollinated by flies of the genus *Chiastocheta* Pokorny (Diptera: Antho-

myiidae) whose only larval host is this plant. Based on previous investigations in large populations it was supposed that *T. europaeus* is

self-incompatible and an obligate outcrosser. The objective of the thesis was to investigate whether *Chiastocheta* flies do not visit small, isolated populations of *T. europaeus*, and whether *T. europaeus* may be autogamous.

2 To test for autogamy, 15 flowers in 16 different populations of *T. europaeus* were bagged in spring 1997 for four weeks. As controls, 20 naturally pollinated flowers per population were collected. In four populations, 20 flowers each were emasculated, bagged and cross-pollinated by hand after seven days. This experiment was conducted to exclude the influence of own pollen on seed set. Seed production per carpel and treatment was estimated.

3 The bagging experiment showed that on average one fertile seed per carpel is produced by autogamy. The differences among individuals revealed that genotypic variation exists for self-incompatibility. At least partly autogamous individuals thus occur, although in small frequency. A higher rate of self-compatibility in small or lowland populations was not observed. *Trollius europaeus* populations without *Chiastocheta* were found.

4 Ten *Chiastocheta* males in each population were collected to improve the knowledge about the number of *Chiastocheta* species occurring in Switzerland. Since a proper identi-

fication of the fly species is only possible by comparing the male genitalia, exclusively male flies ($n = 56$) were sampled.

5 The identification of the flies revealed six different species: *Chiastocheta dentifera*, *C. lophota*, *C. macropyga*, *C. rotundiventris*, *C. setifera* and *C. trollii*, although prior to this study, only three species were known from Switzerland. Six *Chiastocheta* species out of eight known in Europe have been identified. In a single population, although four *Chiastocheta* species were found at the most it is very likely that all six species occur in one population.

6 How can *T. europaeus* populations survive if *Chiastocheta* is absent? This study supports the hypothesis that autogamy is one possibility. However, because of inbreeding depression autogamy as main alternative to allogamy is probably out of question. The only possibility for the plant in the absence of *Chiastocheta* is thus to attract alternative pollinators.

7 Regarding the results of the bagging experiments, *T. europaeus* can be described as partly self-compatible. Other insects than *Chiastocheta*, visiting flowers of *T. europaeus* were observed. Further investigations are necessary to assess the role of these insects as alternative pollinators of *T. europaeus*.

Aspects of the transmission mode of *Epichloë sylvatica* and the influence of the endophyte on growth and germination of the host grass *Brachypodium sylvaticum*

Aspekte der Transmission von Epichloë sylvatica und Einfluss des Endophyten auf das Wachstum und die Keimung des Wirtsgrases Brachypodium sylvaticum; 63 pp.

DOMINIK BREM

1 *Epichloë* endophytes (Clavicipitales, Ascomycetes) are mutualistic symbionts of many grasses. In *Brachypodium sylvaticum*, a common woodland grass, the infection rate is usually 100%. Transmission of the endophyte is either horizontal by sexual asco-

spores formed on stromata, or vertical through infected seeds. This study investigated, whether endophyte infection has an impact on parameters of the host fitness of *B. sylvaticum*. Additionally, aspects of the horizontal transmission of the endophyte,

and of the population dynamics of the host grass were examined.

2 Germination and growth experiments were conducted in the laboratory and in a greenhouse with seeds from four populations and half-sib seeds collected from two selected motherplants. To determine whether horizontal transmission of the endophyte occurs, uninfected seedlings were planted into natural populations of the host grass. Four populations with stromata were monitored for a possible coincidence of mature ascospore producing stromata and the flowering time of the grass. Aspects of the population dynamics of the grass were examined in small areas (1 m²) within eight populations of the host grass.

3 Results of the growth experiments were ambiguous. Infected seeds of *B. sylvaticum* exhibited a significantly higher germination rate and infected seedlings had longer leaves and more fresh weight ten days after germination than those of uninfected seeds. However, after four months of growth the above-ground biomass of infected individuals was reduced compared to that of uninfected plants. No effect of the endophyte could be detected on the tillering rate of the grass. New infections by the endophyte were recorded in three (1.8%) of 172 previously uninfected seedlings. None of the plants flowered by the time of the control. In

the examined stromata forming populations the flowering of the host grass and mature stromata coincided. Death of host grasses and recruitment of new plants by seedling establishment were low in natural populations.

4 Data of growth and germination experiments provide evidence that the interaction between endophyte and grass is mutualistic in the early stage of grass development. On the other hand, the significantly lower biomass produced by infected adult plants suggests a fitness disadvantage. The three new infections by the endophyte indicate that horizontal transmission is effective. Loss of seeds due to stroma forming of the endophyte which leads to abortion of grass inflorescences does not seem critical for the maintenance of *B. sylvaticum* populations.

5 Because of the high infection rate of *B. sylvaticum*, we had assumed that the association would be mutualistic. Nevertheless, growth experiments support this hypothesis only partly. Other parameters that are relevant for host fitness (herbivory, competition, seed-yield) might be more important. The study shows that infection under natural conditions does not only occur through entering stigmata as generally assumed. Further investigations dealing with the horizontal transmission mode of endophytes will be of great importance.

Interaction of pathogen infection and stressful environments on plant growth, disease expression and reproduction. An experimental study with *Albugo candida* inoculation on low light tolerant and unselected control plants of *Sinapis arvensis*

Interaktion von Pathogeninfektion und Umweltstress in Bezug auf Pflanzenwachstum, Pathogenexpression und Reproduktion. Eine experimentelle Untersuchung mit Albugo candida auf schattentoleranten und unselektierten Sinapis arvensis; 61 pp.

INEZ COLYN

1 This research project challenges Grime's (1977) C-S-R theory of three distinctive life history strategies in plants (C, competitive; S,

stress-tolerant; R, ruderal). The work focuses on two alternative hypotheses: if the strict definitions of the C-S-R model apply, then

the existence of a distinct stress-tolerant strategy requires genetic trade-offs between stress tolerance and biotic stresses such as pathogens. Plants which have adapted to abiotic stresses should thus be less tolerant of pathogen attack. Alternatively, if there is no difference in the response to abiotic and biotic stress, then plants that are tolerant of an abiotic stress should also be more able to tolerate infection better, and the C-S-R model may be flawed in its assumptions.

2 A pilot study with 200 unselected *Sinapis arvensis* plants tested inoculation techniques with *Albugo candida* and the importance of host growth stage for inoculation. The pilot experiment was terminated at the stage of seed set when plants were collected and dried. The main experiment consisted of plants that had been selected to tolerate a low light environment, and unselected controls. They were grown in a split-plot design with block structure. Each plot received either a high or a low light treatment (with shade cages) and was either inoculated with the pathogen *Albugo candida* or kept as control plot. Data on growth rates and disease induced by fungal infection were analysed for interactions between the selection history of the plants and the treatments.

3 Light and infection strongly influenced growth rates: cotyledons and leaves developed faster in the shade. In full light, infected leaves grew slightly slower than uninfected

ones, in shade infected leaves grew faster than infected ones.

4 Selection history influenced stem growth and the rate of increase in leaf number. In the shade, selected and control plants performed similarly, whereas under near optimum conditions, low light tolerant plants showed a lower stem growth rate and a trend towards fewer leaves. Thus stress-selected plants seem to expend the same amount of metabolic energy to withstand low light stress as controls but they are less effective under normal conditions.

5 We found no significant interaction of selection history and infection on any of the growth traits, nor any difference in lesion size or reproduction of the fungus between selected or unselected plants.

6 Genetic variation determined a part of the responses to infection and low light in each of the growth traits, such as stem, leaf, and relative cotyledon growth. However, no significant genetic effects were found for lesion size or scores of fungal sporulation.

7 The pilot experiment showed that infection at the cotyledon stage delayed the time of flowering, reduced the number of fruits and dry shoot weight. Inoculation at the seedling stage proved to be most devastating for fitness components.

8 So far, these results do not confirm the hypothesis of a generalised tolerance to abiotic and biotic stress. As the pilot study indicates, full information on fitness effects should be considered before rejecting our hypothesis.

Effects of management

on decomposition processes in a limestone grassland near Merishausen (SH)

Einfluss der Bewirtschaftung auf Abbauprozesse in Trespen-Halbtrockenrasen bei Merishausen (SH); 55 pp.

LADINA FILLI

1 Effects of management on species composition and vegetation structure of a limestone

grassland near Merishausen (SH) have been described in many studies, whereas effects on

soil processes have rarely been considered. In a preliminary examination in autumn 1994 slightly different nitrogen mineralization rates in the upper soil were found between plots of different management regimes. This study deals with the effects of different management regimes on decomposition rates.

2 For this reason four management regimes were chosen: cut in July every or every 2nd year, annual burn in spring and abandonment. Experiments were always done on three replicate plots. Aboveground phytomass was determined in autumn 1996 by clipping the vegetation of four quadrats of 50 cm x 50 cm per plot. Decomposition rates on the soil surface were studied using litter bags with plant material from unmanaged plots, while those in the upper soil were measured using cotton strips. During the cotton strip experiment mean exponential temperatures were measured using the "sugar inversion method" and water contents were measured on single days using the TDR (time domain reflectometry) method. Separate decomposition experiments were performed with plant material from annual cut, burned and unmanaged plots and with some of the dominant plant species.

3 The cutting regime affects the amount of aboveground phytomass and their composition. Phytomass was highest in the unmanaged and burned plots and diminished

with increasing frequency of cutting. Plant material from unmanaged plots decomposed more slowly than that of burned and especially that of annually cut plots. Plant material from *Bromus erectus*, *Brachypodium pinnatum* and *Trifolium medium* decomposed faster than that from *Prunella grandiflora* and *Salvia pratensis*.

4 The cutting regime also affects decomposition rates on the soil surface, where plant material from unmanaged plots decomposed significantly faster on unmanaged plots than on others. Probably, the thick litter cover of these plots causes favourable microclimatic conditions for decomposition, but possible effects of faster colonization by an adapted microflora and fauna cannot be neglected. In contrast, decomposition rates of cellulose in the upper soil were not different between the plots, although slightly different water contents and significant different mean exponential temperatures were found. The heterogeneity between plots may prevail possible effects of management.

5 The effect of management on decomposition rates cannot be finally assessed. Studies with plant material from the different management regimes or with an external source of organic material should be carried out to examine whether site conditions are indeed different.

The influence of plant diversity on plant diseases and herbivore damage in experimental plant communities

Zum Einfluss der Biodiversität auf Pflanzenkrankheiten und Frassverluste durch Herbivore in experimentellen Pflanzengesellschaften; 59 pp.

FERNANDE GÄCHTER

1 To determine how plant diversity affects the abundance of herbivores and pathogens I recorded damage in plots of different plant species diversity (1, 2, 4, 8, 32 spp.) in a large

field experiment established by Bernhard Schmid's group (Universities Zürich and Basel) at Lupsingen, Switzerland. I focused on two target plants, the monocot *Dactylis*

glomerata, and the dicot *Taraxacum officinale*.

2 Theory suggests that disease should be more common where biodiversity is lower, because the effective host density is correspondingly higher. The data showed that of the six symptoms of disease or herbivory studied, four were more common in the lower diversity plots (in agreement with theory), but the other two were more common in the higher-diversity plots (violating the theoretical predictions). As expected from agricultural experience, rust fungi on *Dactylis* followed the predicted pattern, with more disease in monocultures and less in mixtures. There are several possible explanations why other symptoms, such as stripe disease, were more common in the higher diversity plots. Specialist herbivores and pathogens would have greater opportunity to increase in monocultures, whereas generalists, or species dependent on more than one host, would perform better in diverse plots. Environmental

factors may have also played a role, for example, in high diversity plots humidity may be higher due to increased cover and shading.

3 In a smaller experiment, separately conducted at the same field site, a reciprocal transplant of *Dactylis* from eight European countries was investigated. The expectation was that locally adapted plants from the study site should be less infected than foreign ecotypes. Contrary to expectation, no statistically significant difference in disease or herbivore damage was found among these ecotypes. Nor was there a significant relationship between disease severity and distance of their origin. However, these findings must be taken as tentative because the sample size was rather small.

4 The results of this study suggest that the relationship between plant pathogens, herbivores and host plant diversity is complex. Further investigations of natural plant communities are needed for more detailed insight into the interactions between host diversity and attack by natural enemies.

Growth experiments on soils of differently managed limestone grassland near Merishausen (SH)

Wachstumsversuche mit Böden verschieden bewirtschafteter Trespen-Halbtrockenrasen bei Merishausen (SH); 49 pp.

ANDREINA GERSTER

1 It was investigated whether different management types (since 20 years) of limestone grassland plots near Merishausen (SH) do not only cause differences in vegetation but also in soil conditions, which, in turn, might influence vegetation. The following management types were compared: annual mowing in July (traditional management), respectively in October, mowing every second year in July, annual controlled burning in February, and abandonment. A bioassay was performed with topsoil (-1 to -6 cm) taken from the three

replicate plots of each treatment in April 1997. In pots in the greenhouse, growth of the following species, grown from seeds collected in the plots, was measured after five, respectively twelve weeks: *Arabis hirsuta* (L.) Scop., *Plantago lanceolata* L., *Bromus erectus* Huds., and *Dactylis glomerata* L. Additionally, P-content as well as N-accumulation in the soil in bare pots were measured after six weeks in the greenhouse.

2 In general, plant growth was low (shoot dry weight after twelve weeks: *A. hirsuta* 3 mg, *P.*

lanceolata 24 mg, *B. erectus* 20 mg, and *D. glomerata* 11 mg) and did not vary significantly among the different management types. However, all species consistently showed the lowest growth on soil of the plots annually mown in July. The low growth on this soil is probably due to the large nutrient exports with this management.

3 There was no correlation of plant growth with nitrate and ammonia accumulation, nor with the phosphate content of the soils. That growth did not correlate with the soil nutrients is a frequent phenomenon of bioassays and could also have methodical causes.

4 The differences in plant growth between the three replicate soils of one treatment were relatively small for plots with annual mowing in July or in October, and relatively large for

the other treatments. Thus, the management which differs only slightly from the traditional management shows only a small between plot heterogeneity in soils (and also in vegetation). The opposite holds true for the plots with treatments very different from the traditional management. Additionally, the differences among the plots of a single management can possibly be due to the heterogeneity of the whole experimental area.

5 Overall, even 20 years of different management caused only slight and probably reversible differences in soil characteristics. Thus, if the traditional management, i.e. annual mowing in July, is taken up again, a regeneration of typical limestone grassland will probably not be hindered by changed soil characteristics.

Species composition and N-cycle of fen meadows influenced by spreading reed

Artenzusammensetzung und Stickstoffhaushalt von verschilften Feuchtgebieten; 82 pp.

BEAT HAUENSTEIN

1 A spread of common reed (*Phragmites communis*) is presently observed in many Swiss fen meadows. This spread is undesirable because it is expected to reduce species diversity. Moreover, evidence from wastewater treatment plants, where the presence of *Phragmites* accelerates nutrient cycles, suggests that the soil nitrogen availability might be increased by a spread of this species.

2 To test these assumptions, the impact of *Phragmites* on nitrogen mineralisation was investigated in three fen meadows near Zurich in the Swiss Midlands. Mineralisation rates were studied in eight blocks of three plots. Two of the plots were located in parts of the sites in which *Phragmites* was abundant. In one of them all *Phragmites* shoots were regularly cut off and removed. The third plot, in which *Phragmites* was naturally sparse or ab-

sent, was situated at a distance of 10–15 m. From April to July 1997, the soil nitrogen mineralisation rates during three one-month periods was determined by *in-situ* incubation. Additionally, the abundance of *Phragmites* (shoot number and percentage cover), the soil water content, the effective soil temperature, the groundwater level and the available nitrogen and phosphorus concentrations were measured. Vegetation relevés were made using the Braun-Blanquet method.

3 The nitrogen accumulation during the incubation was negative in most cases. The N-mineralisation rates differed among sites (ANOVA, $P < 0.05$), but not among treatments, i.e. it was not affected by the presence of *Phragmites*. From May to July mineralisation rates depended on soil temperature and soil water content (multiple regressions, $P <$

0.001). The abundance of *Phragmites* was neither related to the groundwater level, nor to phosphorus availability. An ordination of the vegetation relevés revealed no treatment effects on species composition.

4 The negative mineralisation rates were probably due to the uptake and immobilisation of the mineralised nitrogen by microorganisms, as well as to denitrification. The absence of correlations between N-mineralisation and soil temperature or soil water content suggests that belowground factors, which

were not measured in this study, influenced mineralisation rates more than shading by *Phragmites*.

5 An impact of *Phragmites* on the nutrient availability could not be detected. It is, however, possible that *Phragmites* affects the nutrient availability on a long term by changing the soil structure. Areas in which the abundance of reed is increasing, should be monitored, because negative effects on vegetation might become apparent only after a longer time.

A GIS-based model of soil erosion using the Universal Soil Loss Equation (USLE) for the catchment of Anjeni (W-Ethiopia)

GIS-gestützte Erosionsmodellierung mit der Universal Soil Loss Equation (USLE) im Einzugsgebiet von Anjeni (West-Äthiopien); 113 pp.

ANDREAS HEINIMANN

1 In the last decades soil erosion has developed to a major threat for the natural resources and the living base of millions of people in the highlands of Ethiopia. The Soil Conservation Research Project (SCRCP), which was founded in 1981 by the Geographic Institute of the University of Bern in collaboration with the Ethiopian Ministry of Agriculture, investigates the problem of soil erosion in Ethiopia. The study area of Anjeni is one of six research units of the SCRCP in Ethiopia where soil erosion relevant data have been collected for the last twelve years. Based on these data the amount and the spatial distribution of soil loss in the catchment of Anjeni were modelled.

2 As erosion model a form of the Universal Soil Loss Equation (USLE) adapted to the Ethiopian conditions was chosen. A Geographic Information System (GIS, ARC/INFO) was used as a tool to implement the USLE, and to calculate a Digital Terrain Model (DTM). In a further step different re-

lief-factors relevant for erosion (e.g. slope, curvature, aspect) were extracted from the DTM by a GIS based relief-analysis.

3 The amount and the spatial distribution of soil loss were modelled for two scenarios. In the first the assumption was made that no soil conservation measurements are implemented in the catchment of Anjeni. The second scenario is based on the assumption that all cultivated fields in the catchment are conserved by physical soil conservation structures.

4 As comparative figures to the modelled soil losses different data from the SCRCP measurements in Anjeni were used. On plots of 180 m² each the loss of soil was measured under conserved and unconserved conditions. The comparison of the ratio of the respective soil losses shows a high correspondence to the corresponding modelled ratio (first to second scenario). Even though a direct comparison between the modelled and the total amount soil loss of all fields in the catchment measured at the hydrological station is not possi-

ble, it can be stated that the second scenario gives realistic values.

5 The interpretation of the modelled spatial distribution of soil loss in the catchment of Anjeni has to be done with caution. New publications show that different factors, which are

not integrated in the USLE may have a huge effect on the spatial distribution of soil loss. Despite this it can be stated that the used model gives a fairly good first impression of the amount and spatial distribution of soil loss in the catchment of Anjeni.

Seed dispersal in high-alpine grasslands

Diasporenfall und -eintrag in hochalpinen Standorten; 93 pp.

KATHRIN KOFLER

1 Seed rain was studied in grassland, a machine-graded un-restored ski run and restoration plots at c. 2500 m a.s.l. in the alpine surroundings of Davos (NE Swiss Alps). Dry funnel traps randomly distributed in the study sites were used to assess seed rain and species composition in autumn 1996 and throughout the following growth period 1997. An additional case study was undertaken to obtain more information on the fate of diaspores after their primary deposition; in this study, marked seeds of *Gentiana punctata* were dispersed in five sites and checked up after one month for possible secondary movement.

2 Contrary to expectations, the highest mean density of seed rain (242 ± 89 seeds m^{-2}) was found in the degraded ski run. Seed rain in the studied restoration plots was also rather dense (164 ± 43 seeds m^{-2}). On the other hand, the corresponding value in grassland was surprisingly low (54 ± 21 seeds m^{-2}). The differences among sites were highly significant. Distribution of seeds in the traps was mostly clumped.

3 Seed rain of the un-restored ski run included the highest number of identified species (15). The second highest diversity (11 species) was recorded in the restoration plots. On the other hand, only nine species were identified in the samples from the grassland. The seed rain of the grassland was dominated by one or two species in all three study sites.

4 Most diaspores were produced and deposited *in situ* because virtually all species identified in the seed rain occurred in the standing vegetation of the respective sites as well. A possible deposition of diaspores from outside sources was observed only twice in the ski run. The possible dispersal distances of diaspores were short in most cases.

5 The case study on *G. punctata* revealed that diaspores of this species moved both vertically and horizontally over short distances.

6 In conclusion, the importance of seed rain studies for planning and implementation of restoration above the timberline is discussed.

Relations between relative growth rate, turnover and leaf tissue density in *Dactylis glomerata* L. ecotypes under contrasting light and nutrient availabilities

Beziehung zwischen der relativen Wachstumsrate, dem Turnover und der Blattgewebedichte in Abhängigkeit von Licht und Nährstoffen bei Dactylis glomerata L. Oekotypen; 34 pp.

CHRISTIAN MARFURT

1 Habitats with a low productivity are usually dominated by species with a low relative

growth rate (*RGR*). However, in short-term experiments species from productive sites

with a high inherent *RGR* grow faster even at low nutrient supply. The slow-growing species have a long-term advantage due to their slow tissue turnover and reduced loss rates. Comparative studies among ecologically contrasting species have shown an unchanged ranking of *RGR* under different environmental conditions, which is a result of an association between plant tissue density and the inherent *RGR*. In the present study ecotypic variation in *RGR* and tissue density were studied among different ecotypes of *Dactylis glomerata*. The aim was to assess, whether the ranking of ecotypes with respect to tissue density is influenced by light and nutrient availability, and if ecotypes with low tissue density show faster growth regardless of environmental conditions.

2 Eight ecotypes of *Dactylis glomerata* L. from different parts of Europe were investigated under two light and two nutrient levels in a factorial design. *RGR* and leaf tissue density were measured in a common garden experiment. Since the experiment for the assessment of turnover-rates over two growing sea-

sons was seriously damaged by pathogens and severe frosts, turnover-rates were calculated in a short-term experiment using the ratio of the dead leaves to totally produced leaves.

3 Light and nutrients had a significant influence on *RGR*. Increase in nutrients and decrease in irradiation led to an increased *RGR* in all ecotypes. Tissue density was higher at high irradiation, whereas nutrient supply had no effect. Among all treatments there was a negative correlation between leaf tissue density and *RGR*. The ranking of the ecotypes according to their leaf tissue density remained similar in all treatments. The ranking according to *RGR* was also similar for both nutrient treatments, whereas some differences were observed between the two light treatments.

4 The data about leaf turnover were not conclusive due to experimental problems.

5 The results support the hypothesis that tissue density is an important determinant of *RGR* and that ecotypes with a high inherent *RGR* grow faster regardless of irradiation or nutrient supply.

Archaeobotanical study of vegetal macroremains from Nabataean and Late Roman periods, ez Zantur, Petra, Jordan

Etude archéobotanique de macrorestes végétaux d'époques nabatéenne et romaine tardive, ez Zantur, Pétra, Jordanie; 142 pp.

DANIÈLE MARTINOLI

1 The study deals with the examination of botanical remains unearthed in archaeological excavations of private dwellings in ez Zantur, Petra. The plant remains belong to three periods: ancient Nabataean (~150 to 50 BC), Nabataean (~50 BC to 100 AD) and Late Roman (4th century AD).

2 In total, 4213 carbonized seeds and fruits, included fragments, were recovered during the archaeological campaigns of the Univer-

sity of Basel (1991–1994); 39 taxa were determined.

3 Naked wheat (*Triticum* sp.) and six-rowed hulled barley (*Hordeum vulgare*), lentils (*Lens culinaris*), olives (*Olea europaea*) and grapes (*Vitis vinifera* cf. *vinifera*) were the most numerous plants in the material. The fruits and seeds identified are described and supplemented by photographic pictures.

4 Grapes were found in large quantities in a Nabataean oven. The pressing of grapes and the use of the waste of this processing as fuel is supposed. The grape seeds were biometrically analyzed and attributed to the cultivated subspecies, with some reserve. The use of this method is discussed.

5 The olives were numerous and frequent in all three periods. The assumption of olive oil production and the use of the waste products as fuel is expressed, in correlation with the large amount of fragments coming from ovens and hearths.

6 The botanical material recovered allows conclusions on the assortment of crop plants and some speculations on the fields. The identified taxa are classified in six groups: cereals, cultivated pulses, cultivated fruits, gathered wild fruits, potential ruderals and "others". The alimentary crop plants represent the main material in the three periods. Fruit remains (mainly olives and grapes) of ancient Nabataean time are relatively scarce, they increase considerably in the later periods. This may indicate an intensification of horticulture and/or a larger use of the fruits. The gathered wild fruits, *Pistacia* spp. and *Crataegus* cf. *aronia*, were absent in the late Roman period, implying a deterioration of the local vegetation. The

potential ruderals found in the three periods probably grew in the fields as well as in the natural environment of steppe or desert type. Only two plant species from ancient Nabataean and Nabataean period (*Cynodon dactylon*, *Panicum* cf. *repens*) need moist conditions. The presence of an important number of potential ruderals in the Nabataean samples suggests local cultivation. Typical ruderals of wintercrops (*Lolium typus temulentum*, *Bupleurum* cf. *lancifolium*) have been found at the same period. There is no botanical evidence for irrigation in the material of the three periods. At the Nabataean and late Roman periods, two plants of other origin (*Acacia* spp. and *Chenopodiaceae*) have been found. They could be used as fuel or fodder. These plants have also been identified by the analysis of charcoals; they are typical for semi-arid vegetation.

7 Written sources describe the Nabateans as nomadic people in the 3rd century BC, but sedentary 300 years later. The analysis of the archaeobotanical material shows that the way of life in the ancient Nabataean period (~150 BC to 50 BC) cannot be considered as strictly nomadic. Since the Nabataean period (~50 BC), an important increase of the cultivated fruits could imply a significant sedentarization.

Investigations of changes in reed distribution and bank structure of three Swiss lakes since 1953

Veränderung von Schilfbeständen an drei ausgewählten Schweizer Seen seit 1953; 60 pp.

KATHARINA MERKEL

1 Reed areas (*Phragmites communis* stands) are characteristic elements of the landscape around lakes and rivers in Switzerland. With its tangle of rhizomes *Phragmites* consolidates the banks and protects them from erosion. It also offers shelter for many aquatic birds, fish and insects.

2 In the 1960s large areas of limnic reed started to disappear. In the following years the causes and consequences of dying reed were thoroughly investigated. The combined impact of many different factors, such as artificially consolidated banks, eutrophication and mechanical stress are the most important causes.

3 In this thesis the changes of the reed area around the Zuger-, Aegeer-, and Greifensee between 1953 and 1993 and the present conditions of the reed stands were examined. The main goal of this work was to find out if the protection measures of the last 25 years helped to stabilize the reed stands, or if they have even recovered and started to expand again towards the open water.

4 The development of the reed areas were analyzed on the basis of black and white aerial photographs from the 1950s and color photos from the 1990s. To register the present structure of the reed front, the number of shoots per squaremeter, the diameter and the height of the shoots were measured.

5 The evaluation of the data revealed that in the three lakes the reed has retreated from the open water for the last 40 years. But it was also found that at most places the reed seems to have physically recovered and shows the potential to expand again towards the open water. This can be seen as a local success of the protection measures taken in the past decades (for instance sewage purification in the 1970s).

6 It is desirable to preserve the currently good condition of the reed stands in the examined areas as well as in other areas with healthy stands which are not under protection. Dams built out of wickerwood or brushwood can help to re-establish this unique habitat and to prevent further erosion.

The ecological significance of pyrrolizidine alkaloids in *Senecio vulgaris*

Die ökologische Bedeutung der Pyrrolizidinalkaloide in Senecio vulgaris; 47 pp.

RAPHAEL NEUBURGER

1 The management in agricultural ecosystems can have various impacts on plants which live in these habitats. To investigate the influence of the type and intensity of agricultural management on weeds a cosmopolitan species which is present in different habitats was analysed biochemically. It was tested whether the original habitat, the application of fertilizer, or herbicide resistance may have any effect on the pyrrolizidine alkaloids (*pa*) content of flower heads of *Senecio vulgaris* (groundsel).

2 Seeds from *Senecio vulgaris* were collected from three different habitats: flower-strips, vineyards and vegetable fields. In addition, seeds of two nearly identical lines of *Senecio vulgaris*, which differed only in their herbicide resistant and the non-resistant chloroplast genome, were used. From these seeds plants were grown in a greenhouse under equal conditions apart from the application of nitrogen-fertilizer to one half of the offspring from each

mother plant. At the point of flowering the flower heads were harvested and their *pa* content was analysed with HPLC.

3 The more intensive the agricultural management in the original habitat the lower the *pa* content in the offspring was expected to be. No significant differences in the *pa* concentration of *Senecio vulgaris* plants from different habitats were found. Thus, *pa* concentration of the flower heads is possibly not an effective indicator for the intensity of habitat management.

4 It was tested if the application of fertilizer affects the *pa* content and if fertilized plants have a higher content of *pa*'s per gramm fresh weight. The unfertilized plants showed significantly higher *pa* concentrations in the flower heads than the fertilized ones. This result was unexpected: a possible explanation could be that the better the resource conditions are the less investment in chemical defense may be

necessary. Compensation of losses due to herbivory under high-resource conditions would then be less costly. The problem of applying this theory is discussed.

5 The herbicide-resistant biotype was expected to have a lower investment in alkaloid

production than the non-resistant biotype. Yet no significant differences were found. A possible explanation of this findings is that herbicide-resistant plants are not less protected against herbivores than non-resistant plants.

Diaspore dispersal above the timberline

Ausbreitung durch Diasporen in der alpine Vegetationsstufe; 89 pp.

KASPAR PFLUGSHAUPT

1 Seed rain of alpine plants was studied within the vegetation period 1997 in a natural grassland, a stabilised grassy tongue and a degraded downhill ski run at the Jakobshorn Mountain (2500 m a.s.l., NE Swiss Alps). Dry funnel traps randomly placed in each plot were used, each site containing several plots. Seasonal patterns of seed rain density and species composition as well as relationships between the seed rain and the standing vegetation were assessed within each plot and then compared within and between sites. The results obtained in the study year were also compared to those obtained in the previous year.

2 An additional case study on *Luzula spadicea* included spatial population structure, diaspore production and seed rain. To measure dispersal distances in this study, lawn-carpet diaspore traps were placed around selected tussocks.

3 In the intact grassland, small-scale heterogeneity of seed rain was considerable although there were hardly any significant differences between plots. The seed rain density, number of species and species composition varied in each respective plot throughout the study season. Almost all species found in the seed rain formed part of the standing vegetation, but only half of the species in the plant cover occurred in the seed rain. Some immigrating species were found as well.

4 On the ski run only few diaspores were recorded. The seed rain density and number of species did not differ significantly between plots but species composition was different in each plot. There was an inverse proportion between the species number in the standing vegetation and the number of immigrating species per plot.

5 The difference in seed rain density and species composition between the ski run and the intact grassland was highly significant. Of the latter group, the grassy tongue included more species, diaspores of grasses and rushes produced in the previous year clearly prevailing. In the grassland plots, the species composition of the seed rain was more balanced.

6 Compared to the data from 1996, the seed rain in 1997 included more diaspores and more species, the increase being significant only in the case of the number of diaspores. This difference is possibly due to more favourable weather conditions in the year of study.

7 The case study on *Luzula spadicea* brought about a circumstantial evidence of short dispersal distances although direct measurements were not possible. It seems that at least some part of this species' diaspores remain on the mother plants throughout the winter.

8 The above results contribute to a better knowledge of dispersal in alpine plants. They also show that seed rain investigations are

valuable for planning, implementation and monitoring of restoration schemes above the timberline.

Experiments on the impact of *Arion lusitanicus* on early secondary succession

Experimente zum Einfluss von Arion lusitanicus auf Frühstadien einer Sekundärsukzession; 46 pp.

NAOMI PORRET

1 The present study examined the influence of *Arion lusitanicus* Mabille, on secondary succession under different nutrient conditions. Seedlings from the natural seedbank of the study site were used for this investigation. In addition, an agricultural seed mixture with *Lolium perenne* L. and *Trifolium repens* L. was sown on the experimental plots. The following questions were addressed: (1) Do slugs influence species diversity? (2) Do they preferentially feed on plants grown on soil with high nitrogen concentration?

2 Four treatments were applied on the experimental plots: There were plots with slugs and plots without slugs, half of each plot was fertilized by adding ammonium nitrate. The cover was determined by taking photographs of subunits of the half-plots every second day for 18 days. The resulting pictures were scanned and the coverage determined with the programmes Photoshop and NIH. Two harvests were performed and the dry matter of the different plant species was weighed separately for each plot. Species numbers, diversity indices, total biomass and biomass of the most frequent species were recorded.

3 The mean cover was distinctly lower in plots with slugs than in those without, and was higher in the subplots with added nitrogen than in those without added nitrogen. There was no interaction between the treatments. At the first harvest, species number

was reduced by the slug treatment and increased by added nitrogen. For the second harvest no influence of neither grazing by slugs nor addition of nitrogen was found. The diversity indices were increased by nitrogen application. In general, the rarer species were more reduced by grazing than common species. At the first harvest, slugs had a clearly negative effect on total biomass while added nitrogen had a positive effect. The effect of nitrogen was reversed at the second harvest, when plots without nitrogen treatment produced a slightly lower biomass than the control plots.

4 The experiment shows that slugs can have a negative effect on both total biomass and species numbers at the beginning of a succession. The slugs displayed an anti-apostatic grazing, tending to feed disproportionately on the rarer species. Once the vegetation was established, the major influence on the individual plants shifted from grazing pressure to competition, and an effect of slugs could not be detected any more. Taken separately, the plant species showed different reactions both to the slug and nitrogen treatments.

5 The influence of slugs was limited to the early stages of the secondary succession. Few plants were influenced in their abundance by slug grazing in established vegetation. There is evidence of an interaction between grazing and nitrogen fertilization only for a few plant species.

Genetic studies on *Silene vulgaris* s.l. (Caryophyllaceae): genetic differentiation among subspecies and spatial distribution of genotypes across a soil boundary

Genetische Untersuchungen an Silene vulgaris s.l. (Caryophyllaceae): Genetische Differenzierung zwischen Unterarten und räumliche Verteilung der Genotypen in einem Übergangsbereich zwischen Serpentin und Silikat-Boden; 76 pp.

BETTINA A. SCHMID

1 *Silene vulgaris* s. l. is an outcrossing, self-compatible perennial plant which is widespread in Europe. In Switzerland, three subspecies, ssp. *vulgaris* (Moench) Garcke, ssp. *prostrata* (Gaudin) Chater & Walters, and ssp. *glareosa* (Jordan) Marsden-Jones & Turrill are recognized. *Silene vulgaris* s.l. occurs in a wide range of habitat types and is one of the characteristic species found on metalliferous soils such as serpentine, on which heavy metal tolerant populations have evolved. The high contents of nickel and chromium in serpentine and other unfavourable characteristics make plant growth on this soil type generally very poor. The purpose of this study was to investigate some genetic aspects of the *S. vulgaris* s.l. complex: (1) the genetic differentiation among subspecies, (2) the genetic differentiation between serpentine and non-serpentine populations of *S. vulgaris* s.l. from Davos-Wolfgang (Kt. GR) and from the Val d'Hérens (Kt. VS), and (3) the spatial genetic structure of a population of *S. vulgaris* ssp. *vulgaris* over a natural contact zone between serpentine and silicate soil at Davos-Wolfgang.

2 The genetic structure of *S. vulgaris* was analysed by using isozyme starch gel electrophoresis. In populations of different subspecies genetic variation at five isozyme loci was assayed. Their genetic differentiation was determined with Wright's *F*-Statistics and Nei's genetic distance. The spatial distribution of genotypes of *S. vulgaris* ssp. *vulgaris* was determined by examining eleven enzyme loci and analysed with spatial autocorrelation analysis, using Moran's *I*.

3 In each of five regions of Switzerland, two populations of different subspecies were sampled. All ten populations showed extensive genetic variability. In spite of the strong morphological differences between subspecies no genetic differentiation was found. The intensity of genetic differentiation and the geographic origin of the populations were not correlated. Two of the above mentioned population pairs consisted of a population from serpentine and a population from an adjacent non-serpentine site each. They showed high within-population variability but low genetic differentiation. To analyse the spatial genetic structure of *S. vulgaris* ssp. *vulgaris* over a soil type boundary, a 100 m x 50 m area was investigated by constructing a grid in which the genotype of the plant next to each grid node was determined. Genetic variability in the sample was extensive but no spatial structure of genotypes was found.

4 The absence of genetic differentiation between sympatric populations of different subspecies suggests that extensive genetic exchange does occur and that no strong crossbreeding barriers exist. The fact that the morphological integrity of subspecies is maintained nevertheless, suggests that these characters are under selection, whereas the investigated isozyme loci are selectively neutral and not tightly linked to traits under selection. An equivalent explication can be invoked to account for the low genetic differentiation between populations on soils with high and low contents of heavy metals, respectively.

5 To assess the importance of natural selection for the maintenance of morphological differences among subspecies of *S. vulgaris* and between heavy-metal tolerant and sensitive populations further studies are needed.

garis and between heavy-metal tolerant and sensitive populations further studies are needed.

Impact of mowing in winter on the turnover of organic matter in two fen meadows

Auswirkungen der Wintermahd auf den Umsatz des organischen Materials in zwei Flachmooren; 56 pp.

SAMUEL STAHEL

1 The impact of mowing in winter on the rates of accumulation and mineralization of the organic matter in the soil was investigated in two fen meadows (*Caricetum elatae*, *Orchio-Schoenetum nigricantis*) on the south bank of Lake Neuchâtel (Switzerland). At each of the two sites three plots had been mown in winter annually or every 2nd year since 1982; they were compared with three unmown plots.

2 The variables measured were dry weight of the biomass and litter in April and in August, the particle size distribution and the organic C and total N content of the soil organic matter, the concentration of nitrate and ammonium in the soil, the monthly average temperature of the topsoil (sugar inversion method), the rate of nitrogen mineralization (incubation *in situ* and in the laboratory), and the rate of litter decomposition (weight loss of litter bags).

3 The amount of biomass as well as the ratio of the total phytomass (biomass + litter) to the biomass were lower in the mown plots than in the controls. Accumulation in the untreated plots led to amounts of litter that were about three times higher than in the mown plots. No treatment effect was observed on the biomass production between April and August, nor on the rate of litter decomposition. A higher proportion of particles >200 µm was found in the soil organic matter of mown plots compared with the

unmown plots. The organic C and total N content of the organic matter did not differ between the treatments, but the soil of mown plots contained more available nitrogen (mostly ammonium). In spite of the one to three degrees higher average soil temperature in mown plots, the rates of N mineralization did not differ from those in the controls. Rates of N mineralization were mostly negative (-0.5 to -4 mg N/100 g dry soil). This result was probably due to the incorporation of the available nitrogen in the biomass of microorganisms and due to losses of nitrogen through denitrification. A weak treatment effect was observed in the laboratory incubation where rates were more negative in the samples from mown plots. Higher incorporation of the nitrogen because of higher microbial activity in the treated plots probably caused this difference.

4 The results indicate that mowing increased the biomass turnover (indicated by the phytomass-to-biomass ratio), the production of roots (indicated by the particles >200 µm), and the microbial activity (indicated by the available nitrogen and the N mineralization in laboratory).

5 Both the abiotic conditions and the management had influenced the turnover of organic matter. The influence of the management, however, was too small to significantly affect the site conditions after fifteen years of different management.

Ecological studies on the effects of the beech leaf-mining weevil *Rhynchaenus fagi* L. on the beech *Fagus sylvatica* L.

Untersuchungen zum Einfluss des Buchenspringgrüsslers Rhynchaenus fagi L. auf die Buche Fagus sylvatica L.; 57 pp.

GABI TITGEMEYER

1 The interactions of the larvae of *Rhynchaenus fagi* and young beech leaves were investigated in this ecological study, with regards to the survival rates of the larvae as well as morphological and physiological changes in the beech leaves. Various aspects of this mutual intercourse were taken into account: The distribution of infestation within a single tree and between trees, the resistance of the beech, expansion of young beech leaves and the increase of chlorophyll, the capacity of photosynthesis, the chemical composition of the leaves and their morphology.

2 The investigations were carried out in the area of Zurich in a forest and in an experimental garden. The infestation was protocolled during two summers. The development of the beech leaves was recorded weekly from budburst until the termination of the growth. Samples were taken for morphological and chemical analyses on several occasions according to the development of the *R. fagi* larvae. Measurements of photosynthesis were made over two months, starting about seven weeks after budburst.

3 The distribution of oviposition sites combined with the results of indoor experiments indicate that some beeches are resistant to *R. fagi*. The growth of the young beech leaves is

retarded after an infestation; the lesser final length is partly compensated by an increased lateral expansion. In infested leaves the synthesis of chlorophyll is enhanced and photosynthesis is more efficient in spring. This positive effect diminishes with time. The concentration of basic chemical compounds as carbon and nitrogen does not vary between infested and healthy leaves; the cation content is increased in affected leaves.

4 The *R. fagi* larvae manipulate the development of the beech leaves to their own advantage. The most essential aspect is to prolong the time in which they are able to tunnel through the leaf, which results in a higher probability to complete the mines and pupate. The beech shows tolerance to the hindering of the leaf expansion; infested leaves partly compensate the limited length growth by widening. Analysed physiologically beeches have a higher amount of chlorophyll in spring and an initially more efficient photosynthesis. Subsequently the loss of photoassimilates is limited until summer.

5 *Rhynchaenus fagi* clearly benefits from the retardation of the leaf growth in spring. For the beech the interference in spring is limited due to compensation but obviously disadvantageous in summer.

PhD theses (5)

Soil water conditions and root growth of seedlings and their importance for species richness in limestone grasslands

Bodenwasserhaushalt und Wurzelwachstum von Keimlingen und ihre Bedeutung für den Artenreichtum von Trespen-Halbtrockenrasen; 70 pp.

GIAN-PIETRO CERLETTI

The main point of investigation was to find mechanisms which contribute to the large species richness in limestone grasslands (up to 40 plant species per square metre). In a limestone grassland (Mesobrometum) in northern Switzerland near Schaffhausen the influence of mature plant individuals on selected soil parameters was studied. It is argued that such influence could differently affect the chances of survival and establishment of various plant species. This would facilitate the coexistence of different species.

Species-specific gaps were created by carefully eradicating large adult individuals of *Bromus erectus* Hudson, *Salvia pratensis* L. and *Plantago media* L. in autumn. The litter was left in the gaps during one winter. During three growing seasons the microclimate and the soil water conditions were measured both in the gaps and in the undisturbed dense vegetation. Soil water content was measured using the Time Domain Reflectometry-Method. The pF-values were calculated using pF-curves.

To obtain information about the root development of the three species used in the gap study seeds were germinated in small pots filled with nutrient poor sand in a greenhouse in Zurich. The seedlings were watered daily with tap water, harvested and measured 2, 4, 8, 12, 16, 24 and 36 days after germination.

1 In gaps the soil water conditions of the top soil fluctuated considerably and the soil water

potential at the centre of gaps (at 1.5 cm below soil surface) reached values of more than pF 4.5 (compared to values of only pF 1.5 in 7 cm below soil surface). Particularly after the mowing, but also in general after several sunny days without precipitation, soil water acquisition is nearly impossible for seedlings and young plants that are only rooted in the top soil.

2 Gaps showed short-term species-specific differences in soil water conditions. At moderate soil water stress (pF \approx 2) gaps generated by removing mature individuals of *B. erectus* lost only half the quantity of water lost in the other two gap types.

3 In dense undisturbed vegetation the soil water conditions are influenced by mature individuals in a species-specific way. At a soil depth of 0–5 cm the soil water content below mature individuals of *S. pratensis* was about 5%vol less than the other two species. On the other hand at a soil depth of 5–10 cm soil water content below individuals of *B. erectus* was about 4–6%vol less than below mature individuals of *S. pratensis*.

4 The microclimatic conditions in gaps vary considerably and can reach extreme values. The most extreme values of light and air temperature as well as humidity occur in the centre of the gaps at noon. (Temperatures of more than 50 °C in the shade 2 cm above soil surface were recorded.)

5 Within four days, roots of *B. erectus* seedlings reached soil depths of at least 4 cm,

where soil water availability is relatively high and fluctuations only small. After 12 days, the root development of seedlings of *B. erectus* was sufficient for an effective acquisition of soil nutrients (herringbone structure). Differences in root development between *B. erectus* and *S. pratensis* were significant but not very large. The largest differences were found between *P. media* and the two other species. Only after 24 days from germination, the seedlings of *P. media* had built up an adequate root system for the ac-

quisition of water and nutrients during a drought period.

6 Pronounced differences in microclimate and soil water conditions within the gaps and between the different gap types were found. Together with the described differences in root development, they lead to species-specific variation in the chances of seedling establishment. All these differences constitute a mechanism enabling coexistence and thus contribute to the large species richness in limestone grasslands.

Problems with invasive alien plants on the islands of Mahé and Silhouette, Seychelles

Probleme mit invasiven Pflanzen auf den Inseln Mahé und Silhouette, Seychellen; 176 pp.

KARL FLEISCHMANN

The Seychelles possess natural forests of considerable botanical interest. These forests are threatened by a gradual invasion of introduced plants. The aim of this study is to investigate the process of this invasion and to provide the scientific basis for the conservation of important biodiversity sites on the islands of Mahé and Silhouette. The study is presented in six parts.

The state of invasion of alien plants

1 A method is presented for a quick and easily repeatable evaluation of the state of invasion of alien woody plants and the ecological status (prominence value, diversity, singularity, rejuvenation) of potentially important biodiversity sites in the Seychelles.

2 The survey revealed 34 species as invasive alien species, the most prominent being *Cinnamomum verum*, *Psidium littorale*, *Aedenanthera pavonina* and *Tabebuia pallida*.

3 The greatest intensity of invasion was recorded in intermediate forests on moderate or gentle slopes and in stream ravines pro-

tected from desiccating winds and insolation. "Mountain mist forests", "palm forests" and "glacis" are the least invaded vegetation types.

4 Prominence values and percentage frequency of invaders are exceeded by the endemic palm *Phoenicophorium borsigianum* which is able to maintain itself in areas suffering from forest destruction and topsoil erosion.

The change of habitat potentials

1 Tree populations in five mature biodiversity sites and in four sites that have been disturbed by human activity over the past 150–200 years were surveyed.

2 For the analysis of stand structures count-plot analysis was used, and a new plotless sampling technique has been designed to analyse prominence and importance values of trees in extreme topographic situations.

3 The reproduction dynamics of tree species was investigated and changes in habitat potentials were predicted from the analysis of survival curves.

4 The endemic *Camptosperma seychellarum*, *Dillenia ferruginea* and *Northea hornei* showed the highest importance values (*IV*) in the study area. However, lack of sufficient recruitment together with low prominence values (*PV*) make it questionable whether these species will be able to maintain themselves in future.

5 The aggressively invasive alien *Cinnamomum verum* had the highest *PV* for both, adult trees and juveniles. The alien *Psidium littorale* was less important and less prominent than *Cinnamomum* v. but the high *PV* of *Psidium* l. saplings indicates an increasing prominence of this alien species in the future.

6 *Phoenicophorium borsigianum* showed the second highest *PV*. Together with its high rate of recruitment this species is probably the only endemic taxon in the study area which is able to successfully compete with *Cinnamomum* v. and *Psidium* l.

7 The following species (the five most important listed in decreasing order of significance) showed a tendency to increase their abundance in the future: *Ochna ciliata*, *Dracaena reflexa*, *Memecylon eleagni*, *Psidium littorale*, and *Cinnamomum verum*. Species that will maintain their abundance in the study area are *Adenanthera pavonina*, *Paragenipa lancifolia* and *Phoenicophorium borsigianum*. Taxa who potentially decrease (listed in decreasing order of significance) their abundance in the future are: *Northea hornei*, *Camptosperma seychellarum*, *Dillenia ferruginea*, and *Nephrosperma vanhoutteana*.

Photogrametric estimation of light regimes

1 A computerized technique for the analysis of hemispherical photographs of 32 microsites in mountain mist forest and intermediate forest habitats on Mahé island is described. The technique appears particularly useful for providing relative comparisons between sites

without making continuous light measurements over a period of time.

2 The analysis yields estimates of diffuse site factors (*DifSF*) from weighted canopy openness. The technique was evaluated by comparing the *DifSF* estimates from photographs with measured photosynthetically active photon flux density (*PFD*) and by comparing computer data with manually derived *DifSF* according to a method described by Anderson (1971).

3 The programmes sampled a total of 130'797 pixels per cm². Measured *PFD* correlated strongly ($r = 0.98$) with the predicted *DifSF* and the computerized picture analysis correlated significantly ($r = 0.92$) with Anderson's manual method. The manual analysis of a canopy photograph took between 1 and 1 1/4 hours, while the computerized analysis usually needed 15–20 min.

4 The 32 microsites on Mahé island could be subdivided into four arbitrary light environments: very dark sites with a mean *DifSF* of 11% (palm forest at La Réserve), dark sites with a mean *DifSF* of 19% (mountain mist forest at Congo rouge), medium-light sites with a mean *DifSF* of 36% (secondary forest at Mt. Brulée), and open sites with a mean *DifSF* of 99% (intermediate forest in post-fire succession).

Seedling response to forest light regimes

1 The performance of seedlings in low-canopy sites (*DifSF* > 29%) was compared with seedling performance in high-canopy sites (*DifSF* < 29%), and the performance of common species was compared with that of rare species.

2 It was investigated whether rare species have different population dynamics or respond differently to canopy height than common species, and whether the invasion of woody alien plants (e.g. *Cinnamomum verum*,

Psidium littorale etc.) can potentially be controlled by changing the specific light environment in which pronounced competition between native plants and invaders takes place.

3 *DifSF* was significantly correlated with height growth over the previous 12–24 months. For most species that were tested, growth among the surviving seedlings was significantly faster in low-canopy sites. This was not true for the endemic palm *Phoenicophorium* which grew better in darker plots. The poor growth performance of *Cinnamomum* in deep shade, coupled with low survival rates in high-canopy sites may indicate that this aggressively invasive species is unable to survive extended periods as suppressed seedlings under a high canopy. However, in low canopy sites *Cinnamomum verum* demonstrated a high competitive ability. In very high levels of light, the endemic *Memecylon eleagni* and *Deckenia nobilis* seem to have a competitive advantage over *Cinnamomum* which showed reduced relative growth rates in height (*RGRH*) in exposed and open areas. In general, palms demonstrated higher *RGRH* over the range of light levels than deciduous trees, but both groups showed a threshold rather than a monotonic response to increasing light availability.

4 Seedling mortality was size dependent. The smallest, and presumably youngest seedlings had a higher probability of dying than larger ones. Mortality was negatively correlated to *DifSF*. The mean mortality in dark sites (*DifSF* < 15) was 17%, in medium-light sites (*DifSF* 15–30) 12%, in light sites (*DifSF* 30–45) 6.5% and in open sites (*DifSF* = 99) 5.4%. There were two exceptions: the endemic palms *Phoenicophorium borsigianum* and *Deckenia nobilis* survived equally well in low- and in high-canopy sites. From the five most prominent seedlings the fastest growing species tended to survive less well.

5 Seedling damage of the five most prominent species was positively correlated with the mortality rates of the corresponding species. Species that grew rapidly showed also greater annual seedling damage.

Seedling establishment and competitive ability of two ecologically important species

1 The light intensity in terms of diffuse site factors (*DifSF*) was estimated in 32 microsites from hemispherical photographs using a computerized image analysis system.

2 A new plant growth analysis function, the so-called leaf area/height index (*ALHI*) has been introduced, and a principal components analysis (*PCA*) was carried out to evaluate the seedling performance of *Cinnamomum* and *Phoenicophorium*.

3 Competition between *Cinnamomum* and *Phoenicophorium* was greatly influenced by the amount of available photosynthetically active radiation (*PAR*). For both species there was a negative correlation between mean leaf area of seedlings and light levels.

4 *Phoenicophorium* responded significantly stronger in terms of *RGRAL* and *ALHI* to low gap light levels than *Cinnamomum*. Both species showed no further response to direct sunlight with levels of 99% diffuse site factor.

5 *Phoenicophorium* and probably other palms like *Deckenia nobilis* and *Roscheria melanochaetes* act as a filter affecting the distribution and abundance of establishing *Cinnamomum* seedlings. Mortality of *Cinnamomum* was strongly negatively correlated with levels of *PAR* while *Phoenicophorium* showed no such correlation. Unlike *Phoenicophorium*, *Cinnamomum* could establish and regenerate only in light levels >7.5% of diffuse site factor.

6 Leaf damage and terminal meristem damage were positively related to seedling density.

7 There were significant correlations between the demographic variables and levels of avail-

able *PAR*. For *Cinnamomum* these correlations were positive for *RGRAL*, *RGRH* and survival, i.e. *Cinnamomum* demonstrated higher competitive ability with increasing light levels while *Phoenicophorium* performed better in more shady forest sites.

The conservation of inselbergs

1 The flora and vegetation of eight inselbergs on the islands of Mahé, Silhouette and Praslin was investigated. In four study sites the ecological status of the vegetation was quantitatively assessed and compared with habitats in the immediate vicinity of inselbergs.

2 Most habitat types were found which are also characteristic for inselbergs in other tropical regions; only monocotyledonous mats and ephemeral flush vegetation were absent.

3 Species richness of Seychelles inselbergs was considerably lower compared to the vegetation of rock outcrops in tropical mainland

areas. Differences in the species inventories of the inselbergs investigated were not significant, i.e. β -diversity was low. Phytogeographical affinities of the rock outcrop flora were more directed to south-east Asia than towards Africa or Madagascar.

4 Though relatively poor in species, the Seychelles rocky outcrops harbour a considerable number of palaeoendemics (e.g. *Medusagyne oppositifolia*, *Nepenthes pervillei*). Quantitative investigations showed that indigenous and endemic species are the most prominent components of the rock outcrop vegetation, whereas alien species, such as *Cinnamomum verum* play only a minor role.

5 In terms of conservation all sites investigated revealed outstanding floristic and ecological values. The still high regeneration rates of native species suggest that rock outcrops are not yet seriously endangered by invasion of alien plants.

Evaluation and management of fen meadows invaded by common reed (*Phragmites australis*)

Bewertung und Bewirtschaftung von verschilfenden Streuwiesen; 173 p.

SABINE GÜSEWELL

1 Common reed (*Phragmites australis* Trin.) has been frequent since long in fen meadows of the Swiss Plateau. In the last thirty years, however, it became more abundant at many sites. This spread raised the question whether *Phragmites* would affect the conservation value of fen meadows and how a further spread could be prevented. This thesis investigated relations among *Phragmites* plant species composition and site conditions. Moreover, the effect of mowing at different dates on the biomass and on the nitrogen and phosphorus economy of *Phragmites* and the other species was assessed.

2 The plant species composition of 241 plots (4 m²) was surveyed using the Braun-Blanquet method. The aboveground biomass of *Phragmites* (*ABP*) in August was estimated based on shoot density and mean shoot length. The aboveground biomass of the other phanerogams was determined for 72 of the plots.

3 The *ABP* ranged from 0 to 1270 g dry weight per m² (0–85% of the total aboveground biomass). Plots dominated by tall herbs (alliance Filipendulion) had on an average higher *ABP* than plots dominated by heath grass or small sedges (alliances Moli-

nion and Caricion davallianae). Alliances differed more in average shoot size than in shoot density. In each alliance the contribution of *Phragmites* to total aboveground biomass was positively correlated with this biomass, i.e. with site productivity; *ABP* was not related to the ground water level.

4 High *ABP* was, on an average, associated with low conservation value in terms of species richness, number of rare or endangered species and proportion of characteristic fen species. Strong differences were, however, found among the three alliances. The conservation value of Filipendulion plots was generally low and decreased significantly with increasing *ABP*. The conservation value of Molinion and Caricion plots was generally high and not related to *ABP*, i.e. a displacement of mire species through shading by *Phragmites* was not observed in these two alliances. Consequently, the abundance of tall herbs appeared to determine the conservation value of fen meadows more than the abundance of *Phragmites*. Since in the alliances Molinion and Caricion increasing abundance of *Phragmites* was associated with an increasing proportion of Filipendulion species, a future loss of conservation value of reed-invaded fen meadows appeared probable.

5 The late seasonal development of *Phragmites* probably contributed to the above results. The shading impact of *Phragmites* was low until mid June at most sites. Therefore, species completing most of their seasonal growth early in the vegetation period were likely to be less affected by this shading than species developing later in summer. The earlier and faster development of *Carex acutiformis* (abundant at high *ABP*) compared with *Carex panicea* (abundant at low *ABP*) was consistent with this assumption. Results suggest that a spread of *Phragmites* might indirectly affect the conservation value of fen

meadows by promoting tall herbs which, in turn, would displace the mire species.

6 Two mowing experiments were carried out to evaluate the impact of mowing in summer on the abundance of *Phragmites* in fen meadows. One experiment had been established in 1982 by A. Buttler (University of Neuchâtel); treatments were (a) mowing in August, (b) mowing in January–February and (c) no mowing. Treatments were applied every year from 1982 to 1987, and every other year since then. The abundance of *Phragmites* (shoot size, shoot number, *ABP*), which had been investigated in 1983–1986 by A. Buttler, was reinvestigated in 1995–1997. It decreased between the two periods in the mown plots, but did not change in the unmown plots. There was no difference between mowing in August and mowing in winter, making it unlikely that mowing in August would suffice to reduce *Phragmites* in invaded fen meadows.

7 The other experiment was started in 1995; the two treatments compared were (a) mowing in early September (*S*) and (b) mowing in late June and early September (*JS*). During the three years of the study, additional mowing in June reduced neither the shoot density nor the shoot size of *Phragmites*. In the third year of the experiment, the biomass of *Phragmites* was still the same in *JS*-plots as in *S*-plots. Conversely, the biomass of the other species was, on an average, 21% lower in *JS*-plots than in *S*-plots. Mowing twice removed 90% more nitrogen and 181% more phosphorus from *Phragmites* than mowing once. Only 30% more nitrogen and 64% more phosphorus were removed from the other species. Thus, the impact of additional mowing in June was ambiguous: on the one hand, the biomass of *Phragmites* had been increased in comparison to the biomass of the other species, suggesting that *Phragmites* had been promoted on the short term. On

the other hand, the impact of mowing in June on nutrient budgets appeared stronger for *Phragmites* than for the other species. Whether *Phragmites* would be reduced on a longer term, or whether it would retain its advantage over the other species could not yet be predicted.

8 Nevertheless, mowing twice had favourable effects. It removed more nutrients than

mowing once, reduced total aboveground biomass and created a more open vegetation structure. These effects appeared to be more decisive for the conservation value of the fen meadows than a complete eradication of *Phragmites*. There is probably no optimal mowing regime, therefore, a more flexible management with some spatial and temporal variation seems to be the best strategy.

Herbivore-carrying capacity of grasslands in the Swiss National Park

Herbivoren-Tragfähigkeit des Graslandes im Schweizerischen Nationalpark; 71 pp.

OTTO HOLZGANG

1 The Swiss National Park (168 km²) is located in the eastern Central Alps within the subalpine and alpine zones. The density of ungulates is assumed to be very high in the Swiss National Park. Therefore, data on phytomass available for ungulates were needed to get a basis for further discussions of the herbivore-carrying capacity.

2 By means of a Geographic Information System the grasslands (20 km²) of the study area (106 km²) were classified into 41 categories by habitat factors. In 31 categories, covering 99% of the grasslands, 76 sample points were selected. In 1996, the green phytomass was assessed at each sample point with a radiometer. In addition, the accuracy of the radiometric technique was investigated. Using the data of the radiometric measurements, the phytomass was then modelled for the study area for three scenarios: (a) "present", (b) "maximum possible", and (c) "no" grazing pressure. The differences (c)–(a) and (c)–(b) were assumed to be the phytomass offtake under present or maximum possible grazing pressure, respectively. The calculated offtake was compared to the requirements of ungulates, rodents and grasshoppers to evaluate the plausibility of the model and to calculate

the herbivore-carrying capacity of the Swiss National Park.

3 In order to assess the energy balance as well as the impact of ungulates on fodder quality of subalpine grasslands, both a productive and a less productive grassland were studied by using a paired-sample design (grazed and ungrazed plots) between May and August 1995.

4 Accuracy of radiometric technique. The 95% confidence interval of prediction for calculating the dry weight of green and total above-ground phytomass (20 measurements) was $\pm 28\%$ and $\pm 45\%$, respectively.

5 Fodder quality and energy balance. The productive grassland investigated showed a mosaic pattern of short turf and tall vegetation, which was caused by grazing. Steady grazing during the growing season resulted in a smaller increase of crude fibre and in a smaller decrease of crude protein content in the short turfs compared with (a) the taller vegetation areas of the productive grassland, as well as (b) the entire less productive grassland. This resulted in better fodder quality. On both subalpine grasslands, ungulates consumed less than 56% of the energy available in phytomass. In May and July, the ungulates

occurring in high density covered all their energy demands on the productive grassland; in June their energy intake on the same site was only 60%. On the less productive grassland, the ungulates occurring in low density covered their energy demands from May to July only to 40–74%, although phytomass was not limited. They grazed in the surrounding forests or in the nearby alpine grasslands instead.

6 Productivity and herbivore-carrying capacity. Under the actual grazing pressure of 1996 the net community productivity of the sub-alpine and alpine grasslands varied between 1.5–2.2 t ha⁻¹ yr⁻¹ and 0.8–1.2 t ha⁻¹ yr⁻¹, respectively. The green phytomass production of the 20 km² grassland amounted to 1750 t yr⁻¹, 642 t yr⁻¹ and 2723 t yr⁻¹ for the scenarios of “present”, “maximum possible” and “no” grazing pressure. The calculated offtake was 973 t yr⁻¹ (36% of the highest possible green phytomass production) under “present” and 2081 t yr⁻¹ (76%) under “maxi-

imum possible” grazing pressure. The requirements of all considered consumer groups accounted in 1996 for 85% of the calculated offtake under present grazing pressure. Because this is within the confidence interval of the radiometric measurements ($\pm 28\%$), the model applied seems to be plausible. The number of herbivores present in 1996 used only 40% of the maximum available phytomass. Therefore, it could be concluded that the herbivore-carrying capacity of the Swiss National Park is about 2.5 times the present number. This conclusion must be treated with caution, because heavy grazing pressure is known to reduce productivity, and production as well as herbivore density are subjected to annual variations. In addition, data of only one summer were available. Thus, it is probably more appropriate to say that the present number of herbivores attained the summer-time herbivore-carrying capacity of the Swiss National Park to two thirds.

Short-term response of the ground vegetation in a montane forest ecosystem under increased nitrogen deposition – influence of light and competition

Kurzfristige Auswirkungen erhöhter Stickstoffdeposition auf die Bodenvegetation eines voralpinen Waldökosystems – Einfluss des Lichtes und der Konkurrenz; 118 pp.

NATHALIE MÜLLER

1 The increase of nitrogen deposition during the last forty years may have induced the long term floristic changes observed in many European forests at the end of the 80's. The nitrogen, considered as limiting growth factor in most forest ecosystems, may have generated an eutrophication causing the extension of some plant species and the disappearance of some others. Nitrogen addition experiments were started in European forest stands under the *NITREX* project with the aim of investigating the role of the anthro-

pogenous loads in the evolution of the vegetation, soil and water quality.

2 Two plots were delimited on the sub-alpine site of Alptal (Central Switzerland) in a mixed forest, where the spruce (*Picea abies*) is the dominant species in association with the fir (*Abies alba*). One plot repeatedly receives low doses of NH₄NO₃ diluted in rainwater and the other (control) the same amount of water without N. The treatment (30 kg N ha⁻¹yr⁻¹) triples the natural N deposition; the supplement of water represents 7% of the ambient

precipitation. The vegetation and the soil of both plots have been mapped. Permanent quadrats (50 cm x 50 cm) were installed for the long term monitoring of the herbaceous and moss layers. The maps and relevés of the quadrates were first used without distinguishing control and treatment for characterising the initial botanical composition.

3 The ground vegetation of the site is a mosaic of three plant communities: one dominated by *Vaccinium myrtillus* and *Vaccinium vitis-idaea*, another dominated by *Caltha palustris* and *Petasites alba* and a third dominated by *Poa trivialis* and *Carex ferruginea*. The pH, the humus form and the nutrient content of the soil are the main factors differentiating the first community from the others: this appears on an acid and nutrient poor raw humus, whereas both other communities grow on a less acid and nutrient rich anmoor humus. Light conditions and related factors (daily light regime, water regime, biological and chemical processes in the soil) separate these communities.

4 After the treatment has begun, the relevés of the treatment plot were compared to those of the control plot to detect a possible nitrogen effect on the relative abundance of plant species. As the information gained from the relevés is inadequate to detect a short term effect, the monitoring was completed by a systematic sampling of five dominant species in both plots. The above-ground parts of the plants were harvested and measured (dry matter, leaf area and length of the current year shoots in the perennial species). The environmental conditions are furthermore qualified at each sampling point with measurements of the relative light radiation and analyses of soil samples.

5 After two years of addition, no nitrogen effect has been detected with either of the two survey methods. However, it has been ob-

served that the mosses *Hylocomium splendens* and *Sphagnum nemorum* tended to become brown respectively pale on the treatment plot.

6 A competition assay with or without N addition was conducted parallel to the main experiment to determine if N may modify the relation between two plant species. Three pairs of species growing in the same conditions were chosen. Individuals of each pair were collected on the site and planted in mono- or mix-culture (intra- respectively inter-specific competition). Both culture types received rainwater with or without N.

7 The experiment revealed that the growth of *Vaccinium myrtillus* was enhanced by the addition of nitrogen, while that of *Vaccinium vitis-idaea* was reduced. The competitive balance between these species may change in the long term to the advantage of *Vaccinium myrtillus*, though the interaction of N and competition could not be shown by the experiment. The growth of *Ranunculus aconitifolius* was positively affected by competition with *Knautia dipsacifolia*, and conversely the growth of *Knautia dipsacifolia* was negatively affected by competition with *Ranunculus aconitifolius*, however, nitrogen had no influence on these responses.

8 The forest of Alptal has an open canopy. Consequently, the light conditions are heterogeneous. As energy source for the photosynthesis, the light may influence the response of the plants to nitrogen. Therefore, an additional experiment was carried out in an experimental garden at Zurich exposing four species from the site to different shade conditions.

9 In this trial, light was an important factor regulating the growth of *Poa trivialis* and *Melica nutans*, but no interaction with the N could be observed. However, both species allocated less biomass to roots in response to nitrogen addition. Though the N availability

of the pot substrata was relatively important, the plant used the supplement of nitrogen.

10 At the plot scale, the effect of increased nitrogen deposition on the herbaceous layer of the Alptal forest has not yet been detected. However, the results of the competition experiment indicate that the *Vaccinium* community, which grows in a poor soil, may be more sensitive to the N addition than the communities of nutrient-rich environments. These findings are in accordance with the theory. The tunnel experiment showed that the plants may respond even in a soil where N is not limiting. That may have long term consequences on the development of plant communities. The monitoring of the quadrats and the sampling of biomass must continue to confirm the experimental results at the plot scale.

