

Summaries of diploma and PhD theses (2001)

Diploma theses (11)

Problems with *Paraserianthes falcataria*

Die invasive Baumart Paraserianthes falcataria; 65 pp.

MICHAEL ANDEREGG & FRANK WIEDERKEHR

- 1 *Paraserianthes falcataria* was introduced to the Seychelles in the 1930s. It is presently widely distributed and is regarded as one of the main threats for the native flora. This study aims to improve our understanding of the ecology and hence provide a basis for the control of *Paraserianthes falcataria*.
- 2 We studied three sites differing in the degree of invasion by *P. falcataria* (heavy, moderate and no invasion). At each site rejuvenation and future development of tree abundance were investigated using stand structure analysis. As the seeds of *Paraserianthes falcataria* seem to germinate preferably in bright light conditions (high *PAR*) and since *P. falcataria* is a nitrogen fixing plant, light climate and soil nutrient content were also investigated.
- 3 Soil nitrogen content was highest in the heavily invaded site and lowest in the moderately invaded site; the distributions of phosphorus contents were similar; this indicates that seedling establishment could be favoured by high nutrient availability.
- 4 Photosynthetic active radiation (*PAR*) was highest at the heavily invaded site and lowest at the non-invaded site, and the abundance of seedlings was positively correlated with diffuse light. Establishment of saplings was only observed at light intensities higher than 19%. This means that the rejuvenation of *P. falcataria* depends strongly on the amount of available *PAR*. The lack of saplings and young trees in dense stands of *P. falcataria* suggests that the rejuvenation of *P. falcataria* is largely impaired by low levels of *PAR* caused by self-shading from mature *P. falcataria* trees.
- 5 Preventive control methods against *P. falcataria* should focus the control of the light regime. The already implemented ring barking program should be continued. Reforestation is needed to close the gaps formed by human activities. Further monitoring is needed to obtain more information about the actual status of the species.
- 6 A management plan for the control of *P. falcataria* is proposed. It is recommended that control measures be taken as soon as possible to avoid a similar impact of *P. falcataria* on the native flora as already seen with *Cinnamomum verum*.

Do grass endophytes increase herbivore resistance of their hosts?

Erhöhen Grasendophyten die Herbivorieresistenz ihrer Wirte? 67 pp.

CHRISTINE BIBER

- 1 *Epichloë* and *Neotyphodium* endophytes (Clavicipitaceae, Ascomycota) are mutualistic symbionts of many grasses: The fitness of the infected hosts can be improved through enhanced growth and seed yield, higher competitiveness and increased resistance against drought and herbivory. These benefits are thought to be associated with certain secondary metabolites of the fungi (alkaloids).

- 2 Most previous research has focused on agronomically important grasses and their interactions with grazers and invertebrate herbivores. In this study we examined grasses of natural and seminatural habitats (woodland and nutrient poor meadow) and tested whether infected plants are more herbivore-resistant than uninfected ones.
- 3 In no-choice feeding assays, larvae of *Spodopterafrugiperda* were fed with either infected or uninfected grasses (*Brachypodium pinnatum*, *Bromus benekenii*, *Bromus erectus*, *Elymus europaeus* and *Lolium perenne*). To examine whether larval development was affected by the infection status of their diet, larvae were weighed three or four times during their development as well as after pupation, and time elapsed to pupation and to adult eclosion was recorded.
- 4 The survival of all larvae was high and independent of the diet. However, in four of five grasses, larvae feeding on infected diet developed more slowly and gained less weight than those feeding on uninfected diet. These results are consistent with the idea that endophytic fungi increase herbivore resistance in infected grasses, but it seems that fungal alkaloids act as a feeding deterrent rather than as a metabolic toxin.
- 5 Results for *Brachypodium pinnatum* contrasted with those for the other grass species: the larvae feeding on infected diet performed better. A possible explanation is that genetic differences between infected and uninfected plants were more important for the development of the larvae than the infection status itself.
- 6 In the second part of this study, herbivore damage was recorded on leaves of *Brachypodium sylvaticum* growing in natural populations. The number of damaged leaves and the leaf area damaged were higher in flowering, endophyte-free shoots than in stroma-forming, infected shoots. This supports our hypothesis of increased herbivore resistance in infected grasses. However, the damaged leaf area of infected but flowering shoots was highest. These results contrast with those of a previous study, which suggests that seasonal and annual climatic differences, by influencing the herbivore fauna and plant condition, could also cause differences in the effect of endophyte infection on feeding damage.

Appreciation of plants in nature preserves by means of experience stations

Inwertsetzung von Pflanzen in Naturschutzgebieten durch Erlebniswege; 75 pp.

VERENA DOPPLER

- 1 Nature conservation areas are mainly visited to enjoy nature and particularly, to observe and experience animals. Information to visitors therefore tends to focus on animal themes, even though plants offer the opportunity to experience nature through a multitude of sensations. This study developed and tested a new method for increasing the visitors' interest in plants.
- 2 Plants were presented on so-called experience stations to visitors of two nature preserves near Rottenschwil (AG) and Greifensee (ZH), respectively. These stations were outdoor installations (between 0.5 and 2 m in size) inviting people to experience and investigate plants. They dealt with the following topics: "Healing and conjuring with plants", "The manifold life of a fen meadow", "Stinging nettle, a weed?", "Waterlilies", "Ingenious construction: culm of grass". Stations on four additional topics were designed for future realisation: "basis of our nutrition, the grasses". "senescence and development", "fertilised meadows – unfertilised meadows", "Pioneers become established".

- 3 The five experience stations were evaluated by four focus groups ($n = 6-11$) from the fields of nature conservation and environmental education as well as two groups of young people (approximately 16 years old) living near the nature reserve. After each focus group had tested the stations, a group discussion took place; each discussion was recorded, transcribed and analysed.
- 4 Six aspects emerged as being particularly valuable in plant experience stations: (a) relation to everyday life; (b) presentation of well known, e.g. abundant, prominent species; (c) information provided through an entertaining story; (d) variation in design (e) use of head, heart and hand, and (f) focus on characteristics of plant species and vegetation. As main difficulties in plant observation, participants mentioned seasonal changes in appearance and the fact that individual plants are hardly perceived as such because they tend to be 'lost' in the uniformly green vegetation. These issues need to be addressed by plant experience stations, e.g. by pointing out the characteristic shapes of leaves.
- 5 Members of the focus groups found it positive that they could express their opinion on the experience stations before the complete experience trail was realised.
- 6 The study has shown that on the whole, experience stations or trails offer a good possibility of making plants better known to the general public. If experience stations are implemented, regular maintenance is necessary, and modifications should always be possible to meet new requirements. To avoid vandalism and weather damage, experience stations should be used flexibly and should be mobile.

Allozyme variation and population structure of *Ranunculus alpestris* along a predictable snow melt gradient

Genetische Variation und Populationsstruktur von Ranunculus alpestris entlang einem Schneeschmelzgradienten; 46 pp.

JEAN-DAVID GERBER

- 1 An analysis of genetic structure and local population differentiation was conducted in the obligatory outbreeding perennial *Ranunculus alpestris* to assess the effect of snow melt timing on the genetic structure of the population. Three populations located along an environmental gradient caused by gradual melting of snow were sampled on the mount Pizol in the Swiss Alps. In each population, plants were collected along 2 transects perpendicular to the snow melt line in order to obtain maximal differences in flowering time between plants located in the early- or late-melting parts of the transects. The phenology of each plant was recorded prior to removal.
- 2 Flowering time was highly correlated with the position of the plants along the transect and thus, with the snow melt time. A simple regression model revealed that in some transects, overlap in flowering time occurs between early- and late-flowering individuals.
- 3 Hardy-Weinberg equilibrium analyses on the basis of 3 polymorphic loci showed that the 3 sampled populations were not panmictic. However, random mating may exist at the subpopulation level. Most genetic differentiation occurred among populations and not among subpopulations within populations, although overall differentiation was relatively low.
- 4 Because subpopulation differences occurred not only across the snow melt gradient, but

also among subpopulations that flower simultaneously, it is concluded that the structuring effect of the snow melt gradient is rather weak and probably counteracted by seed dispersal along the gradient. Instead,

isolation by distance seems to play the most important role in structuring the sampled populations.

Mating system of *Silene vulgaris*

Fortpflanzungssystem von Silene vulgaris; 48 pp.

ANNINA GERET

- 1 Serpentine-adapted populations of *Silene vulgaris* can be found in one of the largest outcrops of serpentine soil in Switzerland situated in the vicinity of Davos (GR). These populations clearly differ both morphologically and physiologically from neighbouring populations of *Silene vulgaris* on silicates. This study compared the mating systems of two *Silene vulgaris* populations growing on serpentine and on silicate, respectively, to investigate whether inbreeding might act as an isolating mechanism between the two populations.
- 2 Plants from both populations were collected in the field and cultivated in the greenhouse; progeny arrays were assayed for 7 allozyme markers to estimate mating system parameters.
- 3 Both the serpentine and the silicate populations were predominantly outcrossed (multilocus outcrossing rate, $t_m = 0.852$ for the serpentine population and 0.872 for the silicate population). Biparental inbreeding ($t_m - t_s$) was significant in both populations ($t_m - t_s = 0.087$ and 0.153). The single-locus outcrossing rate t varied considerably between plants, ranging from 0.40 to 1.14 (mean = 0.69) in the serpentine population and from 0.50 to 1.65 (mean = 0.77) in the silicate population. All these results indicate the existence of a population substructure, in particular the occurrence of more inbred genetic neighbourhoods, probably due to the clustering of related plants combined with limited pollen flow.
- 4 Parental inbreeding coefficients (F) did not differ significantly from zero, but a significant positive correlation of paternity (probability that sibs shared the same father) was found in both populations, suggesting either a limited pollen pool or non-independent mating events as a consequence of pollinator behaviour.
- 5 The serpentine and silicate populations did not differ significantly in any parameter. This similarity together with the high outcrossing rates suggest that strong inbreeding depression might have prevented the evolution of self-fertilisation in these *Silene vulgaris* populations, and that isolating mechanisms other than selfing may have caused the observed differences in morphology and physiology between plants on serpentine and on silicates.

A study of the significance of newly established hay meadows as a habitat for butterflies by means of a quantitative inventory of caterpillars and imagines.

Untersuchung der Bedeutung neu angelegter Heuwiesen als Habitat für Tagfalter mit Hilfe quantitativer Erfassung der Raupen und der Imagines; 25 pp.

RENÉ GRISON

- 1 Inventories and mapping of butterflies are presently mostly based on imagines. However, appropriate methods also make it possible to efficiently inventory the pre-imaginal stages, e.g. the hoop-net method. This efficient and time-saving method was used for the quantitative mapping of butterfly caterpillars in the present study.
- 2 Butterfly caterpillars were searched with the hoop-net method at three test sites in May and June 2001. However, most of the collected animals were caterpillars of moths and larvae of gall wasps. Only very few butterfly caterpillars were caught. Thus, the hoop-net method proved to be unsuitable for a quantitative mapping of butterfly caterpillars.
- 3 The significance of newly established hay meadows for butterflies was investigated using the transect method at the same three test sites. Flower density was partly highly correlated with the number of butterfly species. The new hay meadows in Berg and in Seewadel appeared to be a highly favourable habitat for butterflies and to contribute to species diversity. The combination of farmland with extensive meadows also increases the heterogeneity of the landscape.
- 4 The results and the comparison with related studies clearly shows that animal populations are never completely determined by the vegetation. Depending on the local environment, other factors may play a more important role than the dietary or structural composition of the vegetation.

Field margins as ecological compensation areas?

Säume als ökologische Ausgleichsflächen? 83 pp.

CLAUDE THÉATO

- 1 Agricultural intensification has led to a considerable loss of species in the cultural landscape, mainly due to the disappearance of specific landscape features. As a countermeasure, Swiss agricultural policy offers various types of ecological compensation areas since 1993.
- 2 Field margins, i.e. herbaceous strips along fields and meadows, are a potential element of ecological compensation, but not yet recognised as such. Herbaceous strips are defined here as species-rich permanent vegetation types between crop fields, along meadows, pastures, lanes, ditches and wood. Once established, these strips are mowed only once each year or every second year, and no fertilisers or pesticides are applied. The project „Species-rich field margins in the lowlands of Switzerland“ was set up to assess the contribution of herbaceous strips along fields to enhancing the ecological value of the cultural landscape.
- 3 In this thesis, a floristic survey of existing strips along crop fields and meadows was carried out to establish a reference for the evaluation of sown strips. Differences between strips as well as the factors determining species richness were investigated. In addition, qualitative interviews were conducted with farmers to investigate their attitude towards strips.

- 4 Species composition and species richness varied strongly among geographic regions, and many species were recorded in only one of the regions. The total species number per strip correlated positively with the length and width of the strips and negatively with the average nutrient indicator value of the vegetation. Species richness in strips along fields was lower than in those along meadows. Species-rich strips were characterised by a higher cover, biomass and diversity of legumes (Fabaceae) than species-poor ones.
- 5 The interviewed farmers viewed strips rather negatively. The margins of large fields were the only place where they could conceive establishing strips. Farmers were concerned about practical issues and about problems with weeds or pests. They disliked the idea of taking valuable ground out of production and questioned the ecological value of herbaceous strips.
- 6 Several recommendations for the successful integration of strips in the cultural landscape can be derived from this study. First, it is important that the vegetation of strips does not include problematic weeds that might disperse into adjacent farmland. Second, strips should not be compared to fallows as regards their ecological function, but rather to hedge margins, which are also narrow linear landscape features in the intensively cultured farmland. Third, the mowing date should not be fixed, but adapted to the vegetation development, so that farmers can use the hay and get some benefit from the strips.

The impact of cattle ranching on the large-scale vegetation structure of a coastal savanna in Tanzania

Der Einfluss der Beweidung auf die grossräumige Vegetationsstruktur einer Küstensavanne in Tansania;
35 pp.

MATHIAS TOBLER

- 1 Bush encroachment in savanna ecosystems is often ascribed to grazing pressure by domestic herbivores. To study the effects of 50 years of cattle ranching on the vegetation structure of a large ranch on the coast of Tanzania a vegetation map was created using a Landsat TM satellite image. Sixteen different vegetation types were identified. A multispectral classification using the maximum likelihood algorithm gave good results even in this patchy and heterogeneous environment.
- 2 The comparison of the vegetation on the ranch with an adjacent game reserve showed that open grasslands covered larger areas in the game reserve. The bushland/grassland ratio, which was used to quantify bush encroachment, decreased from 1.2 in the more intensively used part of the ranch to 0.4 in the game reserve. This indicates that cattle ranching led to a strong increase in bush cover compared to the game reserve where native herbivores were present.
- 3 Bush encroachment showed a clear pattern in relation to the paddocks where cattle were kept at night. It was highest between 300 and 2500 m from the paddock and showed a peak at about 900 m, after which it decreased with increasing distance. Differences between paddocks could mostly be explained by the amount of available grazing area. Paddocks with larger grazing areas had a lower overall bush encroachment.
- 4 More than 50% of the area of the ranch lay within the zone of high bush encroachment as a result of the relatively short distances between paddocks (4-8 km). While the total stocking rate was probably still within the carrying capacity of the ranch, areas close to

the paddocks were under strong grazing pressure and showed high rates of bush encroachment. Grazing patterns therefore play an important role in range management.

- 5 By using a vegetation map derived from a satellite image not only could the pattern of the total bush cover be described, but also

different bushland vegetation types be distinguished. It could be seen that different bushland types are dominant in different areas of the ranch.

Nature meets Pasture. Landscape ecological survey within the project 'Feld-Wald-Weide' (research farm Litzibuch)

Nature meets Pasture. Landschaftsökologische Grundlagenerhebungen im Rahmen des Projektes Feld-Wald-Weide (Forschungsbetrieb Litzibuch); 40 pp. + App.

GEORG VON ARX

- 1 Diversity and heterogeneity in vegetation is mainly determined by the type of management and the intensity of land use. Landscape structures such as field edges and hedgerows play a key role in landscape diversity, particularly in intensely used agricultural areas. The objective of the project „Feld-Wald-Weide“ is to upgrade the farmyard Litzibuch ecologically by creating edge structures and hedgerows. This study investigated the spatial distribution of diversity and heterogeneity in agricultural vegetation in relation to management and to the proximity of edge structures with higher diversity.
- 2 Vegetation was sampled according to a systematic design in both edge structures (along ways and forests) and agricultural land of Litzibuch. Four types of management with declining intensity were distinguished: cereal field > high-production meadow > permanent pasture > low-production meadow. Various measures of diversity were calculated; the spatial distribution of vegetation diversity and heterogeneity was related to management type and to the distance from edge structures by means of GIS.
- 3 Edge structures showed the greatest diversity and supported almost all plant species

recorded in the study area, whereas agricultural land supported hardly more than half of the species. Vegetation diversity and heterogeneity increased significantly with declining land use intensity and declined (slightly) with increasing distance from edges. Heterogeneity varied more along these gradients than diversity. Intensity of land use proved to be a key factor explaining the distribution of diversity and heterogeneity, and within a particular management type, the effects of distance from edge were not obvious.

- 4 Edges as diversity ‘hotspots’ seem to have only a minor radiating effect into neighbouring agricultural areas. They are still an important habitat for many (threatened) plant and animal species. Therefore, efforts should be made to increase the value of existing edges. Wildflower strips could represent an additional different and valuable habitat type.
- 5 As crop production remains the main target of Litzibuch, there is no free choice of management type. A crop rotation could still substantially increase the heterogeneity of landscape structures, and thereby of species communities.

Fen rotation fallow near lake Greifensee (ZH): botanical and conservational assessment after 14 years of management

Ried-Rotationsbrache am Greifensee (ZH): botanische und naturschützerische Bewertung nach 14 Jahren Bewirtschaftung; 79 pp.

MANUEL WINTELER

- 1 Traditionally, fen meadows were annually mown in relatively small plots at different dates during autumn. This management resulted in a richly structured habitat for many animal and plant species. In the seventies, this management was replaced by large-scale simultaneous mowing for economical reasons. This resulted in a loss of vegetation structure, which endangers many arthropods. An alternative form of management is fen rotation fallow (German: Ried-Rotations-Brache, RiRoBra), which, in regular cycles, always leaves certain strips unmown. This should counteract the decrease of arthropod diversity. Such a RiRoBra test area (0.9 ha) was set up in 1987 in a *Schoenus* fen near lake Greifensee (canton Zurich); strips of 10 m by 60 m are left unmown every fifth year in a rotation scheme.
- 2 In this study the vegetation of the RiRoBra plots was investigated after 14 years of management and compared to the condition at the very start as well as to the vegetation of neighbouring control plots mown annually. Moreover, within the RiRoBra area, fallow strips were compared with strips mown in the previous year. Differences in species composition, vegetation structure, phytomass (above ground biomass and litter) as well as phenology and vitality of individual species were assessed to evaluate how RiRoBra management affects the vegetation structure in the short term and whether it reduces species richness or promotes undesirable plant species in the long term.
- 3 One-year fallow clearly affected the vegetation structure and microclimate. At the beginning of the vegetation period (May 2001) the phytomass at 0-10 cm in the fallow strips was twice that in the mown strips (479 g m^{-2} versus 239 g m^{-2}), and the same applied for total phytomass (674 g m^{-2} versus 299 g m^{-2}). In the course of the vegetation period the difference decreased slightly (total phytomass at the beginning of August: 823 g m^{-2} versus 456 g m^{-2}). A smaller proportion of sunlight reached the soil surface in the fallow strips compared to the mown strips: in May 14% versus 52%, in June 8% versus 30%. There were also fewer vegetation gaps (sunflecks) in the fallow strips than in the mown (in May 1.2% versus 38%).
- 4 Early Marsh Orchid (*Dactylorhiza incarnata*) blossomed at least one week later in the fallow than in the mown strips. Furthermore, infructescences were 16% shorter in the fallow strips than in the mown ones. This shows a negative effect of fallow on the vitality of this species, but also that recovery is achieved in the following years with mowing.
- 5 Tall-growing forbs or shrubs did not spread noticeably during the 14 years of RiRoBra management. Only the two rhizomatous plants Fen Rush (*Juncus subnodulosus*) and Common Reed (*Phragmites australis*) increased in frequency since 1989 by 100%

and 17%, respectively. Several orchid species as well as Grass of Parnassus (*Parnassia palustris*) and Devilsbit Scabious (*Succisa pratensis*) decreased in the RiRoBra area between 1987 and 2001. But similar changes also occurred in the surrounding annually

mown area, so that an effect of RiRoBra can be practically excluded.

- 6 From a botanical point of view, fen rotation fallow over a period of 14 years is not negative as long as the cyclical fallow phases are limited to one or at most two years.

Effects of wet-dry cycles on the germination of wild plant species

Einfluss von nass-trocken-Zyklen auf die Keimung von Wildpflanzenarten; 36 pp.

SERGE ZAUGG

- 1 In nature many seeds experience fluctuations in moisture conditions ('wet-dry cycles'). Such fluctuations may indicate times favourable for seedling establishment (e.g. the formation of a vegetation gap). It is therefore possible that wet-dry cycles have a signal function for seeds, stimulating their germination when establishment is most likely to be successful, or inhibiting germination when establishment success is likely to be low. However, rather little is known about the effects of fluctuations in moisture conditions on the germination of wild plant species
- 2 This thesis tested the following hypotheses: (a) wet-dry cycles can either increase or decrease the percentage of seed germination, depending on the species and on the number of cycles; (b) species from wet and dry habitats respond differently; and (c) responses depends on the seed size.
- 3 The effect of 24-hour wet-dry cycles (14 h on filter paper saturated with water and nearly 100% air humidity ; 10 h on dry filter paper and 50-60% air humidity) on seed germination of 20 wild plant species was investigated. The seeds were exposed to one,

three or eight consecutive wet-dry cycles, and their subsequent germination was compared to a control without wet-dry cycles by determining the percentage of seeds germinated after 84 or 69 days at 20 °C, 14 h photoperiod and nearly 100% air humidity.

- 4 The percentage of germination of *Cirsium palustre* increased significantly after one and three wet-dry cycles. The percentage of germination of *Helianthemum nummularium* and *Potentilla argentea* increased significantly after eight wet-dry cycles. For all three species the percentage of germination after treatment was 20-25% higher than control. The percentage of germination of *Teucrium botrys* and *Galium palustre* decreased to about half after eight wet-dry cycles. Overall the percentage of germination of the 20 species was lower after 8 wet-dry cycles than after 1 or 3 such cycles.
- 5 It is concluded that 24-hour wet-dry cycles are of relatively little importance for a majority of species. In some species, wet-dry cycles may contribute to regulating the time and place of germination. However, responses were not related to the species' natural habitat (wet vs. dry) nor to their seed size.

Ph.D. Theses (7)

The dynamics of thicket clumps in the Kagera savanna landscape, East Africa

Die Dynamik von Gebüsch in der Kagera-Savannenlandschaft in Ostafrika; 306 pp.

URS BLOESCH

- 1 The Kagera savanna landscape in East Africa covers about 30'000 km² in the border area of Rwanda, Uganda and Tanzania. The tree-grass ratio of this savanna landscape continuously changes according to site-specific dynamics. A better understanding of this dynamics and its driving forces is a prerequisite for an appropriate savanna management. This thesis studied vegetation dynamics at the transition from thicket clumps to open savanna, both on plain with grass savanna and on hillside with shrub savanna.
- 2 A survey of the vegetation structure, floristic composition and soils of 32 thicket clumps and their surrounding savannas showed that the two vegetation types have distinct structure and floristic composition and are separated by a sharp ecotone. Soils also differ, with higher pH and nutrient contents and distinct texture in thicket clumps although both vegetation types have the same parent material. These differences suggest that the presence of dense tree or shrub cover and termites (especially on plain) has profoundly altered the soil properties of thicket clumps, and that the genesis of the analysed thicket clumps must have started at least some decades ago to allow such changes to occur.
- 3 Several factors proved important in determining vegetation dynamics. As regards climate, the rainfall patterns within the Kagera Region are remarkably irregular in time and space, causing varying primary production, which in turn affects herbivory and fire hazard. Fire regime is determined by human influence in the Kagera Region, as natural fires occur seldom since most thunderstorms do not coincide with dry periods and are accompanied by rainfall. Changes in land use modified the fire regime: the traditional pastoral late burning regime became more of an agricultural early burning regime. Also, due to political insecurity in recent decades, most current firing happens in an uncontrolled way at the beginning of the dry season and is not in relation to land use. Thicket clumps (semi-deciduous forests) and gully forests are quite resistant to fire since burning only scorches the edge of these forest formations. Therefore, hot late burning only causes a small gradual regress of the edge, whereas low-intensity early burning and even more, no burning promote the expansion of thicket clumps. Intense browsing, mainly by elephants, may lead to a regress of thicket clumps. Termite (*Macrotermitinae*) mounds favour the growth of woody plants, especially on seasonally waterlogged plains, by providing fire protection, better drainage and often increased soil fertility.
- 5 Factors determining the tree-grass ratio proved to be strongly interactive. They do not only determine the savanna dynamics through a continued impact of similar importance (e.g. climatic conditions), but often act as abrupt, short-lasting disturbances (e.g. stormflow). A simulation of thicket clump dynamics on hillsides underlined the importance of fire and browsing on slope.
- 6 The main determinants of the tree-grass-ratio and its dynamics appeared to depend on the geomorphologic position. On plain, thicket clumps are restricted to termite mounds. Since intraspecific competition dictates a minimal distance between neighbouring *Macrotermitinae* colonies, thicket clumps do not grow together. Fire and the current herbivory may only slightly modulate the

physiognomy and extension of the thicket clumps. The longevity of the termitaria (recolonisation of abandoned mounds) and their mutualism with the vegetation allows a stable vegetation mosaic over centuries. By contrast, on stony hillside the dynamics of the vegetation mosaic is high and determined by several factors together. New thicket clumps can arise on termite mounds or in areas with a high proportion of stony blocks or bare soil providing a certain fire protection. Thicket clumps can expand if the intensity and frequency of fires is low and if browsing impact remains modest. This process is accelerated by a high proportion of stony blocks and reverted by intense fires or increased browsing impact.

7 The results of this study show that thicket clumps and semi-deciduous forests are not relicts of previously large forests, but dynamic parts of the savanna landscape. More generally, results imply that savannas are not intermediates between grassland and forest. Rather, they represent an own biome, with typical floristic composition, structure and function. Under the current climatic conditions, all savannas with the exception of derived ones would have a savanna climax with the proportion of woody plants depending on the aforementioned main determinants as well as on past and current disturbances.

The role of the transmission mode for grass endophyte evolution

Die Funktion der Übertragungs-Art für die Evolution von Gras-Endophyten; 134 pp.

DOMINIK BREM

1 Fungi of the genus *Epichloë* (Ascomycota, Clavicipitaceae) and their asexual descendants of the genus *Neotyphodium* are endophytes of many grasses in the subfamily Pooideae. Their two alternative modes of reproduction characterize two types of symbiosis with the host plant. In the sexual cycle, the fungus is parasitic, since flowering and seed set is suppressed by the formation of stromata (choke disease). In contrast, asexually reproducing endophytes are asymptomatic and invade the host seeds for dissemination. This symbiosis is mutualistic, as endophyte infection causes enhanced herbivore and pest resistance, increased drought tolerance and superior competitive abilities. Whereas most previous studies focused on important pasture grasses in an agronomic context, this thesis focused on wild endophyte-grass associations.

2 *Epichloë sylvatica* is a host-specific endophyte of the common woodland grass *Brachypodium sylvaticum*. In nature, all *B. sylvaticum* plants are infected predominantly

by asexual genotypes, whereas choking strains are rare and restricted to small clusters within some populations of *B. sylvaticum*. Questions asked in the thesis were: (1) why is the endophyte *E. sylvatica* so successful in nature and (2), how frequent is horizontal transmission of *E. sylvatica* and which are the routes of contagious infections?

3 A herbivory bioassay, using *Spodoptera frugiperda*, showed that infected *B. sylvaticum* plants were better protected from herbivores than uninfected plants. However, in an intraspecific competition experiment in the greenhouse, infected *B. sylvaticum* plants performed worse than uninfected plants. By contrast, infected *Bromus benekenii* plants, naturally occurring in the same habitat, performed significantly better than the uninfected plants. Therefore, effects of different factors have to be considered in a more holistic view to understand endophyte associations of wild grasses. Under natural conditions, many factors are interacting and the outcome is a combination of beneficial and less beneficial effects.

- 4 Transmission of *E. sylvatica* by means of ascospores was assessed with a transplanting experiment and in an experimental field plot. Results indicated that contagious spread of *E. sylvatica* to uninfected plants is very frequent. At two sites where sexual stromata of *E. sylvatica* were present, 34% and 17%, respectively, of the uninfected transplants became infected after two years. This was confirmed in the experimental field plot. However, the previously assumed route of infection via the stigmata of the host florets could not be verified experimentally.
- 5 Aspects of speciation and coevolution of the endophyte symbiosis were investigated in *Epichloë bromicola*. This endophyte infects at least three different grass species of the genus *Bromus*. On *B. erectus*, only sexual reproduction is observed, while on two other hosts, *B. benekenii* and *B. ramosus*, the endophyte is asexual. Results from AFLP fingerprinting analysis and from phylogenies based on *tub2* and *tefl* sequences indicated that asexual and sexual isolates of *E. bromicola*, isolated from three different *Bromus* species did not belong to a single, randomly mating population, but form genetically differentiated subpopulations. Asexual strains infecting *B. benekenii* and *B. ramosus* appeared to be descendants of the ancestral sexual species on *B. erectus*. Adaptation and reproductive isolation after host shift presumably resulted in the observed host specificity of strains infecting *B. benekenii* and *B. ramosus*. Hence, asexual endophytes of *E. bromicola* probably represent a distinct incipient species.

Mechanisms and extent of vegetation changes in differently managed limestone grasslands

Mechanismen und Ausmass von Vegetationsveränderungen in verschieden bewirtschafteten Halbtrockenrasen; 88 pp.

BARBARA KÖHLER

- 1 As a semi-natural vegetation, limestone grasslands need management to maintain high species richness including rare and endangered species. The traditional management in northern Switzerland, annual hay-making in July, is no longer economical for farmers and therefore subsidised by nature conservation authorities. To assess whether less expensive forms of maintenance would be sufficient to preserve the botanical diversity, a management experiment was set up in 1977–78 in two nutrient-poor *Mesobrometum* grasslands near Schaffhausen. Each of six treatments (mowing in July annually, every second year or every fifth year; mowing annually in October, controlled burning in February–March and no management) was replicated three times per site in plots of 10 m x 5 m.
- The aim of this thesis was to assess the long-term effects of the treatments on vegetation and soil.
- 2 Vegetation changes from 1977 to 1999 were investigated with correspondence analysis. In plots with controlled burning and without management, the species composition varied most among replicate plots. The 16 most abundant and/or most typical limestone grassland species responded similarly to management at both sites. Besides considerable annual fluctuations partly explained by fluctuations in annual precipitation, directional changes due to management were apparent for the whole vegetation and for single species. A species composition typical of each management had established itself after 13 years and the changes continued up to year 22 in the same way. At the best site the number of species

in the traditional management was 50 species per 36 m²; this number decreased under burning or abandonment to 36 species per 36 m². The intensity of shrub encroachment depended strongly on the distance of the forest fringe and its species composition. All together, these results indicate that the timing, frequency and form of management considerably influence the plant species composition. Since each treatment proved favourable to some typical limestone grassland species, a combination of management types would lead to maximal diversity.

- 3 The role of various plant traits in determining species performance under different management types was analysed, based on differences in species composition and above-ground phytomass observed after 21 years of management at one of the sites. The following traits were considered for a total of 91 species: plant height, growth form, capacity of below-ground nutrient storage, below-ground lateral spread, leaf persistence, and start of flowering. Plant traits helping to retain nutrients in the plant biomass proved to be decisive. In regularly mown plots, such traits are primarily low height and rosette growth form, which minimise the loss of biomass caused by mowing. In plots managed less frequently or later in the year, the ability to withdraw nutrients in autumn is increasingly important. Tall growth, fast lateral spread and large nutrient storage capacity are promoted in burnt or unmanaged plots; species with these traits constitute a potential threat to the rare species of limestone grassland vegetation under burning or abandonment.
- 4 The availability and limitation of nitrogen and phosphorus were assessed in a bioassay with soil from plots mown annually in July and

from plots unmown for 21 years at one of the sites. The phytometer species were *Galium mollugo s.str.* L. and *Raphanus sativus ssp. oleiferus* (DC) Metzg. The former were grown for 8.5 weeks and the latter for 5 weeks in pots supplied weekly either with a complete nutrient solution or with solutions lacking N or P or both. Both N and P limited plant growth, but P was slightly more limiting. This was only apparent with *Galium* seedlings because *Raphanus* seedlings had relatively high P reserves in their seeds. The availability of N and P was generally extremely low in the studied soils. The availability of N (but not P) was slightly higher in the soil of unmown plots than in the soil of annually mown plots. However, this difference probably has only a small effect on the vegetation because of the prevailing P limitation. Overall, abandonment only caused small changes in soil N and P.

- 5 According to the results from this long-term study, the best strategy for achieving and maintaining a high species diversity is probably a mosaic of different management types. Mowing every second year in July resulted in a species composition similar to the traditional management and could therefore be applied to reduce management costs. Annual mowing in October can also be recommended within a mosaic of different management types, unless a site is exposed to seed rain of thermophilous forest fringe forbs: the latter can become dominant under late mowing, especially at more productive sites. A mosaic of different management types would avoid large areas being mown at the same time, and thus maintain a highly diverse habitat also for animal species.

On the ecology and evolution of seed transmission and choke formation in *Epichloë sylvatica*, a grass endophyte of *Brachypodium sylvaticum*

Über die Ökologie und Evolution der Übertragungsmechanismen beim Erstickungsschimmel Epichloë sylvatica, ein Endophyt von Brachypodium sylvaticum; 70 pp.

GERRIT MEIJER

- 1 The Grass endophyte *Epichloë sylvatica* (Clavicipitaceae, Ascomycetes) is specialised on *Brachypodium sylvaticum*, a caespitose woodland grass, and can express both sexual and asexual reproduction cycles on this host. In natural populations almost all host plants are infected by the endophyte. Infections are mostly asymptomatic (no choking) and only in a few populations sexual reproduction is observed. The main question of this thesis was: how and why has asexual seed transmission evolved, and is sexual reproduction maintained in *E. sylvatica*?
- 2 A genetic survey using isozymes revealed that fungal populations consist of asexual and sexual subpopulations that are differentiated at the tiller level. Grass clumps were infected by up to three different fungal genotypes. The sexual subpopulations showed always genetic variation and were not geographically structured (representing a single mating population). The asexual subpopulations were also variable, but only in populations where choke-forming plants occurred, and they were geographically clearly structured. By contrast, only a single genotype was found in all examined populations without sexual reproduction.
- 3 A factorial field experiment with three environmental factors (atmospheric CO₂ concentration, nutrient level, and shading) and a genetic factor (nine natural combinations of host plants and fungi) investigated which factors determine the reproduction mode of *E. sylvatica* and whether the two reproduction modes differ in their effect on plant fitness. Plant growth and the proportion of reproducing tillers that were choked were recorded. About 80% of the total measured variation in choke rate was explained by the genetic factor, the combination of host and fungus. The unintended high rate of horizontal infections during the experiment suggested that uninfected plants are more susceptible to horizontal infections by choking strains than plants infected by seed-transmitted strains. These horizontal transmissions were more frequent in shaded plots than in unshaded plots .
- 4 In a further experiment, I artificially infected seedling families (= seedlings with the same mother) with selected fungal strains to determine whether the plant or the fungal genome determines the reproduction mode of *E. sylvatica*. The artificial combinations were evaluated for their choke rates, which clearly showed that the fungal genome controls the reproduction mode.
- 5 It is proposed that the sexual subpopulation can only persist if the local environment allows for sufficient horizontal transmissions, while the ability to superinfect already infected host plants is essential for this process. At the same time superinfection imposes a selective pressure on the host in favour of infections by seed-transmitted strains, which explains the success of seed-transmitted strains in the presence of choke forming strains. The genetic uniformity of *E. sylvatica* in asymptomatic populations and the high prevalence of infection in these populations may be explained by the superior, for the host most beneficial character of this fungal strain.
- 6 With regard to directional selection on asexuality and mutualism of *E. sylvatica* it is difficult to draw conclusions, because these traits are tightly linked to vertical transmission and seed dispersal. A strong

selection on the mode of dispersal might override a weaker selective force on the other

traits.

Effects of afforestations with non-indigenous (foreign) conifers on the mycoflora in the deciduous forest belt in Southern Switzerland (TI, S. Antonino, Copera)

Einfluss von Aufforstungen mit standortsfremden Nadelbaumarten auf die Pilzflora im Laubwaldgürtel in der Südschweiz (TI, S. Antonino, Copera); 208 pp.

NERIA RÖMER

- 1 This thesis investigates the impacts of planted non-native conifers on the local mycoflora associated with broadleaf trees. The aim was to determine to what extent changes in the diversity of macromycetes, in ectomycorrhizal presence on fine roots of host trees and in humus formation can be explained by host specificity, by changed site conditions or by the introduction of non-native fungus species.
- 2 Between July 1995 and December 1998, macromycetes were surveyed in 17 permanent plots (216 m²) within the afforestation area of Copera near Bellinzona (southern Switzerland), at an altitude of 500–800 m a.s.l. Four reference plots were located in autochthonous deciduous forests (*Castanea sativa* and *Fagus sylvatica*), and 13 plots under planted, allochthonous conifers viz. *Pseudotsuga taxifolia*, *Picea excelsa*, *Pinus sylvestris*, *P. strobus*, *P. nigra* and *Larix decidua*. Physical and chemical properties of the soil, precipitation, minima and maxima of temperature, and the morphology of the ectomycorrhiza on rootlets of the host trees were monitored. All basidiomes of ectomycorrhizal fungi occurring in and close to the plots were mapped.
- 3 On 119 sampling occasions, a total of 13'131 basidiomes was recorded, taxonomically belonging to 342 species, of which 93 % were Basidiomycetes, 5 % Ascomycetes, 1 % Myxomycetes and one species Zygomycetes. A total of 114 ectomycorrhizal species, 17 lignicolous and 40 terricolous saprobic species and 10 parasites were also registered. The phytosociological survey yielded only 78 species of phanerogams and eight species of pteridophytes.
- 4 The different forest types studied in Copera were better differentiated by macrofungi than by plant species composition. The diversity of macromycetes in autochthonous deciduous forests was higher than in plots with planted exotic conifers. The ratio of ectomycorrhizal to saprobic fungi was 1.0 in chestnut forest, but only 0.3 in Douglas-fir stands. Average values of this ratio in stands of deciduous and of coniferous trees were 0.7 and 0.4, respectively.
- 5 Basidiomes of all observed fungal species appeared earlier in the season in exotic conifer forests than in deciduous forests. Basidiomes of most species occurred closer to the trunks of trees under spruce (distance of 0.6 - 1.0 m) and Douglas-fir (0.6 - 2.0 m) than in broadleaf stands (distance of 2.1 - 2.5 m). On the rootlets of host trees, 18 morphotypes were distinguished for chestnut, 7 for beech, 4 for spruce, 6 for White pine and 10 for Douglas-fir. On many rootlets of exotic conifers, in particular those of Douglas-fir, no ectomycorrhizal sheaths at all were detected.
- 6 Mormoder is the most frequent type of humus under coniferous trees, whereas mullmoder dominates in soil profiles of the autochthonous deciduous forests. In general the two types of forests did not differ regarding pH and nutrient content nor in climatic parameters (precipitation, T max., T

min.). The differences in fungal species diversity were therefore not due to changes in abiotic conditions, but can rather be

explained with the host specificity of the fungi and the presence of introduced species.

The influence of management on the floristic composition of hay meadows

Einfluss der Bewirtschaftung auf die Artenzusammensetzung der Vegetation von Mähwiesen; 80 pp.

SYBILLE STUDER

- 1 This study assesses at a regional scale the effects of different management practices on the plant species composition of agricultural grasslands in the Schaffhauser Randen in Northern Switzerland. Three types of grasslands were investigated: (1) "Extensively" used grasslands are not fertilized and are cut only once, in July or August; (2) "Less intensive" management comprises moderate fertilization (manure) and two cuts per year; (3) "Medium intensively" managed sites are cut two or three times per year and are fertilized with slurry or mineral fertilisers. The following three questions were investigated : How has the species composition of grasslands been affected by management, past and present? What roles do seed and recruitment (microsite) limitation play in differently managed grasslands? Do species that occur in differently managed grasslands show genetic adaptation to the different habitats?
- 2 The vegetation of grasslands was surveyed with a spatially stratified design to describe the different types of grassland and relate their species composition to management history. Management had strongly affected the grassland communities in terms of species composition and dominance structure. Species richness was considerably lower in more intensively used grasslands and a large part of the variation in species composition could be explained by management intensity. Where management intensity had been reduced from medium intensive to less intensive, soil fertility was reduced and species composition increased within a few years (since 1992).
- 3 A two-year seed addition experiment was carried out to investigate whether species diversity is limited by seed availability. Seeds of 24 species were sown in established vegetation of the differently managed grasslands. Half of the experimental plots were disturbed by scraping the soil surface and removing mosses. Most species were able to establish, though the numbers of individuals were generally low. Establishment tended to be higher in extensively used sites than in intensively used ones. Disturbance played a minor but significant role in promoting recruitment.
- 4 The results suggest that seed limitation can be an important factor limiting species richness in these grasslands, but that recruitment limitation occurs in intensively managed grasslands, where the recruitment of some species was probably prevented by low light availability in the dense vegetation. Less intensively managed sites did not provide more favourable conditions for establishment than medium intensive sites. We conclude that a more considerable change in vegetation structure is needed to enhance microsite availability for germination.
- 5 Genetically determined variation in plant traits of three species that occur in all three grassland types (*Plantago lanceolata*, *Lotus corniculatus* and *Campanula rotundifolia*) was investigated in a common environment experiment. The aim was to assess the role of genetic adaptation in enabling these species to survive in strongly differing grassland types. *Plantago lanceolata* showed

an increased growth rate of the flower-stalk, indicating an adaptation in timing of flowering to the earlier cutting of the vegetation. *Campanula rotundifolia* showed higher root biomass in plants originating from extensively used sites. Increased allocation of resources to root biomass can be seen as an adaptive response to enhanced

nutrient acquisition in habitats with low nutrient availability. These results suggest that genetic adaptation may develop within a relatively short period (15–30 years) as a consequence of changes in management practices.

The influence of wildflower strips on plant and insect (Heteroptera) diversity in an arable landscape

Der Einfluß von Buntbrachen auf die Diversität von Pflanzen und Insekten (Heteroptera) in einer Ackerlandschaft; 127 pp.

KARIN S. ULLRICH

- 1 Wildflower strips are strips of land at least 3 m wide running across or along the edge of an arable field. They are usually sown with a mixture of indigenous arable weeds and species of ruderal sites and meadows. This study investigates the plant and insect diversity establishing in wildflower strips in the Klettgau, an arable landscape in Switzerland, and the factors influencing this diversity. The aim was to evaluate the contribution of wildflower strips to biodiversity on a landscape scale, and to generate recommendations for their optimal management. The true bugs (Heteroptera) were chosen as an indicator group for total insect diversity.
- 2 The vegetation of wildflower strips differing in age since establishment (1 to 5 years), substrate, seed mixture and management was surveyed to establish the factors affecting floristic diversity, the presence of rare arable weeds, and the vegetation types found in wildflower strips; vegetation types were described both in terms of plant species composition and in terms of species traits. A total of 234 plant species were recorded, of which the vast majority had recruited spontaneously. Results showed that species diversity and the number of rare species are highest in the first year after establishment (on average 29 species in four 1-m² plots).

First-year strips also have a distinct species composition compared to older strips. From the second year on, the seed mixture applied also has a strong influence, and site factors like the soil conditions and surrounding land use become increasingly important. While spontaneous annual therophytes dominate in the first year, sown perennial species are taking over from the second year on, which are again gradually replaced by spontaneous perennial species. This rapid succession means that wildflower strips will only maintain a diverse vegetation for several years if the pressure of grasses and agricultural weeds is relatively low.

- 3 The soil seed bank was studied in six wildflower strips and adjacent arable fields. Wildflower strips had significantly more species in the seed bank than arable fields (a total of 51 vs. 24 species were found in the uppermost 7 cm of soil), but rare species remain scarce. Thus, the recovery of rare populations in wildflower strips could be greatly assisted by *in* and *ex situ* propagation. The species composition of the seed bank differed from that of the vegetation; these differences could be explained in terms of the seed longevity, life form and life history of the various species.
- 4 The abundance and species composition of true bugs was surveyed in 20 of the wildflower strips with a sweep-net method

during a whole growing season. Colonization and establishment patterns of bugs were analysed in terms of responses of species traits to successional change and environmental factors. Many of the bug species appear able to colonise new strips rapidly. Nevertheless, the number of species and the number of individuals were lower in first-year strips than in older ones. Both were positively correlated with the number of perennial plant species and with the structural diversity of the vegetation. Bug species composition depends on the age and grass cover of wildflower strips. Specialized bug species (in terms of food selection) mostly occur in older strips, as do species with only one generation per year and species overwintering in the egg stage.

- 5 A dispersal experiment tested the ability of bugs to colonize monocultures of their host plants at various distances (0 to 138 m) from a wild flower strip serving as dispersal source. The results showed that wildflower strips serve as a source of dispersal for at least some bug species, and that most bug species occurring in wildflower strips are relatively mobile. However, bug species differ in the speed, distance and patterns of dispersal.
- 6 It is concluded that wildflower strips can support a high diversity of plants and insects. In both plant and bug communities, species composition is very variable and responds more strongly to environmental factors than does species number. A high grass cover has a negative effect on the species composition of plants and bugs, and tends to enhance a few common species. Therefore, sites known to have a high pressure of grasses or to contain other problem weeds should be avoided when establishing wildflower strips. Rare plant and bug species tend to have a local distribution. To maximise species diversity wildflower strips should be managed heterogeneously and should be well dispersed across the landscape.