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## Summaries of diploma and PhD theses (2000)

### Diploma theses (14)

#### **Mechanical anchorage of saplings and cuttings of woody pioneer species in the floodplain of the Tagliamento river, north-eastern Italy**

*Mechanische Verankerung von Jungpflanzen und Stecklingen von Pioniergehölzen in den Wildflussauen des Tagliamentos, Nordostitalien; 56 pp. + App.*

SILVIO BLASER

1 Periodic flood events are responsible for frequent disturbance of differing intensity in natural river ecosystems. Therefore, the establishment of pioneer plants requires not only effective sexual and vegetative regeneration, but also rapid anchorage to the substrate, so that minor floods can be resisted.

2 In the present study the growth form and anchorage of two woody pioneer species, *Salix eleagnos* and *Populus nigra*, were investigated at the Fiume Tagliamento in NE-Italy, one of the last large unimpacted Alpine rivers. Anchorage was measured as pullout resistance, using a special gauge for measuring maximal force during vertical uprooting. The influence of sediment type and growth parameters on uprooting resistance was investigated in saplings and cuttings of both species. Cuttings were planted in a field experiment in the study area as well as in a garden experiment in the Botanical Garden of the University of Freiburg im Breisgau (D).

3 Naturally grown saplings of *S. eleagnos* required a significantly higher force for uprooting ( $723 \pm 59$  N) than those of *P. nigra* ( $542 \pm 47$  N). Pullout resistance strongly correlated with aboveground biomass, root surface area and sediment type. Growth forms of *Salix eleagnos* and *Populus nigra* already differed in the juvenile stage. Saplings of *P. nigra* grew higher than saplings of *S. eleagnos* with similar above-ground biomass. Under undisturbed

conditions, *P. nigra* should therefore have an advantage in terms of light competition, whereas *S. eleagnos* should benefit from better anchorage in a more disturbed environment.

4 Planted cuttings of *S. eleagnos*, and to a lower extent those of *P. nigra*, were severely affected by the harsh growth conditions of the floodplain, so that resprouting rate, biomass production and uprooting resistance were lower in the field than in the garden. The pullout resistance of cuttings was very low compared to naturally grown saplings with same biomass.

5 The results of this work indicate that river regulation measures reducing the intensity of floods would result in an advantage of *P. nigra* compared to *S. eleagnos*, since *P. nigra* grows more rapidly under undisturbed conditions.

## Preservation of bulbous geophytes in vineyards of north-eastern Switzerland

*Erhaltung der Zwiebelgeophyten in Rebbergen der Nordostschweiz*; 102 pp.

ANNE-CATHERINE BRUNNER

1 The abundance of bulbous geophytes is decreasing in vineyards of north-eastern Switzerland. These plants depend on traditional vineyard management, which maintains bare soil by hacking every spring. This management method is time-consuming and promotes soil erosion. In contrast, modern vineyard management allows a herbaceous undergrowth to develop between rows. As a result, bulbous geophytes are subject to competition by other plants and to undergrowth management. The aim of the present study was to determine how site conditions and management history influence the abundance of bulbous geophytes in vineyards of north-eastern Switzerland.

2 The survey included 60 vineyard plots in the canton of Zürich containing at least one of the three bulbous geophyte species *Gagea villosa*, *Muscari neglectum* and *Ornithogalum umbellatum*, and 35 vineyard plots in the very close vicinity, with the same slope and exposure, but lacking the three focus species.

3 The distribution of the three geophyte species could partly be explained by climatic conditions: *Gagea* was only found in the north of the canton, where the climate is warmest and driest, whereas *Muscari* and

*Ornithogalum* occurred in the whole canton. Composition and structure of the undergrowth were apparently of minor importance for the distribution of geophytes. Only plots with the highest abundance of *Muscari* and *Ornithogalum* were characterised by a high cover of forbs and a high forb:grass ratio.

4 Management practices have a large impact on the three studied geophyte species, which were most abundant in plots that were not disturbed by undergrowth management from October till May. Tillage before or after this period promotes geophyte dispersal by separating daughter bulbs from the mother bulb. For small bulbs like *Gagea*, the tillage should be fine and only 10 cm deep; for large bulbs like *Ornithogalum*, it should be coarser and up to 20 cm deep. Tillage for *Muscari* should be intermediate. Soil compaction appeared detrimental to bulbous geophytes, especially *Gagea*.

5 Specific management measures are required to preserve and promote the three studied geophyte species. The accompanying expenditures need to be remunerated. Specific eco-points for label-production or well-directed marketing measures may lead to a competitive advantage for vine growers taking care of bulbous geophytes in their vineyard.

## Influence of ground water table, nutrients and competitors on the establishment and growth of four fen-meadow species

*Einfluss von Grundwasserstand, Konkurrenz und Nährstoffen auf Etablierung und Wachstum von vier Feuchtgebietsarten*; 47 pp.

ALEXANDER BURKARDT

1 Around Lake Nussbaumen in northern Switzerland, 50 ha of former agricultural land

will be restored to semi-natural wet grasslands similar to those before drainage in 1943.

This involves re-establishment of the characteristic plant species. In previous experiments, the establishment of target species by seeding or planting was more effective when the topsoil was removed. However, this method can hardly be applied on a large scale for practical reasons. The question is therefore whether it could be replaced by a method with lower environmental impact.

2 The three main factors influenced by topsoil removal are relative water table (distance from soil surface), nutrient conditions and competing plant species from the soil seed bank. If a single factor could be identified as inhibiting (directly or indirectly) the establishment of the target species, it might be possible to manipulate only this one factor and thus to avoid topsoil removal.

3 In two cross-factorial field experiments these three factors were tested for their effects on the germination rate of four wetland species (*Carex hostiana*, *Centaurea angustifolia*, *Iris sibirica*, *Lychnis flos-cuculi*) and on their

growth 72 days after planting on peat soil. Two levels (high, low) of relative water table and nutrients and three levels of competition (high, medium, low) were applied in each experiment.

4 A higher relative water table enhanced the germination rates of the target species by about 80% but had no effect on their mean biomass. The effect of relative water table on germination rates was stronger in the presence of competitors. Competition reduced the mean biomass of the planted species by 50 to 80%. The nutrient level had no significant effect on the biomass of the target species nor on their germination rate.

5 The results of this study suggest that if the topsoil cannot be removed, depletion of the soil seed bank to reduce competitors is the most effective method for the restoration of fen meadows, at least in the short term. Long-term studies with more levels of the factors are needed to substantiate this recommendation for wetland restoration.

### **Nunataks as glacial refugia during the Last Glacial Maximum? A molecular phylogeographic case study with *Draba aizoides* L. (Brassicaceae)**

*Nunatakker als Glazialrefugien in der letzten Eiszeit? Eine molekular-phylogeographische Fallstudie mit Draba aizoides L. (Brassicaceae); 67 pp.*

RENÉ FÜCHTER

1 During the Last Glacial Maximum, most parts of the Alps were covered by ice. Alpine plants could have survived this period either in peripheral refugia ("tabula rasa hypothesis") or within the Alps, on single mountain tops surmounting the general ice level ("nunatak hypothesis"). The aim of this study was to test the two hypotheses for the Brassicaceae species *Draba aizoides* L. by comparing chloroplast and nuclear genome data from refugial and newly founded populations.

2 Chloroplast DNA was studied in samples of 19 populations from the Swiss Alps, one from the Italian Alps and one from the French Pyrénées. A total of 500 individuals of *Draba aizoides* were analyzed to assess the distribution and frequency of seven groups out of a total of eleven haplotypes by a designed PCR-RFLP test. Nuclear genetic structure was investigated with starch gel electrophoresis of isozymes for 15 of the populations. The maternally inherited, non-recombining chloroplast genome was sup-



posed to show mainly historically grown structures, whereas the biparentally inherited, and hence more dynamic nuclear genome would rather provide information about the present state of the populations, as expressed by their fixation index ( $F_{ST}$ ), the inbreeding coefficient ( $F_{IS}$ ) and the heterozygosity ( $H$ ).

3 The geographical distribution of chloroplast DNA haplotypes revealed a generally low haplotypic diversity in the northern Alps. However, three nunatak areas (Säntis, Faulhorn and Stockhorn) had a higher haplotype diversity and harbored haplotypes which were otherwise only found in the central Alps, in the Pyrenées and in the Monte Baldo region in Italy. This occurrence of haplotypes unusual for the northern Alps might indicate that these three nunataks acted as glacial refugia.

4 Haplotypic diversity was generally much higher in the central than in the peripheral Alps. Three rare haplotypes were even found there exclusively. This pattern strongly suggests the additional existence of central or southern Alpine glacial refugia.

5 No effect of “isolation by distance” was found for nuclear DNA as indicated by isozyme loci, suggesting that postglacial recolonization history has had a strong impact on the genetic constitution of extant populations. Heterozygosity and genetic variability (mean number of alleles) did not generally differ between nunataks and recolonized areas of the same region. This may indicate considerable inter-populational flow of nuclear genes through pollen dispersal. However, on the Dent de Morcles (lower Rhone valley) a strongly diverging population was found in the summit region compared to lower areas (very high pairwise  $F_{ST}$  values) indicating that this mountain was probably also a nunatak acting as a glacial refugium.

6 As a whole, the results of this study make a postglacial recolonization from only outside the Alps very unlikely. The “tabula rasa hypothesis” was hence not supported by the available data, but results were consistent with the “nunatak hypothesis”.

## Extensive mowing of hay meadows in the Swiss Alps: an ecologically sensible management?

*Wildheuen: ökologisch sinnvoll oder Relikt aus alter Zeit?* 41 pp.

BEATRIX KÜTTEL

1 “Wildheuwiesen” are extensively used hay meadows in the Swiss mountain regions. They are cut once a year or only every second to forth year. The traditional use of these meadows has decreased over the last years owing to the intensification of favourable sites, the abandonment of low-profit areas, constructing activities, reforestation, and changed structures of agricultural production.

2 This study examined correlations between the landuse history of subalpine hay meadows, floristic diversity, the degree of erosion,

and the shrub cover to assess whether the maintenance of extensive mowing is preferable to other forms of management from an ecological point of view.

3 A total of 29 study sites were surveyed in the subalpine zone in the “Schächental” (Bürglen and Unterschächen) and in the “Maderanertal” (Bristen). The history of use was registered by questioning the farmers and by gathering data from a cultivation map from 1925. Plant species composition was recorded according to Braun-Blanquet on a scale from one to five.

Erosion and shrub cover were assessed qualitatively on a scale from one to four.

4 The use of hay meadows in corporate property has decreased over the last twenty years. In private meadows this tendency was weaker, but changes in cultivation occurred, e.g. from hay meadow to pasture. Meadows for which ecological payment is contributed experienced less change in use than those for which no payment is given.

5 Floristic diversity (number of plant species recorded per site) differed on average among the three study regions, probably due to differences in climate, soil chemistry, and historic management. The current type of management also greatly influenced the number of plant species, with an increase from perma-

nent pastures (85) to fallows (87), pastures with intermittent mowing (97), hay meadows (102), and finally, to mixtures of pasture and meadow (116). Thus, for the preservation of floristic diversity, the change of meadows to permanent pastures or their abandonment should be avoided.

6 Erosion and shrub cover were positively correlated. Both shrub cover and the degree of erosion were lowest in cut meadows and highest in fallows.

7 Since any change in the use of subalpine hay meadows leads to a higher erosion rate, higher shrub cover and reduced floristic diversity, it is recommended to further mow these meadows extensively, with a facultative sheep grazing.

## Role of birds in the dispersal of exotic plants

*Zur Bedeutung der Vögel für die Ausbreitung von exotischen Pflanzen*; 81 pp.

ALICE MÜLLER

1 Exotic fleshy-fruited woody species are currently spreading in the surrounding of towns in Switzerland. The purpose of this study was to examine whether birds can contribute to this dispersal. Two feeding experiments investigated the preferences displayed (1) by birds in the transitional silvan/urban habitat on the outskirts of the city of Zurich (free-range experiment) and (2) by two individual blackbirds (cage experiment) towards native and non-native fruits. Feeding preferences were compared with the chemical composition of the fruits.

2 In the free-range experiment, birds were offered exotic and native fruits using bird-specific feeders in ten gardens on the western slope of Mount Zurich. Two experimental series were run ("autumn fruits": 10 species, "winter fruits": 3 species), and the proportion of eaten fruits was recorded in 5-day and 2-

day cycles, respectively. In the cage experiment, birds were fed the autumn fruits with experimental cycles of half a day.

3 In the free-range experiment, fruit species differed significantly in the degree to which they were eaten. *Magnolia grandiflora* and *Sorbus aucuparia* were preferred most, and *Cornus sanguinea*, *Ligustrum vulgare* and *Berberis rubrostilla* least. Fruits of the exotic group were eaten more than those of the native group. Eating rates displayed high spatial and temporal variability. Differences in eating rates could best be explained in terms of overall profitability with respect to the fat and energy content of the fruits. This result agrees with predictions made by the optimal foraging theory.

4 In the cage experiments, individual differences between the two blackbirds were apparent. The preferred fruit species was *S.*

*aucuparia*. A large proportion (90%) of the seeds contained in eaten fruits could be recovered from faeces or regurgitated leftovers. Blackbirds may thus contribute, as legitimate seed dispersers, to the dispersal of plants with fleshy fruits.

5 Results from the free-range and the cage experiments differed most for the exotic fruits. A possible explanation for these differences is that the birds, being unfamiliar with such fruits, may vary in their reaction to them

on an individual basis. This can be seen as an indication that there is no close mutualism between frugivorous birds and plants with fleshy fruits.

6 It is concluded that potential dispersers for exotic plants with fleshy fruits exist in the city of Zurich, and that gardens provide diaspore sources for such plants. To assess whether an exotic species can disperse successfully, additional factors should be taken into account.

### **The identity and insect-mediated reproduction of systemic rust infections of *Berberis vulgaris***

*Die Identität von systemischen Rostinfektionen auf Berberis vulgaris und die Bedeutung von Insekten für deren sexuelle Fortpflanzung*; 44 pp.

ANDREAS NAEF

1 Witches' brooms on *Berberis vulgaris* are relatively common in Switzerland. They are induced by a systemic infection of a rust fungus pathogen, called *Puccinia arrhenatheri*. Similar to stem rust of wheat, this rust fungus has a life cycle with host alternation to a species in the Gramineae.

2 I sequenced the internal transcribed spacer (ITS) region of ribosomal DNA of systemic infections from different populations of *B. vulgaris* to determine intraspecific variation. I only found small sequence variation in the sequence of the ITS region of the pathogen among different populations.

3 I collected samples of grasses with rust fungus infections underneath infected *B. vulgaris* bushes and sequenced the fungal ITS region to identify primary grass hosts of the rust fungus. On an individual of *Melica nutans*, I found a pathogen that had an identical ITS sequence as systemic infections of *B. vulgaris*. This suggests that *M. nutans* may be used as primary host, in addition to the experimentally proven host alternation to *Arrhenatherum elatius*.

4 Sexual reproduction of rust fungi may depend on gamete transfer by insects. Witches' brooms on *B. vulgaris* bear yellow discolored leaves upon which the fungus presents its gametes (spermatia) in a sugary nectar. During the reproductive phase these leaves spread a strong scent, most likely to attract insects.

5 I used an insect-exclusion experiment to evaluate whether successful reproduction of *P. arrhenatheri* on *B. vulgaris* depends on gamete transfer by insects. Reproductive success was defined by the fungus' ability to produce aeciospores. Aeciospores are dikaryotic spores that are distributed by wind to the Gramineae host. The production of aeciospores was significantly higher on witches' brooms with insect visitation suggesting that the sexual reproduction of the pathogen requires out-crossing by insects. By excluding either crawling or flying insects, I could also show that crawling insects, such as ants, only play a minor role in the reproduction of the pathogen.

6 In addition to the exclusion experiment, I simultaneously observed witches' brooms and uninfected branches of similar size. I observed a high diversity of visitors, mainly insects but also some spiders. The most frequently recorded taxa belonged to the Diptera and Hy-

menoptera, but depending on the locality, different genera and species dominated. Higher visitation rates and longer visits on witches' brooms indicate that the leaves on witches' brooms attract insects, and that the fungal nectar on them is an attractive food source.

## **Dispersal of fleshy-fruited species in an agricultural landscape**

*Ausbreitung endozoochorer Gehölzarten in einer Agrarlandschaft*; 63 pp.

BERT PIEST

1 Little is known about dispersal of fleshy-fruited species in the agricultural landscape. The present study focuses on the effects of landscape structure on seed dispersal. The study was guided by the hypothesis that the activity of frugivorous birds might be influenced both by the structure of hedgerows and isolated trees and by the surrounding landscape.

2 In northern Switzerland (Canton of Schaffhausen) a structurally rich landscape ("Randen") was compared with a poorly structured area, which also had a lower density of forest edges ("Klettgau"). The presence of frugivorous birds was recorded at all study sites. Fruit removal by birds was investigated for natural fruit displays (*Cornus sanguinea*, *Crataegus monogyna*, *Ligustrum vulgare*) and artificial displays (six species). Seed rain of fleshy-fruited species was recorded in a total of 200 seed traps (50 cm x 50 cm) placed at 1.5 m distance from one of 36 hedgerows (26 in Klettgau, 10 in Randen) or at 2.5 m distance from one of 23 isolated fruit trees (9 in Klettgau, 14 in Randen). The traps were exposed from August 1997 to January 1998. The landscape structure within a radius of 100 m around the study sites was analysed with a geographical information system (ArcInfo).

3 In the structurally rich landscape more individuals of frugivorous birds were registered. The fraction of fruits removed from natural fruit displays during the winter was not significantly different between the two landscape types, but there was a tendency of faster fruit removal in the structurally rich landscape. Seed removal was also higher in *Cornus sanguinea* compared with *Crataegus monogyna* and *Ligustrum vulgare*. Removal from artificial fruit displays was low in both study areas. Seed rain around isolated fruit trees was low and did not differ significantly between the two landscapes (8.5 and 6.3 seeds m<sup>-2</sup>, respectively). Seed rain around hedges was slightly lower in the structurally rich landscape (84 versus 98 seeds m<sup>-2</sup>). Hedgerow and landscape structure explained only a minor part of the variation in seed rain. Seed rain was highest in September, and in both areas *Cornus sanguinea* was the most abundant species.



**Porrentruy Jura: a storage of lentils in the Hôtel-Dieu. Cultivated and wild plants of the Middle Age.**

*Porrentruy JU: une réserve de lentilles à l'Hôtel-Dieu. Plantes cultivées et flore adventice au Moyen Âge*; 83 pp.

VALÉRIE PARRAT

1 This study investigated remains of plants in a charcoal layer (late Middle Age) and two older pit remains in foundations of ancient buildings discovered in 1991 under the Hôtel-Dieu, a museum in Porrentruy (JU). Together samples had a water-saturated volume of 7.4 litres and contained more than 15'500 seeds and about 30 pieces of wood. All the material was carbonized and relatively well preserved. Wood carbons originated from three tree species (*Abies alba*, *Fagus silvatica*, *Quercus* sp.), and seeds from 40 taxa, including both cultivated and wild plants.

2 Cultivated plants were mainly represented by legumes and cereals. Legumes were mostly lentils (*Lens culinaris*; over 13'000 seeds), common vetch (*Vicia sativa*), and peas (*Pisum sativum*; only a few seeds). Cereals were in order of decreasing importance rye (*Secale cereale*), naked wheat (*Triticum aestivum/durum/turgidum*), spelt wheat (*Triticum dicoccum/spelta* and *Triticum* cf. *monococcum*), oat (*Avena sativa*) and millet (*Panicum miliaceum* and *Setaria italica*). Some species typically cultivated and eaten in the Middle Age were missing, e.g. buckwheat (*Fagopyrum esculentum*), flax (*Linum usitatissimum*) and marijuana (*Cannabis sativa*).

3 Wild plants were attributed to five plant communities according to the modern phytosociological classification: weed fields associated with cereal or flax crops (*Agrostemma githago*, *Bromus secalinus*, cf. *Centaurea cyanus*, *Lolium temulentum*), arable and garden weeds (*Setaria pumila*, *Chenopodium album*), ruderal weeds (cf. *Artemisia absin-*

*thium*, *Galium aparine*, *Plantago lanceolata*) and weeds of meadows and pastures (*Galium* cf. *mollugo* agg., *Luzula* cf. *multiflora*, *Trifolium* cf. *pratense*, *Phleum* cf. *pratense*).

4 Based on habitat requirements of wild plants and on the number and state of preparation of seeds of crop plants, it was possible to reconstruct two types of cultivation. First, a mixed culture of rye and corn, called "méteil" and characteristic of the medieval period. Second, a mixture of lentils and barley, for which three hypotheses can be formulated: (1) barley was used as undercrop in lentil cultures, (2) the two species were cultivated separately and mixed before storage, or (3) the species became mixed involuntarily during fire. The first hypothesis seems to fit best with the requirements of the culture of lentils and the medieval methods. The second hypothesis seems less probable, but would explain the absence of the pod of lentils and of the glumes of barley.

5 This study shows how a mixture of cultures was often used to secure a harvest under different climatic conditions and without herbicides, insecticides and chemical fertilizers. It also emphasizes the importance of legumes in a diet with little meat.

## Zonation of the vegetation of Praslin National Park, Seychelles, including its importance for the Vallée de Mai and its ecological value

*Zonierung der Vegetation im Nationalpark Praslin, Seychellen*; 63 pp. + App.

ANDREAS REINHARDT & MANUEL VOELLMY

1 The Praslin National Park on Praslin Island, Seychelles, includes the UNESCO World Heritage site *Vallée de Mai*, famous for its stands of the endemic tree species *Lodoicea maldivica*. This study investigated the National Park area surrounding *Vallée de Mai*. The aims were to describe the main vegetation types, the species composition and the population structure of forest vegetation, to evaluate the value of the area for nature conservation, to predict its future development, and to formulate recommendations for its management as a buffer zone for *Vallée de Mai*.

2 The tree species composition of the study area was recorded along transects following all available trails within the park (total length about 7 km, subdivided into sections of 200 m). Each trail transect section was attributed to one of five vegetation zones based on the dominant tree species: *Swietenia* Forest, Native Forest, Palm Forest, Invaded Forest, and Invaded Forest with Palm Rejuvenation. Prominence values of all tree species (based on their relative abundance and frequency) and an index of protection value (based on the occurrence of native and alien species, red list species and rejuvenation) were calculated for each transect section.

3 A total of 24 alien tree species were identified, of which five species were regarded as invasive: *Cinnamomum verum*, *Tabebuia pallida*, *Chrysobalanus icaco*, *Sandoricum koetjape*, and *Hevea brasiliensis*. The most prominent tree species in the park was the invader *Cinnamomum verum*, followed by the endemic palm *Deckenia nobilis*. Transect sec-

tions in the vegetation zones Palm Forest and Native Forest were attributed higher protection values than those in the three other zones.

4 Stand structure was recorded on ten permanent plots chosen to represent the five vegetation zones. Data were used to determine the survivorship of juveniles, from which the future development of forest vegetation could be extrapolated. High survivorship of the following species indicated that they would become more abundant in the future: *Cinnamomum verum*, *Chrysobalanus icaco*, *Deckenia nobilis*, and *Phoenixophorium borsigianum*. Species whose low survivorship indicated a future decrease were *Swietenia macrophylla*, *Callophyllum inophyllum* and *Paragenipa wrightii*.

5 No general correlation was found between the degree of invasion of a particular site and its distance to settlements. However, the abundance of alien species was on average much higher in the National Park area surrounding *Vallée de Mai* (36.3%) than in *Vallée de Mai* itself (11.6%), which confirms the buffer function of the surrounding area against alien invasion.

6 *Fond Ferdinand*, an area of Praslin Island outside the Praslin National Park was also investigated because an extension of the Park to include this area is planned for a better protection of the endemic tree species *Lodoicea maldivica*. The prominence value of *Lodoicea* was higher in *Fond Ferdinand* (29) than in *Vallée de Mai* (19), and some parts of *Fond Ferdinand* had higher protection value than *Vallée de Mai*.



7 Recommendations for management include the establishment of a buffer zone for the *Vallée de Mai*, the link of *Vallée de Mai* to *Fond Ferdinand* through an extension of the

Praslin National Park, eradication campaigns for invasive alien plants, reforestation with native taxa, and the development of ecotourism.

## Assessment of restoration success for a river in the Reuss valley (Uri, CH)

*Erfolgskontrolle im Uferbereich eines renaturierten Baches im Urner Reusstal*; 83 pp.

MARTIN SCHIBLI

1 A melioration channel in Central Switzerland ("Altdorfer Giessen") was restored between 1995 and 1997. The river channel and the river banks were rebuilt to achieve a natural-like state, which would be valuable as habitat for animals and plants and as a recreational area for the public. Special structures were created to promote various endangered animal species.

2 To assess whether the measures had led to an improvement, the present plant species composition and the distribution of vegetation types were analysed and compared to the situation before restoration. The value of the river banks for animals was expressed by the numbers of nestling birds, reptiles, butterflies, dragonflies, ground beetles, and locusts.

3 Compared to the state before restoration, the number of both plant and animal species had increased. The high number of different habitat types allowed a high diversity of animals, including some species that are rather uncommon in this area.

4 Several characteristic animal species had already recolonised the river banks. However, the recolonisation seemed to proceed slowly, presumably due to landscape fragmentation and the resulting isolation of the restored river from similar habitats. Of the animal species for which special structures were created, *Cinclus cinclus* and *Lacerta agilis* successfully recolonised the river, but *Riparia riparia* and *Alcedo atthis* did not.

5 The desired vegetation types did not all re-establish due to the tendency of reed and tall forbs to dominate the grasslands and suppress lower plant species. Without regular maintenance, the river banks would rapidly be overgrown by shrubs and reed. In addition, selective and regular measures are needed against the development of undesired vegetation types.

6 A survey among the residents close to the river showed that these people evaluate the restoration mostly from an aesthetic point of view. The restoration is broadly accepted. Most of the people appreciate this area as an extended recreation site besides the Reuss delta.

7 Based on these results, additional restoration aims were formulated for the "Altdorfer Giessen", and recommendations for maintenance were adjusted accordingly.

## Habitat use and diet selection of chamois (*Rupicapra rupicapra*) on a abandoned sheep pasture

*Raumnutzung und Äsungswahl von Gemsen (Rupicapra rupicapra) auf einer aufgegebenen Schafalp*; 44 pp.

SABIN SCHLATTER

1 The mountain "Schafberg" near Amden has been used as a summer pasture for sheep since approximately 1400 AD. However, it was assumed that the sheep displaced the chamois (*Rupicapra rupicapra*) into nearby mountain forests, where the latter would cause browsing damage. Therefore, sheep grazing was discontinued at Schafberg with the expectation that the chamois would return to their normal habitat.

2 This study examined the habitat use of chamois one year after the cessation of sheep grazing, with particular emphasis upon diet selection. The aim was to provide information for a management scheme which may reduce or prevent chamois damage to trees in the Schafberg forest. A second aim was to determine how long-term sheep grazing had affected the soil fertility on Schafberg.

3 Observations of chamois behaviour made in the study area (65 ha) between June and August 2000 showed that chamois did not use the Schafberg intensively during this period. Apparently, the habitat use and diet selection of the chamois on Schafberg did not

change dramatically in the first summer without sheep grazing.

4 Pastures at the western side of the Glattchamm offered better pastures for the chamois in terms of standing crop than more shaded areas such as the Schafberg Kessel. This difference was most noticeable in the early summer. A positive relation between standing crop and sheep dung deposition during the previous year was only found in early June.

5 Soil phosphorus content varied over a broad range within the study area (155–7046 kg ha<sup>-1</sup>), probably as a result of former sheep grazing. However, soil P content was not correlated with sheep dung deposition during the previous year.

6 A simulation model with 1400 AD as starting point and assuming a constant annual stocking rate predicted a soil P level of 1969.3 kg ha<sup>-1</sup> on an area representing 10–20% of the whole pasture. This would correspond to the area used intensively by the sheep. We found almost exactly the same value (2258.6 kg ha<sup>-1</sup>) as predicted by our model.

## Sexual reproduction of *Salix* species and *Populus nigra*

*Sexuelle Reproduktion bei Salix-Arten und bei Populus nigra*; 59 pp.

MARIANNE SUTER

1 The habitat structure of unregulated rivers is controlled by unpredictable periodical disturbance, i.e. flooding, dry spells, erosion and sedimentation. Willows, poplars and alder species are particularly equipped to withstand

these types of disturbance and thus occur as the most abundant pioneer species in an active floodplain.

2 The Tagliamento in NE-Italy is the last major alpine river that is unregulated in most

reaches. The study site of the thesis is situated in an island-braided reach along the middle course of the river. Five willow species (*Salix daphnoides*, *S. purpurea*, *S. eleagnos*, *S. triandra* and *S. alba*) and one poplar (*Populus nigra*) are found on the wooded islands of this reach.

3 The focus of the study was on differences in the reproductive effort and the regeneration niche of the six Salicaceae. The two main questions were: How are these species differentiated in terms of seed production, and how in terms of seed longevity?

4 The number of seeds per plant and seed mass were determined for 20–30 individuals of each species. Seed longevity was analysed in germination experiments as the time period after which 50% of the seeds were still viable.

5 *Populus nigra* developed the heaviest seeds (0.8 mg) with highest longevity (21.5 days), whereas seed longevity of the five willow species was 6–15 days. Seed mass of the species was significantly different. Seed longevity and

seed mass were positively correlated across species with exception of *S. triandra*, whose small seeds (0.2 mg) were relatively long-lived.

6 *Salix triandra* produced the highest number of seeds (>1 million seeds per plant), whereas only 23'000–230'000 seeds plant<sup>-1</sup> were observed for the other species. Species with small seeds produced highest seed numbers, but no trade-off between seed size and seed number was found when individuals were compared within species. The reproductive effort in terms of biomass allocation to seeds was higher in the shrub species *S. triandra* (2.4%) and *S. eleagnos* (1.7%) compared with the trees *S. alba* (0.8%) and *P. nigra* (0.6%).

7 Regeneration niches strongly differed among the six species, suggesting that the temporal sequence of seed dispersal and the habitat dynamics are the main factors allowing coexistence of the various Salicaceae. Regulation of a floodplain ecosystem may therefore lead to local extinction of at least some of the species.

## Effects of wildflower strips on the diversity of bug fauna and seed bank in the soil of an agricultural landscape

*Einfluss von Buntbrachen auf die Diversität der Wanzenfauna und des Samenvorrates im Boden in einer Ackerlandschaft*; 87 pp.

GABRIELA UEHLINGER

1 Biodiversity in intensively used agricultural areas has decreased during the last 40 years. In the last decade ecological compensation areas (ECA) in agricultural landscapes have been introduced to enhance the diversity of agricultural areas. One kind of ECA are wildflower strips, i.e. strips within crops sown with mixtures of native weeds, ruderal and arable species. In 1993 only few wild flower strips existed in the investigated area (Klettgau, Canton Schaffhausen), but during

the last six years many more have been added.

2 One question addressed in this study was whether insect diversity had changed between 1993 and 1999 in the investigation area. We selected the Heteroptera as an indicator group for general insect diversity. Arthropod samples collected in 1993 by the Vogelwarte Sempach in several ECAs as well as in conventional or less intensively managed crops were compared to samples taken in 1999 in

wildflower strips, meadow strips, field paths, and extensively managed wheat or potato fields. We collected the bugs by sweep net during a ten-week period starting at the end of April 1999.

3 A second question was whether a seed bank builds up in the soil of wildflower strips over a period of several years. Three age categories of wildflower strips were investigated (7 years, 5 years, 2 years). In August/September 1999 a total of 120 samples were taken from 6 wildflower strips and their neighbouring (control) fields, with 5 samples per field at 2 soil depths (0–7 cm, 15–22 cm). Samples were exposed in the greenhouse for 21 weeks, and the emerging seedlings were determined and counted.

4 A total of 69 Heteroptera species were collected, 44 species in 1993 and 64 in 1999. The highest number of species (37) was found in the 1999 wildflower strips. The diversity indices of Heteroptera were highest in the wildflower strips, and also high in the meadow strips and the wheat fields. Evenness was high in wildflower strips, but low in meadow strips. The increasing number of bug species between 1993 and 1999 could be due to the influence of wildflower strips, which offer a wide range of host and food plants, as well as sites for hibernation. Furthermore, many bugs and other arthropods escape from disturbed areas such as treated fields or cut meadows into edge habitats like hedges, field margins and wildflower strips. However, the increased bug diversity may also reflect the generally less intensive agriculture during the last 5–10 years.

5 A total of 58 plant species germinated from the seed bank. Canonical correspondence analysis (CCA) revealed strong differences in species composition among the three age categories, but no difference between soil depths. In contrast, the total number of germinated

seeds and their species richness differed between soil depths, but not among age categories. No rare or endangered species were found. Most species contained in the original seed mixtures were also found in the seed bank, particularly many perennial plants. Some of these species were found in the lower soil level, indicating that a relocation of seeds into lower soil levels takes place. The proportion of annual species decreased with the age of wild flower strips, suggesting that after 3–4 years there should be a soil treatment in wildflower strips to promote annual species.

6 It is concluded that wildflower strips are valuable habitats in the agro-ecosystem, which help to increase the diversity of plants and animals in agricultural areas.

## Ph.D. Theses (7)

### Effects of nutrient inputs and water regime on wetland vegetation and the performance of wetland species

*Auswirkung von Nährstoffeinträgen und Wasserstand auf die Feuchtgebietsvegetation und das Wachstum von Feuchtgebietsarten*; 145 pp.

URSULA BOLLENS

1 Wetlands in Switzerland are protected by law, but their species richness is still endangered by nutrient inputs and interference with the water table. In this thesis the relative effects of these two impacts were investigated at three levels: natural plant communities in wetlands, individual plants in a growth experiment, and artificial species mixtures on an experimental field.

2 Vegetation change between 1977 and 1997 was studied for two wetlands in the canton of Zürich. Filipendulion vegetation could expand in areas formerly covered by Magnocaricion vegetation. Molinion vegetation expanded in many areas covered by Magnocaricion or Caricion davallianae 20 years earlier. A survey of the present vegetation and site conditions suggested that the expansion of Filipendulion was due to nutrient inputs, whereas the decrease of tussock-forming Magnocaricion vegetation was due to drying. Thus, both impacts had caused obvious changes in the vegetation at the community level.

3 Responses of 16 wetland species to enhanced nitrogen and phosphorus supply as well as to different water regimes were studied over a period of two years in a growth experiment. In the first growing season all species responded to enhanced nitrogen supply with enhanced biomass production. In the second year plants mainly responded positively to the addition of phosphorus; the type of nutrient limitation was not clearly related

to nutrient concentrations or N:P ratios in plant biomass. All species were inhibited by periodic flooding in both years; some species were promoted by periodic dryness. Nutrient concentrations were enhanced by the flooding treatment, indicating that reduced growth at high water levels did not result from reduced nutrient uptake.

4 Although the 16 species originated from wetland sites with different productivity and water level, the effects of nutrient supply or water regime in this experiment were not related to the species' natural occurrences. Species differed in that some produced more biomass in the second year than in the first, while other did not. In the low-N-high-P treatment, species characteristic of nutrient-poor sites tended to have higher biomass in the second year (*Molinia caerulea*, *Carex elata*, *Carex flava*, *Succisa pratensis*, *Lysimachia vulgaris*, *Silene flos-cuculi*, *Schoenus* sp., *Ranunculus flammula*, *Selinum carvifolia*), whereas species from more productive sites showed no enhanced growth in the second year (*Filipendula ulmaria*, *Lycopus europaeus*, *Anthoxanthum odoratum*, *Lythrum salicaria*, *Centaurea angustifolia*). In the high-N-low-P treatment, only *Molinia caerulea*, *Schoenus* sp., *Carex elata* and *Carex flava* increased their biomass between the first and second year.

5 In a second experiment the same 16 plant species were planted at 5.5 cm distance in 1x1-m<sup>2</sup> plots on an experimental field after topsoil removal. Plots received nutrient sup-



plies between 0.5 and 120 kg N ha<sup>-1</sup>yr<sup>-1</sup>, and corresponding P and K supplies (N:P:K 3:1:5.7). In the first year differences in biomass resulted mainly from nutrient addition, with greatest differences in the range between 0.5 and 10 kg kg N ha<sup>-1</sup>yr<sup>-1</sup>. In the second year the plots were flooded for a long period of time as a result of exceptionally high rainfall in spring. The biomass production was markedly reduced by flooding. The species differed in their responses to nutrient

supply, with a tendency for species from productive sites to increase their biomass along the nutrient gradient more than those from nutrient-poorer sites.

6 It is concluded that the specific growth form and the life cycle of species need to be taken into account when results from short-term pot experiments are to be compared to the field situation. The study also emphasized the importance of an adequate water regime for the conservation of wetlands.

### **Insect diversity in agricultural grasslands: The effects of management and landscape structure**

*Einfluss von Bewirtschaftung und Landschaftstruktur auf die Insektenvielfalt von Mähwiesen; 79 pp.*

MANUELA DI GIULIO

1 This study investigates the influence of management and landscape structure on insect diversity of hay meadows. Meadows cover a large part of the agriculturally used area in Switzerland and therefore represent an important structure of cultural landscapes. The four chapters of the thesis deal with the following questions: 1) How does management affect the insect diversity of grasslands? Do different grassland types have characteristic insect communities? 2) How important are the various grassland types for species diversity on a landscape level? How does the surrounding landscape affect the insect community of single meadows? 3) How valuable are the meadows of the research area for the bug fauna of Switzerland? 4) How does plant species diversity influence the insect diversity of grasslands? Does host plant diversity affect the larval development of oligophagous insects?

2 True bugs (Heteroptera) were chosen as an indicator group for insect diversity because they are ecologically very diverse and typically live in meadows. The research area was located in the Schaffhauser Randen in Northern

Switzerland, an extensive forested area with a number of more or less isolated enclaves of agricultural land. Four such enclaves with varying mixtures of arable and grassland habitats were selected for the study. Within each enclave we investigated two grassland management types ("medium intensive" and "extensive") with three sites per management type.

3 Management was found to greatly affect the heteropteran bug diversity of grasslands. Extensive meadows were richer in species than medium intensive ones. Further, species differed in their response to management, and thus species composition was also affected. Two species were most abundant in medium intensive meadows. Both develop two generations per year and are relatively mobile; it is argued that these characteristics enable them to survive in highly disturbed habitats. Six species were most abundant in extensively managed meadows. Most of these overwinter as eggs, and larval development takes place in spring. Frequent and early cutting may therefore prevent larval development and reproduction. Ground living spe-



cies, which need a warm and dry microclimate, were also less abundant in medium intensive meadows, probably due to the dense and closed vegetation.

4 The bug fauna of extensive meadows differed greatly between the areas investigated. By contrast, the medium intensive sites differed little in species richness and composition. Many bug species occurred only in individual areas and appeared to have restricted ranges, even though most of them could reach high densities locally. It is therefore crucial to preserve many different sites in order to maintain species diversity at the landscape level.

5 Species composition could partly be explained by the structure of the surrounding landscape, particularly the proportion of arable land. Some meadow species apparently benefit from the presence of this habitat type. However, the spatial scale used in this study was too coarse to understand how insects are affected by their surrounding habitats.

6 To evaluate the importance of meadows in the research area for the bug fauna of Switzerland, an updated species list of Heteroptera for the Canton Schaffhausen was given and compared to data from other regions of Swit-

zerland. The results indicate that the extensively managed meadows of the Schaffhauser Randen are comparatively very species-rich habitats for the heteropteran fauna of Switzerland.

7 A laboratory experiment was carried out to explore how host plant diversity and food quality affect the larval development of two bug species (*Stenodemini*) which are strictly phytophagous and capable of feeding on a wide range of different grass species. The development of insects reared on grass monocultures was compared with the development of insects reared on mixtures of four species. In addition the host grasses were grown under two nitrogen regimes to test if protein content is the key factor determining host plant switching during ontogenesis. The results indicate that host plant diversity significantly increases larval survival and that crude protein content is not the main factor responsible for the effect. A highly diverse meadow might therefore enhance insect diversity by increasing larval survival of herbivores and, indeed, the field data indicates that host plant diversity is positively correlated with the species richness of *Stenodemini*.

### **Ecophysiological investigation into the potential biochemical impact of *Cladophora glomerata* on *Phragmites australis***

*Ökophysiologische Untersuchungen zur Möglichkeit einer biochemischen Schadwirkung von Cladophora glomerata auf Phragmites australis*; 134 pp.

JÖRG IPSEN

1 Severe reed die-back has occurred on many European lakeshores during the last few decades. It has been suggested that substances specific to the green-alga *Cladophora glomerata* (L.) KÜTZING, a species promoted by lake water eutrophication, might be one of the causes. Indeed, irreversible withering symptoms are observed on reed

plants (*Phragmites australis* (CAV.) TRIN. ex STEUDEL) following experimental exposure to filamentous green-algae, in particular *Cladophora glomerata*. The purpose of this study was to investigate the causes of this loss of turgor pressure and to test whether they are indeed specific to *Cladophora glomerata*.

2 *Phragmites* plants were cultivated from rhizomes collected on the shore of lake Constance (D) to a size of 120–150 cm. Effects of a wide range of liquid test substrates (suspensions or extracts of algae or higher plants, cultivation media for microorganisms, antibiotics) on the plants were tested by immersing roots of pre-grown plants for 60 hours in the substrates, followed by replanting in pots with soil and measurement of the transpiration rate as indicator of photosynthetic activity during four days. The effect of single substances isolated from the test substrates with various fractionation methods was investigated similarly.

3 Experiments with suspensions of both algae and cormophytes which had previously been disintegrated by fermentation or by mechanical or thermal processes indicated that the significant damaging effects of *Cladophora* on *Phragmites* are not specific to this green-alga, but can be caused by all plant species providing their tissue has been sufficiently disintegrated. Thus, the hypothesis of *Cladophora* substances being involved in reed die-back was not confirmed.

4 Experiments with substrates containing antibiotics or synthetic cultivation media showed that the decline in transpiration rate and the loss of turgor pressure observed in *Phragmites* following immersion in plant suspensions are actually caused by microbial metabolism in the test substrates. The decisive factor causing these damaging effects is the microbial activity in the rhizosphere of *Phragmites*. Microbial activity is stimulated by soluble substances in plant suspensions as well as by the synthetic cultivation media. If the rhizome microflora was inhibited by antibiotics, immersion in plant suspensions, even fermented ones, did not cause recognizable damage to the *Phragmites* plants.

5 Experiments with unfermented *Cladophora* suspensions showed that these substrates do not have any inhibiting effects on *Phragmites*. *Cladophora* does therefore not have an allelopathic potential towards *Phragmites*, as had been hypothesized.

6 GC/MS-analysis of the test substrates revealed that plant suspensions and nutrient solutions decomposed by the rhizome microflora of *Phragmites* contain phenol and phenol derivatives such as cresol and methoxyphenol. Additionally, short-chain fatty acids such as acetic acid, butyric acid, capronic acid and propionic acid were found. Both groups of substances are known to be phytotoxic. In experiments with pure forms of these phenols and fatty acids, they caused the same decline in transpiration rate and loss of turgor pressure as the tested plant suspensions and cultivation media.

7 It can be concluded that the formation of phytotoxic substances by the rhizome microflora of *Phragmites* itself is responsible for damages which had formerly been attributed to allelopathic effects of *Cladophora*.

## The Late Neolithic lakeshore settlement Saint-Blaise/Bains des Dames (Lake Neuchâtel, Switzerland): Vegetation, agriculture and diet of the Auvernier cordé culture (2640–2450 BC)

*Die Endneolithische Seeufersiedlung Saint-Blaise/Bains des Dames NE. Botanische Untersuchungen zur Vegetation, Landwirtschaft und Ernährung in der Auvernier Cordé-Kultur (2640–2450 Bc); 151 pp. + App.*

OLIVIER MERMOD

1 The Late Neolithic lakeshore settlement Saint-Blaise / Bains des Dames on lake Neuchâtel, Switzerland, was excavated in 1986–88 and attributed to the cultural layer of the Auvernier cordé (2640–2450 BC). We analysed plant material collected during this excavation in order to reconstruct the surrounding natural vegetation, agricultural practices and human diet of the Auvernier cordé culture.

2 We analysed 50 samples in detail, which yielded a total of 48'000 fossil plant remains from 285 taxa. Of these macrofossils 92% were non-carbonised and 10% were fragmented. The organic material was well preserved. A less detailed analysis of 489 additional samples yielded 22'000 seeds or fruits and three additional taxa. Eleven further taxa were found as wood remains or pollen.

3 The plant species found in the samples belonged to 26 different plant communities and together drew a clear picture of the Late Neolithic environment. Various species of water plant communities (Charetea, Potamogetonetea) and many marsh species reflected the strong influence of the lake water on the settlement. Species from reed stands and tall sedge swamps (Phragmitetalia) were rare, with *Schoenoplectus lacustris* belts as the main community type. In contrast, lake shore pioneers were well represented with species of various plant communities (Agropyro-Rumicion, Isoëto-Nanojuncetea and Bidentetea). Together, the wetland species found at the site suggest that the lake water was rather mesotrophic.

4 Moist forests (classe Alnetea and alliance Alno-Ulmion) did apparently not grow in the vicinity of the settlement. By contrast, beech-oak forests (classe Fagetalia without the alliance Alno-Ulmion) covered large areas in the lower parts of the settlement. The inhabitants probably promoted *Quercus* as food resource and construction wood. The frequent occurrence of species of forest edge scrub or hedges (Prunetalia), of fringe communities at sunny forest edges (Trifolio-Geranietea) and of forest clearings (Epilobietea) indicated that forest had an open canopy structure.

5 Moist meadows and pastures (Molinietalia, Arrhenatheretalia) existed around the settlement. These grasslands probably served as pastures for the domestic animals. On a dry slope, xerothermic mixed oak woods (Quercetalia pubescenti-petraeae) and dry chalk grasslands (Festuco-Brometea) formed a natural mosaic. The intense human activity was reflected by numerous plants of nitrophilous ruderal communities (Artemisietea).

6 The 60 potential crop weeds (Chenopodietea and Secalinetea) found at the site indicate that arable fields were located near the village. These fields had probably been established in clearings within the beech-oak forests or in former moist forests. The weed species found and pollen analyses suggest that crop fields were rather small.

7 The estimated minimal population, the height of the harvest, the weed spectra, the topography and the climate together suggest an

agricultural system with short-term fallow. Different cereals, flax, opium poppy and a small amount of pea were cultivated. The most important cereal was barley (*Hordeum vulgare*), followed by emmer (*Triticum dicoccon*), naked wheat (*Triticum aestivum/durum/turgidum*) and a small amount of einkorn (*Triticum monococcum*). Tetraploid naked wheat (*Triticum durum/turgidum*) and hexaploid naked wheat (*Triticum aestivum* s.l.) were also present at the study site. The cereals were sown as both winter and summer crops and threshed within the village.

### **Genetic variation, mating system, and nectar robbery in *Aconitum lycoctonum* (Ranunculaceae)**

*Genetische Variation, Fortpflanzungssystem und Nektarräuber von Aconitum lycoctonum (Ranunculaceae)*; 106 pp.

ANNA-BARBARA UTELLI

1 The mating system of a plant species and population size are the strongest determinants of the distribution of genetic variation among and within populations. Members of the genus *Aconitum* (monkshood) (Ranunculaceae) are typically bee-pollinated plant species. The yellow-flowered *A. lycoctonum* L. emend. Koelle is pollinated by long-tongued bumblebees. Its flowers are protandrous, and the species was thought to be self-incompatible. It has also been assumed that insect pollination favors outcrossing. In addition to the long-tongued bumblebees as pollinators, the flowers of *A. lycoctonum* are visited by short-tongued bumblebees as nectar robbers. Nectar robbers can have positive or negative effect on plant reproduction, thus they could also influence the genetic structure of a species. *A. lycoctonum* is widely distributed across central and southern Europe. Because of its high morphological variability, the systematics of this species has long been unclear, and many taxa at different taxonomic rank have been described.

8 Gathering wild fruits (*Prunus spinosa*, *Malus sylvestris*, *Physalis alkekengi*), berries (blackberries, strawberries, raspberries) and nuts (hazelnut, acorns) was an important addition to the human diet. Numerous other edible, tinctorial (e.g. *Anthemis tinctoria*) or medical plants (e.g. *Hypericum perforatum*) were found in the samples. Different crops and edible wild plants were found in every household, suggesting that households functioned as independent units.

2 To elucidate the patterns of genetic variation in this species in central and southern Europe, I used allozyme markers. My results showed that more selfing and/or mating with close relatives occurred in these populations than had been predicted. I found low levels of heterozygosity and positive inbreeding coefficients in more than half of the investigated populations. A neighbour-joining tree revealed that *A. lycoctonum* probably survived the glaciation period in the south of the Iberian Peninsula and in eastern or south-eastern Europe. Thus, glaciation and subsequent recolonisation might have caused bottleneck effects in *A. lycoctonum*, potentially leading to reduced heterozygosity. The results concerning the mating system of *A. lycoctonum* showed that at least some populations were self-compatible, and that spontaneous autofertilisation also occurs in this species. Moreover, I concluded from observations of pollinators that selfing by geitonogamous pollen was common in *A. lycoctonum*. This result



could explain the positive inbreeding coefficients.

3 An experiment on the influence of nectar robbery by bumblebees did not show any effect of robbery on female success of *A. lycoctonum*. Thus, nectar robbery did not affect the distribution of genetic variation in *A. lycoctonum*. Furthermore, bumblebees that most often act as nectar robbers in *A. lycoctonum* populations at high elevation sometimes also act as pollinators. At low elevation, the holes in the flowers, thought to be caused by nectar robbers, were caused by pollen eating beetles (*Meligethes viridescens* Fabricius).

4 Concerning the systematics of *A. lycoctonum* and its closest relatives, allozyme data as well

as sequence data of nuclear and chloroplast DNA showed very low genetic variation within the yellow-flowered *A. lycoctonum*. These results suggest that there is only a single species in central and southern Europe. The analysis of morphological characters verified that high morphological variability is present, but showed that the measured traits were useless as systematic characters because they vary within and among populations. Moreover, since sequence divergence is also minute among *A. lycoctonum* and its closest relatives *A. septentrionale* Koelle, *A. moldavicum* (Hacquet) Jalas, *A. lasiostomum* [Reichenb. ex] Besser, and *A. orientale* Mill., I suggest that all these taxa belong to one morphologically highly variable species.

### The ecological significance of interspecific variation and phenotypic plasticity in root tissue structure of grasses

*Die ökologische Bedeutung der interspezifischen Variation und phenotypischen Variabilität in der Gewebestruktur in Graswurzeln*; 80 pp.

STEFAN WAHL

1 Species from productive or disturbed habitats have a higher inherent relative growth rate (RGR) and resource acquisition capacity than species from unfavourable habitats. Acquisition capacity for below-ground resources is associated with an extensive root system. For a given biomass, thinner roots, with a low tissue mass density increase root system length and nutrient uptake. However, a low tensile strength and the short life-span of thin roots with a low tissue mass density set limits to the maximisation of root length. The aim of the present study was to investigate how these ecologically important constraints are reflected in root anatomy.

2 Root tissue mass density (TMDr), root diameter and several characteristics of root anatomy were investigated in 19 grass species

from different habitats and related to the ecological behaviour of the species. We found a dichotomy between root anatomical characteristics associated with interspecific variation in relative growth rate (RGR) and those associated with variation in plant height at maturity. RGR correlated negatively with anatomical characteristics that contribute to robustness, i.e. dry matter content in leaves, TMDr, and proportion of stele on root cross-sectional area. For a given root diameter, species with lower RGR had smaller but more numerous xylem vessels, indicating a higher resistance against cavitation and protection against embolisms. Plant height correlated positively with characteristics related to root transport capacity, i.e. root cross-sectional area, total xylem area and mean vessel area.

Interspecific variation in TMDr was explained by the proportion of stele of the root cross-sectional area and the proportion of cell wall in the stele. TMDr was associated with the ecological behaviour of a species, correlating with indicator values for nitrogen.

3 For species growing at low-productive sites a high tissue mass density might not be an advantage by itself, but rather a reflection of anatomical traits important for an efficient nutrient conservation through long-living tissues. Thus we investigated the relationship between turnover of roots, RGR and TMDr and its related anatomical parameters. Root turnover correlated with leaf life-span of the species, obtained from literature. Both traits correlated with TMDr and indicator values for nitrogen, reflecting the close relationship between life-span, TMDr and the productivity of the natural habitats. The proportion of cell wall in the stele was the anatomical trait which correlated best with leaf or root life-span, indicating a pivotal role of the stele for the longevity of roots. RGR was not correlated with tissue life-span. This may have been a result of measuring RGR and leaf- and root life-span at different life stages of the plants.

4 Changes in resource availability may influence the tissue structure. Plasticity in TMDr and root anatomy in response to variation in resource availability was investigated for eight ecologically contrasting grass species. High photon flux density (PFD) and high nutrient availability lead to high biomass production and to thick roots. In shade and at high nutrient supply plants built roots with a relatively higher transport capacity by producing relatively larger xylem vessels and a higher ratio of xylem area on root cross-sections. This may reflect the high leaf area ratio and transpiration under such conditions. In contrast to DM/FMa, which was already lower at 30% PFD, TMDr was only lower when growth was limited at 5.5% PFD. Additionally, nutrient limitation increased DM/FMa, but not TMDr. Under 100% PFD higher nutrient supply did not affect xylem vessels. The reduction in growth under 5.5% PFD also reduced the number of stele cells, leading to a smaller proportion of stele and lower TMDr. Interspecific differences in plastic responses to light availability were not related to their ecology.

## Laurophyllisation in Switzerland

*Grenzlagen der Laurophyllierung in der Schweiz*; 140 pp.

GIAN-RETO WALTHER

1 In recent decades numerous non-indigenous species of the evergreen broad-leaved (laurophyllous) type have started to colonise Swiss lowland forests. Nowadays, in southern Ticino, there are forest patches on southern slopes, especially along the Insubrian lakes, which are dominated by exotic laurophyllous species.

2 The present study provides an overview of the most important exotic species and their

invasion history. Field experiments gave evidence on the crucial ecological factors for seedlings establishment of exotic species. Relevé plots from the seventies were resurveyed in Switzerland both North and South of the Alps.

3 On the northern side of the Alps, the first occurrence of the frost-hardier exotic laurophyllous species was recorded. The observed trends point generally to more mesic condi-



tions; the species' changes suggest habitat conditions which are moister, richer in nutrients and generally shadier. The change towards warmer conditions is reflected by both the decreasing number of montane species and the increasing number of thermophilous species, and in particular the aforementioned evergreen broad-leaved exotic species.

4 On the southern side of the Alps, especially in areas lower than 600 m a.s.l., the structure and composition of forests has completely changed due to the shift in the shrub layer from deciduous to evergreen broad-leaved species. The exotic laurophyllous species must be considered as naturalised and ecologically important components of the affected ecosystems. The particular character of these species and species groups, as well as the fact that their increase in abundance has occurred in the last thirty years, strongly implies changes in environmental factors within that period. The twofold set of climatic parameters, smaller absolute minimum temperatures and lower frequency of frost, suggest an important influence of climate on the establishment of exotic evergreen broad-leaved species.