Diss. ETH No. 14104

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

A dissertation submitted to the

SWISS FEDERAL INSTITUTE OF TECHNOLOGY ZURICH

for the degree of

DOCTOR OF NATURAL SCIENCES

presented by

Karin Susanne Ullrich

Dipl. Biol. Albert-Ludwigs-Universität Freiburg

born 7 October 1966

German

accepted on the recommendation of

Prof. Peter Edwards, examiner

Prof. Peter Duelli, co-examiner

2001

Table of contents

Summary

This study investigates the diversity of plants and insects in wildflower strips in an arable landscape in Switzerland. The aim is to assess the plant and insect diversity establishing in wildflower strips and the factors influencing this diversity, in order to evaluate the contribution of wildflower strips to biodiversity on a landscape scale, and to generate recommendations for their optimal management. 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 recommended mixture of indigenous arable weeds and species of ruderal sites and meadows. They are maintained for at least two, but usually for six years, and after the second year typically one half or one third of a strip is mown each year in rotation. Since wildflower strips are comparatively new elements introduced into the intensively used arable landscape to enhance biodiversity, knowledge of their success is still limited. In this thesis the following sets of questions are investigated in four chapters: 1) How effective are wildflower strips in recruiting rare and threatened plant species? What factors influence the species richness of wildflower strips? What impact do wildflower strips have on plant species diversity in the soil seed bank? 2) How do seed mixtures, management and environmental factors affect the development of vegetation in wildflower strips? 3) What roles do colonization and environmental constraints play in the establishment of insect communities in wildflower strips? Are insect communities in wildflower strips restricted to generalist species or do specialist species also manage to establish, and how quickly? Can the insect communities in different types of wildflower strips be distinguished clearly and if so, what environmental factors are responsible? 4) Do wildflower strips serve as a dispersal source for insects? Over what distance and how quickly can insects colonize patches of their host plants? All chapters aim to contribute answers to the question, how wildflower strips should be managed to achieve a maximum biodiversity on a landscape scale.

While the plant species composition of an ecosystem can be surveyed in total, this is impossible for insects. The true bugs (Heteroptera) were chosen as an indicator group for total insect diversity, because they are ecologically diverse and their numbers correlate well with total insect diversity in agricultural landscapes. The study area is the Klettgau (Canton Schaffhausen), an intensively used arable region in the north of Switzerland. It forms a wide, flat valley covered with calcareous river gravels that are locally overlaid by loam and loess. Since 1991, a large number of wildflower strips have been established, mostly in three focus areas within the Klettgau, in the context of a pilot study sponsored by the Swiss Ornithological Institute and the cantonal authorities. In 1996, the vegetation of all wildflower strips was surveyed, and in 1997 and 1998 the vegetation and bug fauna of selected strips

of different ages and degrees of grass cover were investigated. In 1998, experimental plots of host plants were set up at various distances of a wildflower strip to study their colonization by bugs. Within the context of this thesis, in 1999 Gabriela Uehlinger investigated the accumulation of seeds in the seedbank of wildflower strips of different ages as part of a diploma thesis.

In chapter 1, the factors affecting floristic diversity, and particularly the presence of rare arable weeds, in wildflower strips and arable flora reserves are analysed. In sum, 234 plant species were recorded in the vegetation of wildflower strips in the Klettgau, of which the vast majority had recruited spontaneously. Species richness is highest in strips in their first year and decreases with increasing age and grassiness of a site. The species composition is rather variable, so that maximum diversity at a landscape scale is achieved by a high number of widely dispersed strips. Most rare arable weeds which appear spontaneously grow in first year strips, especially on the more stony soils and in strips which have been sown in the autumn. The recovery of rare populations can be greatly assisted by *in* and *ex situ* propagation. In the seed bank of wildflower strips, rare species remain extremely scarce. However, in total the extremely impoverished seed bank of arable fields is enriched quickly in wildflower strips. The species composition in the seed bank differs from that in the vegetation; these differences can be interpreted in terms of seed longevity, life form and life history of the various species.

In chapter 2, factors differentiating the vegetation of wildflower strips are determined by the means of Canonical Correspondence Analysis; the resulting vegetation types are described in terms of plant species composition and species traits. Succession is the dominating differentiating process, especially in the beginning. From the second year on, the seed mixture applied also has a strong influence, and site factors like the soil conditions and surrounding landuse become increasingly important. Strips in their first year are dominated by typical arable weeds, i.e. spontaneous annual therophytes, which mostly form a long-lived seed bank. Subsequently, the vegetation cover increases as sown perennial thero-hemicryptophytes and hemicryptophytes typical of ruderal sites or meadows become dominant. At this stage, the number of species contained in the seed mixture is reflected in the number and cover of sown species in the vegetation, at the cost of species recruited spontaneously. From the third year onwards, spontaneous perennial species gain ground, including various laterally spreading hemicryptophytes and geophytes (including several grasses) with high nutrient requirements; their progress in replacing the sown species is more rapid on fertile sites. Attempts to steer the vegetation development at this stage by cutting or superficially working the soil are not usually successful in the long term. It is therefore concluded that sites known to have a high pressure of grasses or to contain other problem weeds should be avoided when establishing wildflower strips.

In chapter 3, the insect diversity of wildflower strips is studied with a focus on constraints and enhancing factors. Colonization and establishment patterns of true bugs are analysed based on responses of species traits to successional change and environmental factors. For a large number of species, colonization appears to be no problem. Species richness and total abundance of bugs are lower on average in wildflower strips in their first year than in older strips. Both are positively correlated to the number of perennial plant species and to the structural diversity of the vegetation. Bug species composition responds to the age and grass cover of wildflower strips. The proportions of oligo- and monophagous species, of species with only one generation per year, and of species overwintering in the egg stage all increase during succession, either in terms of species numbers or in abundance. A high grass cover promotes generalist species and grass specialists, including many species which also occur on grassy verges in the surroundings. A basic set of rather common species establish in many wildflower strips. Less mobile and rare species tend to have a local distribution and are difficult to promote.

Chapter 4 describes an experimental study of bug dispersal. The results show 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. None of the species caught in this experiment was found only in the wildflower strip; all species moved at least some distance into the crop. Individuals of some species reached a distance of 138 m within a few weeks or one generation. However, species differ in dispersal speeds, distances and patterns.

In summary, wildflower strips have been found to support a high diversity of plants and insects. While plant diversity is highest in strips in their first year, and these also contain the largest numbers of rare plant species, bug diversity is highest in strips in their second year and older, which also contain most specialized bug species. In both plant and bug communities, species composition is very variable and responds more strongly to environmental factors than species number. A high grass cover has a negative effect on the species composition of both plants and bugs, and tends to enhance a few common species. Comparatively rare plant and bug species both tend to have a local distribution, although dispersal is no problem for the majority of bug species. To maximise species diversity wildflower strips should be managed heterogeneously and should be well dispersed across the landscape.

Zusammenfassung

Diese Arbeit befaßt sich mit der Pflanzen- und Insektendiversität in Buntbrachen in einer schweizer Ackerlandschaft. Das Ziel ist, sowohl die sich in Buntbrachen etablierende Pflanzen- und Insektendiversität zu bestimmen, als auch die Faktoren, die diese Diversität beeinflußen. Damit sollen der Beitrag der Buntbrachen zur Biodiversität auf Landschaftsebene bewertet und Empfehlungen für deren optimale Anlage und Pflege entwickelt werden. Buntbrachen sind mindestens 3 m breite Ackerstreifen, die im Inneren eines Feldes oder entlang dessen Randes verlaufen. Sie werden gewöhnlich mit einer empfohlenen Mischung aus einheimischen Ackerwildkräutern, Arten ruderaler Standorte und Wiesenarten angesät. Sie bleiben für mindestens zwei meist aber sechs Jahre bestehen. Nach dem zweiten Jahr wird gewöhnlich eine Hälfte oder ein Drittel des Streifens im jährlichen Wechsel gemäht. Da Buntbrachen vergleichsweise junge Landschaftselemente sind, die zur Förderung der Biodiversität in die intensiv genutzte Ackerlandschaft eingebracht wurden, sind die Erkenntnisse über ihren Erfolg noch begrenzt. In dieser Dissertation werden die folgenden Fragen in vier Kapiteln untersucht: 1) Wie stark fördern Buntbrachen seltene und bedrohte Pflanzenarten? Welche Faktoren beeinflußen den Artenreichtum von Buntbrachen? Welchen Einfluß haben Buntbrachen auf die Pflanzendiversität in der Bodensamenbank? 2) Wie beeinflußen Samenmischungen, Management und Umweltfaktoren die Entwicklung der Vegetation in Buntbrachen? 3) Welche Rolle spielen die Besiedlung und Beschränkungen durch Umweltfaktoren bei der Etablierung von Insektengesellschaften in Buntbrachen? Sind Insektengesellschaften in Buntbrachen auf Generalisten beschränkt oder gelingt es auch Spezialisten, sich zu etablieren und wie schnell? Können Insektengesellschaften in verschiedenen Typen von Buntbrachen klar unterschieden werden, und wenn ja, welche Faktoren sind verantwortlich? 4) Dienen Buntbrachen als Ausbreitungsquelle von Insekten? Über welche Distanz und wie schnell können Insekten Flecken mit ihren Wirtspflanzen besiedeln? Ziel aller Kapitel ist, zur Beantwortung der Frage beizutragen, wie Buntbrachen angelegt und gepflegt werden sollten, um eine maximale Biodiversität auf Landschaftsebene zu erreichen.

Während die Artenzusammensetzung der Vegetation vollständig erfaßt werden kann, ist dies für Insekten unmöglich. Die Wanzen (Heteroptera) wurden als Indikatorgruppe für die Gesamtdiversität an Insekten ausgewählt, weil sie ökologisch vielfältig sind und ihre Zahlen in der Agrarlandschaft gut mit der Gesamtdiversität an Insekten korrelieren. Das Untersuchungsgebiet ist der Klettgau (Kanton Schaffhausen), ein intensiv genutztes Ackerbaugebiet im Norden der Schweiz. Es bildet ein flaches breites Tal, das von kalkreichen Flußschottern bedeckt ist, die lokal von Lehm und Löß überlagert sind. Seit 1991 wurden im Klettgau im Rahmen eines von der Schweizer Vogelwarte Sempach und dem Planungs- und

Naturschutzamt Schaffhausen geförderten Pilot-Projektes eine große Anzahl Buntbrachen angelegt, die vor allem in drei Schwerpunktgebieten liegen. Im Jahr 1996 wurde die Vegetation aller Buntbrachen aufgenommen, sowie 1997 und 1998 die Vegetation und Wanzen-Fauna ausgewählter Streifen unterschiedlichen Alters und Grasdeckung. Im Jahr 1998 wurden Beete mit Wirtspflanzen in mehreren Distanzen zu einer Buntbrache angelegt, um ihre Besiedlung durch Wanzen zu untersuchen. Im Kontext dieser Dissertation hat Gabriela Uehlinger in ihrer Diplomarbeit die Anreicherung von Samen in der Samenbank von Buntbrachen verschiedenen Alters untersucht.

Im 1. Kapitel werden die Faktoren analysiert, die die floristische Diversität und insbesondere die Anwesenheit seltener Ackerwildkräuter in Buntbrachen und Feldflorareservaten beeinflussen. Insgesamt wurden 234 Pflanzenarten in der Vegetation von Buntbrachen im Klettgau gefunden, von denen die große Mehrheit spontan aufgekommen ist. Die Artenzahl ist in einjährigen Streifen am größten und nimmt mit zunehmendem Alter und Vergrasung einer Fläche ab. Die Artenzusammensetzung variiert recht stark, so daß auf Landschaftsebene durch eine große Zahl von weit verstreuten Streifen eine maximale Diversität erreicht wird. Die meisten seltenen Ackerwildkräuter, die spontan aufkommen, wachsen in einjährigen Streifen, besonders auf den steinigeren Böden und in Streifen, die im Herbst angesät wurden. Die Erholung seltener Populationen kann durch in und ex situ Vermehrung stark unterstützt werden. In der Samenbank von Buntbrachen bleiben seltene Arten sehr rar. Dennoch reichert sich die in Äckern extrem verarmte Samenbank insgesamt in Buntbrachen schnell an. Die Artenzusammensetzung der Samenbank weicht von der in der Vegetation ab; diese Unterschiede können bezüglich der Langlebigkeit der Samen, der Lebensform und des Lebenszyklus der verschiedenen Arten interpretiert werden.

Im 2. Kapitel werden mit Hilfe von Kanonischer Korrespondenzanalyse Faktoren bestimmt, die die Vegetation von Buntbrachen differenzieren. Die sich daraus ergebenden Vegetationstypen werden hinsichtlich ihrer Arten-zusammensetzung und Arteigenschaften beschrieben. Die Sukzession ist der dominierende differenzierende Prozeß, besonders zu Beginn. Vom zweiten Jahr an hat auch die ausgebrachte Samenmischung einen starken Einfluß und Standortfaktoren, wie die Bodenverhältnisse und die umgebende Landnutzung, gewinnen an Bedeutung. Streifen im ersten Jahr werden von typischen Ackerwildkräutern dominiert, d.h. spontanen annuellen Therophyten, die größtenteils eine langlebige Samenbank bilden. Danach nimmt die Vegetationsdeckung zu, sobald angesäte ausdauernde Thero-Hemikryptophyten und Hemikryptophyten dominant werden. In diesem Stadium spiegelt sich die Anzahl in der Samenmischung enthaltener Arten, in der Anzahl und Deckung angesäter Arten in der Vegetation wider, was auf Kosten spontaner Arten geht. Vom dritten Jahr an, nehmen spontane ausdauernde Arten zu, darunter verschiedene sich vegetativ ausbreitende Hemikryptophyten und Geophyten (darunter einige Gräser) mit hohem Nährstoffbedarf. Dementsprechend verdrängen sie angesäte Arten auf fruchtbaren Böden schneller. Versuche, die Vegetationsentwicklung in diesem Stadium durch Mahd oder oberflächliche Bodenbearbeitung zu steuern, sind langfristig meist erfolglos. Daraus wird geschlossen, daß Standorte mit bekannterweise hohem Grasdruck oder anderen Problemunkräutern für die Anlage von Buntbrachen gemieden werden sollten.

Im 3. Kapitel wird die Insektendiversität von Buntbrachen mit Schwerpunkt auf einschränkenden und fördernden Faktoren untersucht. Die Besiedlungs- und Etablierungsmuster von Wanzen werden anhand von Reaktionen einiger Arteigenschaften auf Sukzessionsveränderungen und Umweltfaktoren analysiert. Für eine große Zahl von Arten scheint die Besiedlung kein Problem zu sein. Die Artenzahl und Gesamtindividuenzahl von Wanzen ist in erstjährigen Buntbrachen im Durchschnitt geringer als in älteren. Beide sind positiv mit der Anzahl perenner Pflanzenarten und der strukturellen Diversität der Vegetation korreliert. Die Zusammensetzung der Wanzenarten reagiert auf das Alter und die Grasdeckung von Buntbrachen. Sowohl die Anteile oligo- und monophager Arten, als auch die von Arten mit nur einer Generation pro Jahr und die von Arten, die im Eistadium überwintern, nehmen im Laufe der Sukzession zu. Die Zunahme erfolgt entweder in der Arten- oder in der Individuenzahl. Eine hohe Grasdeckung fördert Generalisten und Grasarten, die großenteils auch an grasreichen Wegrändern in der Umgebung vorkommen. Eine Auswahl recht häufiger Arten etabliert sich in vielen Buntbrachen. Weniger mobile und seltenere Arten neigen zu lokaler Verbreitung und sind schwer zu fördern.

Kapitel 4 beschreibt eine experimentelle Studie zur Ausbreitung von Wanzen. Die Ergebnisse zeigen, daß Buntbrachen zumindest für einige Wanzenarten als Ausbreitungsquelle dienen und daß die meisten Wanzenarten, die in Buntbrachen vorkommen, recht mobil sind. Keine der in diesem Experiment gefangenen Arten, wurde ausschließlich in der Buntbrache gefunden; alle Arten bewegten sich zumindest über eine gewisse Distanz in die Kulturen. Individuen einiger Arten erreichten innerhalb von wenigen Wochen oder einer Generation eine Distanz von 138 m. Die Arten unterscheiden sich jedoch in ihren Ausbreitungsmustern.

Insgesamt zeigte sich, daß Buntbrachen eine hohe Diversität an Pflanzen und Insekten fördern. Während die florisitsche Diversität in erstjährigen Buntbrachen am höchsten ist und diese auch die größten Zahlen seltener Pflanzenarten enthalten, ist die Wanzendiversität in zweijährigen und älteren Streifen am höchsten. Letztere enthalten auch die meisten spezialisierten Wanzenarten. Die Artenzusammensetzung von beiden, Pflanzen- und Wanzengesellschaften, ist sehr variabel und reagiert stärker auf Umweltfaktoren als die Artenzahl. Eine hohe Grasdeckung wirkt sich negativ auf die Artenzusammensetzung von Pflanzen und Wanzen aus und fördert vor allem wenige häufige Arten. Vergleichsweise seltene Pflanzen- und Wanzenarten neigen beide zu lokaler Verbreitung, obwohl die Ausbreitung für die meisten der Wanzenarten kein Problem ist. Um die Artenvielfalt zu maximieren, sollten Buntbrachen heterogen behandelt und weit über die Landschaft verteilt werden.

General introduction

The intensification of agriculture in Europe in recent decades, associated with rapid changes in farming methods and landscape structure, has led to a considerable reduction of biological diversity in agricultural systems. This decline has been especially severe in intensively used arable landscapes and is largely due to the elimination of structural elements, other melioration measurements, changes in crop rotation, frequent mechanical disturbance plus pesticide and fertilizer inputs, as well as more thorough cleaning of seeds (Otte A. 1984; Albrecht H. 1989; Albrecht H. & Bachthaler G. 1990b; Hüppe J. 1990). In Switzerland, about half of all arable and other ruderal weed species are extinct or endangered (Landolt E. 1991). Although no equivalent numbers are available for invertebrates, it can be assumed that their decline is at least as severe, as many of them depend on these plant species. For larger animals – for example, birds such as the skylark or grey partridge and some mammals like the European hare – the situation is further aggravated by their large scale habitat requirements (Tucker G.M. et al. 1994; Mühlenberg M. & Slowik J. 1997; Weibel U. 1999; Jenny M. et al. 1999).

During the 1980´s, and especially since the earth summit in Rio in 1992, public awareness of the decline in biodiversity has increased. As a consequence many countries have agreed to introduce measures to enhance biodiversity. In Europe, one focus has been on the extensification of agricultural land, including the subsidy of set-aside land; this approach coincides with demands for measures against agricultural overproduction. In Switzerland, a legal framework to promote the introduction of 'ecological compensation areas' in intensively used agricultural landscapes has been in force since 1993 (Art. 31b of the Agriculture Act). Under this policy, a farmer only qualifies for direct subsidies if 7% of the agricultural area of a farm is maintained as ecological compensation areas. These 'ecological compensation areas' include various types of extensive grasslands, ponds or ditches, fruit-trees or (more commonly in arable land) other trees or groups of trees, hedges, pesticide-free cereal headlands, grassland and wildflower strips. Unlike most other types of 'compensation areas', wildflower strips are not traditional features of the landscape. They are strips of land, at least 3 m wide, running down the middle or along the edge of an arable field, and are sown with a recommended mixture of indigenous arable weeds and ruderal species. They are maintained for at least two years and usually for longer (up to six years) and, after the second year, one half or one third of a strip is typically mown each year in rotation. The effectiveness of these measures to enhance biodiversity was investigated as part of the 'Swiss Priority Programme Environment (SPPE) – Biodiversity' of the Swiss National Science Foundation. The aims of this thesis, which is part of that programme, are:

- to assess the plant and insect diversity of wildflower strips and the factors influencing this diversity,
- to evaluate the contribution of wildflower strips to biodiversity on a landscape scale,
- to make recommendations for the optimal management of wildflower strips.

There have been several experimental studies of wildflower strips, mainly aimed at developing seed mixtures and management regimes which favour a high diversity of plants and invertebrates (Bürki H.-M. & Hausammann A. 1992; Günter M. 2000a; Günter M. 2000b; Häni F. & Zürcher J. 2000; Heitzmann A. 1995; Pfiffner L. & Schaffner D. 2000; Ramseier D. 1994; Salveter R. & Nentwig W. 1993; Schaffner D. & Keller S. 1998; Schaffner D. et al. 2000). There has also been work focussed on wildflower strips as habitats for beneficial arthropods (Schmid A. 1992; Weiss E. & Stettmer C. 1991). As many of these studies have been carried out on a small spatial scale, one object of this thesis is to confirm whether the conclusions can be transferred to large-scale field applications.

The floristic diversity, and particularly the presence of rare plant species in wildflower strips, is only partly due to the species sown. Species recruiting spontaneously also contribute greatly to the overall diversity, though the numbers and identity of species vary according to site conditions (Günter M. 2000a). I analyse differences in floristic diversity and the occurrence of rare plant species depending on the influence of various site and management factors. I also determine the factors influencing the development of the vegetation and describe the characteristics of the resulting vegetation types.

Invertebrate communities often show complex responses to site conditions because they can be influenced by the vegetation composition and plant architecture, as well as by the structure of the surrounding landscape and other environmental factors (Southwood T.R.E. et al. 1979; Saunders D.A. et al. 1991). In addition, factors such as the sequence of immigration and interactions between trophic levels can influence community composition (Lawton J.H. 1978; Southwood T.R.E. 1988; Gibson C.W. et al. 1992). As it was practically impossible to study the whole insect diversity of wildflower strips, I chose the true bugs (Heteroptera) as an indicator group. There were several reasons for this choice. Bugs are an ecologically very diverse group, containing species of all trophic levels and degrees of food specialization, and differing widely in mobility and life cycle traits (Dolling W.R. 1991). They spend their entire life cycle in the same habitat – except the adults of some species which overwinter in special sites – and thus respond sensitively to changes in environment (Morris M.G. 1969; Morris M.G. 1979; Achtziger R. 1995; Otto A. 1996). A comparison of diversities of different insect groups has shown that, in the agricultural landscape, bug diversity correlates strongly with total insect diversity (Duelli P. & Obrist M. 1998). In a study of a long-term secondary succession, bug diversity also mirrored age-dependent changes in total exopterygote diversity closely (Brown V.K. & Southwood T.R.E. 1983). Last, but not least, numbers of bug species occurring in the arable landscape are large enough to allow statistical analysis but manageable from a practical view-point. So far, bug diversity and species composition have rarely been studied in the context of secondary succession (Brown V.K. 1985; Greiler H.-J. 1994), and never in sown wildflower strips. I analyse which environmental factors influence bug species composition, and try to separate the effects of colonization from those of site factors.

In previous studies of wildflower strips, the seed mixtures used, site factors and management have varied widely, as well as the experimental set up (Ramseier D. 1994; Heitzmann A. 1995; Günter M. 2000a; Schaffner D. et al. 2000). It is therefore difficult to reach general conclusions about the development of the vegetation and insect fauna of wildflower strips, or about the most effective ways to manage them for diversity. In this thesis I attempt to generalise about the flora and fauna by relating the life history characteristics of plants and bugs to habitat factors. Various schemes have been proposed for classifying habitats in terms of the factors important for life history evolution. All of these schemes recognise a gradient from highly disturbed sites to stable sites, and some also recognise an independent quality/adversity gradient (Grime J.P. 1979; Southwood T.R.E. 1977; Southwood T.R.E. 1988). The various schemes agree that typical colonising or ruderal species ('r-species') occur in highly disturbed sites, while competitive species which are usually closely adapted to local site conditions ('C'- or 'K-species') occur in more stable sites. Both strategies are associated with a series of species traits which tend to be underdispersed in the respective sites, while a random distribution of traits is expected under intermediate conditions (Keddy P.A. 1992; Weiher E. & Keddy P.A. 1995; Belyea L.R. & Lancaster J. 1999). While effects of overdispersion of traits due to niche avoidance can be excluded in young sites such as wildflower strips, phylogenetic constraints may bias the distribution patterns of traits if only a narrow taxonomic range is considered (Weiher E. & Keddy P.A. 1995; Felsenstein J. 1985). In this thesis, I investigate the responses of species traits in wildflower strips to different successional stages and environmental factors. While such an approach has frequently been used in vegetation studies, generalizations based on species traits are rare in entomological studies (Brown V.K. 1985; Brown V.K. 1986; Novotny V. 1994; Novotny V. 1995).

Dispersal of organisms as a means to colonise new habitats is a crucial precondition for the establishment of a diverse flora and fauna in wildflower strips. In plant species, dispersal can occur in time as well as in space, through the germination of species stored in the seed bank (Hodgson J.G. & Grime J.P. 1990). Many species of arable habitats form a seed bank and, accordingly, the diversity and species composition of plants in the soil seed bank of arable fields has been investigated in detail (Albrecht H. 1989; Albrecht H. & Bachthaler G. 1990a; Albrecht H. 1994; Froud-Williams R.J. et al. 1983; Otte A. 1992). Although several studies have examined changes in the soil seed bank of set-aside sites (Tischew S. & Schmiedeknecht A. 1993; Jödicke K. & Trautz D. 1994), much less is known about the seed bank of wildflower strips. This was studied by Heitzmann (1995), who compared the seed bank of three year old strips with those of arable fields. In the context of the present study, Uehlinger (2000) investigated the seed bank of wildflower strips of different ages and compared it with that in adjacent fields.

In contrast to plant dispersal, rather few studies deal with the dispersal and colonization of insects in agricultural landscapes. In particular, there has been only one major study on the dispersal of heteropteran bugs (Southwood T.R.E. 1960), though a few other studies are also relevant. One of these concerns the distribution of bugs caught in flight in a landscape transect, and others deal with potential pest species (Brown E.S. 1965; Stöckli E. & Duelli P. 1989). I designed an experiment to investigate the ability of bugs to colonise isolated patches of their host plants planted into adjacent cultures at various distances.

Data for this study were collected between 1996 and 1999 in the Klettgau (Canton Schaffhausen), an intensively used arable region in the north of Switzerland. It forms a wide, flat valley covered with calcareous river gravels that are locally overlaid by loam and loess. Since 1991, a large number of wildflower strips have been established in the context of a project of the Swiss Ornithological Institute to promote the grey partridge (*Perdix perdix*) and the European hare (*Lepus europaeus*). Wildflower strips were also sponsored by the cantonal authorities. The Klettgau thus offered good conditions for the purposes of this study.

This thesis is organised in four main chapters. Chapter 1 investigates the factors affecting floristic diversity (and particularly the presence of rare arable weeds) in wildflower strips and arable flora reserves. In chapter 2, factors differentiating the vegetation of wildflower strips are determined, and the resulting vegetation types are described in terms of plant species composition and species traits. Chapter 3 concerns the diversity of heteropteran bugs in wildflower strips, with a focus on the factors influencing species diversity. The responses of species traits to successional change and environmental factors are also analysed. Chapter 4 describes the experimental study of bug dispersal.

References

Achtziger, R. 1995. Die Struktur von Insektengemeinschaften an Gehölzen: Die Hemipteren-Fauna als Beispiel für die Biodiversität von Hecken- und Waldrandökosystemen. Bayreuther Forum Ökologie 20.

Albrecht, H. 1989. Untersuchungen zur Veränderung der Segetalflora an sieben bayerischen Ackerstandorten zwischen den Erhebungszeiträumen 1951/68 und 1986/88. Borntraeger, Stuttgart-Berlin.

Albrecht, H. 1994. Modelluntersuchung und Literaturauswertung zum Diasporenvorrat gefährdeter Wildkräuter in Ackerböden. Schriftenreihe „Aus Liebe zur Natur" der Stiftung zum Schutze gefährdeter Pflanzen 5: 123-140.

Albrecht, H. & Bachthaler, G. 1990a. Unkrautsamengehalte und Bodeneigenschaften von Ackerflächen in Bayern. Weed Research 30: 101-108.

Albrecht, H. & Bachthaler, G. 1990b. Veränderungen der Segetalflora Mitteleuropas während der letzten vier Jahrzehnte. Verhandlungen der Gesellschaft für Ökologie 19: 364-372.

Belyea, L.R. & Lancaster, J. 1999. Assembly rules within contingent ecology. Oikos 86: 402-416.

Brown, E.S. 1965. Notes on the migration and direction of flight of Eurygaster and Aelia Species (Hemiptera, Pentatomidae) and their possible bearing on invasions of cereal crops. Journal of Animal Ecology 34: 93-107.

Brown, V.K. 1985. Insect herbivores and plant succession. Oikos 44: 17-22.

Brown, V.K. 1986. Life cycle strategies and plant succession. In: Taylor, F. & Karban, R. (eds.) The evolution of insect life cycles, pp. 105-124. Springer-Verlag, New York.

Brown, V.K. & Southwood, T.R.E. 1983. Trophic diversity, niche breadth and generation times of exopterygote insects in a secondary succession. Oecologia 56: 220-225.

Bürki, H.-M. & Hausammann, A. 1992. Überwinterung von Arthropoden im Boden und an Ackerunkräutern künstlich angelegter Ackerrandstreifen. Agrarökologie 7.

Dolling, W.R. 1991. The Hemiptera. Oxford University Press.

Duelli, P. & Obrist, M. 1998. In search of the best correlates for local biodiversity in cultivated areas. Biodiversity and Conservation 7: 297-309.

Felsenstein, J. 1985. Phylogenies and the comparative method. The American Naturalist 125: 1-15.

Froud-Williams, R.J., Chancellor, R.j. & Drennan, D.S.H. 1983. Influence of cultivation regime upon buried seeds in arable cropping systems. Journal of Applied Ecology 20: 199-208.

Gibson, C.W., Brown, V.K., Losito, L. & McGavin, G.C. 1992. The response of invertebrate assemblies to grazing. Ecography 15: 166-176.

Greiler, H.-J. 1994. Insektengesellschaften auf selbstbegrünten und eingesäten Ackerbrachen. Agrarökologie 11.

Grime, J.P. 1979. Plant strategies and vegetation processes. Wiley, Chichester.

Günter, M. 2000a. Anlage und Pflege von mehrjährigen Buntbrachen unter den Rahmenbedingen des Schweizerischen Ackerbaugebietes. Agrarökologie 37: 154.

Günter, M. 2000b. Sukzession von Buntbrachen. In: Nentwig, W. (ed.) Streifenförmige ökologische Ausgleichsflächen in der Kulturlandschaft: Ackerkrautstreifen, Buntbrache, Feldränder, pp. 55-76. Verlag Agrarökologie, Bern.

Häni, F. & Zürcher, J. 2000. Vermehrung, Ausbreitung und Regulierung der Ackerkratzdistel Cirsium arvense – Ökoflächen im Fokus. In: Nentwig, W. (ed.) Streifenförmige ökologische Ausgleichsflächen in der Kulturlandschaft: Ackerkrautstreifen, Buntbrache, Feldränder, pp. 93-112. Verlag Agrarökologie, Bern.

Heitzmann, A. 1995. Angesäte Ackerkrautstreifen - Veränderungen des Pflanzenbestandes während der natürlichen Sukzession. Agrarökologie 13.

Hodgson, J.G. & Grime, J.P. 1990. The role of dispersal mechanisms, regenerative strategies and the seed banks in the vegetation dynamics of the British landscape. In: Bunce, R.G.H. & Howard, D.C. (eds.) Species dispersal in agricultural habitats, pp. 65-81. Belhaven Press, London.

Hüppe, J. 1990. Die Genese moderner Agrarlandschaften in vegetationsgeschichtlicher Sicht. Verhandlungen der Gesellschaft für Ökologie 19(2): 424-432.

Jenny, M., Weibel, U. & Buner, F. 1999. Der ökologische Ausgleich in intensiv genutzten Ackerbaugebieten des Klettgaus und seine Auswirkungen auf die Brutvogelfauna. Mitteilungen der Naturforschenden Gesellschaft Schaffhausen 44: 203-221.

Jödicke, K. & Trautz, D. 1994. Veränderungen der Samenbank im Boden von Ackerbrachen. Natur und Landschaft 69: 258-264.

Keddy, P.A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3: 157-164.

Landolt, E. 1991. Gefährdung der Farn- und Blütenpflanzen in der Schweiz, mit gesamtschweizerischen und regionalen roten Listen. Bundesamt für Umwelt, Wald und Landschaft, Bern.

Lawton, J.H. 1978. Host-plant influences on insect diversity: the effects of time and space. In: Diversity of insect faunas. Symposium of the Royal Entomological Society of London. Mound, L.A. & Waloff, N., (eds.). 105-125.

Morris, M.G. 1969. Differences between the invertebrate faunas of grazed and ungrazed chalk grassland. III. The heteropterous fauna. Journal of Applied Ecology 6: 475-487.

Morris, M.G. 1979. Responses of grassland invertebrates to management by cutting. II. Heteroptera. Journal of Applied Ecology 16: 417-432.

Mühlenberg, M. & Slowik, J. 1997. Kulturlandschaft als Lebensraum. Quelle & Meyer Verlag, Wiesbaden.

Novotny, V. 1994. Association of polyphagy in leafhoppers (Auchenorrhyncha, Hemiptera) with unpredictable environments. Oikos 70: 223-232.

Novotny, V. 1995. Relationships between life histories of leafhoppers (Auchenorrhyncha - Hemiptera) and their host plants (Juncaceae, Cyperaceae, Poaceae). Oikos 73: 33-42.

Otte, A. 1984. Änderungen der Ackerwildkraut-Gesellschaften als Folge sich wandelnder Feldbaumethoden in den letzten drei Jahrzehnten - dargestellt an Beispielen aus dem Raum Ingolstadt. Cramer, Vaduz.

Otte, A. 1992. Entwicklung im Samenpotential von Ackerböden nach dem Aussetzen von Unkrautregulierungsmaßnahmen. Landwirtschaftliches Jahrbuch 69: 837-860.

Otto, A. 1996. Die Wanzenfauna montaner Magerwiesen und Grünbrachen im Kanton Tessin (Insecta: Heteroptera) - Eine faunistisch ökologische Untersuchung. Dissertation. ETH Zürich, Zürich.

Pfiffner, L. & Schaffner, D. 2000. Anlage und Pflege von Ackerkrautstreifen. In: Nentwig, W. (ed.) Streifenförmige ökologische Ausgleichsflächen in der Kulturlandschaft: Ackerkrautstreifen, Buntbrache, Feldränder, pp. 41-54. Verlag Agrarökologie, Bern.

Ramseier, D. 1994. Entwicklung und Beurteilung von Ansaatmischungen für Wanderbrachen. Veröffentlichungen des Geobotanischen Instituts der ETH, Stiftung Rübel 118: 134.

Salveter, R. & Nentwig, W. 1993. Schwebfliegen (Diptera, Syrphidae) in der Agrarlandschaft: Phänologie, Abundanz und Markierungsversuche. Mitteilungen der Naturforschenden Gesellschaft Bern 50: 1-45.

Saunders, D.A., Hobbs, R.J. & Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5: 18-32.

Schaffner, D., Günter, M., Häni, F. & Keller, M. 2000. Ökologische Ausgleichsfächen in der Landwirtschaft: Ergebnisse mehrjähriger Versuche zur Anlage und Pflege blütenreicher Buntbrachen. Schriftenreihe der FAL 34.

Schaffner, D. & Keller, S. 1998. Praxiserfahrungen mit Buntbrachen und Ackerrandstreifen in der Schweiz. Schriftenreihe der Landesanstalt für Pflanzenbau und Pflanzenschutz 6: 45-54.

Schmid, A. 1992. Untersuchungen zur Attraktivität von Ackerwildkräutern für aphidophage Marienkäfer (Coleoptera, Coccinellidae). Agrarökologie 5.

Southwood, T.R.E. 1960. The flight activity of Heteroptera. Transaction of the Royal Entomological Society London 112: 173-220.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 46: 337-365.

Southwood, T.R.E. 1988. Tactics, strategies and templets. Oikos 52: 3-18.

Southwood, T.R.E., Brown, V.K. & Reader, P.M. 1979. The relationship of plant and insect diversities in succession. Biological Journal of the Linnean Society 12: 327-348.

Stöckli, E. & Duelli, P. 1989. Habitatbindung und Ausbreitung von flugfähigen Wanzenarten in naturnahen Biotopen und Kulturlandflächen. Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie 7: 221-224.

Tischew, S. & Schmiedeknecht, A. 1993. Vegetationsentwicklung und Dynamik der Diasporenbank und des Diasporenfalls einer Ackerbrache unter den Bedingungen des Mitteldeutschen Trockengebiets. Verhandlungen der Gesellschaft für Ökologie 22: 162-173.

Tucker, G.M., Heath, M.F., Tomialojc, L. & Grimmett, R.F.A. 1994. Birds in Europe: their conservation status. – Birdlife International, Cambridge.

Uehlinger, G. 2000. Einfluß von Buntbrachen auf die Diversität der Wanzenfauna und des Samenvorrats im Boden einer Ackerlandschaft. Diplomarbeit. ETH Zürich.

Weibel, U. 1999. Effects of wildflower strips in an intensively used arable area on skylarks (Alauda arvensis). Dissertation. Swiss Federal Institute of Technology Zürich, Zürich.

Weiher, E. & Keddy, P.A. 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. Oikos 74: 159-164.

Weiss, E. & Stettmer, C. 1991. Unkräuter in der Agrarlandschaft locken blütenbesuchende Nutzinsekten an. Agrarökologie 1.

Chapter 1. The role of wildflower strips in enhancing floristic diversity in an intensive arable landscape

Karin S. Ullrich, Gabriela Uehlinger and Peter J. Edwards

Abstract

This paper investigates the success of sown wildflower strips and arable flora reserves in promoting a high diversity of arable weeds in an intensively used arable landscape. The study was located in the Klettgau, a region in Northern Switzerland which is used for intensive arable agriculture. Soil conditions are favourable to support a high diversity of arable species, and historical records reveal that many threatened species were formerly present, although many of these have now declined or disappeared. A large number of wildflower strips have been planted in the region since 1990 as part of a scheme to promote biological diversity, and particularly to increase populations of certain bird species. During surveys of the vegetation of these wildflower strips 234 species were found, of which the vast majority had recruited spontaneously. Species richness was highest in strips in their first year and decreased with increasing age and grassiness of a site. The species composition of individual sites is rather variable, so that maximum diversity at a landscape scale is achieved by a high number of widely dispersed strips. Most rare arable weeds which appear spontaneously grow in first year strips, especially those on more stony soils and which have been sown in the autumn. The recovery of rare populations can be greatly assisted by *in* and *ex situ* propagation.

A seed bank study revealed that the extremely impoverished seed bank of arable fields is enriched quickly in wildflower strips. However, rare species remain extremely scarce. The species compositions of the vegetation and the seed bank are different. These differences can be interpreted in terms of seed longevity, life form and life history of the various species. Based on the results of this study, recommendations are presented of how the floristic diversity of intensive arable areas can be enhanced.

Keywords: Arable flora reserve, Correspondence Analysis, life form, landscape scale, life history, rare arable weeds, Red List, seed bank, Switzerland, seed longevity

Introduction

The decline of biodiversity in Europe in recent decades has been especially severe in intensively used arable areas. Many populations of arable and ruderal plant species have been lost because their habitats have been destroyed or altered. Important changes include more frequent mechanical disturbance, changes in crop rotation, increased use of pesticides and fertilizers, and more thorough cleaning of seeds (Albrecht H. 1989; Albrecht H. & Bachthaler G. 1990; Hüppe J. 1990; Otte A. 1984). In Switzerland, where the work described in this paper was performed, arable and ruderal weeds make up roughly one quarter of the flora; however, about half the species are extinct or endangered (Landolt E. 1991). Invertebrates and larger animals which depend on these plant species, or on the habitats in which they occur, have also been severely affected.

A variety of measures have been taken in Switzerland to reduce or even reverse the loss of biodiversity; these include extensification of agricultural land and, since 1993, also the creation of new landscape elements. Among the latter are wildflower strips, of which large numbers have been sown in intensively used arable areas. These are strips of land which are at least 3 m wide and may either run through or along the edge of an arable field. They are usually sown with a recommended mixture of indigenous arable weeds and ruderal species. They are maintained for at least two, but usually for six years; after the second year one half or one third of a strip is typically mown each year in rotation.

Part of the purpose of wildflower strips is to increase biological diversity, especially of rare species and of beneficial organisms such as natural enemies of pest species (Heitzmann A. & Nentwig W. 1993; LBL 1996; Nentwig W. 1993; Nentwig W. 1992; Ramseier D. 1994). In this paper we are interested in the potential of wildflower strips to enhance spontaneous recruitment of plant species and promote a diverse arable flora. The study was carried out in an intensively used arable area where a large number of wildflower strips have been introduced during the last decade. By means of vegetation surveys and seed bank studies we investigate the following questions:

- How effective are wildflower strips in recruiting rare and threatened plant species?
- What factors influence the species richness of wildflower strips?
- What impact do wildflower strips have on plant species diversity in the soil seed bank?

Research area

The study area is the Klettgau (Canton Schaffhausen), an intensively used arable region in the north of Switzerland. It forms a wide, flat valley with calcareous river gravels which are locally overlaid by loam and loess; soil conditions are mostly rich in bases but vary in depth and texture and thus also in fertility and water permeability. The area ranges in altitude between 400 and 470 m a.s.l.. In comparison to other parts of the Swiss Midlands, the climate is relatively dry and warm in summer (915 mm precipitation per year; 18.4°C Temp. average in July; 8.5°C annual Temp. average), which leads to a frequent deficit in water balance between April and August (data from the Swiss Meteorological Institute 1996). Cereals are the main crop type and cover about half of the surface of the agricultural area; these are followed, in declining order of abundance, by root crops, maize, rape, and locally also by grassland. The average parcel size in the region is about 0.88 ha, i.e. very small. The study area is divided into three districts, Widen, Langfeld and Plomberg, which together with the surrounding area comprise the region known as the Klettgau.

Table 1. Characteristics of the districts comprising the majority of wildflower strips in the Klettgau (based on Jenny M. & Weibel U. 1999).

Characteristics	**Widen**	**Langfeld**	**Plomberg**
Location	NE of Neunkirch	W of Neunkirch	W of Wilchingen
Area of district	5.3 km^2	2.4 km^2	4.7 km^2
Soil depth	10 - 50 cm	50 - 100 cm	50 - 100 cm
Stone cover	0 - 60%	mostly 0%	mostly 0%
Soil texture (according to Schröder 1984)	stony, loamy clay (– silty loam)	clay loam, little sand	silty loam, 10 - 30% sand
Fertility	less fertile	very fertile	very fertile
Grassland	12%	6%	17%
Trees + hedgerows	locally (area of a former fen)	some	few
Specialities	base rich, rare arable weeds, arable flora reserves, area of a former fen with a stream and pond included	canalised streams	few wildflower strips
Age of strips	1 - 5 years	1 - 5 years	2 - 3 years
No. of wildflower strips:			
total	26	14	8
subsections in 1st yr	15	9	0
arable flora reserves	9	0	0

The region used to have a rich arable flora consisting mainly of species associated with the Caucalidion lappulae, an alliance of calcareous cereal fields and to a lesser degree the Fumario-Euphorbion, an alliance of calcareous root crops (Isler K. 1976;

Kelhofer E. 1920; Kummer G. 1937; Oberdorfer E. 1994). Some of the more rare species associated with these alliances can still be found, especially in the Widen district.

As part of a project to improve habitat conditions for the grey partridge and the European hare, a large number of wildflower strips of various kinds have been created in the Klettgau since 1992 (Jenny M. & Weibel U. 1999; Jenny M. et al. 1999). They are concentrated mainly in the three districts Widen, Langfeld and Plomberg while only few are located elsewhere in the region (Table 1). Records about the management of these areas are held by the Swiss Ornithological Institute and the cantonal authorities as well as by some farmers, and are not always complete. Here we refer to wildflower strips and arable flora reserves. The latter are fields or parts of fields managed to promote rare arable weeds by sowing cereals at low density in favourable sites and also by adding seeds of selected rare species. In contrast, in wildflower strips a variety of standard seed mixtures have been used at one time or other (App.1). Sometimes, additional unknown species have been sown in particular strips, referred to as 'Additions'. Some of these 'Additions' are from rare arable species, which had been collected locally and propagated both *in* and *ex situ*.

Methods

Vegetation survey

In 1996 the vegetation of all the then existing wildflower strips and arable flora reserves in the Klettgau (62) was surveyed (4th June – 22nd July). Subsections of strips that had experienced different management or for some other reason had developed a distinctive vegetation were treated as distinct sites. Wherever possible, information was gathered for each site concerning the following: the age ('1st year', '2nd year', '3rd year' and '≥ 4th year'), the season of establishment ('Spring', 'Autumn'), whether a seed mixture was applied recently ('Newly sown'), the seed mixture applied ('Spontaneous', 'Kanton93', 'Rams.o', 'Rams.r', 'UFA94', 'UFA95/96', 'Klettgau', 'Ackerfl94', 'Additions'; App. 1) and later maintenance impacts, i.e. the renewal of a site ('Old strip'). In addition, the surrounding landuse was mapped for each site ('Cereals', 'Other Crops', 'Grassland', 'Roads', 'Wood', 'Other') and the quantity of stones on the soil surface was recorded as percentage cover classes ('Stones 0-15%', 'Stones 16-30%', 'Stones 31-45%', 'Stones > 45%').

In each of the 156 sites thus recognised four 1 m^2 quadrats were located regularly along the length of the strip. In each quadrat the top cover of every plant species was estimated (to the nearest 1% between 1 and 20%, and to the nearest 5% above 20% cover).

The surveys were repeated in 1997 (2nd – 10th June) in 20 sites, all situated in the district Widen. These sites belong to 4 main types, differentiated by age and grass cover in spring (1st year, 2nd year, ≥ 3rd year not grassy, ≥ 3rd year grassy), represented by 5 replicates each. In 1998 (25th June – 2nd July), a further 18 sites were surveyed; these were distributed all over the Klettgau and belonged to 3 types (1st year, 2nd year, 3rd year not grassy) with 6 replicates of each.

Seed bank study

For the seed bank study, soil samples were taken in 1999 from 2 young (3rd year), 2 medium old (5th-6th year) and 2 old (7th year) wildflower strips (W). Reference samples were taken from the adjacent fields (F), in which cereals were grown, except for one field with sugar beet (F young 1). Differences in soil characteristics could not be avoided entirely; however to keep these to a minimum the sites were all situated within the Widen district. Another source of variation is in the seed mixtures used, which varied slightly between years (App.2).

Between August 21st and September 1st five samples were taken from each site. Each sample was derived by mixing 8 subsamples extracted in a regular pattern from an area of 2 m^2. The first sample was taken 20 m from the end of a strip and the others at 20 m intervals along the strip. The same pattern was followed within the adjacent field at 20 m distance to the strip. A soil corer of 7 cm diameter was used to take a subsample from the upper soil layer (0-7 cm depth). After deepening the hole to 15 cm with a Richard-borer or a spade, a second core was taken (15-22 cm depth). Greater depths below the ploughing horizon could not be reached due to the high stone content. The 8 subsamples of each layer were well mixed in a bag before 2 l of the roughly 2.15 l sample were measured out for further processing.

The soil was soaked with water in a bucket and then passed through a sieve of 4 mm mesh to separate out stones and other coarse particles. It was then passed through a sieve of 0.2 mm mesh width to get rid of clay and loam particles while retaining even the smallest seeds. This material was washed into a funnel furnished with a fine gauze. After surplus water had drained away, the samples had a wet-weight of between 400 - 500 g. The samples were returned into a plastic bag and stored for 2 to 13 days at 12 - 15°C in the dark until they were required.

On September 7th, the samples were spread in 15 x 15 cm^2 compartments on top of propagation trays (30 x 45 cm) prepared with a layer of perlit covered by a woollen fleece. The propagation trays stood in low basins filled with water to provide the samples with a constant water supply. Seedlings were determined at weekly intervals for 21 weeks, with the aid of the following guides: Csapody (1968), Cremer (1991), Aichele (1991), Hanf (1990), Hubbard (1985), Klapp (1990), Lauber (1996), Schmeil (1993), Vögeli (1993).

Comparative plant ecological data

For all species recorded, the following information (referred to as species 'traits') was assembled from published sources (Baskin C.C. & Baskin J.M. 1998; Hanf M. 1990; Hodgson J.G. et al. 1995; Landolt E. 1991; Schneider H. & Paulsen J. 1994; Thompson K. et al. 1997; Ødum S. 1974; Fitter A.H. & Peat H.-J. 1994; Korsmo E. 1930): Red List status in Switzerland and NE Switzerland, natural habitat affinity, life history, life form according to Raunkiaer (1934), longevity of seeds in the seed bank, and indicator values according to Landolt (1977). Information about the former occurrence of Red List species was assembled from local floristic records, and about their affinity to phytosociological taxa from other sources (Isler K. 1976; Kelhofer E. 1920; Kummer G. 1937; Oberdorfer E. 1994; Welten M. & Sutter R. 1982).

Analyses

All multivariate analyses were run using Canoco version 4.02 (ter Braak 1997-1999). For the 36 strips in their 1st year, cover data for spontaneous species (+ those derived from 'Additions') were entered in a Correspondence Analysis (CA). Only species occurring in at least 3 strips were entered in the analysis. The remaining species, a series of environmental variables and a responding variable 'No. of Red List species' were included by the means of indirect gradient analysis. The analysis was run using log-transformed data and with no down-weighting of rare species.

The influence of various site and management factors on the spontaneous vegetation of strips in their first year was investigated by Canonical Correspondence Analysis (CCA), using the same species and settings as in the CA. Forward selection of environmental variables (Table 1) was used to eliminate variables which are collinear or in general do not contribute significantly to an explanation of the variation in species abundances (Monte Carlo Test with 599 unrestricted permutations; $P \leq 0.01$). The explained variation in the vegetation data was partitioned according to the contribution of single factors or factorial groups (Borcard D. et al. 1992; Økland R.H. & Eilertsen O. 1994; ter Braak C.J.F. & Smilauer P. 1998; Whittaker J. 1984). For each of these factors or factorial groups the variance contributed was partialled out and tested for significance (Monte Carlo Test with 599 unrestricted permutations; $P \leq 0.01$).

The influence of the factors age of the site (old, medium, young), soil layer (upper, lower), type of site (wildflower strip, field) and site number (1-6), as well as the interaction of the latter two on the species composition in the seed bank, was also analysed by the means of CCA. All species were included in the analyses without transformation or down-weighting of rare species. As for the vegetation data, the variance was partialled out for the single factors and tested for significance (Monte

Carlo Test with 199 unrestricted permutations; P≤0.001). Separate analyses have been run on the total data set as well as on the wildflower strip data by themselves.

Diversity analyses

For the 1996 data, several measures of species diversity were calculated for each site, including species number, Simpson-Index, Shannon-Index and evenness. The diversity measurements were compared between sites of different age and for those ≥ 3 years age also between non-grassy (grass cover < 20%) and grassy strips (grass cover > 20%) using the Tukey-Kramer HSD Test. For the 1997 and 1998 data diversity was also calculated for quadrats and for vegetation types. For this purpose the data originating from the quadrats were successively aggregated according to site, vegetation type, and total for all wildflower strips, and the diversity measures recalculated at each level (hierarchical analysis of diversity (Lande R. 1996)).

Results

The flora of wildflower strips

Between 1996 and 1998 we recorded a total of 234 plant species in 194 wildflower strip sites (776 1 m^2 quadrats). About one quarter of the species found had been sown somewhere (App. 1; Table 2), while a further 9% are crop plants (e.g. *Triticum* spec., *Brassica napus*). The remaining species are wild plants that recruited spontaneously. Most species are typical arable weeds (22.6%), occur in both arable and ruderal sites (22.2%), or mainly in ruderal sites (29.9%); there were also a few species of meadows (14.5%) and forest edges (fringe species 0.9%, wood species 4.7%).

Forty-three of the species we found appear in the Red List for NE Switzerland (Landolt E. 1991) (34 within quadrats, 9 outside quadrats). These include 5 which are classified as not present in NE Switzerland, 4 classified as extinct, 18 as very endangered, and the remaining 15 as endangered. Thirty-two of them are also on the Red List for Switzerland (Landolt E. 1991). In this list one species is classified as not present, one as extinct, 14 as very endangered and 16 as endangered.

Most of the Red List species, of which approximately 60% are known to have been sown somewhere in the study area, are arable weeds (Table 2). However, the sowing records suggest that at least 75% of the arable weeds on the Red List have recruited spontaneously in at least some wildflower strips.

Table 2. Red list (RL) species found in wildflower strips in the Klettgau: habitat affinity, seed source, Red List status, trends in their population development based on historical floristic inventories (Kelhofer E. 1920; Kummer G. 1937; Isler K. 1976) and 'today' = surveys between 1996 and 1998 + accidental observation; NE-CH = North-East Switzerland, CH = Switzerland.

		Habitat	Source	RL		Historical documentation				Trend
				NE-CH	CH	Kelhofer	Kummer	Isler	today	(1920-1976)
S = also found in seed bank		A=arable Ru=ruderal M=meadow	A=added (sown) S=spontaneous A/S=both occurs	0=not present Ex=extinct E=very endangered V=endangered U=not endangered		W=Widen, L=Langfeld, P=Plomberg K=Klettgau elsewhere, ?=location ? x=present in larger area, in general: C=common, S=scarse, R=rare A=adventitious, ()=mistake in spec.?				–=negative +=positve ?=uncertain *=overlooked? n=new (Klettg.)
RL-spec. within quadrats										
Adonis flammea		A	A/S	E	E	WR	WR	W	W	–
Agrostemma githago		A	A/S	E	E	WLPKC	R,K?	–	WLPK	–
Anagallis foemina		A	S	V	U	WS	KS,LP?	–	W	–?*
Anthemis tinctoria	S	A	A(/S?)	V	E	WC	KS	–	WLPK	–
Asperugo procumbens		A	S	0	V	R	R	–	W	–
Bifora radians		A	A/S	E	E	W	WR	–	WL	–
Bromus secalinus		A	A/S	E	V	C,WL?	S	x	R	–
Buglossoides arvensis		A	A/S	V	U	C	C	x	WLK	–
Bupleurum rotundifolium		A	A(/S?)	Ex	E	S,WLP?	R	–	WL	–
Camelina sativa		A	A/S	E	V	R	R	–	WLK	–
Caucalis platycarpos		A	A/S	E	V	C	W	(W)	W	–
Centaurea cyanus	S	A	A/S	V	U	C	S	W	WLPK	–
Consolida regalis		A	A/S	V	V	WC,P?	WS	W	WL	–
Dianthus ameria		Ru/M	A/S	V	U	C,WP?	LC	x	WL	–?
Epilobium obscurum		Ru	S	V	U	R	–	–	L	n
Euphorbia cf. falcata		A/Ru	S	0	V	–	–	–	W	n
Falcaria vulgaris		A/Ru	S	E	E	WS	WS	x	W	–
Fumaria vaillantii		A	S	E	V	WLC	WLC	x	W	?
Kickxia spuria		A	S	V	U	WC,LP?	C	x	WL	?
Lathyrus tuberosus		A/Ru	S	V	V	WS,LP?	PKS	x	W	?
Legousia hybrida		A	S	Ex	Ex	W	WK	–	W	–?*
Legousia speculum-veneris		A	A/S	E	V	C	WS,L?	x	WLPK	–
Orlaya grandiflora		A	A	Ex	E	KR,WLP?	R	–	W	–
Picris echioides		A/Ru	A/S	E	E	WLR	K,WLP?	x	LK	–
Ranunculus arvensis		A	A/S	V	V	C	WPC	xS	W	–
Reseda luteola		Ru	A	E	V	A	R	–	WLP	–
Scandix pecten-veneris		A	S	E	E	WL,P?	WL	x	WL	–
Silene noctiflora	S	A/Ru	A/S	V	V	WC,L?	WC	x	WLK	–?
Stachys annua		A/Ru	A	V	V	C	C	x	LK	–
Tanacetum vulgare	S	Ru	A(/S?)	V	U	R	R	x	WLPK	+
Tragopogon orientalis		M	A/S	E	U	C	C	x	WLPK	?
Vaccaria hispanica		A	A(/S?)	E	E	R,L?	R	–	WLK	–
Vicia angustifolia		M	S	0	U	WC,L?	WC	x	W	–?
Xeranthemum annuum		Ru	A	0	0	–	–	–	L	n
RL-spec. outside quadrats										
Adonis aestivalis		A	S	0	V	S,W?	WS	W	W	–
Aphanes arvensis	S	A	S	V	U	WLKS	WPC,L?	C	W	?
Asperula arvensis		A	A	E	E	S	–	–	W	–
Crupina vulgaris		M	A	0	E	–	–	–	L	n
Filago arvensis		A	S	Ex	V	L	KR	–	L	–?
Gagea arvensis		A	S	V	E	WPC,LK?	C	–	W	–
Galium spurium		A	S	V	U	W,L?	WLPS	–	W	–?*
Neslia paniculata		A	A?	E	V	–	C,not K	–	W	n
Papaver argemone		A	A?	E	V	WPS	WLPR	P	W	–?

Most of the 43 Red List species are mentioned in historic records for the Canton Schaffhausen, and some information is available on their former abundance and distribution (Kelhofer E. 1920; Kummer G. 1937; Isler K. 1976). For many species, the documentary evidence allows us to assess how populations have changed during the last century or so. The records show that at least 24 of the 43 Red List species declined between the early part of the 20th century and the 1990's, when wildflower strips were introduced (Table 2). A further 8 species probably also declined, though the records are less clear. For example, *Galium spurium* and *Legousia hybrida* might have been overlooked due to their strong similarity to the related and more frequent species, *Galium aparine* and *Legousia speculum-veneris*, respectively.

The general decline in abundance is also illustrated by the decreasing number of species recorded as 'common', from 22 in 1920, to 11 in 1937, and to one in 1976. In contrast, the numbers of species recorded as 'scarce' went up from 7 to 10 between 1920 and 1937, while the number of 'rare' species increased from 8 to 12. Eleven species recorded by Kelhofer (1920) and/or Kummer (1937) were not found again around 1976, although seven of them were present within a larger mapping unit in the period 1966-1979 (Welten M. & Sutter R. 1982). In contrast, one species, *Tanacetum vulgare*, which is known to have spread along railway embankments, apparently became more frequent (Isler K. 1976).

In our survey we recorded 5 Red List species which had not previously been documented in the Klettgau. Two of these, *Xeranthemum annuum* and *Crupina vulgaris*, probably originate from a seed mixture containing non-indigenous species. Two others, *Epilobium obscurum* and *Neslia paniculata*, are known from herbarium proofs for a larger mapping unit (Welten M. & Sutter R. 1982). Only one species, *Euphorbia falcata*, is entirely new to the area, the nearest herbarium proofs originating from about 50 km away in Aargau. For five species no clear trend could be made out from the sources available.

Influence of environmental conditions on the distribution of rare arable weeds

Most of the Red List species we recorded are annual species and tend to be most abundant in young wildflower strips. For example, in 1996, > 75% of the Red List species were recorded in 1st year strips (including arable flora reserves). However, even within 1st year strips, the occurrence of rare species is very variable, and we therefore analysed their distribution patterns in relation to environmental factors. Fig. 1 shows an ordination diagram based on a CA of these 1st year sites, in which only 'spontaneous' Red List species are shown (though the analysis was based on all species occurring in at least three sites). The diagram also shows those environmental variables which are significantly related to the species patterns. The CA produces one large, distinct group of Red List species in the lower left hand corner of the diagram and a number of other species scattered over the remaining area. This group consists of species belonging to the class Secalietea (e.g. *Agrostemma githago*, *Buglossoides arvensis*, *Ranunculus arvensis*), which includes associations of cereal fields. More specifically many of the species are characteristic of the order Centauretalia (e.g. *Centaurea cyanus*) and the alliance Caucalidion (e.g. *Consolida regalis, Fumaria vaillantii, Legousia hybrida, Legousia speculum-veneris*) or of associations belonging to the latter (*Orlaya grandiflora, Silene noctiflora*) (classification according to Müller T. & Oberdorfer E. 1993; Oberdorfer E. 1994). Several other species associated with the Caucalidion, but typical for heavier and intermittently moist soils, are situated at some distance from this group (e.g. *Kickxia spuria, Lathyrus tuberosus*). Although *Vaccaria hispanica* is also associated with the Caucalidion and prefers dry sites, it does not group with other species of the alliance in the CA. This may be because it has been sown in some strips and its distribution is not 'spontaneous'. The remaining, more scattered species in the diagram are associated with a variety of other vegetation types, including the Sisymbrion, i.e. the Polygono–Chenopodietea of the root crops (Asperugo procumbens), communities of ruderal sites (*Falcaria vulgaris, Anthemis tinctoria*), and meadows (*Tragopogon orientalis*).

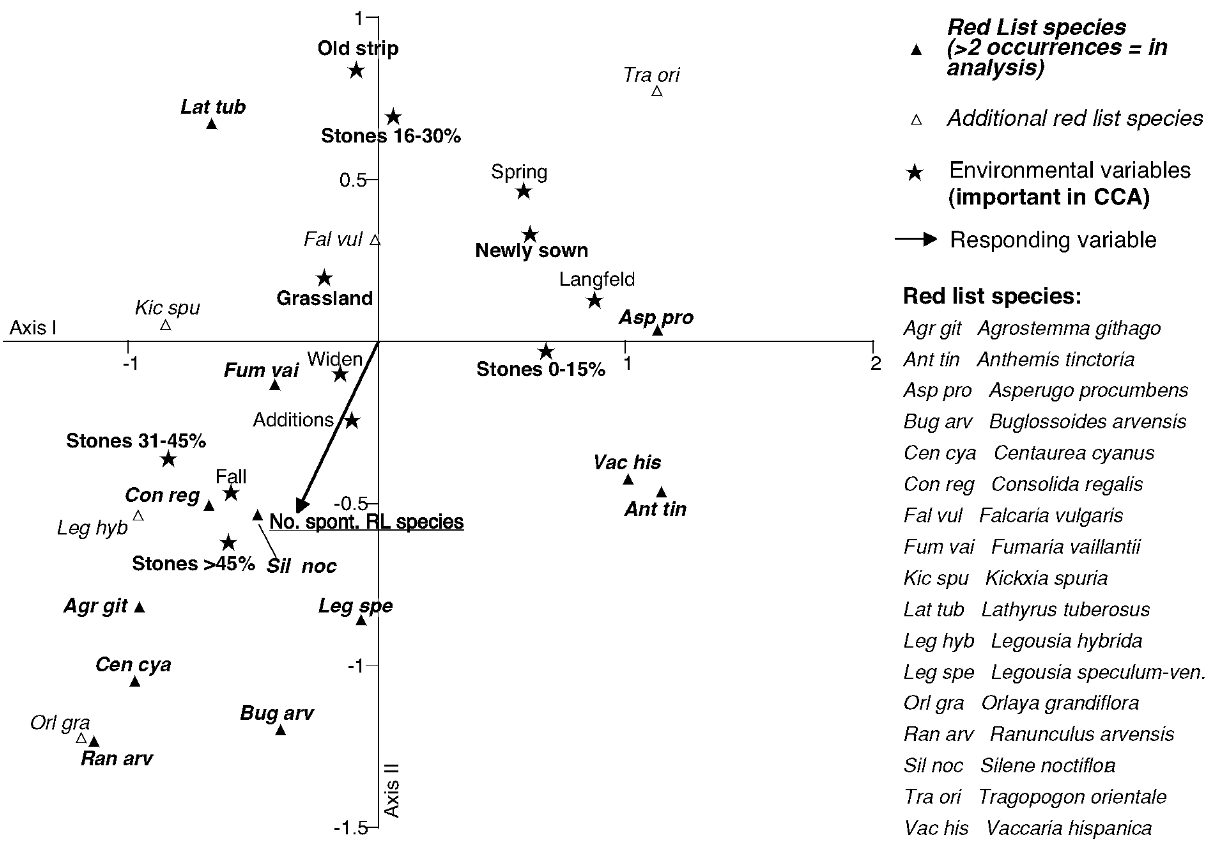


Fig. 1. Correspondence Analysis (CA) of wildflower strips in their 1st year (including arable flora reserves) based on species recruited spontaneously occurring in more than two sites. Only Red List species and important environmental factors are shown (indirect gradient analysis; eigenvalues Axis I = 0.39, Axis II = 0.272; total inertia = 3.019). Species typical of cereal fields on shallow calcareous soil group in the lower left-hand corner, where stone cover is also highest.

The Red List species associated with the Caucalidion occur mainly on sites with shallow soils with a high stone content. However, interpretation of this finding is complicated because of the confounding of variables; the sites on shallow soils are mainly sown in the autumn, and these sites have also been frequently sown with additional species (i.e. 'Additions'). In contrast, few 'spontaneous' Red List species occur on the heavier, loamy soils, which are mainly sown with a seed mixture in spring. Despite this uncertainty, it is probable that many of the Red List species have appeared spontaneously.

A Canonical Correspondence Analysis reveals that 30.1% of the variation in spontaneous species in 1^{st} year wildflower strips can be explained by a model containing four environmental variables (Fig. 1). Stone cover is the most important factor, explaining altogether 14.5% of the species variation. The factor 'newly sown', i.e. sown with a seed mixture, explains a further 9.3% of the species variation, though 3.5% of these cannot be separated from the effect of stone cover. The factors 'old strip' and 'adjacent grassland' each explain 4.9% of the variation, with almost no overlap with other factors.

Patterns of species diversity

In a separate paper we show that age strongly influences the plant species composition of wildflower strips, but only in younger strips (Chapter 2). In these, species composition changes rapidly, but in older strips it stabilizes and the variation between strips increasingly reflects site and management factors. Amongst the older strips, a major distinction is between grassy (grass cover > 20%) and non-grassy strips. We therefore calculated mean species numbers and diversity indices separately for strips of various age groups and degrees of grassiness. Various diversity indices were calculated, but since they all indicate the same trends, only the results for the Simpson index are shown in Fig. 2.

While species numbers decrease significantly from the first to the third year, Simpson's index does not vary significantly (Fig. 2). From the third year on, age does not influence diversity strongly, although diversity does vary widely between sites. For example, both species number and Simpson's index are significantly lower in grassy sites than in none grassy sites.

A hierachical analysis of diversity was performed for 15 wildflower strips from the Widen district (1997 data). For comparison, an identical analysis was performed for a set of 15 wildflower strips throughout the Klettgau (1998 data). These analyses show that the average species number increases steeply from the level of quadrats to sites, and even more so from the level of sites to types, and further on to total species number (Fig.3). The data set from the Klettgau shows a slightly greater increase in

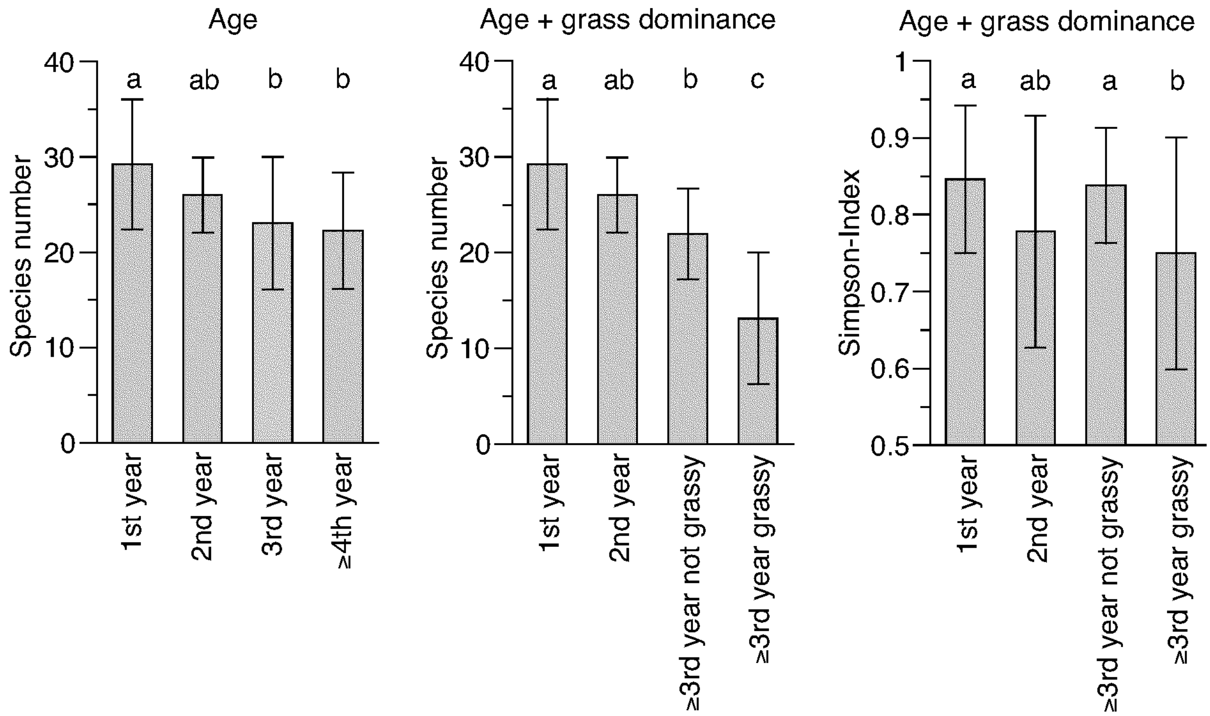


Fig. 2. Mean species numbers and Simpson-Indices in sites of different types of wildflower strips from all over the Klettgau in 1996 (SD). Letters a–c indicate significant differences between types (Tukey-Kramer HSD Test, P<0.05).

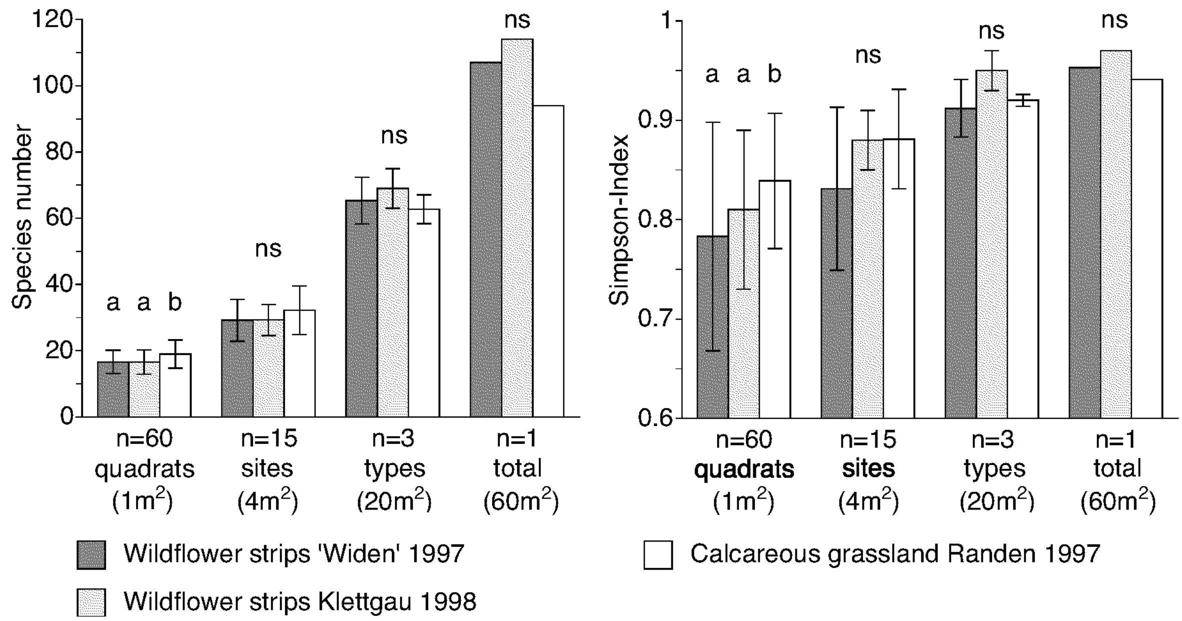


Fig. 3. Hierarchical diversity analysis: species numbers and Simpson´s Indices of wildflower strips are compared with data from calcareous grassland on different landscape scales using data from 1997 exclusively from the Widen district, from 1998 from all over the Klettgau and grassland data from 1997 from the Schaffhauser Randen (S. Studer unpublished data). Types of wildflower strips: 1[st] year, 2[nd] year, ≥ 3[rd] year not grassy; types of grassland: extensive, little intensive, medium intensive; letters a–b indicate significant differences, ns not significant (Tukey-Kramer HSD Test, P<0.05); (SD).

species numbers from site to type level and a larger total number of species than thedata set restricted to the Widen. This difference reflects the larger area sampled and the more variable site conditions in the Klettgau than in the Widen.

A similar hierarchical analysis was performed based on species diversity rather than species number. The large standard deviations indicate that diversity varies considerably, especially at the quadrat and site levels. In general diversity indices increase less steeply from level to level than species numbers.

The seed bank of wild flower strips and adjacent fields

From soil samples of six wildflower strips and adjacent crops, a total of 3806 seedlings germinated, belonging to 58 species. Both numbers of species and numbers of individuals were significantly higher in wildflower strips than in crops (Kruskal-Wallis test χ^2=70.8 resp. χ^2=62.3; P<0.0001; Table 3). Twenty-eight species were present both in samples from wildflower strips and crops, while 27 species were found exclusively in wildflower strip samples, and only four were confined to crops.

Table 3. Total numbers of species and seedlings found in the seed banks of wildflower strips (W) and adjacent fields (F). Conversion factor for No. of seedlings/m^2 (/7 cm depth) = 35.

	Species No.		Seedling No.	
Site	**Upper layer**	**Lower layer**	**Upper layer**	**Lower layer**
W old 1	28	15	1521	193
W old 2	25	19	238	107
W medium 1	21	14	351	130
W medium 2	22	13	202	49
W young 1	23	8	158	58
W young 2	31	25	434	137
W total	**51**	**41**	**2904**	**674**
F old 1	2	0	10	0
F old 2	17	16	43	43
F medium 1	11	10	35	27
F medium 2	4	3	11	16
F young1	1	3	1	3
F young 2	9	9	18	21
F total	**24**	**22**	**118**	**110**

In wildflower strips, species numbers and seed density were much higher near the soil surface (Table 3). Between 21 and 31 species and an average of ca. 17000 seeds m^{-2} were recorded from the uppermost 7 cm of soil, compared with 8-25 species and an average of ca. 3900 seeds m^{-2} from the lower layer (15-22 cm) (Kruskal-Wallis-Test χ^2=20.5 resp. χ^2=24.0; P<0.0001). One of the flower strips contained extremely high numbers of *Poa trivialis* seeds. If this species is excluded from the calculations, the mean seed density in the upper soil of wildflower strips is 4320 seeds m^{-2} , compared to 1537 in the lower layer. There were no significant differences in numbers of species or individuals between wildflower strips of different ages. In the adjacent fields, species numbers and seed density were roughly the same in both soil layers, with 0-17 species and an average of 670 seeds m^{-2}.

A Canonical Correspondence Analysis of the total data set from the seed bank study shows that 19.4% of the species variation can be explained by the variables 'age', 'type' and 'site' (Fig. 4a). The factor 'type', i.e. differences between strips and fields, explains only 3.6% of the variation. Most of the variation is associated with differences between wildflower strips (30.1% of the variation among these explained by 'age' and 'site'; Fig. 4b) rather than between fields (5.2% of the variation among these explained by 'site'). Differences in species composition between soil layers are insignificant and are not included in the models. The age of the wildflower strips has the greatest impact, both in the total model and that for wildflower strips alone (Fig. 4a+b). The factor 'site', representing samples from a strip and the adjacent field, also explains a considerable portion of species variation in both analyses, although the bigger portion of its influence cannot be separated from that of age.

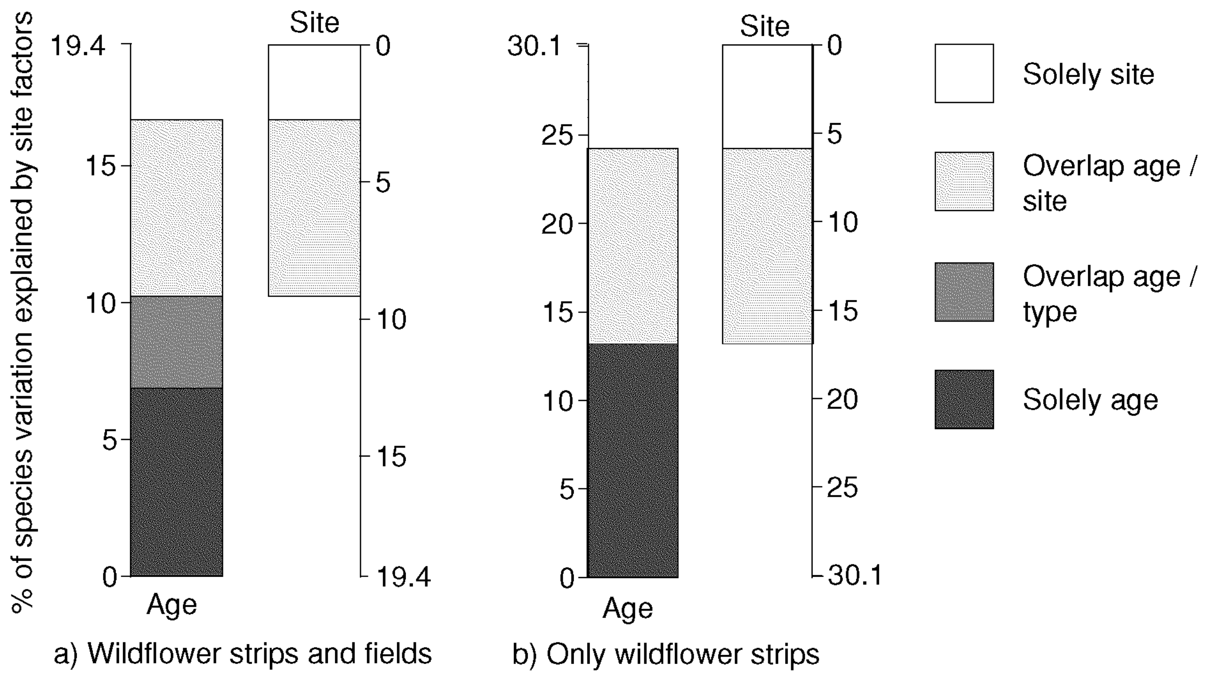


Fig. 4. Variation in species data of the seed bank of wildflower strips explained by environmental variables based on CCAs (total inertia 3.019; Monte Carlo Permutation tests with 599 unrestricted permutations; P≤0.01).

Between 19 and 45% of the sown species germinated from the soil samples (Table 4, App. 2). The presence of these species in the seed bank is clearly related to the longevity of their seeds. While none of the species with very short lived seeds

Table 4. Percentage of sown species recorded in soil samples from wildflower strips, their seed longevity and life history. W = wildflower strip, U = upper soil layer, L = lower soil layer; species maximum longevity of seeds: < 5 years, > 5 years; species life cycle: A = annual, M = monocarpic perennial, P = polycarpic perennial, I = intermediate; characteristics of < 5 sown species not included in statistics.

Age of strip		old					medium						young					
Seed mixture		Rams.o					UFA 95			UFA 94			Klettgau			UFA 96		
Site		No. of sown species	W 1		W 2		No. of sown species	W 1		No. of sown species	W 2		No. of sown species	W 1		No. of sown species	W 2	
Soil layer			U %	L %	U %	L %		U %	L %		U %	L %		U %	L %		U %	L %
Species recorded		31	32	19	26	19	19	37	26	23	30	22	11	45	27	19	32	32
Seed longevity	>5 years	17	53	29	41	35	11	64	55	14	43	29	8	63	38	10	60	60
	<5 years	10	10	0	10	10	8	13	0	6	17	17	3	33	0	8	13	13
Life history	A	10	20	20	10	10	*4*	*25*	*25*	*4*	*25*	*25*	*3*	*67*	*33*	*4*	*25*	*25*
	M	8	38	38	38	13	6	33	33	6	33	17	5	40	20	6	67	50
	P	11	27	9	27	27	7	57	29	12	25	25	*2*	*50*	*50*	7	14	14
	I	*3*	*67*	*0*	*33*	*33*	*2*	*0*	*0*	*18*	*100*	*0*	*1*	*0*	*0*	*2*	*0*	*50*

Table 5. Percentage of spontaneous species with different period of seed longevity and types of life history in soil samples. W = wildflower strip, F = field, U = upper soil layer, L = lower soil layer; maximum longevity of seeds in seed bank: < 5 years, > 5 years; species life history: A = annual, M = monocarpic perennial, P = polycarpic perennial, I = intermediate; samples < 5 individuals not included in statistics.

		Total	Wildflower strips												Fields											
Age of strip			old				medium				young				old				medium				young			
Site			W1		W2		W1		W2		W1		W2		F1		F2		F1		F2		F1		F2	
Soil layer			U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L
No. of species		51	19	9	16	12	14	9	15	8	17	4	24	19	2	0	17	16	11	10	4	3	1	3	9	9
Seed longevity	>5 years	88	74	78	81	92	93	89	80	75	82	*100*	88	89	*100*	–	82	81	100	90	*100*	*67*	*100*	*100*	89	100
	<5 years	10	21	11	6	0	6	0	7	13	8	*0*	18	11	*0*	–	12	13	0	0	*0*	*0*	*0*	*0*	11	0
	?	2	5	11	0	0	6	8	7	11	7	*13*	0	0	*0*	–	6	6	0	10	*0*	*3*	*0*	*0*	0	0
Life history	A	55	58	67	63	58	64	67	67	63	71	*100*	75	74	*50*	–	76	69	82	80	*75*	*67*	*100*	*67*	100	78
	M	6	0	0	0	0	0	0	0	0	0	*0*	0	0	*0*	–	6	13	9	10	*0*	*0*	*0*	*0*	0	11
	P	33	42	33	38	42	36	33	27	38	8	*0*	21	21	*50*	–	18	13	9	0	*25*	*33*	*0*	*0*	0	11
	I	6	0	0	0	0	0	0	0	0	12	*0*	4	5	*0*	–	6	6	0	0	*0*	*0*	*0*	*33*	0	0

(< 1 year) and only 0-20% of the species with a seed longevity of 1-5 years were found, 29-64% of the species with a seed life span > 5 years were recorded. The differences in seed longevity of sown species were not significantly related to the age of the strips, but there were significant differences in plant life history (Table 4). The proportion of annual species was higher in the younger strips (Kruskal-Wallis-Test χ^2=8.5, P=0.004). A similar but not significant tendency can be observed for monocarpic perennials, their recovery rate ranging from 10-38% in old and medium old strips, and 20-67% in young strips. For polycarpic perennials the recovery rate was 9-57%, and no age dependent differences could be detected.

Numbers of species recruited spontaneously were significantly higher in wildflower strips than in fields (Kruskal-Wallis-Test χ^2=5.8, P=0.016; Table 5, App. 3). Between 74-100% of these have seeds with a longevity of > 5 years. Between 58-100% of the species were annuals, the proportion being highest in fields followed by young wildflower strips (Kruskal-Wallis-Test χ^2=12.8, P=0.002). Polycarpic perennials (0-42% of all spontaneous species) were more abundant in wildflower strips, i.e. in old and medium old ones (Kruskal-Wallis-Test χ^2=13.5, P=0.001), while monocarpic perennials were absent from the wildflower strips and seldom in the fields (Kruskal-Wallis-Test χ^2=11.7, P=0.001).

Comparison of the species composition of the seed banks and vegetation

The vegetation of the wildflower strips (recorded in 1996 and 1997) has a different plant species composition from that found in the seed banks in 1999. A total of 88 plant species were recorded for the six strips used in the seed bank studies. Of these, 38 occurred in both the vegetation and the seed bank, whereas 30 were found only in the vegetation and 20 only in the seed bank (Table 6). The majority of species found in the seed bank are rather common; only five are Red List species, of which *Anthemis tinctoria*, *Centaurea cyanus* and *Tanacetum vulgare* were recorded in the vegetation of the same strips, while *Silene noctiflora* and *Aphanes arvensis* have been recorded in other strips. With the exception of *Aphanes arvensis*, all these species are contained in at least some seed mixtures (Table 2, App. 2 and 3).

Certain life forms are over- or under-represented in the seed bank in comparison with the vegetation (Table 6). For example, geophytes are only found in the vegetation, while therophytes are over-represented in the seed bank. Most plants with a mixed therophyte/hemicryptophyte strategy occur both in the vegetation and the seed bank. Almost half of the hemicryptophytes are restricted to the vegetation and another third is also present in the seed bank, whereas only 21% are missing in the vegetation.

Table 6. Comparison of numbers and characteristics of species found in the seed bank of wildflower strips or adjacent fields, in their vegetation or in both.

		Only seedbank		Seedbank and vegetation		Only vegetation (only strips)		Total	
		No. spp	% spp only in seed bank	No. spp	% spp in seed bank + vegetation	No. spp	% spp only in vegetation	No. spp	% all spp
Total		20		38		30		88	
Only wildflower strips		10	50	17	45	30	100	57	65
Wildflower strips + fields		9	45	19	50			28	32
Only fields		1	5	3	8			4	5
Life form	Geophytes	0	0	0	0	4	13	4	5
	Therophytes	6	30	6	16	4	13	16	18
	Thero-/Hemicryptoph.	7	35	20	53	7	23	34	39
	Hemicryptophytes	7	35	11	29	15	50	33	38
	Chamaephytes	0	0	1	3	0	0	1	1
Life history	Annuals	8	40	21	55	8	27	37	42
	Monocarpic perennials	1	5	5	13	2	7	8	9
	Polycarpic perennials	8	40	11	29	18	60	37	42
	Intermediate	3	15	1	3	2	7	6	7
Seed longevity	>5 years	16	41	35	57	15	25	66	75
	<5 years	3	8	3	8	12	22	18	20
	(unknown)	1	5	0	0	3	10	4	5

The type of life history also has an influence on the presence of species in the vegetation or seed bank. In the total of 88 species recorded in either the vegetation or seed bank, annuals and polycarpic perennials occur with the same frequency and are much more common than monocarpic perennials and intermediate strategies (Table 6). Of this total, species occurring only in the seed bank consist of similar proportions of annuals and polycarpic perennials. The set of species found in both the vegetation and the seed bank is dominated by annuals, followed by polycarpic perennials and a few monocarpic perennials. In contrast the majority of species occurring in the vegetation but not in the seed bank are polycarpic perennials.

The seeds of almost half of all species found are reported to survive in the soil for more than 20 years; 28% can survive for 5-20 years, while 21% survive for less than 5 years. However, species with short lived seeds are strongly under-represented in the seed bank. For example, 66% of the 18 plant species with a seed longevity of < 5 years were recorded only in the vegetation, compared with 23% of the 66 species with a seed life > 5 years (Table 6).

Discussion

Factors influencing species diversity in wildflower strips

The data presented here reveal that wildflower strips can provide the habitat for a large diversity of species, including many which are not sown but appear spontaneously. Many factors, including management, soil conditions and successional time, influence the diversity of species which may be present. At a site level, species numbers decrease from the first to the third year. This is partly due to the loss of annual species (and a few perennials) as a result of increasing competition from a few dominant perennials. However, it also reflects patchiness in the vegetation due to the increasing size of some perennial plants, with the consequence that many species may be absent from 4 m^2 plots. This effect is especially strong where some grass species invade, spreading laterally to form large patches which suppress other species. The patchy dominance of a few species is also reflected in the decline in Simpson's index with increasing age (especially at grassy sites), and in the large standard deviations.

Conclusions about biological diversity are strongly influenced by the spatial scale at which data are analysed. Lande (1996) showed how species richness and diversity can be analysed hierarchically across a range of spatial scales. At small spatial scales, we expect an increase of species number as the survey area is increased, simply because a certain minimum area is needed to record the majority of species. For arable weed communities and grasslands, this minimum area usually lies between 25 and 100 m^2 (Ellenberg H. 1996). Although the minimum area is not reached by the 4 m^2 surveyed in a site and not even by the 20 m^2 in a type, the hierarchical analysis of species richness reveals a much steeper increase in species number from the level of the site (mean 29 species) to that of type (mean 65 species) than to be expected due to a minimum area curve. This increase is mainly due to variation between strips in the spontaneous species, the set of sown species being similar everywhere.

Comparisons with other studies are difficult because of differences in the sampling schemes. However, the diversity in the Klettgau study area does seem to be particularly high. We found an average of 65 species per type of wildflower strip (based on 20 1x1 m^2 quadrats). This value is considerably higher than the mean of 40 species found in 300 m^2 of conservation headlands containing similar arable weed associations in Upper Bavaria (Mattheis A. & Otte A. 1994). A particularly interesting comparison can be made with data for a number of calcareous grassland sites in the Schaffhauser Randen area (only a few kilometres from the study area). These data were collected and analysed using similar methods to those applied here (unpublished grassland data S. Studer). Both the mean number of species and Simpson's index are significantly lower in individual quadrats in wildflower strips than in grassland (Fig. 3). However, at larger spatial scales, the mean values for species richness and Simpson's index in wildflower strips increase more steeply than in grasslands and reach higher maximum values. The reason for the difference may be that the grasslands are much older communities in which community composition is determined by competitive interactions, with the result that species composition is similar on similar substrates throughout the region. In contrast, the wildflower strips are new, unstable communities in which species composition is strongly affected by the chance presence or absence of particular species and by limitations in the dispersal ability of species. The important conclusion for management is that the spontaneous species in wildflower strips tend to be distributed patchily at a landscape scale, and a large number of strips is required to include the majority of species.

Factors promoting the occurrence of rare species

Wildflower strips and arable flora reserves in the Klettgau promote a large number of rare species, including 43 Red List species among which 35 are arable weeds, and many other arable weeds which are no longer common, although they are not on the Red List. The spontaneous occurrence of most of these rare species somewhere in the Klettgau, combined with the historical documentation of their former presence shows, that a certain potential for the reestablishment of a rich arable flora still exists.

Most of the Red List species found in wildflower strips in the Klettgau are annual arable weeds which grow in 1st year wildflower strips. In general, calcareous or base-rich soils, which are common in the Klettgau, favour the occurrence of rare arable weeds, and especially those associated with the Caucalidion (van Elsen T. & Günther H. 1992; Müller T. & Oberdorfer E. 1993). Results from the CA and CCAs show that these species occur chiefly in sites with a high stone content. This is probably because these soils, with their high permeability and reduced fertility, support rather sparse vegetation cover and offer favourable conditions for rare arable weeds. Earlier records also indicate that most of the Red List species we recorded were formerly present in the Widen district (Kelhofer E. 1920; Kummer G. 1937; Isler K. 1976). In contrast, sites on heavier, more fertile soils with a low stone content usually develop a dense vegetation cover of sown species rather quickly, and contain but few spontaneous Red List species, as was also found in other studies (Günter M. 2000a; Schaffner D. et al. 1998).

Although the correlation between soil type and the presence of the rarer arable weeds seems clear, caution is needed in interpreting the results. Because the lighter and shallower soils in the Widen district were identified as being potentially good sites for rare arable weeds, such areas were chosen for arable flora reserves. Since most of these, as well as some wildflower strips, were sown with particular species ('Additions'), it is often hard to say whether species have appeared spontaneously or been sown. However, some 'old sites' in the Widen district that were renewed contain few Red List species. These sites often have a comparatively high cover of annual or geophyte problem weeds, which might have been the reason for their renewal. Most sites adjacent to grassland also contain few spontaneous Red List species, probably due to grass growing in from the side increasing the vegetation cover. The presence of adjacent grassland has a significant positive effect on the grass cover of wildflower strips (Kruskal-Wallis test χ^2=7.9; P = 0.005). (Günter M. 2000a) found, that the presence of grasses previous to the establishment of a wildflower strips also leads to a high grass cover.

Although we cannot always be certain whether particular populations of rare weeds have been sown (with seed of local origin) or not, there is little doubt that the provision of young wildflower strips and arable flora reserves has promoted the spontaneous recurrence of several Red List species. It is clear that many species do still exist, either in the seed bank or as small, overlooked populations, and that wildflower strips, and even more so, arable flora reserves provide a habitat in which their populations can recover.

Contribution of wildflower strips to potential plant diversity in the soil seed bank

The density of seeds in the fields is very low, ranging between 140-3000 seeds/m^2 per 14 cm soil layer (upper layer 0–7 cm plus lower layer 15–22 cm depth). The values are low compared with those reported for arable fields elsewhere (e.g. 1800 seeds/m^2 (per 0–13 cm soil depth) – 19´000 seeds/m^2 (per 0–6.5 cm soil depth) (Fix K. & Poschlod P. 1993) or 4´742–73´350 seeds/m^2 (per 0–15 cm soil depth) (Cavers P.B. & Benoit D.L. 1989)) and reflect the intensive landuse and high herbicide use in the region. As a result of ploughing, there are no significant differences associated with depth in the seed bank of the fields.

In contrast the concentration of seeds in wildflower strips is much higher, ranging between 7´560–60´000 seeds/m^2 (per 14 soil layer, see above), which lies in the range of published values for arable set-aside (e.g. 4300–21´600 seeds/m^2 per upper 15 cm soil layer (Jödicke K. & Trautz D. 1994) or 15´000–40´000 seeds/m^2 per upper 10 cm soil layer (Tischew S. & Schmiedeknecht A. 1993)). The youngest sites in our study were only three years old, indicating that the seed bank can build up very quickly. Seeds tend to be more concentrated near the surface in wildflower strips, reflecting the fact that they are not ploughed for several years. We found that the concentration of seeds at 15-22 cm ranged from 12-45% of that in the top 7 cm. The CCA shows no significant differences in species composition at the two levels.

In spite of the large number of seeds, we found very few seeds of rare species, even in the wildflower strips. This may be partly because of the sample size; many more samples would have been necessary to detect some of the rarer species (Albrecht H. 1994; Froud-Williams R.J. et al. 1983). The almost complete lack of rare species may also be due to the sampling time, which was unfavourable for species with seeds ripening only after late August or requiring a seed dormancy period (Baskin J.M. & Baskin C.C. 1989).

Ecological characteristics of species in the seed bank and the vegetation

The species compositions of the actual vegetation of wildflower strips and of the seed bank differ significantly. These differences can be interpreted in terms of the life forms and life histories of the various species. For example, therophytes mostly fail to germinate in old, dense vegetation stands while they thrive in freshly disturbed sites. Accordingly, in comparison to the 'old' vegetation in wild flower strips, they are over-represented in the seed bank, where they persist waiting for favourable conditions, i.e. renewed disturbance. Species with a mixed therophyte-/hemicryptophyte strategy, on the other hand, are successful competitors in dense vegetation as well as in freshly disturbed sites, and thus perform extremely well in wildflower strips, usually being present in both the vegetation and the seed bank. In sum, this is also the case for most annuals, which are partly therophytes and partly thero-/hemicryptophytes, and which comprise the majority of spontaneous species. Pure hemicryptophytes, which are mostly also polycarpic perennials, on the other hand, gain ground during the succession of wildflower strips but fail to build a large seed bank (Baskin C.C. & Baskin J.M. 1998).

Significance for the conservation of rare arable weeds

In spite of its intensive agriculture, the Klettgau is an exceptional region with respect to its richness in rare arable weed species. This is due to its largely shallow, stony, calcareous soils and its location at low altitude, both factors favourable for rare arable weeds associated with the Caucalidion. Although the study area is in many respects unusual, we believe that our main conclusion – that wildflower strips can be used to restore floristic diversity in an intensively used arable landscape – is transferable to other regions. This is suggested by the similar conclusions reached from the analysis of two different data sets. One concerned the small, rather uniform Widen district, which is especially species rich; the other comprised data for a number of more heterogeneous, but less exceptional, sites from all over the Klettgau. Both analyses revealed similar trends concerning average species numbers and diversity at different spatial scales.

We list below what we believe are the main lessons to be learnt from our study concerning the conservation of arable weeds.

- By the introduction of wildflower strips, a high floristic diversity consisting not only of sown species, but also of many that recruited spontaneously, can be achieved. Even a small area of wildflower strips will contribute something, but diversity increases rapidly with an increasing number of strips, especially where these are dispersed across the landscape.

- Individual sites should be located and managed to prevent grass from spreading, since this is likely to reduce floristic diversity, especially in older strips (Günter M. 2000b). A renewal of such strips does not usually bring back a diverse flora including rare able weeds, even when these are sown (differentiating influence of factor 'old strip' in CCA; Fig. 1). Once grasses reached a certain dominance they reestablish a dense cover quickly after renewal, inhibiting other species.
- Rare species can be promoted by the creation of wildflower strips and arable flora reserves of low vegetation density. Their numbers may increase rapidly simply by providing favourable conditions in promising sites, but *in* or *ex situ* propagation of specimens derived from local populations accelerates this process.
- Arable flora reserves, which are renewed every year, have a greater potential to promote rare arable weeds than wildflower strips. This applies probably also to unsprayed crop edges and wildflower rotation fallows, which remain in place for only 1.5 – 2.5 years (the latter have been introduced since 1998). The opposite is the case for diversity in species composition, which is enhanced by the successional and structural variety of the vegetation developing in wildflower strips over time.

Conclusions

Many arable weeds have become rare or disappeared altogether since the early part of the 20th century. In spite of a low weed diversity in the vegetation and seed bank of intensively used arable fields, the remaining potential for diversity can still be remarkably high. The creation of wildflower strips or arable flora reserves provides habitats in which many arable plant species can thrive. Because these species are often patchily distributed in the landscape, a large number of widely dispersed sites are needed to achieve maximum effect. Where rare species still occur, or are known to have occurred, there is a good chance of re-establishing viable populations, at least of some species. In addition to creating suitable habitats, *in* and *ex situ* propagation of these species may be desirable to accelerate the process of building up populations. However, it is important to act quickly. Although some species may still persist in the seed bank, their longevity is limited (Bekker R.M. et al. 1998; Schneider C. et al. 1994).

References

Aichele, D. & Schwegler, H.-W. 1991. Unsere Gräser. 10th ed. Franckh-Kosmos, Stuttgart.

Albrecht, H. 1989. Untersuchungen zur Veränderung der Segetalflora an sieben bayerischen Ackerstandorten zwischen den Erhebungszeiträumen 1951/68 und 1986/88. Borntraeger, Stuttgart-Berlin.

Albrecht, H. 1994. Modelluntersuchung und Literaturauswertung zum Diasporenvorrat gefährdeter Wildkräuter in Ackerböden. Schriftenreihe „Aus Liebe zur Natur" der Stiftung zum Schutze gefährdeter Pflanzen 5: 123-140.

Albrecht, H. & Bachthaler, G. 1990. Veränderungen der Segetalflora Mitteleuropas während der letzten vier Jahrzehnte. Verhandlungen der Gesellschaft für Ökologie 19: 364-372.

Baskin, C.C. & Baskin, J.M. 1998. Seeds. Academic Press, San Diego.

Baskin, J.M. & Baskin, C.C. 1989. Physiology of dormancy and germination in relation to seed bank ecology. In: Leck, M.A., Parker, V.T. & Simpson, R.L. (eds.) Ecology of soil seed banks, pp. 53-66. Academic Press, San Diego.

Bekker, R.M., Schaminee, J.H.J., Bakker, J.P. & Thompson, K. 1998. Seed bank characteristics of Dutch plant communities. Acta Botanica Neerlandica 47: 15-26.

Borcard, D., Legendre, P. & Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology 73: 1045-1055.

Cavers, P.B. & Benoit, D.L. 1989. Seed banks in arable soils. In: Leck, M.A., Parker, V.T. & Simpson, R.L. (eds.) Ecology of soil seed banks, pp. 309-328. Academic Press, San Diego.

Cremer, J.R., Partzsch, M., Zimmermann, G., Schwär, C. & Goltz, H. 1991. Acker- und Gartenwildkräuter. 1st ed. Deutscher Landwirtschaftsverlag, Berlin.

Csapody, V. 1968. Keimlingsbestimmungsbuch der Dikotyledonen. Akadémiai Kiadó, Budapest.

Ellenberg, H. 1996. Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. 5th ed. Ulmer, Stuttgart.

Fitter, A.H. & Peat, H.-J. 1994. The Ecological Flora Database. Journal of Ecology 82: 415-425.

Fix, K. & Poschlod, P. 1993. Extensivierung von Grünlandstandorten am Beispiel Wackershofen (Lkr. Schwäbisch Hall; Gipskeuper). Bedeutung von Nährstoffstatus und Diasporenbank. Verhandlungen der Gesellschaft für Ökologie 22: 39-45.

Froud-Williams, R.J., Chancellor, R.j. & Drennan, D.S.H. 1983. Influence of cultivation regime upon buried seeds in arable cropping systems. Journal of Applied Ecology 20: 199-208.

Günter, M. 2000a. Anlage und Pflege von mehrjährigen Buntbrachen unter den Rahmenbedingen des Schweizerischen Ackerbaugebietes. Agrarökologie 37.

Günter, M. 2000b. Sukzession von Buntbrachen. In: Nentwig, W. (ed.) Streifenförmige ökologische Ausgleichsflächen in der Kulturlandschaft: Ackerkrautstreifen, Buntbrache, Feldränder, pp. 55-76. Verlag Agrarökologie, Bern.

Hanf, M. 1990. Ackerunkräuter Europas mit ihren Keimlingen und Samen. 3rd ed. BLV-Verlagsgesellschaft, München.

Heitzmann, A. & Nentwig, W. 1993. Angesäte Ackerkrautstreifen in der Agrarlandschaft: Eine Möglichkeit zur Vermehrung des Nützlingspotentials und zur Kontrolle von Schädlingspopulationen, somit zur Förderung der Biodiversität in der Kulturlandschaft, bei gleichzeitig intensiver landwirtschaftlicher Nutzung. Schweiz. Landw. Forschung 32: 365-383.

Hodgson, J.G., Grime, J.P., Hunt, R. & Thompson, K. 1995. The electronic comparative plant ecology. Chapman & Hall, London.

Hubbard, C.E. 1985. Gräser. Ulmer Verlag, Stuttgart.

Hüppe, J. 1990. Die Genese moderner Agrarlandschaften in vegetationsgeschichtlicher Sicht. Verhandlungen der Gesellschaft für Ökologie 19(2):424-432.

Isler, K. 1976. Beiträge zu Dr. Georg Kummers Flora des Kantons Schaffhausen mit Berücksichtigung der Grenzgebiete. Mitteilungen der Naturforschenden Gesellschaft Schaffhausen 31: 7-121.

Jenny, M. & Weibel, U. 1999. Qualität und Quantität des ökologischen Ausgleichs in drei intensiv genutzten Ackerbauflächen des Klettgaus. Mitteilungen der Naturforschenden Gesellschaft Schaffhausen 44: 107-116.

Jenny, M., Weibel, U. & Buner, F. 1999. Der ökologische Ausgleich in intensiv genutzten Ackerbaugebieten des Klettgaus und seine Auswirkungen auf die Brutvogelfauna. Mitteilungen der Naturforschenden Gesellschaft Schaffhausen 44: 203-221.

Jödicke, K. & Trautz, D. 1994. Veränderungen der Samenbank im Boden von Ackerbrachen. Natur und Landschaft 69: 258-264.

Kelhofer, E. 1920. Die Flora des Kantons Schaffhausen. Botanisches Museum der Universität Zürich, Zürich.

Klapp, E. & Boberfeld, W.O.V. 1990. Taschenbuch der Gräser. 12th ed. Verlag Paul Parey, Berlin.

Korsmo, E. 1930. Unkräuter im Ackerbau der Neuzeit. Springer, Berlin.

Kummer, G. 1937. Die Flora des Kantons Schaffhausen mit Berücksichtigung der Grenzgebiete. Mitteilungen der Naturforschenden Gesellschaft Schaffhausen 8.

Lande, R. 1996. Statistic and partitioning of species diversity, and similarity among multiple communities - Mini Review. OIKOS 76: 5-13.

Landolt, E. 1977. Ökologische Zeigerwerte zur Schweizer Flora. Veröffentlichungen des Geobotanischen Instituts der ETH Zürich, Stiftung Rübel 64.

Landolt, E. 1991. Gefährdung der Farn- und Blütenpflanzen in der Schweiz, mit gesamtschweizerischen und regionalen roten Listen. Bundesamt für Umwelt, Wald und Landschaft, Bern.

Lauber, K. & Wagner, G. 1996. Flora Helvetica. 1st ed. Verlag Paul Haupt, Bern.

LBL. 1996. Mit Buntbrachen die Artenvielfalt fördern – Merkblatt. Landwirtschaftliche Beratungszentrale, Lindau.

Mattheis, A. & Otte, A. 1994. Ergebnisse der Erfolgskontrollen zum „Ackerrandstreifenprogramm" im Regierungsbezirk Oberbayern 1985 - 1991. Schriftenreihe der Stiftung zum Schutze gefährdeter Pflanzen 5: 56-71.

Müller, T. & Oberdorfer, E. 1993. Süddeutsche Pflanzengesellschaften Teil III Wirtschaftswiesen und Unkrautgesellschaften. Gustav Fischer Verlag, Jena.

Nentwig, W. 1992. Die nützlingsfördernde Wirkung von Unkräutern in angesäten Unkrautstreifen. Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz. Sonderheft XIII: 33-40.

Nentwig, W. 1993. Nützlingsförderung in Agrarökosystemen. Verhandlungen der Gesellschaft für Ökologie 22: 9-14.

Oberdorfer, E. 1994. Pflanzensoziologische Exkursionsflora. Ulmer, Stuttgart.

Ødum, S. 1974. Seeds in ruderal soils, their longevity and contribution to the flora of disturbed ground in Denmark. In: 12th British Weed Control Conference. 1131-1144.

Økland, R.H. & Eilertsen, O. 1994. Canonical correspondence analysis with variation partitioning: some comments and an application. Journal of Vegetation Science 5: 117–126.

Otte, A. 1984. Änderungen in Ackerwildkraut-Gesellschaften als Folge sich wandelnder Feldbaumethoden in den letzten 3 Jahrzehnten. Cramer, Vaduz.

Ramseier, D. 1994. Entwicklung und Beurteilung von Ansaatmischungen für Wanderbrachen. Veröffentlichungen des Geobotanischen Instituts der ETH, Stiftung Rübel 118.

Raunkiaer, C. 1934. The life forms of plants and statistical plant geography. Clarendon Press, Oxford.

Schaffner, D., Keller, S. & Fried, P.M. 1998. Spontanbegrünung von Brachen - im Mittelland sinnvoll? Agrarforschung 5: 257-259.

Schmeil, O. & Fitschen, J. 1993. Flora von Deutschland und angrenzender Länder. 89th ed. Quelle und Meyer Verlag, Heidelberg.

Schneider, C., Sukopp, U. & Sukopp, H. 1994. Biologisch-ökologische Grundlagen des Schutzes gefährdeter Segetalpflanzen. Schriftenreihe Vegetationskunde 26: 1 356.

Schneider, H. & Paulsen, J. 1994. Schweizer Flora Arten – Datenbank. Botanisches Institut der Universität Basel.

ter Braak, C.J.F. & Smilauer, P. 1998. Canoco reference manual and user's guide to Canoco for Windows. Centre for Biometry, Wageningen.

Thompson, K., Bakker, J. & Bekker, R. 1997. The Soil Seed Banks of North West Europe. Cambridge University Press, Cambridge.

Tischew, S. & Schmiedeknecht, A. 1993. Vegetationsentwicklung und Dynamik der Diasporenbank und des Diasporenfalls einer Ackerbrache unter den Bedingungen des Mitteldeutschen Trockengebiets. Verhandlungen der Gesellschaft für Ökologie 22: 162-173.

van Elsen, T. & Günther, H. 1992. Auswirkungen der Flächenstillegung auf die Ackerwildkraut-Vegetation von Grenzertrags-Feldern. Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz. Sonderheft XIII: 49-60.

Vögeli, U. & Obrist, R. 1993. Was keimt in meinem Acker? Eine Bestimmungshilfe für die wichtigsten Arten der Ackerbegleitflora. Landwirtschaftliche Lehrmittelzentrale, Zollikofen.

Welten, M. & Sutter, R. 1982. Verbreitungsatlas der Farn- und Blütenpflanzen der Schweiz. Birkhäuser Verlag, Basel.

Whittaker, J. 1984. Model interpretation from additive elements of the likelihood function. Applied Statistics 33: 52-65.

App. 1. List of species in seed mixtures applied in the Klettgau (1992 – 1999). () only in one mixture in one strip, * occasionally also in 'Additions'.

Achillea millefolium
Agrimonia europaea
Agrostemma githago
Anchusa arvensis
Anthemis tinctoria
Arctium lappa/minus
Bromus arvensis
Buglossoides arvensis
*(Bupleurum rotundifolium)**
Camelina sativa
Campanula rapunculus
Carum carvi
Centaurea cyanus
Centaurea jacea
Chamomilla recutita
Chrysanthemum leucanthemum
Cichorium intybus
Consolida regalis
(Crepis foetida)
(Crupina vulgaris)
Daucus carota
Dianthus armeria
Dipsacus fullonum
Echium vulgare
Fagopyrum vulgare
Galeopsis angustifolia
(Galeopsis ladanum)
Galium verum
Hypericum perforatum
(Iberis pinnata)
Knautia arvensis
Legousia speculum-veneris
Leontodon hispidus
Linaria vulgaris
Lotus corniculatus
Malva moschata
Malva sylvestris
*(Melampyrum arvense)**
Melilotus albus
*(Misopates orontium)**
*(Nigella arvensis)**
Oenothera biennis
Onobrychis viciifolia
Origanum vulgare
*(Orlaya grandiflora)**
(Papaver argemone)
Papaver dubium
(Papaver lecoquii)
Papaver rhoeas
Pastinaca sativa
*(Picris echioides)**
Prunella vulgaris
Ranunculus arvensis
Reseda lutea
Reseda luteola
Salvia pratensis
Scabiosa columbaria
Silene alba
Silene noctiflora
Silene vulgaris
Stachys annua
Tanacetum vulgare
Tragopogon orientalis
(Trifolium arvense)
Vaccaria hispanica
Valerianella rimosa
Verbascum densiflorum
Verbascum lychnitis
Verbascum nigrum
Verbascum thapsus
(Xeranthemum annuum)

App. 2. Seed mixtures applied and numbers of seedlings of sown species recorded in soil samples. Conversion factor for No. of seedlings/m² (/7 cm depth) = 35; species = found only where sown (7), *(species)* = sown species found nowhere (19), ***species*** = present where not sown (10), / **x** = in arable field, A = annual (10), M = monocarpic perennial (9), P = polycarpic perennial (18); maximum longevity of seeds in seed bank: 1 = < 1 year, 2 = 1-5 years, 3 = 5-20 years, 4 = > 20 years.

Age	Life history	Seed longevity	old					medium						young					
Seed mixture			Rams.o					UFA 95			UFA 94			Klettg.96 Standard			UFA 96		
Site (W=wildfl. strip, F=field)			W/F 1			W/F 2		W/F 1			W/F 2			W/F 1			W/F 2		
Layer (U=upper, L=lower)			*Seeds g/100m²*	U No.	L No.	U No.	L No.	*Seeds g/100m²*	U No.	L No.	*Seeds g/100m²*	U No.	L No.	*Seeds g/100m²*	U No.	L No.	*Seeds g/100m²*	U No.	L No.
Achillea millefolium	P	4	*0.8*	1	—	2	2/**1**	*3*	5	3	*x*	—	—	*5.5*	—	—	*3*	—	—
(Agrimonia eupatoria)	P	2	*23.9*	—	—	—	—												
(Agrostemma githago)	A	2	*13*	—	—	—	—	*14*	—	—	*x*	—	—	*26*	—	—	*14*	—	—
Anthemis tinctoria	P	3							**52/9**	**34**	*x*	38	15	*1.85*	22	26		**11**	**10**
Arctium lappa od. minus	M	4	*6.1*	14	1	**2**	**3**				*x*	—	—						
(Carum carvi)	P	1						*8*	—	—	*x*	—	—				*8*		
Centaurea cyanus	A	3	*4.3*	—	—	—	—	*8*	—	—	*x*	—	—	*15*	1	—	*8*	—	—
(Centaurea jacea)	P	2	*5.3*	—	—	—	—	*2*	—	—	*x*	—	—				*2*	—	—
Chrysanthemum leucanth.	P	4	*0.9*	13	—	9	3	*4*	13	8	*x*	23	5		**10**	**3**	*4*	10	2
(Cichorium intybus)	M	2	*2.1*	—	—	—	—	*3*	—	—	*x*	—	—	*3*	—	—	*3*	—	—
Daucus carota	M	4	*2.2*	1	1	13/**1**	1/**1**	*5*	2	2	*x*	2	1	*7.5*	—	—	*5*	1	2
(Delphinium consolida)	A	3	*3.5*	—	—	—	—												
Dipsacus fullonum	M	3	*0.3*	13	—	—	—	*0.25*	—	—	*x*	—	—				*0.25*	1	1
(Echium vulgare)	M	2	*1.5*	—	—	—	—	*3*	—	—				*5.5*	—	—	*3*	—	—
(Fagopyrum vulgare)	A	1	*26.7*	—	—	—	—	*22.5*	—	—							*22.5*	—	—
Hypericum perforatum	P	4	*0.6*	7	—	57	26	*2*	1	—							*2*	—	—
Knautia arvensis	P	4	*6*	—	—	—	—				*x*	—	—						**1**
(Legousia speculum-veneris)	A		*4.2*	—	—	—	—				*x*	—	—						
(Linaria vulgaris)	P	3	*1.1*	—	—	—	—												
(Malva sylvestris)	P	4	*1.2*	—	—	—	—	*1*	—	—	*x*	—	—				*1*	—	—
Melilotus albus	M	4	*1*	—	—	1	—												
(Oenothera biennis agg.)	M	4									*x*	—	—						
(Onobrychis viciifolia)	P		*18.9*	—	—	—	—				*x*	—	—						
(Origanum vulgare)	P	3									*x*	—	—						

App. 2. (continued)

Age			old					medium						young					
Seed mixture			Rams.o					UFA 95			UFA 94			Klettg.96 Standard			UFA 96		
Site (W=wildfl. strip, F=field)			W/F 1			W/F 2		W/F 1			W/F 2			W/F 1			W/F 2		
Layer (U=upper, L=lower)	Life history	Seed longevity	*Seeds g/100m²*	U No.	L	U No.	L	*Seeds g/100m²*	U No.	L	*Seeds g/100m²*	U No.	L	*Seeds g/100m²*	U No.	L	*Seeds g/100m²*	U No.	L
(Papaver dubium)	A		*1.4*	—	—	—	—												
Papaver rhoeas	A	4	*6.6*	5	6	17	4/**1**	*6*	10/**4**	4	*x*	13/**4**	7/**12**	*11*	22/**1**	17	*6*	178/**6**	52/**2**
Pastinaca sativa	M	3	*3.5*	—	—	2	—	*9*	—	—/**3**				*17*	1	—	*9*	2	—/**1**
(Ranunculus arvensis)	A		*15.5*	—	—	—	—												
(Reseda lutea)	P	2									*x*	—	—						
(Salvia pratensis)	P										*x*	—	—						
Scabiosa columbaria	P/M	2	*4.1*	1	—	3	1								**1**			**1**	
Silene alba	P/A	4	*2.1*	1	—	—	—	*2*	—	—	*x*	1	—	*3.75*	—	—	*2*	—	2
Silene noctiflora	A	3	*6.1*	4	1	—	—					**1**							
Tanacetum vulgare	P	2	*0.34*	—	—	—	—	*0.5*	3	—	*x*	2	1				*0.5*	—	—
(Tragopogon orientalis)	P/M	2	*7.4*	—	—	—	—	*4.75*	—	—							*4.75*	—	—
(Vaccaria hispanica)	A	2	*4.5*	—	—	—	—												
Verbascum spec.	M	4	*0.4*	—	—	—	—	*2*	3/**1**	1	*x*	6	—	*3.75*	42	1	*2*	18	3
Species number			*31*	10	6	8**+1**	6**+1**	*19*	7**+1**	5**+1**	*23*	7 **+1**	5	*11*	5**+2**	3**+1**	*19*	6**+2**	6**+3**
% of sown species recorded				32	19	26	19		37	26		30	22		45	27		32	32

App. 3. Numbers of seedlings of spontaneous species recorded in soil samples given. Conversion factor for No. of seedlings/m^2 (/7 cm depth) = 35; *species* = spontaneous species also in surveys (37), *species* = spontaneous species additional to surveys (4), ***species*** = species from mixtures present where not sown (10), A = annual (10), M = monocarpic perennial (9), P = polycarpic perennial (18); maximum longevity of seeds in seed bank: 1 = < 1 year, 2 = 1-5 years, 3 = 5-20 years, 4 = > 20 years.

Age	Life history	Seed longevity	old								medium								young							
Seed mixture			Rams.o								UFA 95				UFA 94				Klettg.96 Standard				UFA 96			
Site: W = wildflower strip, F = field			W1 No./m^2		F1 No./m^2		W2 No./m^2		F2 No./m^2		W1 No./m^2		F1 No./m^2		W2 No./m^2		F2 No./m^2		W1 No./m^2		F1 No./m^2		W2 No./m^2		F2 No./m^2	
Layer (U = upper, L = lower)			U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L
Achillea millefolium	P	4								1																
Aethusa cynapium	A	4	1	1			1	2					3	1									4			4
Alopecurus myosuroides	A	3					2	2	3	5			1		1				4				18	5		
Anagallis arvensis	A	4					1	2															1			1
Anthemis tinctoria	P	3									52	34	9										11	10		
Aphanes arvensis	A	4	1																							
Capsella bursa-pastoris	A	4					1	3	1		17	10	1	4									8	3		
Cerastium spec.	P	4	1				1	1																		
Chenopodium spec.	A	4							4			1		1	1					2					2	
Chrysanthemum leucanth.	P	4																								
Dactylis glomerata	P	2	2	1											3								2			
Daucus carota	M	4							1	1																
Epilobium spec.	P	2	16				1		2																	
Erigeron annuus	A	1	2				1			1					1				2							
Erysimum cheiranthoides	A	3									1								1				1			
Fallopia convolvulus	A	4		7											1											
Festuca rubra	P	3	1												3	1										1
Galium aparine	A	2	5						4	2						1			8				4	1	2	
Geranium dissectum	A	3	2																1				5	1		
Geranium pusillum	A	4																	3	1			2	1		
Knautia arvensis	P	4																						1		
Lactuca serriola	A	3	3				1				3	1											19	7	1	
Lamium amplexicaule	A	4								1	1			2									2			
Lamium purpureum	A	4	7	1					1	2	15	7	9	7	2	1	2					1	30	10	1	1
Lolium perenne	P	3	3																							
Lychnis flos-cuculi	P	3						1																		

App. 3. (continued)

Age			old								medium								young							
Seed mixture			Rams.o								UFA 95				UFA 94				Klettg.96 Standard				UFA 96			
Site: W = wildflower strip, F = field	Life history	Seed longevity	W1 No./m²		F1 No./m²		W2 No./m²		F2 No./m²		W1 No./m²		F1 No./m²		W2 No./m²		F2 No./m²		W1 No./m²		F1 No./m²		W2 No./m²		F2 No./m²	
Layer (U = upper, L = lower)			U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L
Medicago lupulina	A/P	4								2																
Mentha arvensis	P	3																	1							
Myosotis arvensis	A	4	4				5	7	7	8				1	5	1			4				27	6		
Papaver rhoeas	A	4								1			4				4	12			1				6	2
Pastinaca sativa	M	3								1				3												1
Poa annua	A/P	4													4				1			1				
Poa trivialis	P	3	1384	153			12	6			9	4			67	11			1				27	1		
Prunella vulgaris	P	3						1	1		1						4									
Rumex obtusifolius	P	4	**1**		3																		1			
Scabiosa columbaria	M/P	2																	1				1	1		
Silene noctiflora	A	3													1											
Sinapis arvensis	A	4												1												
Sonchus asper	A	3		1					4	3					1	1			3				5			1
Sonchus oleraceus	A	4							3																	
Stellaria media	A	4							1	3	4	3	3	4					2			1	9	3		
Taraxacum officinale	P	4			7		3																			
Thlaspi arvense	A	4																						1		
Trifolium repens	P	4					**2**				5								1				6	3		
Verbascum spec.	M	4											1													
Veronica arvensis	A	3	12	10			**75**	**27**	**2**	3	186	48	2	3	20	3	1	2	25	7			23	6	1	2
Veronica filiformis	P		2	1			6	3	6	7	14	5		1	4	1		2								
Veronica hederifolia	A	3					10		1	**2**	1								1				2	3	3	1
Veronica persica	A	4	**11**				10	12			5				2								7	7		
Veronica polita	A	4	**2**	**2**									1						1	1			1	1	1	
Viola arvensis	A	4							1																1	
Number of species		51	19	**9**	**2**	**0**	16	12	17	16	14	9	11	10	5	8	4	3	17	4	1	3	24	19	9	9
Total number of seedlings		2978	1460	177	10	**0**	132	67	43	43	314	113	**35**	**27**	116	20	11	16	60	11	1	3	216	71	18	14

Chapter 2. The vegetation of wildflower strips in a Swiss arable region in relation to age, management and site factors

Karin S. Ullrich and Peter J. Edwards

Abstract

The development of the vegetation of wildflower strips in response to various management and site factors was studied in a large scale field survey. The study area is located in the Klettgau, an intensively used arable region in northern Switzerland where many wildflower strips have been established in recent years.

Successional change in wildflower strips is relatively rapid and, to a considerable extent, predictable. Sites in their 1st year are dominated by typical arable weeds, i.e. spontaneous annual therophytes, which mostly form a long-lived seed bank. From the 2nd year on the vegetation cover increases as sown perennial thero-hemicryptophytes and hemicryptophytes typical of ruderal sites or meadows become dominant. At this stage, the species composition of the vegetation is strongly influenced by the seed mixture which was used. The number and cover of sown species in the vegetation increases with the number of species contained in the mixture. The cover of spontaneous species is inversely affected by the abundance and number of sown species. From the 3rd year onwards, spontaneous perennial species gain ground. Many of these are laterally spreading hemicryptophytes and geophytes (including several grasses) with high nutrient requirements; their progress in replacing the sown species is therefore more rapid on fertile sites. Attempts to steer the vegetation development at this stage by cutting or superficially working the soil, e.g. by rotavation or tine cultivation, are not usually successful in the long term. Therefore, sites known to have a high pressure of grasses or to contain other problem weeds should be avoided when establishing wildflower strips.

Keywords: Correspondence Analysis, life form, life history, management, seed bank, seed longevity, seed mixture, set-aside, succession, Switzerland

Introduction

Swiss agricultural policy supports various types of 'ecological compensation areas', including hedges, extensive grassland or wildflower strips, as a way to reintroduce biological diversity into intensively used agricultural landscapes. This article concerns wildflower strips; these are strips of land at least 3 m wide running across or along the edge of an arable field, and sown with a recommended mixture of indigenous arable weeds and species of ruderal places. They are left for at least two years, and more usually for up to six years. Ideally, such strips should maintain a high plant species diversity over several years without promoting undesirable weeds and grasses. Another objective is to create vegetation with a heterogeneous structure of moderate density and consisting of plants of various heights, since these features are thought to offer a maximum variety of habitats for associated animal species. There may also be benefits for biological diversity at a landscape scale where there is a large diversity of wildflower strips differing in species composition and vegetation structure.

Several factors influence the vegetation of wildflower strips. The potential species pool depends on the seed mixture sown and on the species present in the neighbourhood, including those in the seed bank. The actual vegetation composition developing from the potential species pool is influenced by a range of management and site factors which affect the performance of particular species. Since wildflower strips are new elements in the landscape our understanding of how these factors affect the vegetation is still limited. Several experimental studies have been performed with the aims of developing effective seed mixtures for wildflower strips and determining management regimes which favour a high diversity of plants and invertebrates (Bürki H.-M. 1993; Günter M. 2000a; Günter M. 2000b; Häni F. & Zürcher J. 2000; Heitzmann A. 1995; Pfiffner L. & Schaffner D. 2000; Ramseier D. 1994; Salveter R. & Nentwig W. 1993; Schaffner D. & Keller S. 1998; Schaffner D. et al. 2000; Schmid A. 1992; Weiss E. & Stettmer C. 1991). However, many of these studies have been carried out at a small spatial scale, and it is not clear whether the conclusions can be transferred to large scale field applications. In this paper we present data from a large scale study carried out in the Klettgau region of northern Switzerland. This is an intensively used arable region containing a large number of wildflower strips of different ages, management and site conditions. Our central question is: how do seed mixture, management and environmental factors affect the development of vegetation in wildflower strips? Our objective was to reach conclusions which are useful for the planning and maintenance of wildflower strips and which are generally valid in other regions. To achieve this objective we analyse the influence of environmental factors on vegetation development, not only in terms of species composition, but also in terms of vegetation structure and the frequency of occurrence of contrasting species traits.

Research area

The study area is the Klettgau (Canton Schaffhausen), an intensively used arable region in the north of Switzerland. It forms a wide, flat valley with calcareous river gravels which are locally overlaid by loam and loess; the soils vary in depth and texture and are rich in bases. The area ranges in altitude between 400 and 470 m a.s.l.. In comparison to other parts of the Swiss Midlands the climate is relatively dry (915 mm precipitation per year) and warm in summer (18.4°C Temp. average in July; 8.5°C annual Temp. average), which leads to a frequent deficit in water balance between April and August (Data from the Swiss Meteorological Institute 1996). Cereals are the main crop type and cover about half of the surface of the agricultural area; these are followed, in declining order of abundance, by root crops, maize, rape, and locally also by grassland. The study area is divided in four districts 'Widen', 'Former Fen', 'Langfeld' and 'Plomberg' plus the remaining surrounding area 'Outside'.

Table 1. Characteristics of the districts comprising the majority of wildflower strips in the Klettgau (based on Jenny M. & Weibel U. 1999).

Characteristics	**Widen**	**Widen-Former Fen**	**Langfeld**	**Plomberg**
Location	NE of Neunkirch	E of Neunkirch	W of Neunkirch	W of Wilchingen
Area of district	$5.3\ km^2$ including	Former Fen	$2.4\ km^2$	$4.7\ km^2$
Soil depth	10 - 50 cm	?	50 - 100 cm	50 - 100 cm
Stone cover	0 - 60%	0 - 20%	mostly 0%	mostly 0%
Soil texture (according to Schröder 1984)	stony, loamy clay	silty loam (high content of organic matter)	clay loam, little, sand	silty loam, 10 - 30% sand
Fertility	less fertile	very fertile	very fertile	very fertile
Grassland	12%	along nature reserve	6%	17%
Trees+hedgerows	almost none	forest+hedgerows	some	few
Age of strips	1 - 5 years	1 - 5 years	1 - 5 years	2 - 3 years
Specialities	base rich, rare arable weeds, arable flora reserves	stream+ponds nature reserve	canalised streams	few wildflower strips
Numbers of:				
wildflower strips	26	4	14	8
subsections of strips	76	13	34	16
arable flora reserves	9	0	0	0

As part of a project to improve habitat conditions for the grey partridge and the European hare a large number of wildflower strips of various kinds have been created since 1992 (Jenny M. & Weibel U. 1999; Jenny M. et al. 1999). Here we distinguish between wildflower strips and arable flora reserves. The latter are managed specifically to promote rare arable weeds by sowing cereals at low density in favourable sites and also by adding seeds of selected rare species. In wildflower strips, a variety of standard seed mixtures have been used at one time or other (App.1). Sometimes additional species were sown in particular strips, referred to here as 'Additions'. These strips are mainly concentrated in the four districts while only few are located elsewhere in the region (Table 1). Records concerning the management of the strips are held by the Swiss Ornithological Institute and the cantonal authorities as well as by some farmers, but the information is not always complete.

Methods

Vegetation survey

In 1996, the vegetation of all the then existing wildflower strips and arable flora reserves in the Klettgau (62) was surveyed (4th June – 22nd July). Subsections of strips that had experienced different management or for some other reason had developed a distinctive vegetation were treated as distinct sites. For each site, information on management factors was gathered from the Swiss Ornithological Institute, the cantonal authorities and farmers. These factors include: total age of a site (1st year, 2nd year, 3rd year and ≥ 4th year), season of establishment (Spring, Autumn), seed mixture applied (Spontaneous, Kanton93, Rams.o, Rams.r, UFA94, UFA95/96, Klettgau, Ackerfl94, Additions – compositions in App.1), and later maintenance impacts, i.e. the renewal of a site or other major disturbance since the previous autumn. In addition, for each site the surrounding landuse was mapped (Cereals, Other Crops, Grassland, Roads, Wood, Other) and the quantity of stones on the soil surface was recorded as percentage cover classes (0-15%, 16-30%, 31-45%, > 45%).

In each of the 156 sites thus recognised four 1 m^2 quadrats were located regularly along the length of the strip. In each quadrat the top cover of every plant species was estimated (to the nearest 1% between 1 and 20%, and to the nearest 5% above 20% cover). The cover of moss, litter and bare ground was also estimated, giving a total cover for each quadrat of 100%.

For all species recorded, the following information (referred to as species 'traits') was assembled from published sources: Red List status, natural habitat affinity, life history, life form according to Raunkiaer (1934), longevity of seeds in the seed bank, modes of dispersal, and indicator values according to Landolt (1977) (Table 2).

Table 2. Species traits gathered from various databases (Hodgson J.G. et al. 1995; Landolt E. 1977; Landolt E. 1991; Lindacher R. 1995; Müller-Schneider P. 1986; Thompson K. et al. 1997; Schneider H. & Paulsen J. 1994), dispersal terminology according to van der Pijl (1982).

Type of trait	Categories
Source	Sown species (A=added) Spontaneous species (S)
Rarity	Red List-species (RL)
Habitat affinity	Arable weeds Meadow species Ruderal species (= species of ruderal places) Fringe species Wood species
Life history	Annuals Monocarpic perennials Polycarpic perennials
Life form according to Raunkiaer (1937)	Geophytes Therophytes Hemicryptophytes Thero-/Hemicryptophytes Phanerophytes
Longevity of seeds in the soil seed bank	0-1 years 1-5 years 5-20 years > 20 years

Modes of dispersal	Vegetative dispersal
	Passive ballists
	Zoochorous:
	    Ectozoochorous
	    Myrmecochorous
	    Endozoochorous
	    Dyszoochorous
	Rain wash
	Anemochorous
	Anthropochorous *s. str.*
	Hemerochorous

Indicator values according to Landolt (1977)	Moisture value Intermittently moist Reaction value Nutrient value Humus value Light value Temperature value Continentality value

Analyses

All multivariate analyses were run using Canoco version 4.02 (ter Braak 1997-1999). The influence of the various environmental and management factors on the vegetation was studied using Canonical Correspondence Analysis (CCA). For this purpose the data from the four 1 m^2 quadrats from each site were averaged. Species with a frequency < 5% (i.e. species recorded at < 8 sites) were omitted to minimize sampling errors and random effects. All CCAs were run using log-transformed data and with no down-weighting of rare species. All environmental variables were transformed into classes and entered as nominal data. Forward selection of variables was used to eliminate variables which are collinear or in general do not contribute significantly to an explanation of the variation in species abundances (Monte Carlo Test with 199 unrestricted permutations; P≤0.01). In order to reduce the multifactoriality of the analysis, subsets of the total data were analysed separately using the same settings; in these analyses species that occurred at least four times were included.

The explained variation in the vegetation data was partitioned according to site factor, management and adjacent landuse components (Borcard D. et al. 1992; Økland R.H. & Eilertsen O. 1994; ter Braak C.J.F. & Smilauer P. 1998; Whittaker J. 1984). For each of these factorial groups the variance contributed by single factors (groups of nominal variables belonging to the same factor) was partialled out and tested for significance (Monte Carlo test with 199 unrestricted permutations; P≤0.005).

The data were also analysed using Correspondence Analysis (CA), in order to produce a 2-way vegetation table of sites and species. The groups were checked visually for specificity and homogeneity, and outlier sites were removed from the table. Each vegetation group was characterised in terms of the environmental variables and the frequency and mean abundance of plant species present. An 'importance value' (defined as weight * variance) was calculated for each species; this value indicates the importance of particular species in differentiating the vegetation types in the CA (ter Braak C.J.F. & Smilauer P. 1998). The vegetation of each site was also characterised in terms of frequencies of occurrence or mean values for the various species traits (Table 2). These values were used in the CA of the total data set in an indirect gradient analysis together with significant environmental factors. By plotting the centroids of the environmental factors and the vectors of vegetation characteristics and species traits in ordination diagrams correlations between the two are illustrated.

To investigate successional changes in species composition more closely, the differences in relative frequency and average % cover of plant species between 1st and 3rd year sites were calculated. Species sown only in certain years or mixtures with a strong impact on the CA (importance value) were removed to minimize management artefacts. Changes in plant abundance were related to species traits such as life history, life form and seed longevity.

Limitations of analysis due to confounding of variables

Most environmental factors are not independent of each other, and their influence on the vegetation thus has to be interpreted with caution (Table 3). The problem arises because the wildflower strips were not set up based on an experimental design. Instead their management and spatial distribution developed over the years. In the various districts the establishment of wildflower strips started at different times and their numbers have varied over time. Seed mixtures have also varied; some were only used for only one or two years and some were chiefly sown in either spring or fall. The species composition of 'Additions' is often unrecorded, and we cannot be sure whether certain rare species were sown or recruited spontaneously. For the establishment of arable flora reserves only promising sites in the district Widen with a high stone cover were chosen. A renewal or any kind of disturbance of a strip except mowing was carried out selectively, only where the state of the vegetation was unsatisfactory.

Table 3. Correlations between environmental factors of different factorial groups. ++/– – = correlations > 0.4, +/– = correlations > 0.2, Pearson product-moment correlation, P<0.05; **Age**, ***Season***, **<u>Seed mixture</u>**, <u>District</u>, Stone cover, *Adjacent landuse*.

	1st year	**2nd year**	**3rd year**	**≥4th year**	**Disturbance**	***Fall***	***Spring***	**<u>Spontaneous</u>**	**<u>Kanton93</u>**	**<u>Rams.o</u>**	**<u>Rams.r</u>**	**<u>UFA94</u>**	**<u>UFA95/96</u>**	**<u>Klettgau</u>**	**<u>AckFl94</u>**	**<u>Additions</u>**	<u>Widen</u>	<u>Former Fen</u>	<u>Langfeld</u>	<u>Plomberg</u>	<u>Outside</u>	Stones 0-15%	Stones 16-30%	Stones 31-45%	Stones >45%
Fall	.	+	.	–	.																				
Spring	+	.	–	+	.																				
<u>Spontaneous</u>	.	.	–	+	+	.	.																		
<u>Kanton93</u>	–	–	+	+	.	.	.																		
<u>Rams.o</u>	.	.	.	.	.	+	–																		
<u>Rams.r</u>	.	.	+	–	.	.	.																		
<u>UFA94</u>	–	++	.	–	.	.	.																		
<u>UFA95/96</u>	++	.	–	–	.	.	+																		
<u>Klettgau</u>	+	.	–	.	.	–	+																		
<u>AckFl94</u>	+	.	.	.	.	.	.																		
<u>Additions</u>	++	.	–	–	.	.	.																		
<u>Widen</u>	.	.	–	.	+	+	.	+	–	.	–	.	.	.	.	+									
<u>Former Fen</u>	.	.	+	.	.	.	–	.	+	.	.	.	.	.	.	–									
<u>Langfeld</u>	.	.	–	+	.	–	+	.	+	–	.	–	.	+	+	.									
<u>Plomberg</u>	–	.	+	–	.	.	.	.	–	.	+	+	.	.	.	–									
<u>Outside</u>	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.									
Stones 0-15%	.	.	.	.	–	–	.	.	.	.	+	.	.	.	.	–	– –	–	++	+	+				
Stones 16-30%	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	++	–	–	–				
Stones 31-45%	+	.	–	.	+	.	.	.	–	.	.	+	.	.	.	+	++	.	–	.	.				
Stones >45%	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	–	.	.				
Cereals	.	.	–	.	.	.	.	.	–	.	.	.	.	.	.	+	+	– –	.	.	–	.	–	+	.
Other crops	.	.	+	–	.	+	–	–	.	.	.	.	.	.	.	.	–	+	–	+	+	+	.	.	–
Grassland	.	.	.	.	.	–	+	.	.	–	+	.	.	.	.	.	.	–	.	.	.	.	.	.	.
Roads	.	.	.	.	.	.	.	.	.	.	.	.	–	.	.	.	.	.	.	.	–	.	.	.	.
Wood	.	.	+	.	.	+	–	.	.	+	–	.	.	.	.	.	–	++	–	.	.	–	.	+	.
Other	.	.	.	.	.	+	–	.	.	+	.	–	.	.	.	.	–	++	+	–	.	.	.	.	.

Results

Variation in species composition explained by site and management factors

The vegetation of wildflower strips in the Klettgau is extremely variable due to the diversity of management and site conditions. A total of 38.6% of the variance in the CCA of the total data set can be explained by the environmental and management variables (Fig. 1). Of this total, factors related to the management account for 21.8%, while site factors (including stone cover) account for 5.4%, adjacent landuse for 5.7%, and management and site factors combined for another 2.9%. A closer analysis shows that, among the management factors, seed mixture explains the biggest portion of variance, followed by age and the combined influence of seed mixture and age; season of establishment plays only a minor role.

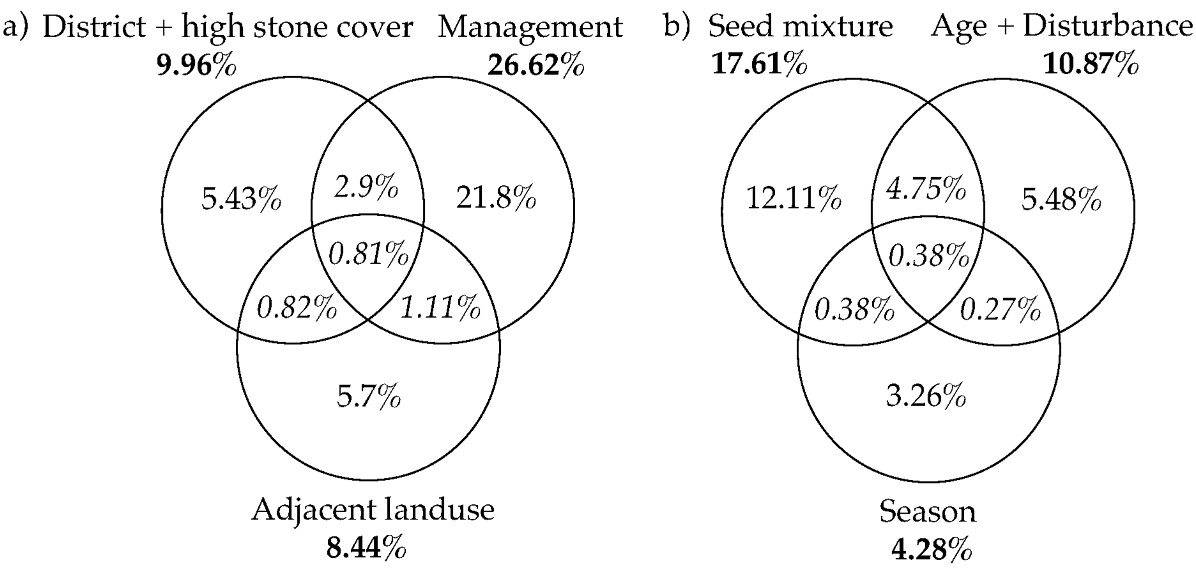


Fig. 1. Variance in the vegetation composition explained by environmental factors based on CCAs of the total data set (total inertia 5.58, sum of all canonical eigenvalues 2.15); a) partitioning of total explained variance (38.57%), b) partitioning of variance explained by management; **total variance explained by a factorial group including overlap with other groups**, variance explained by pure factors, *non-separable i.e. overlapping variance.*

The first two axes of the CA based on the total data set show that strips in their 1st year form a distinct group which is clearly separate from older strips (Fig. 2). To investigate variation in 2nd year and older strips the data for these strips were analysed separately (Figures 3, 4). As in the analysis of the total data, 38.6% of variance is explained by the management and environmental variables. As Figure 3 shows, age plays little role in differentiating these older sites, while seed mixture, location and adjacent landuse are significant factors (Fig. 4). Management impacts like the renewal of a strip by working the soil superficially (e.g. by rotavation or tine cultivation), by mowing of a site, or local abatement of problem weeds show no significant effect when analysed separately.

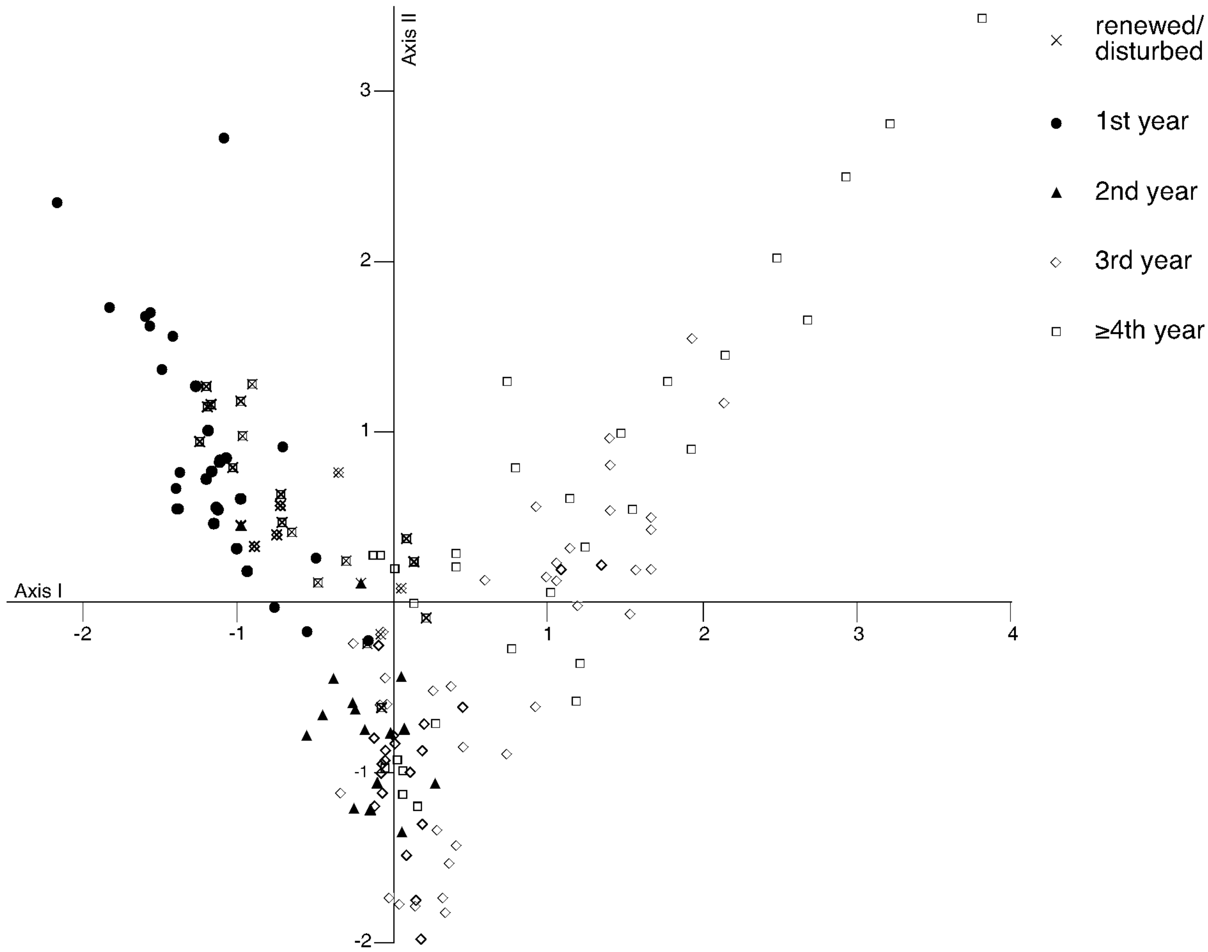


Fig. 2. Ordination diagram of a CA of the total data set showing the sites differentiated according to their age. Sites in their 1st year form the most distinct group, i.e. their species composition is relatively similar in comparison to that of older sites, which differentiate less according to age (Total inertia = 5.58, eigenvalue of axis I = 0.50 and of axis II = 0.37).

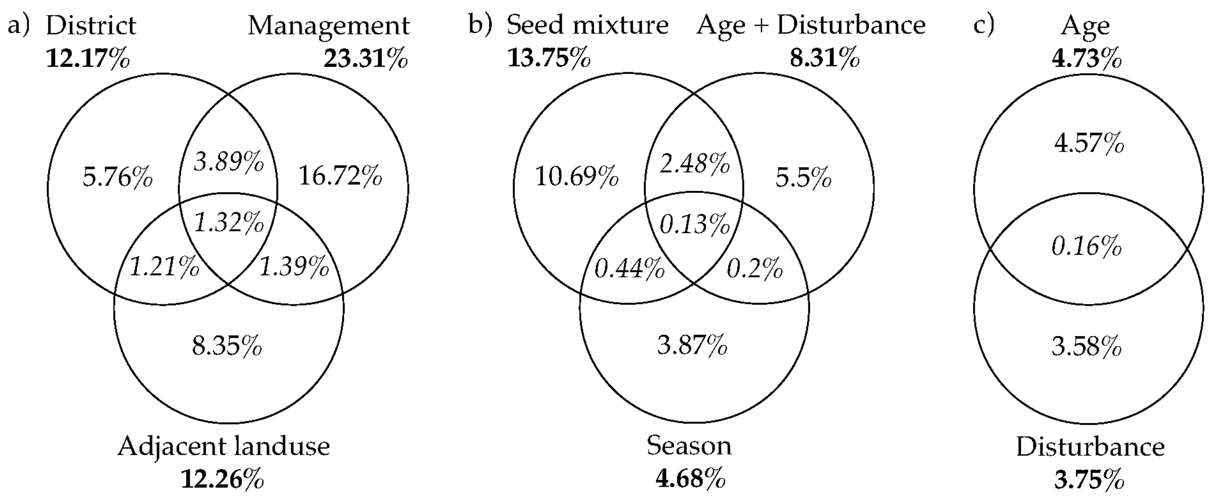


Fig. 3. Variance in the vegetation composition explained by environmental factors based on CCAs of the data subset '≥ 2nd year' (total inertia 5.47, sum of all canonical eigenvalues 2.11); a) partitioning of total explained variance (38.63%), b) partitioning of variance explained by management, c) partitioning of variance explained by age + disturbance; **total variance explained by a factorial group including overlap with other groups**, variance explained by pure factors, *non-separable i.e. overlapping variance.*

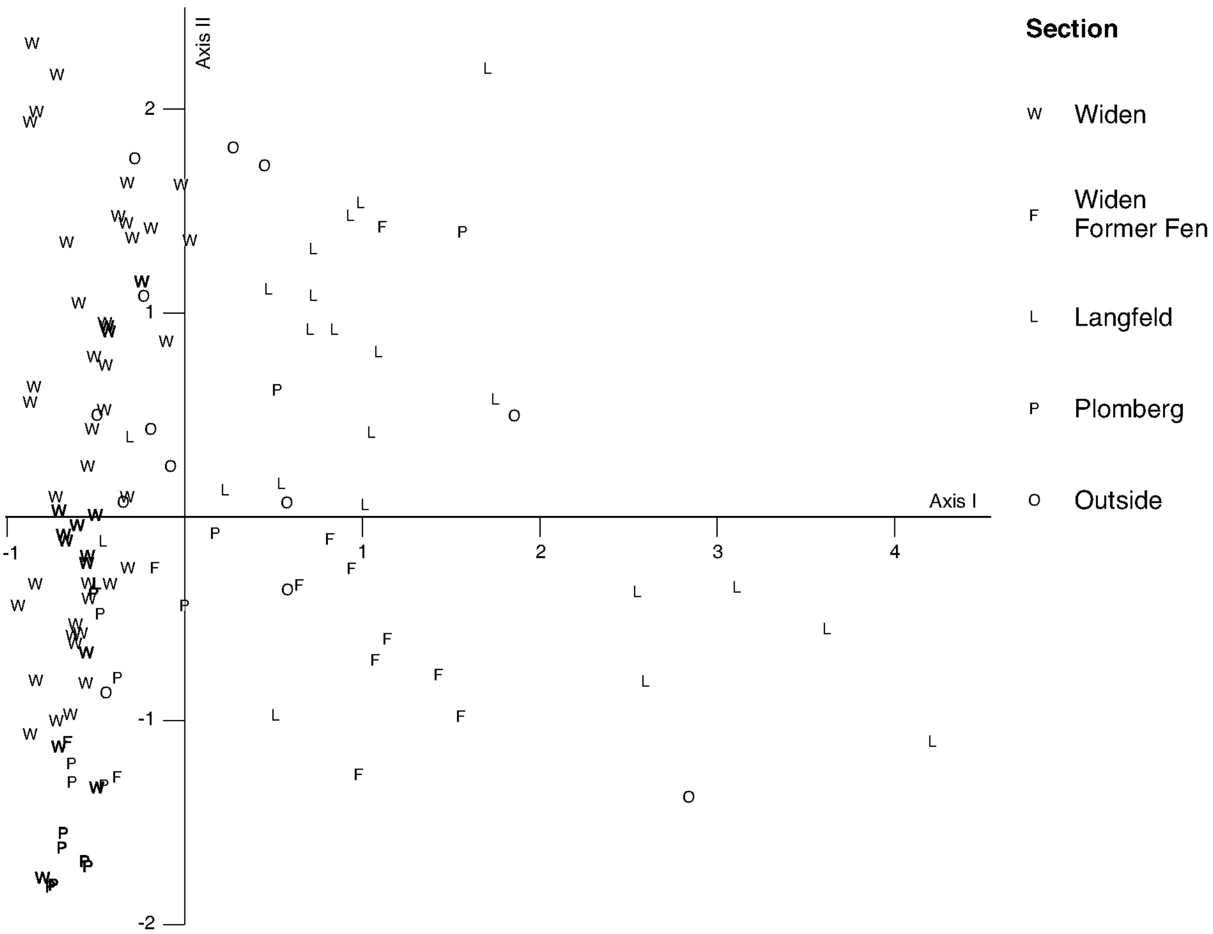


Fig. 4. Ordination diagram of a CA of the data subset '≥ 2nd year' showing the differentiation of the sites according to their location in the different districts. The clear differentiation between the large numbers of sites located in the Widen from those in the Langfeld mainly reflects the reaction of the plant species composition in the wildflower strips to the different soil conditions (Total inertia = 5.47, eigenvalue of axis I = 0.50 and of axis II = 0.36).

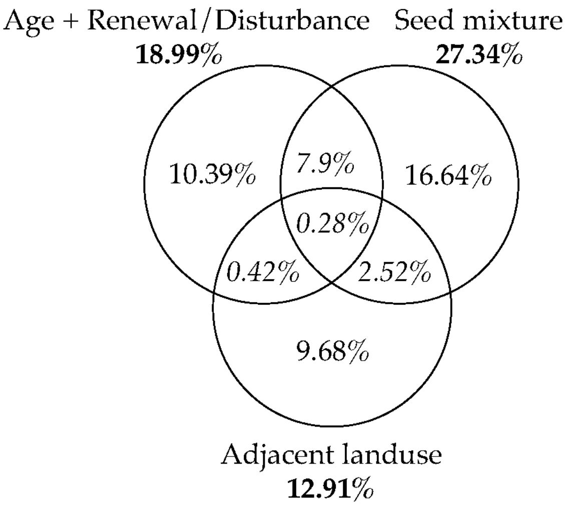


Fig. 5. Variance in the vegetation composition explained by environmental factors based on CCAs of the data subset 'Widen' (total inertia 3.53, sum of all canonical eigenvalues 1.69); total explained variance (47.83%), **total variance explained by a factorial group including overlap with other groups**, variance explained by pure factors, *non-separable i.e. overlapping variance.*

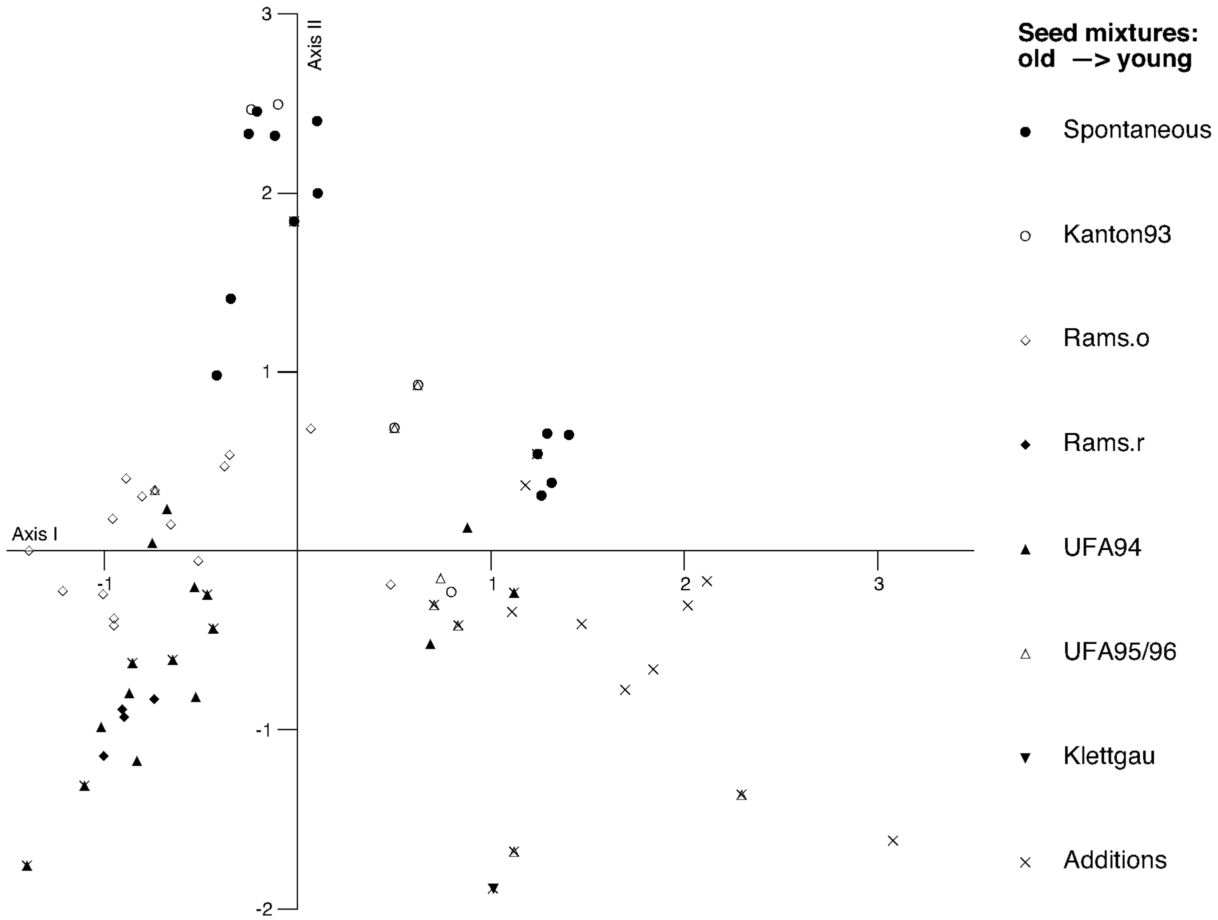


Fig. 6. Ordination diagram of a CA of the data subset 'Widen' showing the sites differentiated according to the seed mixtures applied. Sites sown with the same mixture basically group in the same area of the diagram, i.e. possess similar species compositions (Total inertia = 3.53, eigenvalue of axis I = 0.42 and of axis II = 0.32).

In a separate analysis of the data for Widen, 47.8% of the variance in the species composition could be explained (Fig. 5). Here seed mixture is the most important factor, followed by age (including renewal and disturbance); together these factors account for 38.2% of variance, the remainder being explained by adjacent landuse (Fig. 6).

Classification of the vegetation of wildflower strips (Tables 4 and 5)

Despite the great variability in the vegetation, it is possible to recognise a number of more or less distinct vegetation types based on the CAs. A vegetation table showing these types is presented in Table 4, and details of management and environmental conditions are given in Table 5. The most distinct type of wildflower strips are those in the 1st year (Fig. 2, Table 4, Types 1, 2). These usually have a comparatively sparse vegetation (Fig. 8a) and are dominated by annual arable weeds, often accompanied by young individuals of perennial ruderal or meadow species. The majority of characteristic annual species recruit spontaneously, though a few are contained in most seed mixtures (e.g. *Centaurea cyanus, Agrostemma githago*). Accordingly these 1st year sites are floristically similar, regardless of the seed mixture applied. A distinct subgroup of one year old strips is formed by arable flora reserves (Table 4, Type 1); these have an even lower vegetation cover and often contain cereals at low density as well as various rare arable weeds. They generally lack perennial species, especially those which are sown, but may contain a few geophytes rated as problem weeds (e.g. *Cirsium arvense, Convolvulus arvensis*).

Most similar to 1st year strips are those in the 2nd year (Type 3). These are already dominated by perennial species, though at comparatively low density, and they still contain some annual arable weeds. Unless the vegetation is disturbed, these annual species decline with increasing age of a strip. Even by the 2nd year there is an overlap with older strips in the ordination diagram (Fig. 2).

From the 3rd year on, the differentiation of the vegetation of wildflower strips according to seed mixture and district becomes increasingly evident. 3rd year sites, as well as some older sites, tend to be dominated by sown perennial species, which vary somewhat between mixtures and are responsible for some of the variation in the vegetation (Types 4-7, 11). The sown species are accompanied by a diversity of spontaneous species; of these, annuals occur more frequently in the district Widen (Types 4, 7, 11-13) than elsewhere (Type 5, 6, 8-10).

In the majority of older strips (i.e. > 3rd year), and in some of the 3rd year strips on very fertile soil, most of the sown species are absent (Types 9, 10, 12) or present only at low frequency (Types 9-13). The vegetation is now similar to that in those older strips which were never sown (Types 11, 13). Several spontaneous perennial species are frequent, with considerable differences in species composition between the various districts (Types 9-13). On the fertile soils in the Former Fen and Langfeld various grass species dominate the vegetation or are at least abundant (Types 8-10). In some areas, especially Widen, problem weeds such as *Cirsium arvense, Convolvulus arvensis, Taraxacum officinale* and *Agropyron repens* tend to become abundant, especially but not exclusively on unsown sites (Types 7, 11-13). The abundance of these problem species has often been a cause for the renewal of a site by cultivating the soil (e.g. with a rotavator or tine cultivator) and occasionally by resowing (Type 13), or for extensive mowing, local cutting or spraying of problem weeds (Type 12). In such cases the problem weeds usually remain frequent but may be accompanied by many spontaneous annual species, depending on the severity of the management. In most cases, sown species – annuals as well as perennials – remain scarce, even in sites that were originally sown or resown recently (Types 12, 13). However, in a few cases resowing was so successful that the strips group with those in their 1st year (Type 2).

Table 4. Vegetation types of wildflower strips in the Klettgau (1996 data) characterized by the relative frequency of species within each type. Sites are grouped according to the similarity of the vegetation also showing in the CAs of the total data set and the data subsets ' 2nd year' and 'Widen'. Due to their small number, strips sown with the mixtures UFA94 and Rams.r were left in the same type (4) inspite of differentiating species. Only species occurring with a frequency > 40% in at least one type are shown. The importance value (= weight * variance) indicates the strength of the influence of a species in a CA, species with a strong influence in either of the CAs are marked '++' = 1st-25th highest values and '+' = 26th-50th highest values respectively; Species source: S = species recruited spontaneously, A = species added; FF = relative frequency 70%, F = relative frequency 40%, ◆ = average cover 1%, ◇ = present.

Type description			1st yr		2nd yr	3rd yr			3rd yr						
			Additions	Various	UFA94	UFA94/ Rams.r	Rams.r	Rams.o		Kanton93		Various	Spont.+Kant.93		Various
			Widen Reserves	Various	Widen		Plomb.	Various	Widen	F. Fen	Langfeld		Widen Disturb.		Renewed
Group No.	Import. value	Species source	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
No of sites (strips)			9 (7)	24 (17)	7 (5)	12 (6)	8 (4)	9 (4)	14 (8)	9 (3)	13 (8)	12 (7)	8 (5)	11 (7)	7 (3)
Species no. Ø			3.3	29.2	24.7	26.7	21.1	25.8	27.9	27.1	21.2	13.9	21.6	26.3	25.0
Species no. SD			.7	7.3	1.4	4.8	4.3	6.5	4.1	4.7	4.8	4.5	4.6	7.3	4.8
Annual species, focus in new or disturbed strips															
Cereals	++		FF◆	F◆	◇		◇							◇	◇
Brassica napus	++	S		F◆		◇			◇						
Sonchus asper		S		F◆	◇			◇	◇		◇	◇		◇	◇
Consolida regalis	++	A	F	◇	◇									◇	F◆
Veronica hederifolia	+	S	F◆	◇							◇			◇	FF
Lamium amplexicaule		S	FF	◇		◇			◇			◇			FF
Euphorbia helioscopia		S	◇	◇			◇							◇	FF
Lathyrus tuberosus	++	S		◇	◇				◇						F◆
Senecio vulgaris		S	◇	◇				◇	◇				◇		F
Lamium purpureum		S	F	F	◇	◇	◇			◇		◇		◇	F
Chenopodium album	+	S	FF	FF◆	◇	◇	◇		◇			◇		◆	FF
Capsella bursa-pastoris		S	◇	F◆		◇			◇					F	F
Aethusa cynapium	++	S	F◆	F	◇				◇				◇	F	FF◆
Viola arvensis		S	FF◆	FF◆	◇	F		◇	F	◇			◇	F◆	FF◆
Polygonum aviculare	+	S	FF◆	FF◆	◇	F	◇	◇	F ◇		◇	◇	◇		FF◆
Stellaria media		S	F	F	F	◇	◇		◇		◇	◇		F	◇
Anagallis arvensis		S	◇	F		◇							◇	◇	◇
Legousia speculum-veneris		A	F	◇	◇	F		◇	◇					◇	
Centaurea cyanus	+	A	FF◆	F◆	F	F	◇	◇	◇					◇	◇
Agrostemma githago		A	FF	FF◆	FF◆	F	◇	◇	FF				◇	◇	F
Papaver rhoeas	++	A	FF◆	FF◆	FF◆	F	◇	F◆	FF	◇			◇	FF◆	FF◆
Fallopia convolvulus	+	S	FF◆	F◆	F	F	◇	◇	FF	◇	◇	◇	◇	FF	FF◆
Alopecurus myosuroides	++	S	FF◆	F◆	FF◆	F	◇	FF	FF				FF◆	F	FF◆
Lactuca serriola		S	F	FF◆	F	FF	◇	F	FF	◇ ◇		◇		FF◆	F
Galium aparine		S	FF◆	FF◆	FF◆	FF◆	F	FF◆	FF◆	FF	◇	◇	FF	FF◆	FF◆
Myosotis arvensis		S	F	F	FF◆	F	FF	F	FF	◇	◇		FF	FF	F
Veronica persica		S	◇	F	◇	◇	◇	F	F◆		◇	◇	◇	F	FF◆
Veronica arvensis		S	◇	◇	◇	◇	◇	◇					FF	◇	◇
Perennial species, persistant, sown															
Silene alba	+	A	F	F	FF◆	FF◆	FF◆	F◆	FF◆	F	◆			◇	
Daucus carota		A	F	FF◆	FF◆	FF◆	FF◆	FF◆	FF◆	F◆	◇		◇	FF◆	◇
Achillea millefolium	+	A		F	FF	FF◆	FF◆	FF◆	FF◆	FF◆	◆	◇	◇	F◆	◇
Leucanthemum vulgare	+	A		◇	FF◆	FF◆	FF◆	F	FF◆	FF◆	◇			◇	◇
Pastinaca sativa	++	A	◇	F◆		◇	◇	FF◆	FF◆	◆	◆		◇	◆	
Anthemis tinctoria	++	A	◇	F◆	FF◆	FF◆	FF◆		◇	◇	◇			◇	◇
Arctium lappa	+	A	◇	F	FF◆	FF◆	FF◆	FF◆	FF◆		◇	◇		◇	
Carum carvi		A			F	◇	◇								
Centaurea iacea	+	A		◇	F	FF◆	FF◆	FF◆	FF◆		◇			◇	
Dipsacus fullonum	+	A		◇	F◆	F◆	F◆	◆	F◆		◇				
Onobrychis viciifolia		A		◇	F◆	F	◇	F	F		◇			◇	
Knautia arvensis		A		◇	◇	F	F	◇	F	◇	◇				
Salvia pratensis	+	A		◇	F	FF◆	FF◆			◆	◇				◇
Tanacetum vulgare	++	A		◇		F◆	FF◆	◇	◇		◇				
Cichorium intybus		A	◇	◇		F	FF	◇	◇	◇	◇			◇	
Verbascum densiflorum	+	A		◇	◇	◆	FF◆			F◆	◇				
Origanum vulgare	++	A		◇	F	◇	F			FF◆	F◆	◇		◇	
Agrimonia eupatoria	+	A						F◆	FF◆						
Linaria vulgaris	+	A	◇	◇		◇	◇	FF◆	F◆	FF	◇	◆		◇	
Hypericum perforatum	+	A				◇		F◆	FF◆	F◆	◇			◇	
Echium vulgare		A		◇		◇		◇	◇	F◆				◇	
Galium verum	++	A								F◆	F◆			◇	
Malva moschata		A			F									◇	
Perennial species, persistant, spontaneous															
Cirsium arvense	+	S	F	◇	F	◇	◇	FF◆	FF◆	FF◆	◇	F	F◆	FF◆	◇
Convolvulus arvensis	+	S	F◆	◆	F	F◆		F◆	F	F	F◆	◆	FF◆	FF◆	FF◆
Taraxacum officinale	++	S	F	F	F◆	F◆	F	FF◆	FF◆	F	F◆	F◆	FF◆	FF◆	FF◆
Agropyron repens	++	S	◆	◇	FF◆	F◆	F◆	FF◆	F◆	F	◆	F◆	F	◆	FF◆
Lolium multiflorum	+	S	◇	◇	F◆	◇	◇	F	F	◇	◇	F◆	FF◆	F◆	F
Lolium perenne	++	S		◇	F◆	◇	◇	F	F◆	◇		F◆	FF◆	FF◆	F◆
Trifolium repens	++	S	◇	◆	F	◇	◇	◇	◆	◇	◆	◇	F◆	F◆	◇
Geranium pusillum	+	S		◇	F◆	◇		◇	F◆	◇	◇		FF◆	F◆	FF◆
Poa trivialis	++	S		◇	F ◇	◇		F◆	F◆	FF◆	F◆	FF◆	F	F◆	◇
Trifolium pratense	++	S	◇	◇	◆	◇	F	◇					◇	◇	
Epilobium adnatum		S		◇	F		◇		◇		◇	◇	F	F	
Cirsium vulgare	++	S		◇	◇	◇		◆	◇	F◆		◇	FF◆	◇	FF
Arrhenaterum elatius	++	S		◇						◇	F◆	F◆	◆	◇	◇
Trisetum flavescens		S			◇			◇	◇	FF	FF	◇	F	◇	◇
Dactylis glomerata	++	S		◇	◇			◇	◇	FF◆	F◆	FF◆	◇	◇	
Poa pratensis	++	S		◇			◇		◇	F◆	F◆	F◆	◇	◇	◇
Bromus sterilis	++	S		◇				F	◇	F◆	◇	◆	◇		◇
Geranium dissectum	++	S		◇	F ◇	◇		◇	◇		◇	◇	◇	◇	
Silene vulgaris		S		◇						F	◇			◇	◇
Woody species		S		◇				◇		FF◆					◇
Bromus erectus	++	S								FF◆	◆				
Phleum pratense		S		◇	F			◇			F◆				
Galium mollugo	+	S				◇				◇	FF	◇			
Festuca rubra	++	S	◇			◇				◇	F◆	◇	◇		
Holcus lanatus	+	S								◇	F◆	◇			
Deschampsia cespitosa	++	S									F◆	◇			
Equisetum arvense	++	S		◇		◇					F◆				
Anthoxanthum odoratum		S									F				

Table 5. Types of wildflower strips discerned in the Klettgau (1996 data) are characterized by the relative frequency of occurrence of differentiating environmental and management factors within each type. Sites are grouped according to the similarity of the vegetation also showing in the CAs of the total data set and the data subsets ' 2^{nd} year' and 'Widen'. Due to their small number, strips sown with the mixtures UFA94 and Rams.r were left in the same type (4) in spite of differentiating species. Where the sum of factorial groups is < 1 the factors were unknown for certain sites, where the sum is > 1 several seed mixtures were applied or various landuses abut; * renewal within the last year, () renewal 2 years ago.

Type description			1st yr		2nd yr	3rd yr			3rd yr						
			Additions	Various	UFA94	UFA94/ Rams.r	Rams.r	Rams.o		Kanton93		Various	Spont.+Kant.93		Various
			Widen Reserves	Various	Widen		Plomb.	Various	Widen	F. Fen	Langfeld		Widen		Disturb. Renewed
Environmental factors:		Group No.	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
		No of sites (strips)	9 (7)	24 (17)	7 (5)	12 (6)	8 (4)	9 (4)	14 (8)	9 (3)	13 (8)	12 (7)	8 (5)	11 (7)	7 (3)
Management	Age at establishment	1st year	1	0.79											
		2nd year			1	0.17		0.11	0.07					0.18	
		3rd year		0.04		0.83	1	0.89	0.43	0.89	0.15	0.64		0.45	
		4th year		0.17					0.50	0.11	0.85	0.36	1	0.36	1
	Management impact	Renewal*		0.21					(0.07)						0.43
		Disturbance								0.13			0.25	0.91	0.57
	Season at establishment	Fall	0.89	0.42	1	0.42	1	1	0.93	0.89	0.46	0.18	0.38	0.91	
		Spring	0.11	0.58		0.58			0.07	0.11	0.38	0.55	0.63	0.09	1
	Seed mixture	Spontaneous		0.08								0.27	0.75	0.27	0.71
		Kanton93				0.08				1	1	0.36	0.25	0.18	0.29
		Rams.r		0.04		0.33	1					0.27			
		Rams.o		0.17				1	1					0.36	
		UFA94		0.13	1	0.58						0.09		0.18	
		UFA95/96		0.46					0.07						0.29
		Klettgau		0.29					0.07						
		AckFl94		0.08											
		Additions	1	0.67	0.43	0.33		0.11					0.13	0.09	0.14
Site characteristics	District	Widen (W)	1	0.46	1	0.92			1			1		0.91	1
		Former Fen (M)		0.04		0.08		0.11		0.89					
		Langfeld (L)		0.38				0.22			0.77	0.82			
		Plomberg (P)					1	0.22							
		Outside (O)		0.13				0.44		0.11	0.23	0.18		0.09	
	Stone cover	Stones 0-15%	0.22	0.54	0.29	0.08	1	0.89	0.21	0.11	1	1	0.25	0.09	0.29
		Stones 16-30%	0.11	0.17	0.43	0.42		0.11	0.43	0.89			0.38	0.18	0.71
		Stones 31-45%	0.44	0.21	0.29	0.33			0.07					0.45	
		Stones >45%	0.22	0.08		0.17			0.29				0.38	0.27	
Adjacent landuse	(+Cereals and Roads almost everywhere)	Other crops	0.67	0.67	0.86	0.67	1	0.78	0.43	0.89	0.62	0.55	0.25	0.55	
		Grassland	0.67	0.33	0.57	0.67	0.75	0.22	0.36		0.31	0.82	1	0.18	1
		Woods	0.11	0.17	0.14	0.08		0.56	0.07	1	0.15	0.09		0.55	
		Other	0.11	0.46	0.14	0.08		0.78	0.14	0.89	0.46	0.36		0.64	

Interactions between environmental factors

In the CA diagram, the centroids of environmental factors indicate the influence that the various factors have on the vegetation. Even factors which are not closely correlated in the total data set (Table 3) may occur close together if they have a similar influence on the vegetation. For example, in Fig. 7 the centroid for 1st year strips lies in the upper left hand corner of the ordination diagram. The centroids for Widen and high stone cover also lie to the left of the diagram, indicating that these factors are associated with strips in a typically young condition. In Widen, with its less fertile soils – especially on sites with a high stone cover – vegetation typical of young strips persists for the longest period. The opposite is the case in the districts Langfeld and Former Fen, with its fertile soil and low stone cover, where a vegetation composition more typical of old strips develops comparatively quickly. This indicates that the speed of succession can vary considerably according to site conditions.

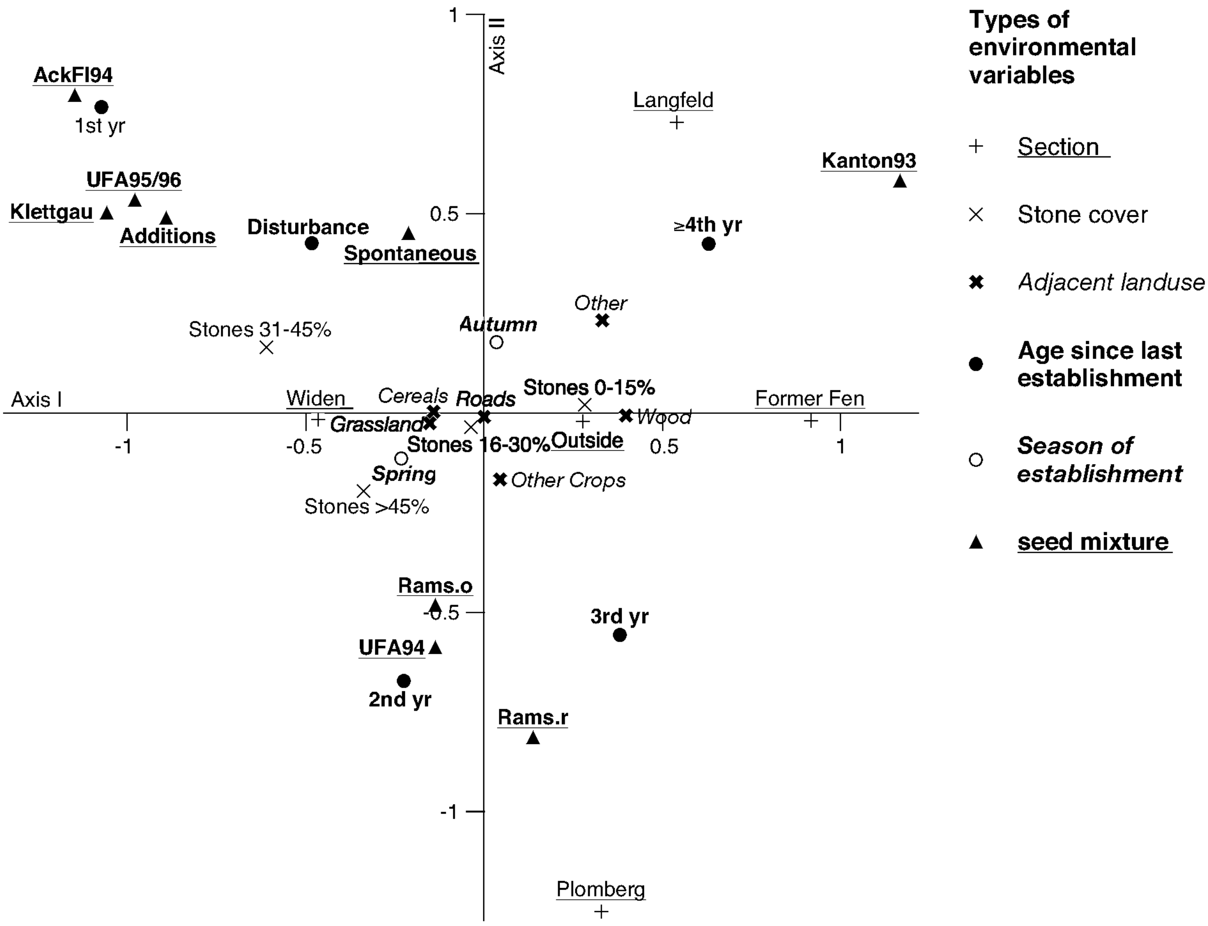


Fig. 7. Ordination diagram of a CA of the 1996 total data set showing the centroids of environmental variables influencing the species composition of wildflower strips. Factors located close to each other or located in roughly the same direction from the origin are either correlated (compare with Table 3) or have a similar influence on the vegetation (indirect gradient analysis; eigenvalues: 1st axis = 0.497, 2nd axis = 0.373, total inertia = 5.582); axes as in Fig. 8.

Reaction of vegetation characteristics and of species with certain traits to site and management factors

Many vegetation characteristics of wildflower strips, including the frequency of occurrence of species with certain traits, are influenced by site and management factors. Since these environmental factors are not independent (Table 5), and reactions to different factors interfere with each other, no absolute correlations can be obtained. However, by means of indirect gradient analysis (CA), relationships can be visualised by relating the location of the centroids of the environmental factors (Fig. 7) to the direction and length of the vectors of the various vegetation characteristics and species traits (Fig. 8).

Total species number reacts only weakly to any of the environmental factors, though it tends to be lowest in the oldest sites. It is also generally lower in the district Langfeld, which has the heaviest, most fertile soil, and highest in sites with a high stone content (Fig. 8a). The total number of species includes both sown and spontaneous species, of which the numbers behave almost inversely. While the number of sown species in the vegetation is highest in 2nd and 3rd year sites, the number of species recruited spontaneously is highest in 1st year sites, on sites with high stone content, and where no seed mixtures have been sown. Vegetation cover is independent of species number, total cover being highest in 3rd year sites. The cover of spontaneous species is highest in 1st year sites, sites > 3 years old, and sites established in autumn. The cover of grass, root weeds, moss and litter are all highest in the oldest sites, of which many were sown with the mixture 'Kanton93', and in the district Langfeld which has almost no stone cover. The chances that problem weeds reach a high cover are similar almost anywhere, the risks being slightly greater in strips left to recruit spontaneously, and lower in well developed 2nd or 3rd year stands of sown species. Red list species, on the other hand, are most numerous in 1st and 2nd year strips, and in sites where stone cover is high. Red list species which appear spontaneously are mainly found in 1st year strips (though some may have been sown as 'Additions'), while sown ones are slightly more frequent in the 2nd year.

The frequency of occurrence of most species traits follows typical successional patterns, although these are influenced by site conditions (Fig. 9). These trends are also evident for the ordination diagrams in Figure 8b–f. For example, most crop species and typical arable weeds are spontaneous annuals (therophyte or mixed thero-/ hemicryptophyte strategy; Fig. 8a–c). These are most common in the 1st year and in the least fertile sites with a high stone cover, although thero-/hemicryptophytes can still be numerous in the 2nd year. Sown ruderal and meadow species are most abundant in the 2nd and 3rd years; these species include the majority of monocarpic perennials but also many polycarpic perennials (mainly thero-/

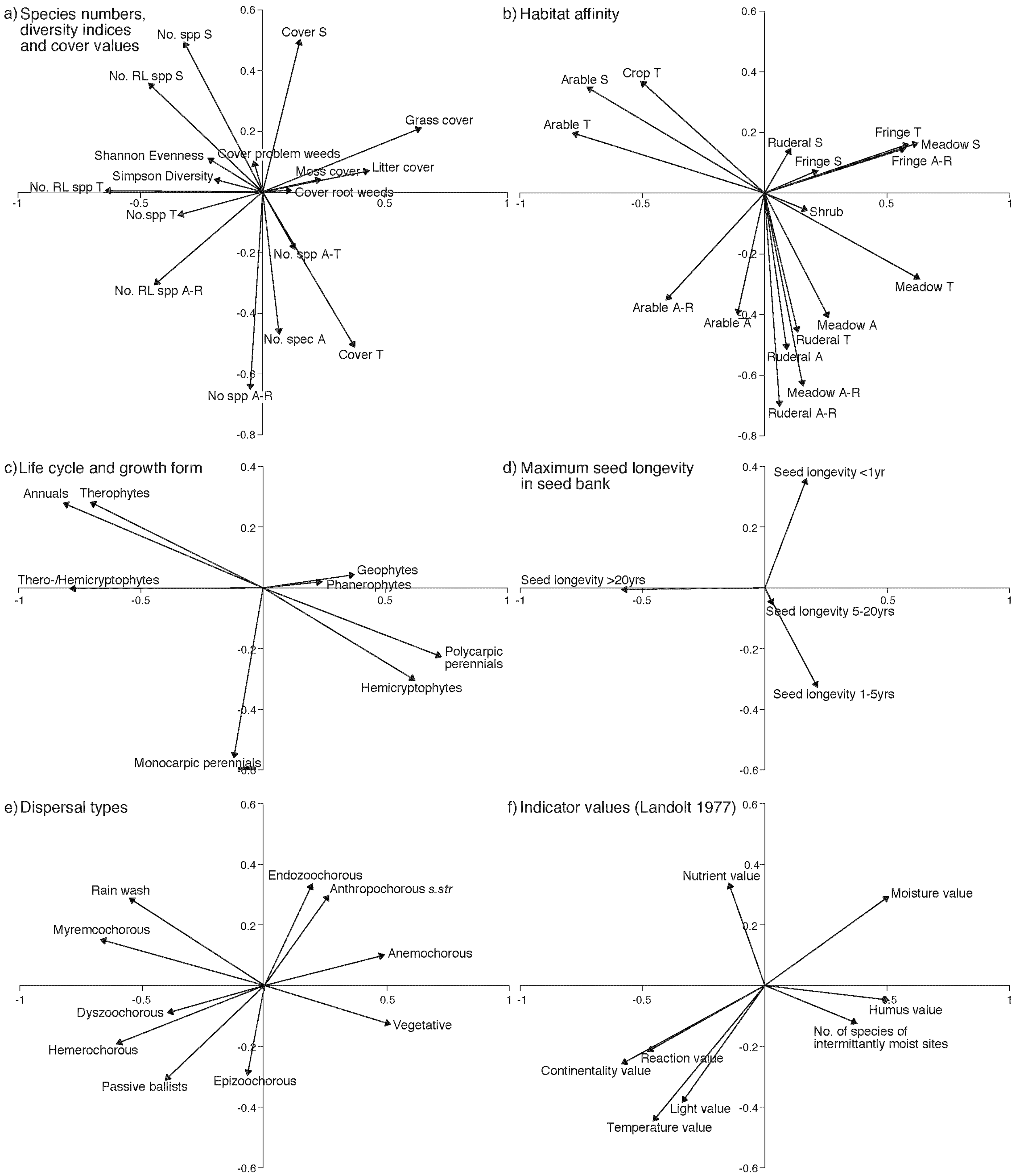


Fig. 8. Ordination diagrams showing general vegetation characteristics and frequencies of certain species traits as vectors derived from a CA of the 1996 total data set (indirect gradient analysis; eigenvalues: axis I = 0.50, axis II = 0.37, total inertia = 5.58). Frequencies or values of the traits increase in the vegetation of wildflower strips in the direction of the vector. The relative lengths of the vectors indicate the strength of the reaction. Traits of which the vectors point in the same direction as the location of the centroids of environmental factors in Fig. 7 show a positive response to these factors. Traits of which the vectors point in the same direction show a similar reaction to environmental factors and in combination characterize the vegetation in different types of wildflower strips; axes as in Fig.7 but shortened; T = all species, S = spontaneous species, A = added species, A-R = added species retrieved, A-N = added species not found, RL = Red List species.

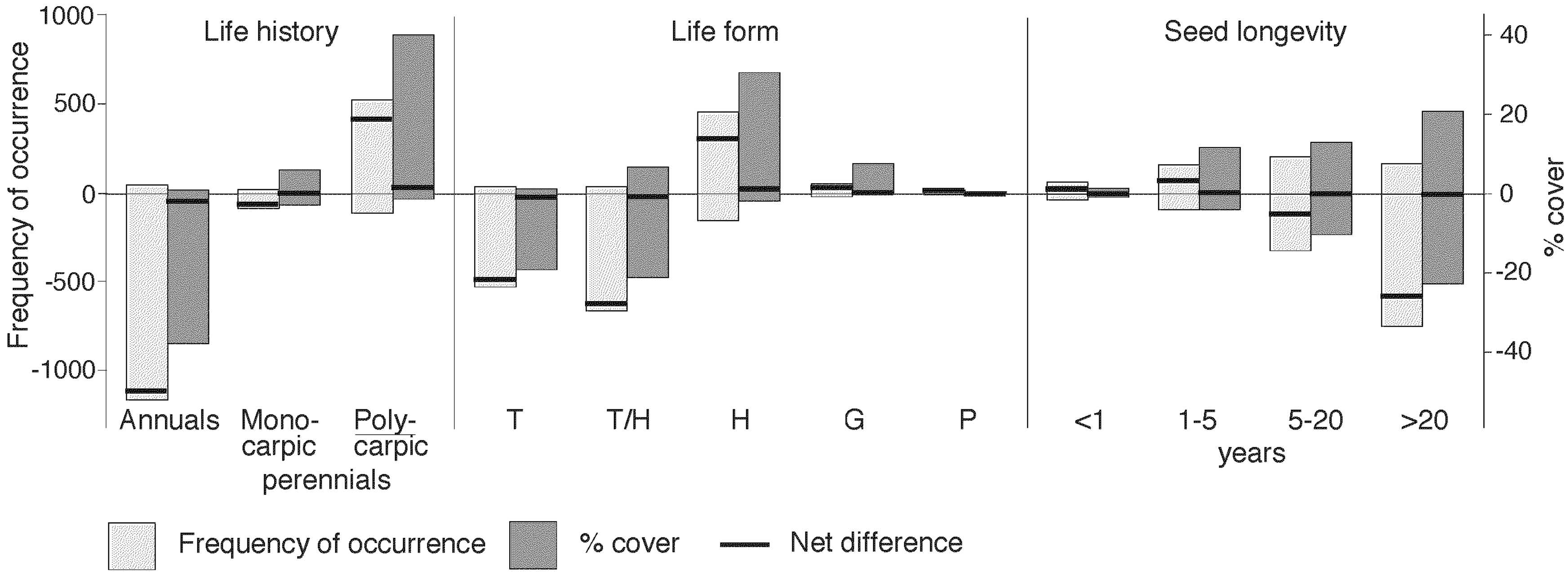


Fig. 9. Differences in frequency of occurrence and % cover of groups of species with different life histories, life forms and seed longevities in wildflower strips in their 1st year and in their 3rd year (values from 3rd year - values from 1st year); T = Therophytes, T/H = Thero-/Hemicryptophytes, H = Hemicryptophytes, G = Geophytes, P = Phanerophytes.

Table 6. Success of various seed mixtures applied in the Klettgau in creating vegetation of high sown versus spontaneous plant species diversity in relation to vegetation cover; sites with several mixtures are excluded; n = number of strips, Age = age of strips, **main age**; 'Additions': seed composition is unknown and thus not included in sown species; '+ Additions' applied only in part of the strips; (mixtures) applied rarely, i.e. numbers are not representative; Tukey-Kramer HSD-Test ($P<0.05$), a-c indicate significant differences Δ between mixtures.

			Average numbers of species									Average % cover of species					
	n	Age	Sown	Sown + retrieved				Spontaneous		Total		Sown		Spontaneous		Total	
			No.	No.	Δ	%	Δ	No.	Δ	No.	Δ	%	Δ	%	Δ	%	Δ
Spontaneous	15	3-≥4	0	0		–		23.9	a	23.9	ab	0		66.7	a	66.7	a
Kanton93	31	3-≥4	19	5.1	a	27%	a	16.3	b	21.4	a	20.6	a	55.1	ab	75.8	ab
Rams.o + Additions	27	3-≥4	31	10.8	b	35%	a	16.5	b	27.3	b	40.5	b	41.2	b	81.7	b
Rams.r + Additions	18	3 ≥4	26	10.6	b	41%	a	13.5	b	24.0	a	44.2	b	30.6	b	74.8	ab
UFA94 + Additions	28	1-3	23	9.6	b	42%	a	14.1	b	23.7	ab	32.0	ab	45.3	b	77.3	b
UFA95/96 + Additions	7	1	19	6.4	ab	34%	a	21.3	a	27.7	b	19.5	ab	39.5	b	59.0	ac
(Klettgau + Additions)	*4*	*1*	*13*	*8.3*		*63%*		*14.8*		*23.0*		*44.1*		*34.5*		*78.6*	
(Ackfl94 + Additions)	*2*	*1*	*22*	*3.5*		*16%*		*24.5*		*28.0*		*13.8*		*58.0*		*71.8*	
Additions	12	1-≥4	?	?		?		?		21.2	ab	?		?		53.5	c

hemicryptophytes and hemicryptophytes). From the 3rd year onwards, spontaneous ruderal and meadow species as well as sown and spontaneous fringe species gradually take over. These are mostly polycarpic perennials and hemicryptophytes, but with some geophytes and phanerophytes, especially in the more fertile sites and those with adjacent woodland or 'other' landuse.

Success of seed mixtures in creating diverse vegetation

The number of species included in the seed mixtures varied between 13 and 31. However, in most cases a few additional species were sown at the same time ('Additions'), and the precise number of species introduced at a particular site cannot always be determined. The mean number of sown species which were recorded in the vegetation varied from 27 – 42% according to the mixture (Table 6). Although most seed mixtures were used for only one or two years, and accordingly the average age of strips varies with the seed mixtures, no trends related to age of the strip are evident in the sown species recorded. The average number of species recruited spontaneously ranges from 13 – 24, and tends to be negatively related to the cover of sown species (Table 7). As a result, the total number of species per site is relatively constant, ranging from 21 to 28 species (mean values per seed mixture).

The average cover of sown species mirrors roughly the number of species sown and also the number recorded in the field survey. The cover of species recruited spontaneously is positively correlated with the number of spontaneous species (Table 7). In 1st year strips, total cover tends to be low and variable, but after the first year it lies in the relatively narrow range of 67-82%, being lowest in the oldest spontaneous strips (Table 6). It is also positively correlated to the number of sown species.

Table 7. Correlations between numbers and cover of sown and spontaneous species; * = 'Cover sown species' transformed $x^{0.61}$ for normal distribution of residuals.

	All sites sown with regular mixtures				All sites	
	No. sown species		Cover sown species		No. spont. species	
	r	P	r	P	r	P
No. sown + retrieved species	0.372	<0.0001	0.793*	<0.0001		
No. spontaneous species		n.s.	-0.235	0.0107		
No. total species	0.189	0.041	0.271	0.0031		
Cover sown species	0.268*	0.0035				
Cover spontaneous species	-0.182	0.0493	-0.895	<0.0001	0.267	0.0012
Cover total species	0.246	0.0075	0.489	<0.0001		

Discussion

Successional changes in wildflower strips

The data presented here for a large number of wildflower strips in the Klettgau region show that their vegetation develops and differentiates following general rules, and that both site and management factors are important. These conclusions largely confirm findings from experimental studies (Günter M. 2000a; Günter M. 2000b; Heitzmann A. 1995; Pfiffner L. & Schaffner D. 2000; Schaffner D. et al. 2000). The dominating process leading to a strong differentiation in the vegetation of wildflower strips is succession. This begins with annual dominated plant communities, which are taken over initially by sown perennials and finally by spontaneous perennials. Species numbers are highest during the transition from annual to sown perennial dominance, and then decrease with age. In contrast, vegetation cover mostly reaches its peak in the third year and then decreases as litter accumulation leads to the formation of gaps. As in many secondary successions, changes in wildflower strips are at first very rapid but become slower after the second year. The speed of succession depends strongly on soil conditions, advancing much faster on fertile soil than on less fertile soil with a high stone content. In addition the direction that succession takes is influenced by soil conditions as well as by the seed mixture applied.

While most seed mixtures contain only a few and mostly similar annual species, from the 2nd year on the composition of perennial species has a strong impact on the resulting species composition. Most sown species are found only at sites where they are sown, and there is little evidence that they disperse more widely (Günter M. 2000a; Kleijn D. et al. 1997; Schaffner D. et al. 2000). Although the proportions of sown species which establish are generally similar for all mixtures, some species are more successful at establishing than others. Accordingly, the composition of established species is different for each seed mixture. Since the cover of sown vegetation is directly related to the number of sown species which establish, the seed mixture applied also influences the composition of species recruited spontaneously. The number of species contained in a seed mixture thus influences the abundance of spontaneous species.

Species composition is also strongly influenced by site factors. The set of spontaneous species varies between districts according to soil conditions, with perennial species profiting from a high fertility, while many annual species are mainly restricted to the less fertile, stony soils. Soil fertility and species presence or performance also lead to differences in vegetation structure, cover being highest on fertile soils. Lower fertility and vegetation cover allow more annual species to persist in wildflower strips beyond the 1st year, while the stronger competition between perennials at fertile sites can soon lead to the dominance of only a few species. Since many spontaneous perennials, especially some grasses and root weeds are more competitive on fertile soil, these often replace sown ones quickly under such conditions.

Which species eventually become dominant may depend on what species are present in the neighbourhood or were formerly abundant on the site. For this reason, adjacent landuse has an influence on the species composition, with adjacent grassland often serving as a source of invading grasses. In a separate analysis of the data subset 'Widen', grass cover is associated with the presence of adjacent grassland. Neighbouring woody vegetation, i.e. woodland, hedgerows or shrubs, was the source of some of the few spontaneous fringe and woody species which were recorded.

In contrast to findings in the literature, our data do not show any tendency for higher establishment of sown species in spring and of spontaneous species in autumn (Schaffner D. et al. 2000). If anything, the reverse is true, though this may simply reflect the irregular sequence of spring and autumn sowing over the years. According to Pfiffner & Schaffner (2000) and West & Marshall (1995), sowing in the autumn enhances grass cover, perhaps because grasses can grow more strongly than forbs during the winter months, thus giving them a 'head start'.

In most cases a renewal or disturbance of a site brought back spontaneous annual species, but few sown annuals or perennials. Many of the spontaneous perennials, especially problem weeds, recovered quickly from the treatment. This means that once grasses or other perennial problem weeds have firmly established themselves in wildflower strips, management measurements often remain without lasting success. In contrast, annual problem weeds decline during succession, though they may hinder an optimal development of the vegetation since early successional stages are decisive for further development (Günter M. 2000a; Schaffner D. et al. 2000). Therefore, sites where annual or perennial problem weeds are known to occur should be avoided for the establishment of wildflower strips.

Environmental factors, vegetation characteristics and species traits

We can never specify precisely what kind of vegetation will develop, since local conditions will determine which of the species sown are likely to perform best; in addition the pool of species which may establish spontaneously varies widely. The succession can be characterised in terms of the changing importance of plants with different life histories, life forms and ecological affinities. The early stages are dominated by fast-growing annual therophytes or thero-hemicryptophytes, i.e. typical arable weeds, which produce only a sparse vegetation cover (Fig. 8b). However, even at an early stage, light tolerant perennial thero-hemicryptophytes and hemicryptophytes are present; these are species typical of ruderal sites which develop more slowly and dominate in the 2nd year, forming a more dense vegetation cover. In these shadier conditions, only more shade tolerant species, mostly polycarpic perennial hemicryptophyte meadow species, can still establish. Monocarpic perennials (species reproducing only once) thus have their peak in the 2nd year and decline subsequently, while some polycarpic perennials (species reproducing several times), ruderal and meadow species, still thrive in the 3rd year and sometimes even longer, depending on site conditions. Once litter starts to accumulate, causing gaps in the vegetation cover, certain grasses and root weeds with a strong lateral spread (i.e. geophytes) tend to gain ground where they are present. Succession in wildflower strips thus shows an 'overlapping species replacement pattern' of the kind expected by the 'initial floristic composition model' (Egler F.E. 1954) and the 'tolerance model' (Connell J.H. & Slatyer R.O. 1977). These models indicate that the entire initial species set by chance present in a site can coexist at the beginning of succession but the species composition is differentiated according to the specific speed of development and longevity of species, which gradually leads to the loss of less competitive species (Barbour M.G. et al. 1987).

The successional sequence of species with seeds with different germination characteristics reflects the varying stability of the plant communities. Many of the plants of 1st year strips show a typical pioneer strategy ('R-strategy'), frequent in unstable communities, where the mostly annual or monocarpic perennial species produce large numbers of long lived seeds which persist in the soil until conditions for germination become favourable (Grime J.P. 1979; Grime J.P. et al. 1988; Hodgson J.G. & Grime J.P. 1990). The association of species with short lived seeds with older, more dense vegetation stages is probably because competition and shade tolerance play a greater role, leading to selection for large seeds which are mostly rather short lived ('C-strategy') (Thompson K. et al. 1998). In addition, the greater stability of the vegetation favours early germination.

Plant dispersal strategies can also be related to environmental factors and vegetation characteristics. Species dispersed externally by animals (ectozoochorous, e.g. *Echium vulgare*) and also species with no obvious long-distance dispersal mechanisms (passive ballists, e.g. *Silene alba*), except with crop seed (hemerochorous, e.g. *Agrostemma githago*), are overrepresented amongst the sown species. Successional changes in the frequency of different dispersal strategies are largely reflected in the spontaneous species set. Short-distance dispersal by rain wash (e.g. *Polygonum aviculare*), ants (myrmecochorie, e.g. *Viola arvensis*), or passive seed scattering (passive ballists, e.g. *Chenopodium album*) is most common among the abundant arable weeds of 1st year sites. Since agricultural impacts like ploughing probably are the main means of dispersal for these species, other dispersal types become secondary, especially in combination with the long viability of the seeds that can be regarded as dispersal in time (Hodgson J.G. & Grime J.P. 1990). The ruderal and meadow species with short-lived seeds – characteristic of the more dense and stable vegetation of the older strips – possess other more effective independent means of dispersal. They follow different strategies including short distance, vegetative dispersal by lateral spread (e.g. *Lolium perenne*), and long distance dispersal by wind (e.g. *Epilobium adnatum*). Dispersal by agricultural processes in general (anthropochorie *sensu sticto*, e.g. *Lamium purpureum*) is important, not only for arable weeds, but for a large number of species occurring in agricultural landscapes (Marshall E.J.P. & Hopkins A. 1990). In sum, to establish in wildflower strips spontaneous species either need to have persistent seeds or effective means of dispersal. The soil seed bank plays a role almost exclusively in the 1^{st} year. From the 2^{nd} year on, when the soil has not been freshly disturbed and gaps start to close, only a few shade tolerant species manage to establish and so vegetative dispersal becomes more important. This is especially true where sown species from the mixtures did not establish well, or problem weeds capable of vegetative dispersal are present, since these quickly close any gaps.

Indicator values are generally only used to describe site conditions in old established communities. In the early secondary successional stages covered by wildflower strips they mainly describe but also help to explain the vegetation development. The correlation of a high average nutrient value with the number of species recruited spontaneously means that the nutrient supply is high everywhere. Species with a lower nutrient value are mostly sown and in the long run outcompeted by the species profiting more from a high nutrient supply.

Implications for the management of wildflower strips

To a certain degree it is possible to predict and steer the development of the vegetation in wildflower strips. However, to do this requires a good knowledge of soil and other site conditions. It also requires an understanding of the ecological properties of the species used in the seed mixtures, and of the species in the spontaneous potential species pool; this includes species formerly present at the site which may still be in the seed bank, and species still present in the surroundings. The most important uncontrollable factors are the climatic conditions during the first vegetation period, and especially in the first few weeks after sowing. Water and temperature conditions play a crucial role in determining the relative success of sown and spontaneous species. For example, by choosing the time of year for the establishment of wildflower strips, certain groups of species can in general be deliberately favoured over others. However, differences in climatic conditions after sowing can interfere with the effects of spring and autumn sowing. This is probably responsible for contrary seasonal results in the establishment success of sown versus spontaneous species found by Ramseier (1994) and Heitzmann (1995).

There are also opportunities to influence the development of a wildflower strip after it has been sown. If spontaneous annual weeds interfere with the establishment of sown species, an early cut is recommended (preferably during weeks 6 to 8) to suppress the weeds and promote growth of the sown species (Günter M. 2000a; Schaffner D. et al. 2000). If perennial problem weeds like *Cirsium arvense* occur, these should be weeded, cut or sprayed individually at an early stage (Häni F. & Zürcher J. 2000; Schaffner D. et al. 2000). Perennial grasses can be a difficult problem; when they become abundant control by cutting or tine cultivation is unlikely to be effective, while rotavation in autumn may have some success (Pfiffner L. & Schaffner D. 2000). The occasional cutting of wildflower strips in autumn after the second year is sometimes recommended; however, it is unclear whether it helps to reduce vegetation cover and thus increase floristic diversity (Pfiffner L. & Schaffner D. 2000).

Conclusions

The dominating process determining the species composition in wildflower strips is succession. However, the speed and direction that succession takes is strongly influenced by site conditions and the potential species pool. Management has the strongest impact at the stage of establishment of a wildflower strip. The development of general vegetation characteristics can be predicted based on the knowledge of site and mangement factors. It is more difficult to predict the performance of individual species, but a knowledge of relevant species traits such as life form and reproductive strategy give some indication of how species may perform.

In practice, no-one can expect a farmer or site manager to have a detailed knowledge of all the complex interactions between the potential species pool and site and management factors. Straightforward guidelines are therefore needed which allow a farmer to establish and maintain wildflower strips which meet the objective of increasing floristic diversity. Based on results from experimental studies, Günter (2000a) and the Swiss Center for Agricultural Extension (LBL 1996) composed guidelines for the establishment and maintenance of wildflower strips. The conclusions presented here are largely consistent with these guidelines.

References

Barbour, M.G., Burk, J.H. & Pitts, W.D. 1987. Terrestrial Plant Ecology. 2nd ed. The Benjamin/Cummings Publishing Company Inc., Menlo Park, California.

Borcard, D., Legendre, P. & Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology 73: 1045-1055.

Bürki, H.-M. 1993. Überwinterung von Arthropoden im Boden unter künstlich angelegten Ackerkrautstreifen. Verhandlungen der Gesellschaft für Ökologie, Zürich 22: 35-38.

Connell, J.H. & Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111: 1119-1144.

Egler, F.E. 1954. Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4: 412-417.

Grime, J.P. 1979. Plant strategies and vegetation processes. Wiley, Chichester.

Grime, J.P., Hodgson, J.G. & Hunt, R. 1988. Comparative plant ecology. Allen & Unwin, London.

Günter, M. 2000a. Anlage und Pflege von mehrjährigen Buntbrachen unter den Rahmenbedingen des Schweizerischen Ackerbaugebietes. Agrarökologie 37.

Günter, M. 2000b. Sukzession von Buntbrachen. In: Nentwig, W. (ed.) Streifenförmige ökologische Ausgleichsflächen in der Kulturlandschaft: Ackerkrautstreifen, Buntbrache, Feldränder, pp. 55-76. Verlag Agrarökologie, Bern.

Häni, F. & Zürcher, J. 2000. Vermehrung, Ausbreitung und Regulierung der Ackerkratzdistel Cirsium arvense – Ökoflächen im Fokus. In: Nentwig, W. (ed.) Streifenförmige ökologische Ausgleichsflächen in der Kulturlandschaft: Ackerkrautstreifen, Buntbrache, Feldränder, pp. 93-112. Verlag Agrarökologie, Bern.

Heitzmann, A. 1995. Angesäte Ackerkrautstreifen - Veränderungen des Pflanzenbestandes während der natürlichen Sukzession. Agrarökologie 13.

Hodgson, J.G. & Grime, J.P. 1990. The role of dispersal mechanisms, regenerative strategies and the seed banks in the vegetation dynamics of the British landscape. In: Bunce, R.G.H. & Howard, D.C. (eds.) Species dispersal in agricultural habitats, pp. 65-81. Belhaven Press, London.

Hodgson, J.G., Grime, J.P., Hunt, R. & Thompson, K. 1995. The electronic comparative plant ecology. Chapman & Hall, London.

Jenny, M. & Weibel, U. 1999. Qualität und Quantität des ökologischen Ausgleichs in drei intensiv genutzten Ackerbauflächen des Klettgaus. Mitteilungen der Naturforschenden Gesellschaft Schaffhausen 44: 107-116.

Jenny, M., Weibel, U. & Buner, F. 1999. Der ökologische Ausgleich in intensiv genutzten Ackerbaugebieten des Klettgaus und seine Auswirkungen auf die Brutvogelfauna. Mitteilungen der Naturforschenden Gesellschaft Schaffhausen 44: 203-221.

Kleijn, D., Joenje, W. & Kropff, M.J. 1997. Patterns in species composition of arable field boundary vegetation. Acta Botanica Neerlandica 46: 175-192.

Landolt, E. 1977. Ökologische Zeigerwerte zur Schweizer Flora. Veröffentlichungen des Geobotanischen Instituts der ETH Zürich, Stiftung Rübel 64.

Landolt, E. 1991. Gefährdung der Farn- und Blütenpflanzen in der Schweiz, mit gesamtschweizerischen und regionalen roten Listen. Bundesamt für Umwelt, Wald und Landschaft, Bern.

LBL. 1996. Mit Buntbrachen die Artenvielfalt fördern – Merkblatt. Landwirtschaftliche Beratungszentrale, Lindau.

Lindacher, R. 1995. Phanart – Datenbank der Gefässpflanzen Mitteleuropas. Veröffentlichungen des Geobotanischen Instituts der ETH Zürich, Stiftung Rübel 125.

Marshall, E.J.P. & Hopkins, A. 1990. Plant species composition and dispersal in agricultural land. In: Bunce, R.G.H. & Howard, D.C. (eds.) Species dispersal in agricultural habitats, pp. 98-116. Belhaven Press, London.

Müller-Schneider, P. 1986. Verbreitungsbiologie (Diasporologie) der Blütenpflanzen. Veröffentlichungen des Geobotanischen Instituts der ETH Zürich, Stiftung Rübel 61.

Økland, R.H. & Eilertsen, O. 1994. Canonical correspondence analysis with variation partitioning: some comments and an application. Journal of Vegetation Science 5: 117–126.

Pfiffner, L. & Schaffner, D. 2000. Anlage und Pflege von Ackerkrautstreifen. In: Nentwig, W. (ed.) Streifenförmige ökologische Ausgleichsflächen in der Kulturlandschaft: Ackerkrautstreifen, Buntbrache, Feldränder, pp. 41-54. Verlag Agrarökologie, Bern.

Ramseier, D. 1994. Entwicklung und Beurteilung von Ansaatmischungen für Wanderbrachen. Veröffentlichungen des Geobotanischen Instituts der ETH, Stiftung Rübel 118.

Raunkiaer, C. 1934. The life forms of plants and statistical plant geography. Clarendon Press, Oxford.

Salveter, R. & Nentwig, W. 1993. Schwebfliegen (Diptera, Syrphidae) in der Agrarlandschaft: Phänologie, Abundanz und Markierungsversuche. Mitteilungen der Naturforschenden Gesellschaft Bern 50: 1-45.

Schaffner, D., Günter, M., Häni, F. & Keller, M. 2000. Ökologische Ausgleichsfächen in der Landwirtschaft: Ergebnisse mehrjähriger Versuche zur Anlage und Pflege blütenreicher Buntbrachen. Schriftenreihe der FAL 34.

Schaffner, D. & Keller, S. 1998. Praxiserfahrungen mit Buntbrachen und Ackerrandstreifen in der Schweiz. Schriftenreihe der Landesanstalt für Pflanzenbau und Pflanzenschutz 6: 45-54.

Schmid, A. 1992. Untersuchungen zur Attraktivität von Ackerwildkräutern für aphidophage Marienkäfer (Coleoptera, Coccinellidae). Agrarökologie 5.

Schneider, H. & Paulsen, J. 1994. Schweizer Flora Arten – Datenbank. Botanisches Institut der Universität Basel.

ter Braak, C.J.F. & Smilauer, P. 1998. Canoco reference manual and user´s guide to Canoco for Windows. Centre for Biometry, Wageningen.

Thompson, K., Bakker, J. & Bekker, R. 1997. The Soil Seed Banks of North West Europe. Cambridge University Press, Cambridge.

Thompson, K., Bakker, J.P., Bekker, R.M. & Hodgson, J.G. 1998. Ecological correlates of seed persistence in soil in the north-west European flora. Journal of Ecology 86: 163-169.

van der Pijl, L. 1982. Principles of dispersal in higher plants. 3rd ed. Springer-Verlag, Berlin, Heidelberg, New York.

Weiss, E. & Stettmer, C. 1991. Unkräuter in der Agrarlandschaft locken blütenbesuchende Nutzinsekten an. Agrarökologie 1.

West, T.M. & Marshall, E.J.P. 1995. Managing sown field margin strips on contrasted soil types in three environmentally sensitive areas. Aspects of Applied Biology 44: 269-276.

Whittaker, J. 1984. Model interpretation from additive elements of the likelihood function. Applied Statistics 33: 52-65.

App. 1. Species composition of seed mixtures; () = falcultative species, * = amount unknown

Species; seeds [g/100m²]	**Kanton93**	**Rams.o**	**Rams.r**	**UFA 94**	**UFA 95/96**	**Klettgau**	**Ackerfl94**
Achillea millefolium	3.5	0.8	0.3	*	3	5	
Agrimonia eupatoria		23.9					
Agrostemma githago		13	2.3	*	14	18	*
Anthemis tinctoria			0.3	*		1.5	
Arctium lappa od. minus		6.1	0.3	*			
Bromus arvensis						(3.5)	
Buglossoides arvensis						(3.5)	
Carum carvi			1.3	*	8		
Centaurea cyanus	4	4.3	3.7	*	8	13.5	*
Centaurea jacea		5.3	1.7	*	2		
Cichorium intybus	3	2.1	1.7	*	3	3	
Daucus carota	3.5	2.2	3	*	5	5	
Consolida regalis		3.5				(3.5)	
Dianthus armeria						(2.5)	
Dipsacus fullonum		0.3	0.1	*	0.25		
Echium vulgare	*	1.5	1.7		3	5	
Fagopyrum vulgare		26.7			22.5		
Galium verum	2.5						
Hypericum perforatum	2	0.6	1		2		
Knautia arvensis		6	1.7	*			
Legousia speculum-veneris		4.2	0.3	*			*
Leucanthemum vulgare	2.5	0.9	0.7	*	4		
Linaria vulgaris	2	1.1					
Lotus corniculatus	0.5						
Malva sylvestris / moschata	-/2.5	1.2	0.7/-	*	1		
Chamomilla recutita	1		0.3				
Melilotus alba		1	0.2				
Oenothera biennis			0.2	*			
Onobrychis viciifolia	1	18.9	3.3	*			
Origanum vulgare	1.5		0.3	*			
Papaver dubium		1.4					*
Papaver rhoeas	1	6.6	1.7	*	6	10	*
Pastinaca sativa		3.5	1.3		9	14	
Ranunculus arvensis		15.5				(5)	
Reseda lutea				*			
Salvia pratensis	6.5			*			
Scabiosa columbaria		4.1					
Silene alba	3	2.1	1.3	*	2	3.5	
Silene noctiflora		6.1					*
Silene vulgaris	2						
Tanacetum vulgare		0.34	0.2	*	0.5		
Tragopogon orientalis		7.4			4.75		
Vaccaria hispanica		4.5					*
Verbascum lychnitis /densifl. / thapsus /nigrum	-/-/2/2	0.4/-/-/-	0.2/0.8/-/-	-/*/-/-	2	3.5	
No of species	**19**	**31**	**26**	**23**	**19**	**16**	**22**

Additional species in Ackerflora94: *Bupleurum rotundifolium*, *Crepis foetida*, *Crupina vulgaris*, *Galeopsis ladanum*, *Iberis pinnata*, *Melampyrum arvense*, *Misopates orontium*, *Nigella arvensis*, *Orlaya grandiflora*, *Papaver argemone*, *Papaver lecoquii*, *Picris echioides*, *Stachys annua*, *Trifolium arvense*, *Xeranthemum annuum* .

'Additions': consist of various species combinations mostly containing rare arable weeds that were found in the reasearch area or close by and propagated in situ.

Chapter 3. Diversity and ecology of insects (Heteroptera) in wildflower strips of different age

Karin S. Ullrich and Peter J. Edwards

Abstract

One attempt to reintroduce biodiversity into intensively used arable landscapes applied in Switzerland is the establishment of sown wildflower strips. These can develop a high diversity of plant species and vegetation types. In this paper we investigate, whether a high insect diversity can also establish, and the factors which influence the diversity of insect species. True bugs (Heteroptera) were chosen as an indicator group as these are an ecologically diverse group, and bug diversity has been found to correlate well with total insect diversity in agricultural landscapes. We analyse colonization and establishment patterns in terms of responses of species traits to the successional change and environmental factors. For a large number of species colonization appears to be no problem. Species richness and total abundance of bugs are, on average, lower in wildflower strips in their first year than in older strips, and are positively correlated to the number of perennial plant species. Bug species composition responds to the age and grass cover of wildflower strips. The proportions of oligo- and monophagous species, of species with only one generation per year, and of species overwintering in the egg stage all increase during succession either in terms of species numbers or of numbers of individuals. A high grass cover promotes generalist species and grass specialists, including many species which also occur on grassy verges in the surroundings. A basic set of rather common species establish in most wildflower strips. Less mobile and rare species have a local distribution and are difficult to promote. To achieve a maximum insect diversity, wildflower strips should have a high plant species and structural diversity, and be managed heterogeneously on a landscape level.

Keywords: agricultural landscape, Correspondence Analysis, insect diversity, insect strategies, life-cycle, secondary succession, Switzerland

Introduction

In response to an increasing awareness of a rapid decline of biodiversity in European agricultural landscapes, a variety of measures are now being introduced to stop or even reverse this process. One method to reintroduce biodiversity into intensively used arable landscapes, widely used in Switzerland, is the establishment of sown wildflower strips. These are strips of land which are at least 3 m wide and may either run through or along the edge of an arable field. They are usually sown with a recommended mixture of indigenous arable weeds and species of ruderal sites and meadows. They are maintained for at least two but usually for six years, and after the second year typically one half or one third of a strip is mown each year in rotation.

Wildflower strips have been found to contain a high diversity of plant species and vegetation types (Chapter 1 and 2). In this paper we investigate whether this is also the case for a group of insects, the heteropteran bugs. Plant species originate partly from seed mixtures, but larger numbers recruit spontaneously either from the soil seed bank, or invade by dispersal from surrounding vegetation. Insect species, in contrast, have to immigrate from the surroundings. The colonization of wildflower strips by insects therefore depends on the species pool present in the region, and on the ability of the various species to migrate to sites offering suitable habitat conditons. While colonization is the dominating process in the inital phase of a secondary succession, environmental constraints and internal dynamics soon gain importance and determine the species composition of both the vegetation and the insect fauna (Belyea L.R. & Lancaster J. 1999). Using a simple classification of wildflower strips based on age and grass cover, we investigate the following questions concerned with the development of the bug community in wildflower strips:

- What are the roles played by colonization and environmental constraints in the establishment of insect communities in wildflower strips?
- Are insect communities in wildflower strips restricted to generalist species or do specialist species also manage to establish, and how quickly?
- Do different types of wildflower strips have distinct insect communities and, if so, which environmental factors are responsible?
- What are the implications of these findings for an optimal management of wildflower strips?

In order to understand general processes shaping the insect community, we analyse the responses of species traits to differentiating environmental factors, assuming that environmental constraints lead to an underdispersion, i.e. more frequent than random occurrence, of species traits (Keddy P.A. 1992; Belyea L.R. &

Lancaster J. 1999). As wildflower strips represent early successional stages, we also assume that competitive interactions are relatively less important than environmental constraints. Such interactions might lead to an overdispersion, i.e. lower than random occurrence of species traits due to niche avoidance, which would have complicated the interpretation of trait frequencies (Weiher E. & Keddy P.A. 1995). Where competitive adversity is low, neutral species traits in theory should be distributed randomly (Weiher E. & Keddy P.A. 1995); however, they might be biased by phylogenetic constraints (Felsenstein J. 1985).

A similar approach has been used by Brown (1985; 1986) to study life cycle strategies of various insect groups (including Heteroptera) in a study on a long-term secondary succession from initial stages to forest in neighbouring sites. In these studies, various species traits i.e. food specificity, number of generations per year, overwintering stage and mobility, were related to the r–K continuum of various habitat templets (Southwood T.R.E. 1977; Southwood T.R.E. 1988). These studies thus provide valuable background information to compare and evaluate our results with those of long-term succession in a more diverse landscape. An important difference, however, is that the wildflower strips we study have been sown, though spontaneous successional processes are also important in their development.

As it was practically impossible to study the whole insect diversity of wildflower strips, we chose the true bugs (Heteroptera) as an indicator group. There were several reasons for this choice. Bugs are an ecologically very diverse group containing species of all trophic levels and degrees of food specialization, which vary in mobility and life cycle traits (Dolling W.R. 1991). They spend their entire life cycle in the same habitat – except the adults of some species that overwinter in special sites – and thus respond sensitively to changes in environment (Morris M.G. 1969; Morris M.G. 1979; Achtziger R. 1995; Otto A. 1996). A comparison of diversities of different insect groups has shown that, in the agricultural landscape, bug diversity correlates strongly with total insect diversity (Duelli P. & Obrist M. 1998). In the study of a long-term secondary succession already referred to, bug diversity also mirrored age-dependent changes in total exopterygote diversity exactly (Brown V.K. & Southwood T.R.E. 1983). Last, but not least, numbers of bug species occurring in the arable landscape are large enough to allow statistical analysis but manageable from a practical view-point.

Materials and methods

Research area and study sites

The study area is the Klettgau (Canton Schaffhausen), an intensively used arable region in the north of Switzerland. It forms a wide, flat valley with calcareous river gravels which are locally overlaid by loam and loess; soil conditions vary in depth and texture and are rich in bases. The area ranges in altitude between 400 and 470 m a.s.l.. In comparison to other parts of the Swiss Midlands the climate is relatively dry (915 mm precipitation per year) and warm in summer (18.4°C Temp. average in July; 8.5°C annual Temp. average; data from the Swiss Meteorological Institute 1996). Cereals are the main crop type and cover about half of the surface of the agricultural area; these are followed, in declining order of abundance, by root crops, maize, rape, and locally also by grassland.

Within the Klettgau the district 'Widen', located to the northeast of Neunkirch, offers comparatively homogenous site conditions, which induced us to concentrate all study sites within its boundaries. It covers an area of 5.3 km^2, and is made up of small fields (average 0.81 ha) interspersed by a dense network of pathways covered or bordered by grass. It is a very open landscape and, apart from a pond and stream accompanied by a little wood and hedgerows near the southern border of the district, other structural elements are mainly absent. As part of a project to improve habitat conditions for the grey partridge and the European hare a large number and variety of wildflower strips have been created in the Klettgau since 1992, of which many are located in the district 'Widen' (Jenny M. & Weibel U. 1999; Jenny M. et al. 1999). These make up most of the 3.2% of the agricultural area in the district classified by Jenny & Weibel (1999) as ecologically valuable.

For our study we chose 20 wildflower strips of 4 types (5 replicates each), differentiated by age and grass cover in early spring: 1st year strips, 2nd year strips, ≥ 3rd year not grassy strips, ≥ 3rd year grassy strips. Due to the heterogeneity of the management of wildflower strips, and even of subsections of individual strips, other site factors could not be kept constant between the strips; instead it was attempted to vary these factors evenly within types. These factors comprise the seed mixture applied, the season of establishment (spring or autumn), the spatial isolation of the strips (isolated, subsection of a larger strip), the new establishment or renewal of a strip, mowing in the previous autumn, the adjacent landuse, and variations in soil conditions (stone cover).

The plant species composition was surveyed in all sites (2nd – 10th June 1997) based on four 1m^2 quadrats located regularly along the length of the strip. In each quadrat the top cover of every plant species was estimated. The number of plant species found in each strip (17 – 32), the number of plant families present (9 – 18), total vegetation cover, the cover of each plant family and of all plant species present in at least 4 sites, were all recorded. The distinction between grassy and non-grassy sites was made in the early spring, and total grass cover had changed by the time of the survey. Nevertheless, for the proportion of grass in total vegetation cover the classification was still valid in June, as strips with a high grass cover in spring had a significantly lower total vegetation cover in June (% grass cover of total vegetation cover in June: 'not grassy' Average = 5.9%, SD = 4.9; 'grassy' Average = 27.9%, SD = 13.5).

Sampling methods

The heteropteran bugs were sampled by a standardised sweep-net method (Remane R. 1958; Bornholdt G. 1991; Otto A. 1996). The sweep-net had a diameter of 40 cm and was fitted with a heavy cloth suitable for use in coarse vegetation. For each sample, 100 sweeps were drawn through the vegetation at a constant pace over a distance of about 80 m. The net was emptied after every 20 sweeps, resulting in 5 subsamples per site and date. Samples were taken 7 times between mid-May and mid-September of 1997. Sampling was restricted to periods with favourable conditions for bug activity, i.e. periods between 10.00 a.m. and 18.00 p.m. (on very warm sunny days exceptionally until 19.30 p.m.) with an air temperature > 17°C, prevailing sunshine and dry vegetation. Samples were always taken on 2 subsequent days and the sampling order was varied.

The adult bugs were determined with the help of entomological handbooks and other relevant publications (Wagner E. 1952; Wagner E. & Weber H.-H. 1964; Wagner E. 1966; Wagner E. 1967; Wagner E. 1970/71; Wagner E. 1973; Wagner E. 1975; Wagner E. & Weber H.-H. 1978; Péricart J. 1972; Péricart J. 1987; Rieger C. 1984). The determination of critical species was checked by R. Heckmann (Germany) and Ch. Rieger (Germany). A large portion of the samples plus the larvae were altogether determined by R. Heckmann (Leston D. & Scudder G.G.E. 1956). The nomenclature follows Günther (1990).

Comparative ecological data on Heteroptera

For all bug species recorded, the following information on their ecology (referred to as species 'traits') was assembled from published sources: type of food (zoophagous, phyto-/zoophagous, phytophagous; the latter two were pooled for analysis as the classification was not always clear), food specificity (polyphagous = feeding on > 1 plant family, oligophagous = feeding on 1 plant family, monophagous = feeding on 1 plant genus or 1 plant species), food plants, number of generations per year, overwintering stage, habitat characteristics (moisture range), mobility and commonness (Kullenberg B. 1944; Wagner E. 1952; Southwood T.R.E. & Leston D. 1959; Afscharpour F. 1960; Southwood T.R.E. 1960; Schwörbel W. 1966; Wagner E. 1966; Wagner E. 1967; Wagner E. 1970/71; Wagner E. 1973; Wagner E. 1975; Wagner E. & Weber H.-H. 1978; Péricart J. 1972; Péricart J. 1983; Burghardt G. 1977; Rieger C. 1979; Péricart J. 1984; Péricart J. 1987; Bernhardt K.-G. 1988; Wachmann E. 1989; Achtziger R. 1991; Achtziger R. et al. 1992; Otto A. 1994; Otto A.

1995; Moulet P. 1995; Vietmeier A. et al. 1996; Hattwig F. 1997; Günther H. et al. 1998). Specifications of traits sometimes originate from only one source and in other cases are contradictory in different sources. As most information originates from studies in spatially limited sites and regions, they do not take account of possible differences in trait characteristics and thus also habitat preferences at different ends of the ecological range of a species (Duffey E. 1978). The reliability of species traits applied to specimens from the research area is thus limited, but is thought to be sufficiently accurate to detect general distribution patterns. The occurrence of the species in other habitats (pathway verges, grassland strips, extensive cereal fields, potato fields) within the Klettgau region was checked by comparison with data from other studies (Uehlinger G. 2000; Ullrich K. unpublished data).

Statistical analysis

For all analyses except the phenological development, the samples were pooled over time, resulting in one sample per wildflower strip. All analyses presented are based on the combined data sets of adults and larvae. Multivariate analyses were run using Canoco version 4.02 (ter Braak 1997-1999). To compare the bug species composition in the wildflower strips, the data (only species > 2 individuals) were entered in a Correspondence Analysis (CA; no data transformation and downweighing of rare species) including all environmental variables (see above) in an indirect gradient analysis. Based on this analysis, environmental factors were preselected according to their apparent influence on bug species composition. The remaining variables were then included in a Canonical Correspondence Analysis (CCA) and tested for significance (Monte Carlo Test with 499 permutations, $P<0.01$). In the resulting model, the amount of variance explained by single factors was determined by variation partitioning (Borcard D. et al. 1992; Økland R.H. & Eilertsen O. 1994; ter Braak C.J.F. & Smilauer P. 1998). For the 35 most common species (> 20 individuals) and for the numbers of species and individuals with specific traits (numbers of individuals ln-transformed), analyses of variance were conducted to examine their response to the key factors age (nominal classes) and grass cover (continuous data).

Results

Characteristics of bug communities in wildflower strips

A total of 81 bug species of agricultural habitats (18´847 individuals consisting of 9´150 adults and 9´697 larvae) were recorded in the 20 wildflower strips (Table 1). A few vagrant species (4 species, each with 1 individual) from wooded, swamp or

Table 1. Numbers of bug species and individuals found in total (n = 20) and in the four originally chosen types of wildflower strips (n = 5); a and b indicate significant differences between types of strips (No. of individuals total: $F = 3.36$, $P<0.05$; No. of individuals larvae: $F = 6.66$, $P<0.005$).

		1st year			2nd year			≥3rd year not grassy			≥3rd year grassy			Total		
		Average /strip	SD	Sum	Average /strip	SD	Sum	Average /strip	SD	Sum	Average /strip	SD	Sum	Average /strip	SD	**Sum**
No. of species	Total	26.4	2.7	50	30.2	4.2	51	31	4.4	56	30.6	5.5	55	29.6	4.4	**81**
	Imagines	24.2	3.3	46	28.8	4	49	29.4	4.7	53	28.6	5	51	27.8	4.5	**76**
	Only as larvae			4			2			3			4			**5**
	Vagrants			1			1			1			1			**4**
No. of individuals	Total	465^{a}	166	2326	1040^{ab}	451	5202	1446^{b}	1063	7230	817^{ab}	377	4089	942	671	**18847**
	Imagines	354	126	1769	599	273	2993	488	165	2441	389	137	1947	458	195	**9150**
	Larvae	111^{a}	42	557	442^{b}	185	2209	958^{b}	943	4789	428^{b}	260	2142	485	553	**9697**
	Vagrants			1			1			1			1			**4**

dung/silage habitats were also collected but have been excluded from the analysis. Pooled with samples from other studies so far 127 bug species (+ 7 vagrants), have been found in wildflower strips in the Klettgau (Uehlinger G. 2000; Schwab A. and Ullrich K. unpublished data).

The average number of species per strip was 29.6, with numbers ranging from 21 to 37 species for individual strips. The average number of individuals per strip was 942, but the range for individual strips was very wide (259-3235). Both numbers of species and individuals were positively correlated with the number of perennial plant species (species: $r = 0.49$, $F = 5.71$, $P<0.05$; individuals: $r = 0.65$, $F=13.24$, $P<0.005$) but showed no correlation to the total number of plant species.

The average number of species was slightly but not significantly lower in strips in the first year than in older strips (Table 1). In contrast, the average number of individuals was significantly lower in 1st year strips in comparison to ≥ 3rd year non-grassy strips ($F = 3.36$, $P<0.05$). Just considering larvae individuals were lower in 1st year strips in comparison to all older strips ($F = 6.66$, $P<0.005$). The mean rank abundance curves indicate that equitability is on average highest in 1st year strips and lowest in 3rd year, non-grassy strips (Fig. 1).

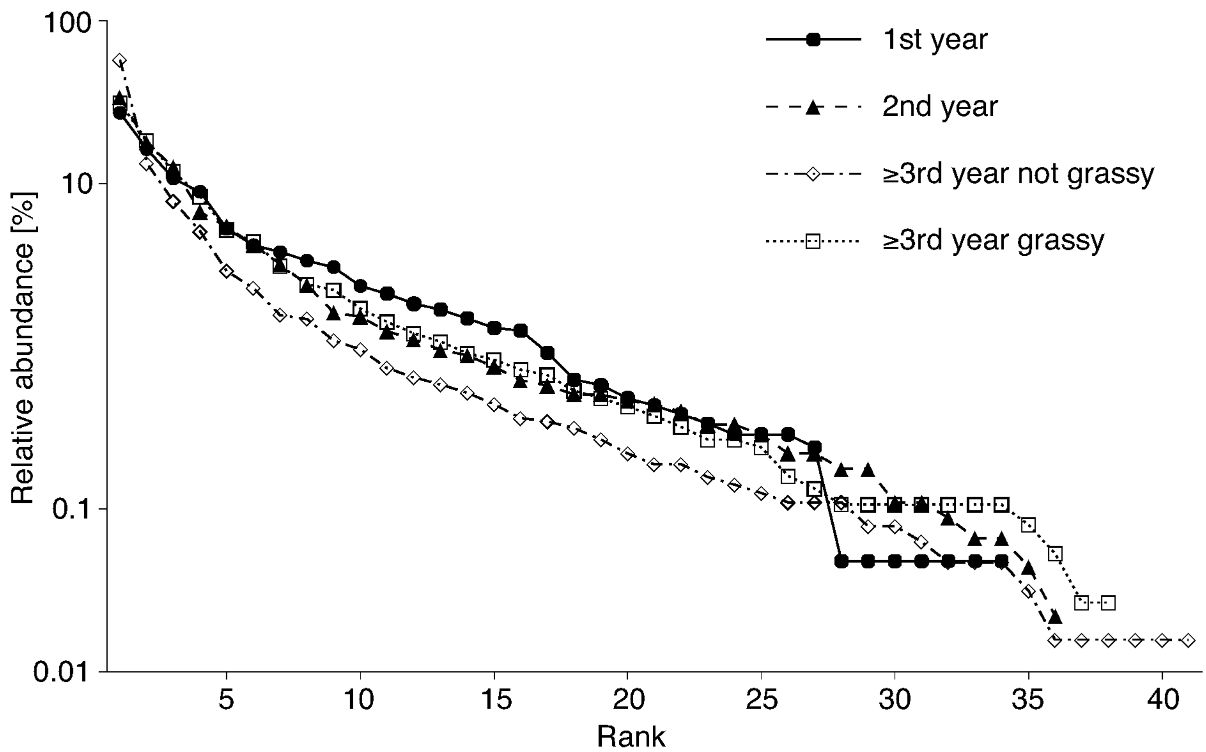


Fig. 1. Average rank abundance distributions of heteropteran communities in wildflower strips of different ages and grassiness.

Table 2. Frequency (*and relative abundance*) of species traits, commonness and habitat characteristics in bugs in 20 wildflower strips and their occurrence in bug families. Where numbers of species within a group of traits do not add up to the total species number, information on some species is missing; Others = Cydnidae (3), Scutelleridae (2), Berytidae (1), Piesmatidae (1), Tingidae (1).

			Trophic level			Feeding specificity			Generations		Overwintering			Surroundings			Commonness			Habitat pref.		
	Total no. species	*% Individuals*	Zoophagous	Phyto-/Zoophagous	Phytophagous	Polyphagous	Oligophagous	Monophagous	>1 Generation	1 Generation	Adult	Egg	Various	Pathway verges	Elsewhere	Nowhere	Very common	Medium common	Scarce-rare	(Xero-)thermophilic	Mesophil./Unspecif.	Hygrophilic
Total no. spp	**81**		**9**	**9**	**63**	**40**	**31**	**9**	**28**	**53**	**55**	**21**	**5**	**29**	**18**	**34**	**45**	**16**	**15**	**30**	**25**	**4**
% Individuals			*8%*	*3%*	*88%*	*46%*	*53%*	*1%*	*27%*	*73%*	*43%*	*56%*	*1%*	*66%*	*32%*	*2%*	*92%*	*6%*	*2%*	*7%*	*43%*	*0.1%*
Miridae	36	*83.5%*	1	3	32	13	17	5	10	26	12	21	3	14	8	14	22	4	8	11	17	3
Lygaeidae	9	*0.5%*		2	7	5	3	1	5	4	7		2		4	5	5	3	1	6	1	1
Pentatomidae	10	*3.4%*		4	6	6	4		1	9	10			4	3	3	6	3		3	3	
Rhopalidae	6	*3.9%*			6	6			4	2	6			1	1	4	3	1	1	5		
Coreidae	4	*0.8%*			4	2	2		2	2	4			1		3	2	1	1			
Nabidae	5	*1.9%*	5			5			1	4	5			3	2		3	2		1	4	
Anthocoridae	3	*5.7%*	3			3			3		3			3			2	1				
Others	8	*0.3%*			8		5	3	2	6	8			3		5	2	1	4	4		

Almost half of the species and 84% of individuals belong to the Miridae (Table 2). The Lygaeidae, Pentatomidae, Rhopalidae, Coreidae, Nabidae and Anthocoridae each contributed between 3 to 10 species, but with few exceptions, the numbers of individuals from these families were small. The majority of species is phytophagous, 9 species are phyto-/zoophagous, and another 9 species (mostly Nabidae and Anthocoridae) are zoophagous. Half of the species are polyphagous, including all of the Rhopalidae, Nabidae and Anthocoridae. Almost two thirds of the Miridae and Pentatomidae are oligo- or monophagous, as well as around half of the Lygaeidae and Coreidae and all species belonging to the 'other' families in Table 2. Nine species are monophagous. Oligophagous species tend to be present in large numbers, whereas monophagous species are often represented by only a few individuals. About two thirds of species, including about 60% of the Miridae and most of the Pentatomidae and Nabidae, produce 1 generation per year, while the remainder, produce > 1 generation. Two thirds of all species overwinter as adults and one quarter – all of them species of Miridae – as eggs; 3 Miridae and 2 Lygaeidae have been recorded to overwinter in various stages (egg, larvae or adult).

Forty-five of the species occurring in wildflower strips have been classified in the literature as very common, 17 as medium common, and another 14 as sparse to rare (no information was found on the commonness of the remaining 5 species). 'Commonness' appears to be related to abundance, very common species amounting to 92% of all individuals. Furthermore, the most abundant species tended to occur, not only in the majority of strips, but also in the surrounding vegetation. Forty-seven species, representing 98% of individuals, were found somewhere in the surroundings – 29 in pathway verges and 18 elsewhere – while the remaining 34 species were only found in wildflower strips. These patterns of abundance are indicated by the positive correlations between species abundance (ln-transformed) and frequency ($r = 0.9003$, $P<0.0001$), species abundance and presence in surroundings ($F = 9.02$, $P<0.01$), and frequency and presence in surroundings ($F = 8.09$, $P<0.01$). Information on habitat preferences in respect of moisture is incomplete, but indicates that with a few exceptions of species characteristic of moist habitats, about half of the species require either dry and warm sites (most Lygaeidae, Rhopalidae and 'Others') while the other half are either mesophilic or tolerate a wide range of moisture conditions. The latter on average are much more abundant than species of dry or moist sites.

Factors differentiating bug species composition

A total of 43% of the variance in the CCA can be explained by the environmental variables 'age of a strip' (i.e. 1st year, 2nd year, ≥ 3rd year; 31% of variance) and 'grass cover in June' (12% of variance). In the CA, the factor age is strongly correlated with

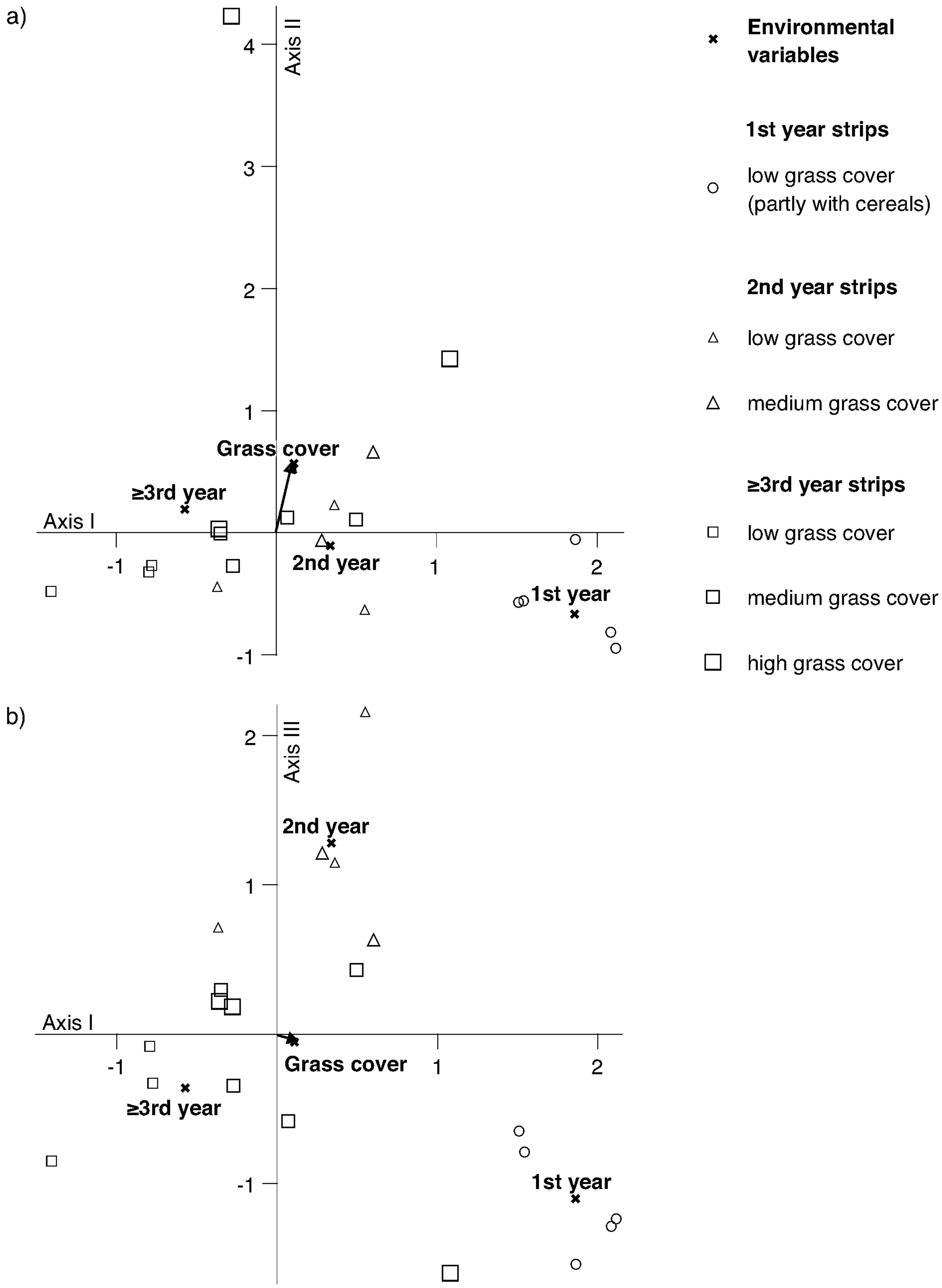


Fig. 2. Ordination diagrams of a CA of the bug species composition (Adults and Larvae) of wildflower strips differentiated according to their age (symbol) and grass cover in June (size of symbol); a) Axes I and II, b) Axes I and III. The environmental variables age (nominal data) and grass cover (continuous data) are included by the means of indirect gradient analysis (eigenvalues: Axis I = 0.44, Axis II = 0.32, Axis III = 0.24, total inertia = 1.827); low grass cover < 3%, medium grass cover > 5% and < 8%, high grass cover > 9%.

the first axis, while grass cover is correlated with the second axis. Strips in their first year form a distinct group in the bottom right hand corner of the ordination diagram for the first and second axes (Fig. 2a). Strips in their second year are focussed in the centre of the diagram but overlap partly with older strips (especially those 2nd year strips that have already developed a considerable grass cover). Among the older strips a clear gradient can be seen from those containing almost no grass in June (< 3%) located in the bottom left hand corner of Figure 2a, to those with a medium grass cover (5-8%) in the centre of the diagram, to those with a higher grass cover (9-18%) mainly found in the upper part of the diagram. The latter are scattered over a larger area, though, which indicates a greater variability in their species composition. On the third axis (Fig. 2b), the 2nd year sites separate clearly from older strips, irrespective of their degree of grassiness.

Changes in species composition in relation to the age of wildflower strips

Twelve out of 35 species show a significant response to the age of wildflower strips (Fig 3). For 3 species the abundance is very low in the first year and increases with age. Of these *Megalocoleus molliculus* occurs in vast but varying numbers in the oldest strips, while *Leptoperna dolobrata* and *Calocoris norvegicus* are already frequent in 2nd year strips and increase only slightly in older sites. A fourth species, *Platyplax salviae,* was only caught in some of the oldest strips. Three species have their maximum in strips in the second year; these are *Dicyphus globulifer* and *Adelphocoris lineolatus,* both of which are very abundant, and *Orthops campestris* which is much less frequent. The abundance of five species decreases with increasing age of the strips. *Lygus rugulipennis* is the most abundant of these, followed in decreasing order by *Lygus pratensis, Eurydema oleraceum, Nabis ferus* and *Palomena viridissima.* For the following 23 species no significant differences were found between wildflower strips of different ages: *Notostira erratica, Orius niger, Stictopleurus puntatonervosus, Nabis pseudoferus, Orius majusculus, Dolycoris baccarum, Amblytylus nasutus, Campylomma verbasci, Coreus marginatus, Carpocoris fuscispinus, Stictopleurus abutilon, Orthops kalmii, Carpocoris purpureipennis, Chlamydatus pulicarius, Capsus ater, Adelphocoris seticornis, Corizus hyoscyami, Plagiognathus chrysanthemi, Rhopalus parumpunctatus, Rhyparochromus pinii, Orius minutus, Charagochilus gyllenhalii, Piezodorus lituratus.*

Some differences associated with the ages of sites are also evident at the family level. The Miridae increased from 41% of all species and 60% of all individuals in the first year, to 50% of species and 83% of individuals in the second year (Fig. 4). The Lygaeidae reached a maximum of 7% of all species in ≥ 3rd year strips, though numbers of individuals remained small. The other bug families showed little or no response to site age.

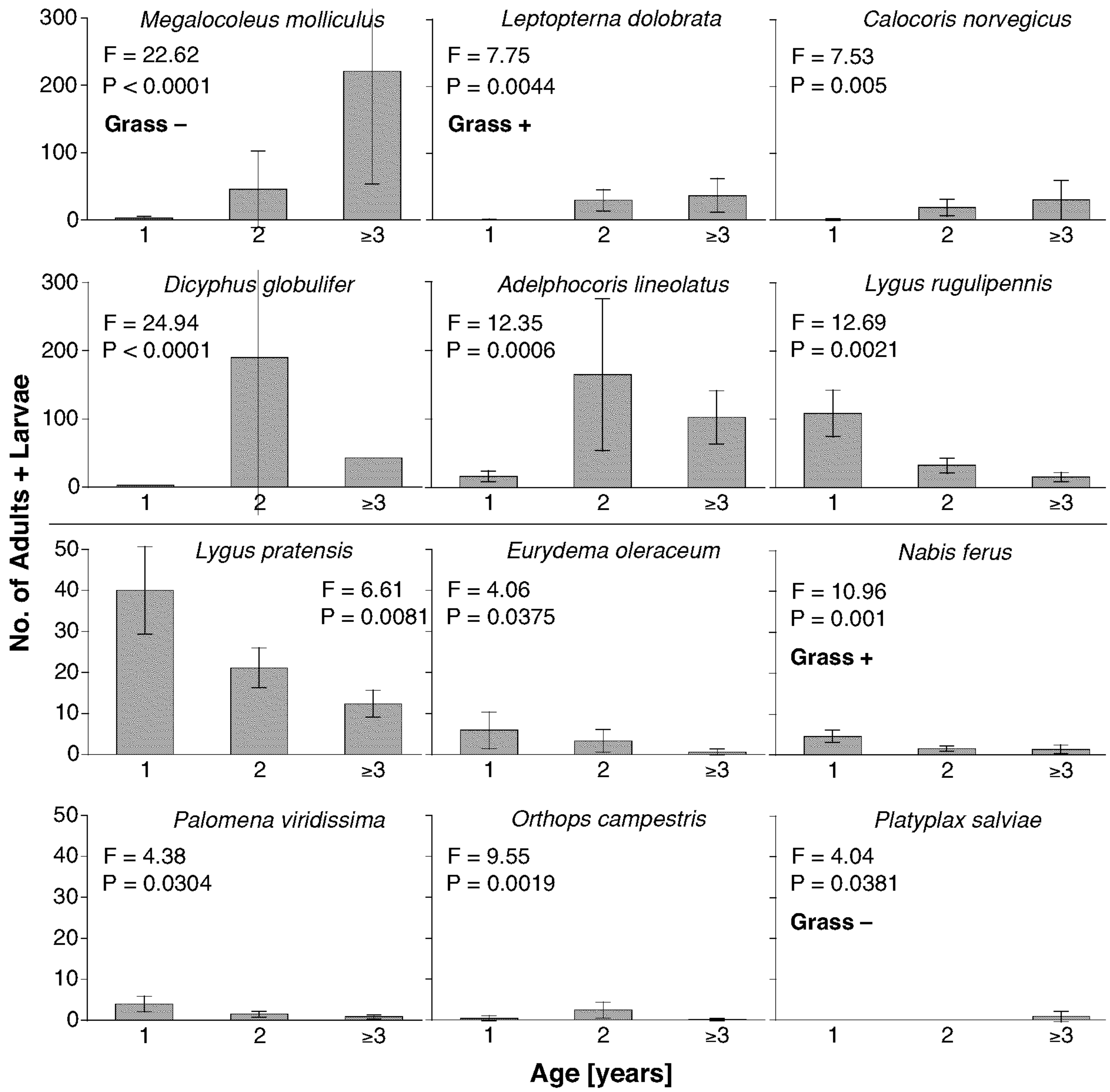
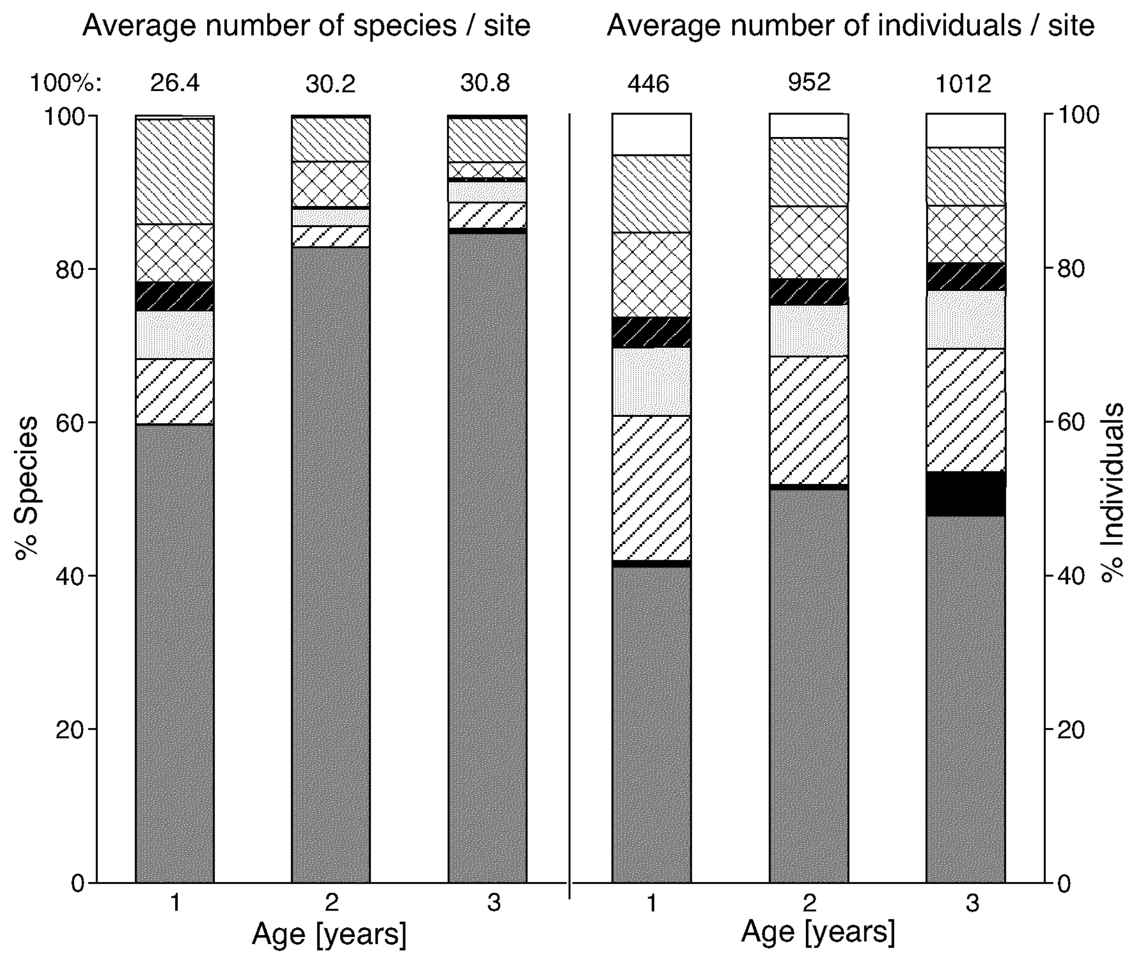


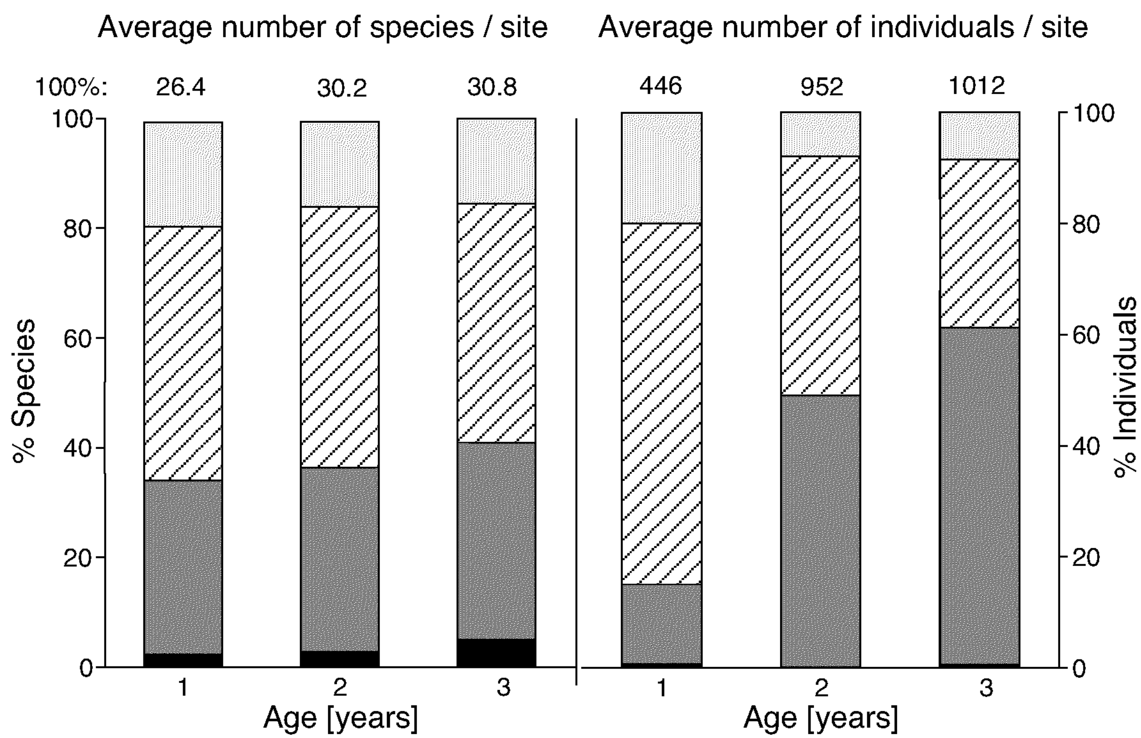
Fig. 3. Responses of individual species (numbers Ln-transformed) to the age of wildflower strips (mean, SD) were tested based on two-way ANOVAs together with the response to grass cover (continuous variable, response indicated as **Grass** + or –). Numbers of individuals vary strongly between strips, years and species; because of the latter different scales on the y-axes have been chosen for the upper and lower two rows. The abundances of *Megalocoleus molliculus*, *Leptopterna dolobrata* and *Calocoris norvegicus* increase from 1st to ≥ 3rd year strips, those of *Dicyphus globulifer*, *Adelphocoris lineolatus*, and *Orthops campestris* show a maximum in the 2nd year, those of *Lygus rugulipennis*, *Lygus pratensis*, *Eurydema oleraceum*, *Nabis ferus* and *Palomena viridissima* decrease with increasing age, and *Platyplax salviae* only occurs in strips ≥ 3rd year.

The relative proportions of zoophagous and phytophagous species do not vary significantly between strips of different ages (Fig. 5), but the number of individuals of phytophagous taxa increases from the first year (80%) to the second year (92%). Among the phytophagous bugs, the proportion of monophagous species is highest in strips ≥ 3 years, but no other trends are evident at the species level. However, the numbers of individuals showing different degrees of feeding specialization do vary.



Bug family	Comparison of age classes: % Species F-Ratio	% Species P-Value	% Individuals F-Ratio	% Individuals P-Value
Others		ns		ns
Anthocoridae		ns		ns
Rhopalidae		ns		ns
Coreidae		ns	7.47	0.0051
Nabidae		ns	8.25	0.0034
Pentatomidae		ns	6.35	0.0094
Lygaeidae	5.98	0.0115 (*)		ns (*)
Miridae	3.88	0.0424 (*)	16.53	0.0001 (*)

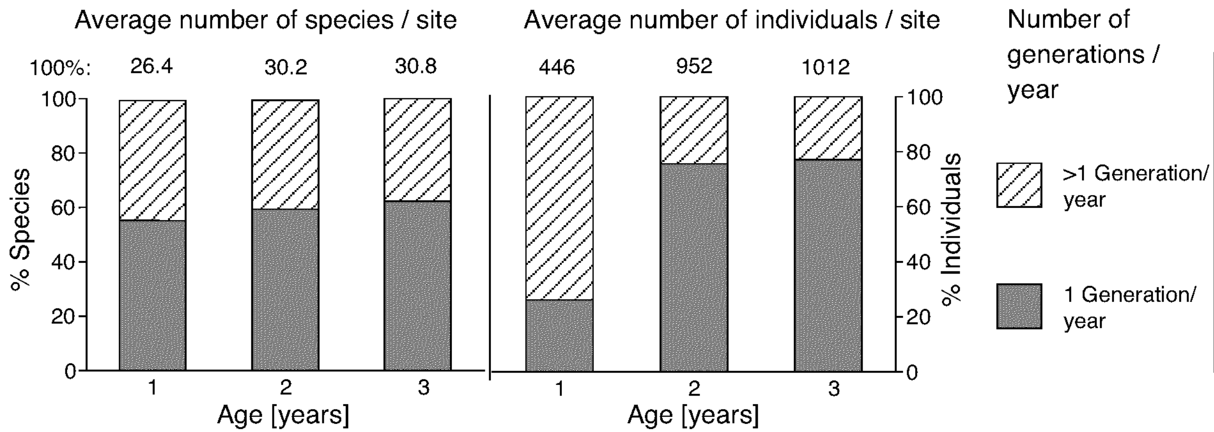
Fig. 4. Average proportions of bug families in the total numbers of individuals and species found in wildflower strips of 1 year (n = 5), 2 years (n = 5) and ≥ 3 years age (n = 10). Where differences between the age classes are significant, the F-Ratio and P-Value is given; ns = not significant, (*) = significant for absolute numbers of individuals or species; above the % columns the average total number of individuals or species found in wildflower strips of the same age class is given (=100%).



Feeding type	% Species F-Ratio	% Species P-Value	% Individuals F-Ratio	% Individuals P-Value
Zoophagous		ns	4.09	0.0366
Phytophagous:		ns	4.17	0.0349
Polyphagous		ns	7.47	<0.0001
Oligophagous		ns	25.71	<0.0001 (*)
Monophagous		ns (*)		ns

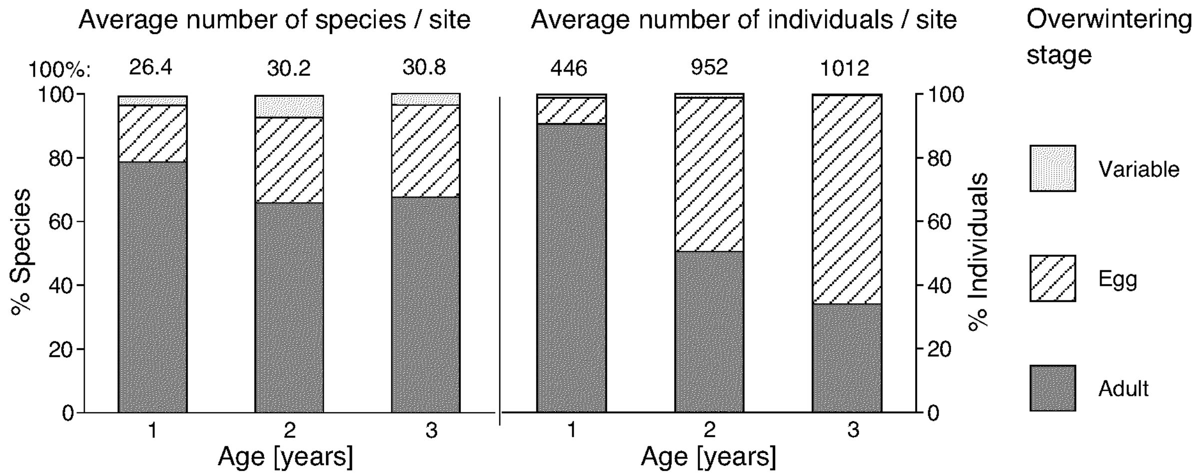
Comparison of age classes

Fig. 5. Average proportions of feeding types in the total numbers of individuals and species found in wildflower strips of 1 year (n = 5), 2 years (n = 5) and ≥ 3 years age (n = 10). Where differences between the age classes are significant, the F-Ratio and P-Value is given; ns = not significant, (*) = significant for absolute numbers of individuals or species; above the % columns the average total number of individuals or species found in wildflower strips of the same age class is given (= 100%).



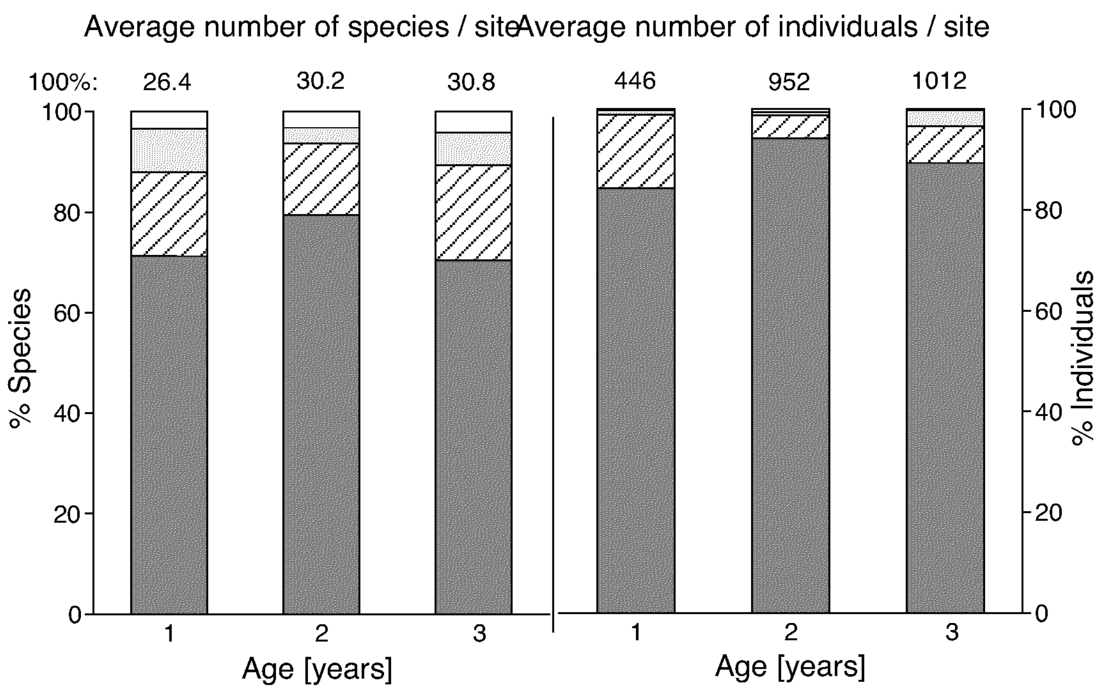
Comparison of age classes	% Species F-Ratio	% Species P-Value	% Individuals F-Ratio	% Individuals P-Value
>1 Generation/ year		ns	38.12	<0.0001 (*)
1 Generation/ year		ns	32.83	<0.0001 (*)

Fig. 6. Average proportions of species with 1 or > 1 generations per year in the total numbers of individuals and species found in wildflower strips of 1 year (n = 5), 2 years (n = 5) and ≥ 3 years age (n = 10). Where differences between the age classes are significant, the F-Ratio and P-Value is given; ns = not significant, (*) = significant for absolute numbers of individuals or species; above the % columns the average total number of individuals or species found in wildflower strips of the same age class is given (= 100%).



Comparison of age classes	% Species F-Ratio	% Species P-Value	% Individuals F-Ratio	% Individuals P-Value
Variable		ns		ns
Egg	7.06	0.0064 (*)	34.64	<0.0001 (*)
Adult	10.24	0.0014	13.75	<0.0001

Fig. 7. Average proportions of overwintering stages in the total numbers of individuals and species found in wildflower strips of 1 year (n = 5), 2 years (n = 5) and ≥ 3 years age (n = 10). Where differences between the age classes are significant, the F-Ratio and P-Value is given; ns = not significant, (*) = significant for absolute numbers of individuals or species; above the % columns the average total number of individuals or species found in wildflower strips of the same age class is given (= 100%).



Commonness	Comparison of age classes: % Species F-Ratio	% Species P-Value	% Individuals F-Ratio	% Individuals P-Value
Unknown		ns		ns
Sparse-rare		ns		ns
Medium common	5.14	0.0189 (*)	3.65	0.0493
Very common	4.1	0.0365 (*)		ns

Fig. 8. Average proportions of very common to rare bug species in the total numbers of individuals and species found in wildflower strips of 1 year ($n = 5$), 2 years ($n = 5$) and ≥ 3 years age ($n = 10$). Where differences between the age classes are significant, the F-Ratio and P-Value is given; ns = not significant, (*) = significant for absolute numbers of individuals or species; above the % columns the average total number of individuals or species found in wildflower strips of the same age class is given (= 100%).

The relative and absolute numbers of oligophagous individuals are low (18%) in the first year and increase strongly in the second year (53%) and in older strips (66%). In contrast, relative numbers of polyphagous individuals decrease with increasing age.

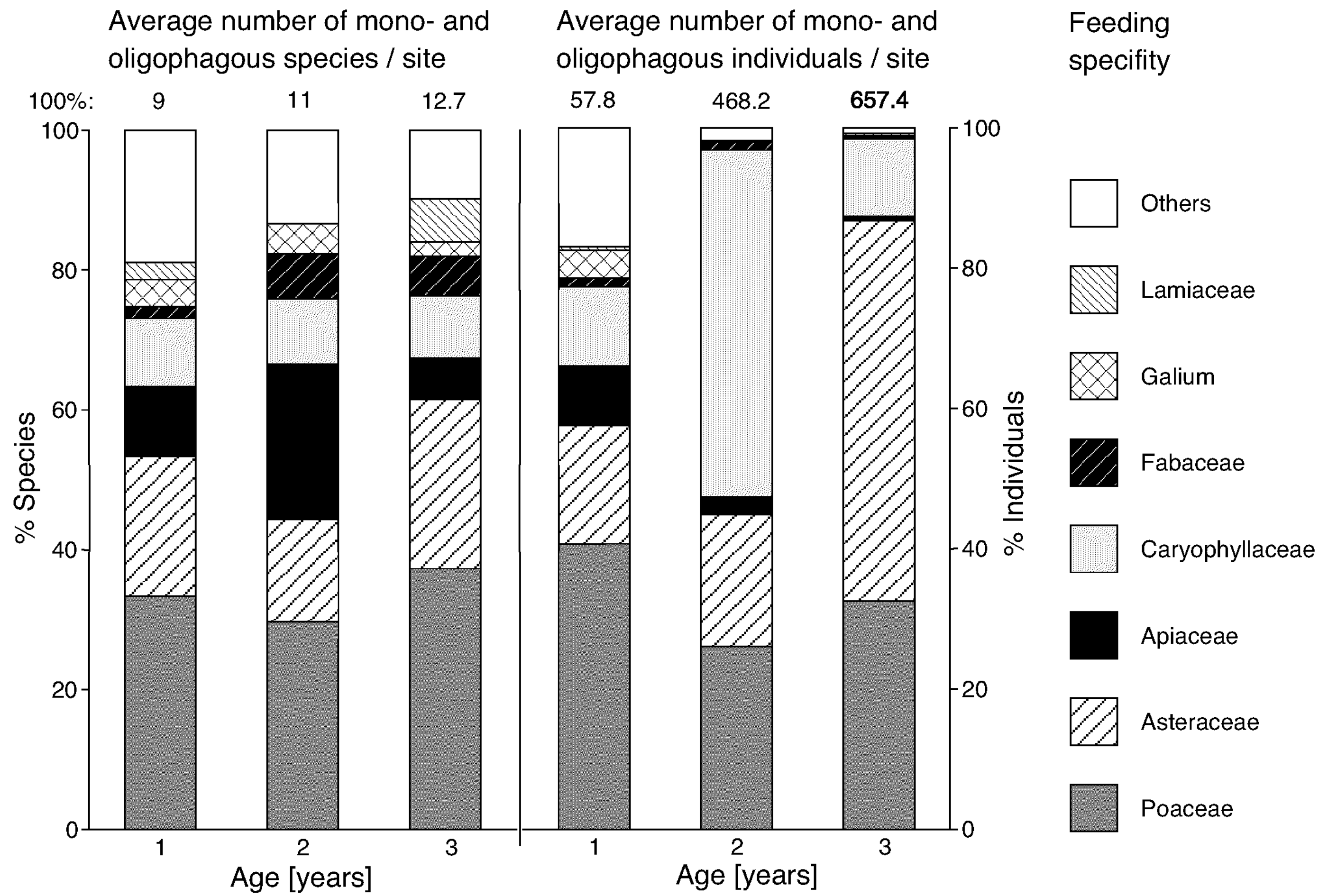
There are no trends in the numbers of species related to the number of generations produced per year (Fig. 6). However, bug species with >1 generation per year are more abundant in the first year, while those with only 1 generation per year dominate from the second year onwards. The proportion of bugs overwintering in the adult stage is very large in the first year (79% of all species and 90% of all individuals) and decreases strongly in the second year and in older sites; the reverse trend applies for bugs overwintering as eggs (Fig. 7). These trends are due mainly to an absolute increase in the numbers of species and individuals overwintering as eggs. In general, there are larger numbers of individuals of species overwintering as eggs than of those overwintering as adults.

The presence of species in the surroundings of the wildflower strips shows no general response to the age of wildflower strips. With regard to commonness, numbers of very common species have a maximum in the second year and numbers of medium common species increase with increasing age of the strips (Fig. 8). Numbers and abundances of sparse to rare species are too low to show a significant response.

Species changes related to plant species composition

Among the mono- and oligophagous bug species, the abundances of those specialized on different plant families, or on certain plant species within these, change with the age of the strips (Fig. 9). Species feeding on Asteraceae are most numerous in ≥ 3rd year strips, both in absolute and relative numbers of species and individuals. Their numbers correlate closely with the abundance of Asteraceae ($r = 0.78$, $F = 27.44$, $P<0.0001$). For species feeding on Apiaceae, i.e. mainly species of the genus *Orthops*, both absolute and relative species numbers as well as absolute numbers of individuals are most numerous in 2nd year strips with a high abundance of Apiaceae. Species specialized on Caryophyllaceae also respond to age, with very high numbers of individuals in the second year; this is largely because of the abundance in these sites of *Dicyphus globulifer* and its host plant *Silene alba*. Bug species feeding on other plant families or genera, i.e. Poaceae, Fabaceae, *Galium* species, Lamiaceae, show no significant response to the age of the strips.

Seven species show a response to grass cover (Table 3). Of the five species reacting positively, *Leptopterna dolobrata, Notostira erratica* and *Amblytylus nasutus* feed on grass, while *Nabis pseudoferus* and *N. ferus* are zoophagous species frequent



Feeding specifity	% Species F-Ratio	% Species P-Value	% Individuals F-Ratio	% Individuals P-Value
Others		ns		ns
Lamiaceae		ns		ns
Galium		ns		ns
Fabaceae		ns		ns
Caryophyllaceae		ns	15.08	0.0002 (*)
Apiaceae	9.11	0.0023 (*)		ns (*)
Asteraceae	11.98	0.0007 (*)	16.36	0.0001 (*)
Poaceae		ns		ns

Comparison of age classes

Fig. 9. Average proportions of bug species specialized on different plant taxa in the total numbers of individuals and species found in wildflower strips of 1 year (n = 5), 2 years (n = 5) and ≥ 3 years age (n = 10). Where differences between the age classes are significant, the F-Ratio and P-Value is given; ns = not significant, (*) = significant for absolute numbers of individuals or species; above the % columns the average total number of individuals or species found in wildflower strips of the same age class is given (= 100%).

Table 3. Reaction of species and species traits to grass cover, based on two-way ANOVAs with age as nominal variables and grass cover as continuous variable (without interaction); only traits showing a significant response to grass cover are shown and their regression statistics are given. 1st choice: response of proportions, 2nd choice: absolute numbers, (*) where absolute numbers also showed a response but no details are given; spp = Species, ind = Individuals; reaction to age: + = increase with age, - = decrease with age, number = age with pronounced maximum; species strongly contributing to characteristics are given in order of decreasing dominance; species (numbers of individuals): *Ade lin* = *Adelphocoris lineolatus* (2330), *Amb nas* = *Amblytylus nasutus* (193), *Cal nor* = *Calocoris norvegicus* (868), *Car fus* = *Carpocoris fuscispinus* (103), *Dic glo* = *Dicyphus globulifer* (1883), *Lep dol* = *Leptopterna dolobrata* (1010), *Lyg pra* = *Lygus pratensis* (513), *Lyg rug* = *Lygus rugulipennis* (1000), *Meg mol* = *Megalocoleus molliculus* (4805), *Nab fer* = *Nabis ferus* (60), *Nab pse* = *Nabis pseudoferus* (239), *Not err* = *Notostira erratica* (733), *Ori nig* = *Orius niger* (726), *Sti pun* = *Stictopleurus punctatonervosus* (477).

Traits	Categories	No. or % of individuals or species	Reaction to: Age	Grass cover b	F-Ratio	P	Species characteristics/ species dominating in category/ numbers of species involved
Bug species	*Leptopterna dolobrata*		+	0.181	9.47	0.0072	grass feeding
	Notostira erratica			0.183	7.18	0.0165	grass feeding
	Amblytylus nasutus			0.143	5.29	0.0353	grass feeding
	Nabis pseudoferus			0.064	4.81	0.0433	meadow species
	Nabis ferus		-	0.120	16.75	0.0008	meadow species
	Megalocoleus molliculus		+3	-0.137	4.51	0.0496	feeding on Asteraceae
	Platyplax salviae		3	-0.103	5.80	0.0285	feeding on Salvia
Bug families	Pentatomidae	No. spp		0.208	5.37	0.0341	10 of 81 species
	Nabidae	No. ind		0.071	5.84	0.0280	*Nab pse*, *Nab fer*
Feeding selectivity	Oligophagous	No. spp		0.430	12.11	0.0031	32 of 81 species (10 grass-feeding species)
	Monophagous	No. spp	+	-0.117	5.48	0.0325	9 of 81 species (herb-feeding species)
Species feeding on certain plant families	Poaceae	% mono-oligoph. ind		0.031	10.99	0.0044 (*)	*Lept dol*, *Not err*, *Amb nas*
	Poaceae	No. spp		0.258	15.66	0.0011	10 of 39 species
	Asteraceae	% mono-oligoph. ind	+,3	-0.026	12.18	0.0030 (*)	*Meg mol*, *Car fusc*
	Asteraceae	% mono-oligoph. spp	3	-0.013	19.34	0.0004 (*)	6 of 39 species
Generations/ year	1 Generation	% ind	2,3	-0.011	6.33	0.0229	*Meg mol*, *Ade lin*, *Dic glo*, *Lep dol*, *Cal nor*
	>1 Generation	% ind	1	0.014	7.63	0.0139 (*)	*Lyg rug*, *Not err*, *Ori nig*, *Lyg pra*, *Sti pun*, *Nab pse*
Species also in surroundings	Pathway verges	No. spp		0.277	10.66	0.0049	29 of 81 species
	Elsewhere	% ind	3	-0.022	18.2	0.0006 (*)	*Meg mol*
Commonness	Medium common	% spp	(1)3	-0.006	5.70	0.0297	18 of 81 species

in meadows. The two species responding negatively to grass cover are specialized on herbaceous plants: *Megalocoleus molliculus* on Asteraceae and *Platyplax salviae* on *Salvia pratensis*. At the family level, both the numbers of species of Pentatomidae (in total 11 species), and the number of individuals of the Nabidae (mainly *Nabis pseudoferus* and *N. ferus*) are positively correlated with grass cover.

Regarding the degree of feeding selectivity, oligophagous species (in total 32 species) become more frequent with increasing grass cover, while numbers of monophagous species (in total 9 species) drop (Table 3). A closer analysis of the response of the set of mono- and oligophagous species to grass cover, shows that those feeding on grass increase in numbers of species (in total 11 species) and relative proportion of individuals. In contrast, for species specialized on Asteraceae (in total 6 species) the relative proportions of species and individuals decrease.

Bug species with > 1 generation per year tend to be more abundant where there is a high grass cover, whereas those with only 1 generation per year decline (Table 3). Bug species with different overwintering stages are in no way affected by grass cover.

Numbers of species also caught in pathway verges (29 species) increase with growing grass cover (Table 3). Where grass cover is high, species that are classed as medium common decrease in species numbers in relation to the total species set dominated by common species.

Correlations between species traits

The various species traits are not entirely independent of each other for the bug species recorded. The degree of food specificity is correlated with the number of generations per year produced by a species (χ^2 = 10.5, P = 0.0333) and with the presence of a species in the surroundings (χ^2 = 27.1, P = 0.0007; Table 4). Monophagous species all produce only 1 generation per year, as is also the case for most oligophagous species feeding on grass (except the 2 *Notostira* species). Among other oligophagous species, as well as polyphagous and zoophagous ones, only a slightly higher proportion produces > 1 generation per year than in the total species set. Although the overwintering stage is not correlated to other species traits, the proportions of species overwintering as eggs or in various stages are over represented in monophagous species as well as in grass specialists. As in the total species set, about two thirds of the other oligophagous and the polyphagous species overwinter as adults, as do all zoophagous species. The majority (67%) of monophagous species could not be found in the surroundings. For oligophagous species, except those feeding on grass, numbers found on pathway verges were still low, but a considerable number was recorded elsewhere in the surroundings.

Table 4. Classification of bug species occurring in wildflower strips according to their food specificity. Food specificity is correlated (*) with the 'number of generations per year' ($\chi^2 = 10.5$, $P<0.05$, 1 generation, > 1 generation) and with the 'presence in the surroundings' ($\chi^2=27.1$, $P<0.001$; P = pathway verges, S = only elsewhere in the surroundings, N = nowhere in the surroundings), but not with the overwintering stage (A = adult, E= egg, V = various). The different categories of food specificity are characterized by species traits cooccurring with a higher frequency than in the total species set (in bold); bug families contained in each class are listed: Anthocoridae (An), Berytidae (B), Coreidae (C), Cydnidae (Cy), Lygaeidae (L), Miridae (M), Nabidae (Na), Pentatomidae (Pe), Piesmatidae (Pi), Rhopalidae (R), Scutelleridae (Sc), Tingidae (Ti).

Food specificity	Total		Generations/ year *		Overwintering stage			Presence in surroundings *			Bug families involved (number of species)
	n	%	1	>1	A	E	V	P	S	N	
Monophagous	9	11%	**100%**	–	56%	**33%**	11%	22%	11%	**67%**	M 5, Cy 2, L 1, B 1
Oligophagous (– grass)	20	25%	55%	45%	70%	20%	10%	15%	**35%**	**50%**	M 9, Pe 3, L 3, C 2, Cy 1, Pi 1, Ti 1
Grass specialists	10	13%	**80%**	20%	60%	**40%**	–	**90%**	–	10%	M 7, Sc 2, Pe 1
Polyphagous	32	40%	59%	41%	66%	28%	6%	25%	28%	47%	M 13, Pe 6, R 6, L 5, C 2
Zoophagous	9	11%	56%	44%	**100%**	–	–	**67%**	22%	11%	Na 5, An 3, M 1
Total	**80**	**100%**	**65%**	**35%**	**69%**	**24%**	**6%**	**35%**	**24%**	**41%**	

All grass specialists were also found in pathway verges, except *Notostira elongata*, which was scarce in wildflower strips, too. Proportions of polyphagous species present in the surroundings depart only little from the average, whereas the majority of zoophagous species was also caught in pathway verges.

Changes in species abundance during the season

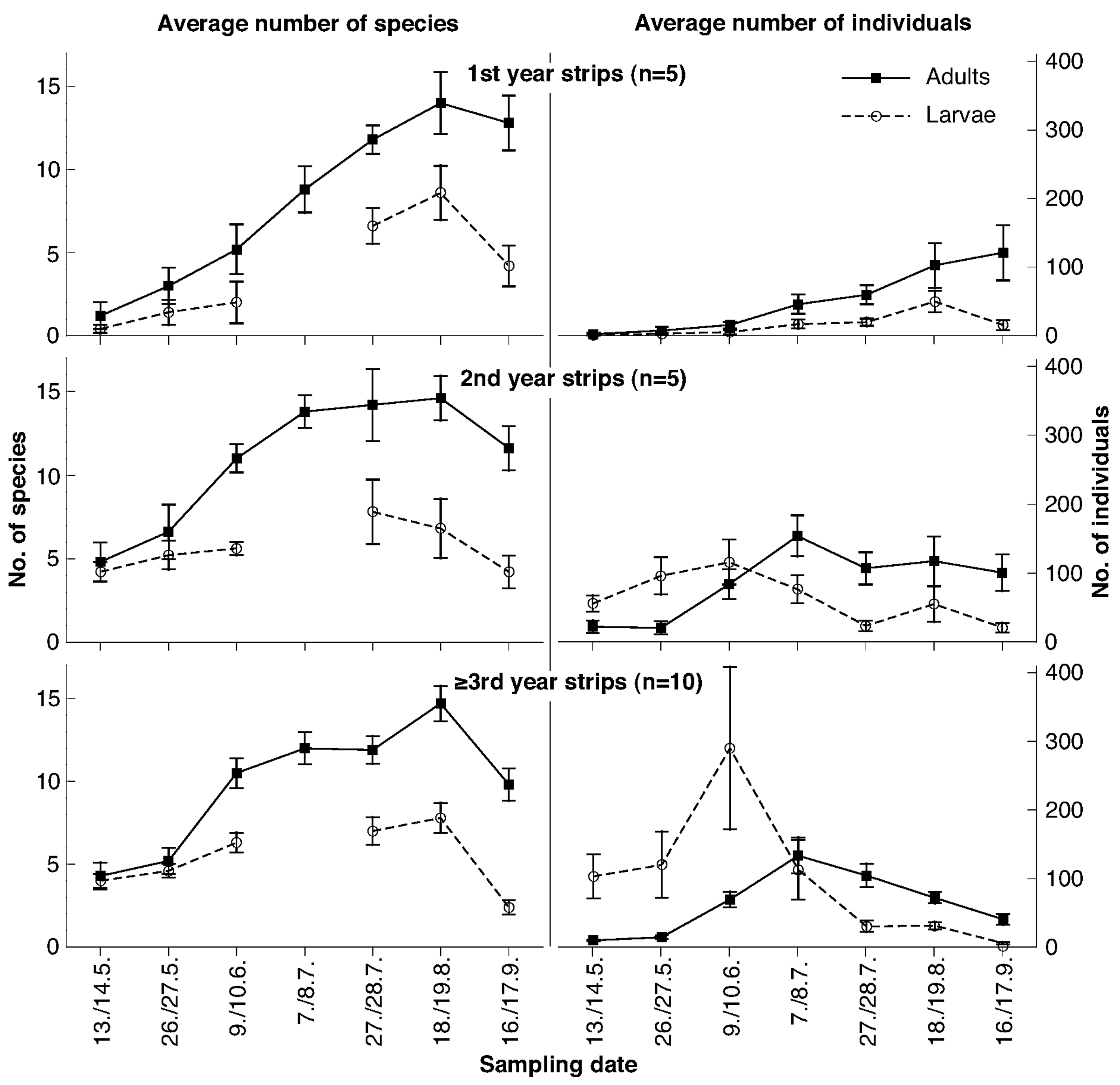


Fig. 10. Phenological development of average numbers of bug species and individuals in wildflower strips in their 1st, 2nd and ≥ 3rd year (1997); numbers of adults and larvae are shown separately (SE).The larvae were only counted but not determined for the date 7./8.7, leaving the number of species unknown.

In wildflower strips in their first year, numbers of species and individuals are very low in spring, but they increase steadily during summer, reaching numbers similar to those in older strips by mid-August (Fig. 10). In older strips, not only are the initial numbers of species and individuals higher than in 1st year strips, but the increase in species numbers is also faster, so that there are > 10 species by mid-June. In strips of all ages, the mean species number reaches a maximum, ranging between 14 and 15 species, in August.

The numbers of species recorded as larvae are always below those of adults, because some larvae were only determined to the level of the genus. In the 1st year strips, numbers of individual larvae remain much lower than those of adults throughout the season. In contrast, there are more larvae than adults in May and June in older strips, and especially in ≥ 3rd year strips (enhanced by extreme numbers of *Megalocoleus molliculus* in one strip). Numbers of larvae reached a maximum around the 10 June. Numbers of adults increase later, surpassing those of larvae until the beginning of July, when they reach their maximum before they slowly decrease again.

Seasonal trends in numbers are different for species which overwinter as eggs and as adults (Fig. 11). Of those species which overwinter as adults, about 40% are present as adults at the beginning of the season; this proportion is rather constant during May and June, and then increases gradually to around 60%. Few larvae of these species are present until the end of May, and thereafter the numbers increase to reach a peak of around 50% of possible species in July. In contrast, no adult individuals of species overwintering as eggs were found in mid-May. Their numbers increased rapidly, though, reaching 20% of the species of this type by the end of May, and over 80% by early June; thereafter the number of species decreased again to below 40% by mid-September. Around 30% of these species were present as larvae in mid-May, and their numbers increased to a maximum at some time between the beginning of June and July, before decreasing to zero by mid-September.

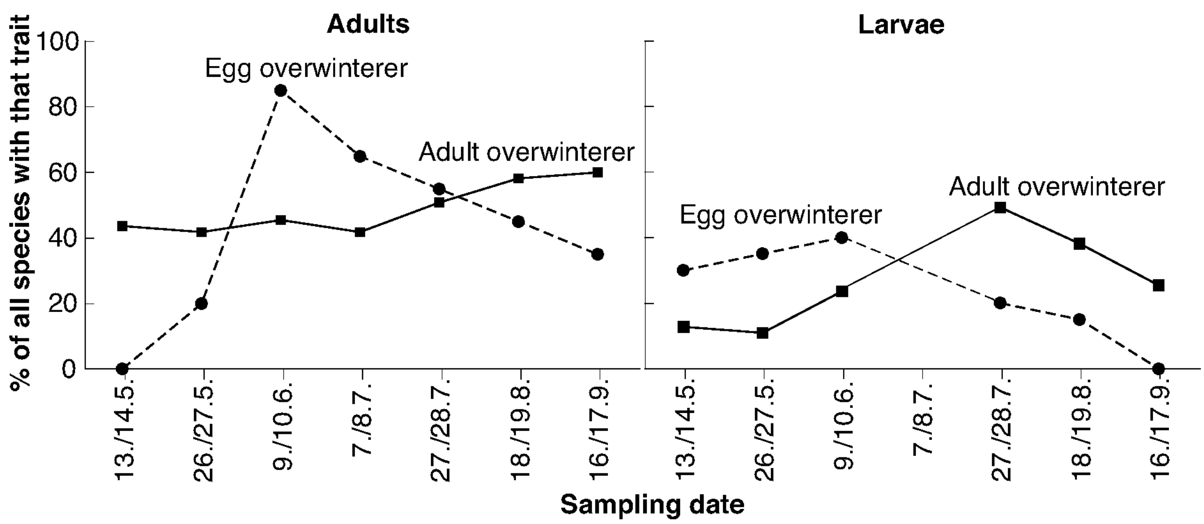


Fig. 11. Phenology of numbers of species overwintering as adult and as egg occurring in wildflower strips of all ages; the relative proportion of species of one overwintering type present at a certain date is shown.

Discussion

Responses of the bug community

The age of the wildflower strips, and thus successional stage, is the most important factor differentiating the bug communities, explaining 31% of the variation found in the CCA. This result appears to be mainly due to variation in the species composition and partly also to low numbers of individuals, especially of larvae, in the first year. Species numbers are only slightly lower in the first year. Both, numbers of species and individuals vary greatly between single strips, and increase only slowly during the first year (Fig. 11). This can partly be attributed to a limited colonization rate, and also to the low abundance of perennial plant species in the first year (Chapter 2).

Findings from other studies concerning the possible correlation of numbers of bug species with those of plant species are contradictory and all regard total species numbers, although specialist bug species mostly feed on perennial host plants (see below). In secondary succession Sanderson (1992) detected no correlation of bug species numbers with age or plant species numbers, while Greiler (1994) recorded a continuous and correlated increase in the numbers of both plant and bug species. Similarly, Southwood, Brown & Reader (1979) reported an initial parallel increase of both plant and bug species until the second year, when numbers of plant species went down again while those of bug species remained high. They showed that the enhanced diversity of bug species was a positive reaction to an increased structural diversity of the vegetation of older successional stages, a finding which was confirmed by Otto (1996).

Grass cover is the second important factor differentiating the bug communities of the sampled wildflower strips, explaining 12% of the species data. Numbers of species and individuals again show no response, indicating that the differences are based on the bug species composition. The effect of grass cover in June is independent of that of age, both factors showing no overlap in the CCA, although grass cover itself is clearly correlated with age, only rarely reaching high values before the third year. The comparatively great variability in bug species composition in grassy sites showing in Fig. 2 reflects a similar increase in variability in plant species composition observed in ≥ 3rd year grassy sites, where different spontaneous plant species dominate increasingly depending on site conditions (Chapter 2).

The total abundance of species is positively correlated with their frequency of occurrence in wildflower strips and the presence of the species in the surroundings. Commonly found patterns of positive correlations between abundance and frequency of closely related, ecologically similar species are described by Hanski (1982) and Brown (1984). Brown (1984) explains these as a result of several premises:

1) species respond to the distribution of suitable sites, 2) the similarity of combinations of required environmental variables decreases with increasing distance between sites, 3) closely related, ecologically similar species mostly differ in few niche dimensions. These patterns lead us to conclude that species abundant in the few wildflower strips sampled, are also likely to be present in strips with similar characteristics, at least in the same region, and in suitable sites in the surrounding arable landscape. Conversely, species which were not found in the surroundings tend to have a low abundance and frequency in wildflower strips. They probably have specific demands from their habitat which are not fulfilled by the surroundings in general and which either are not ideal in the wildflower strips, or the species are little mobile and thus restricted to local populations. Of course there are a few exceptions to this general relationship between abundance and dispersion, such as those species which have a high local abundance but are mostly restricted to single wild flower strips (e.g. *Amblytylus nasutus*).

Responses of bug families

Within the Miridae numbers of species and individuals are lowest in the first year, presumably because not all potential species have arrived. Those which are abundant are typically extreme generalist species such as *Lygus rugulipennis* and *L. pratensis*. From the second year on, more species are present. These include a number of more oligophagous species and species overwintering as eggs, which occur in very high numbers (*Dicyphus globulifer*, *Adelphocoris lineolatus*, *Orthops campestris*, *Megalocoleus molliculus*, *Leptopterna dolobrata*, *Calocoris norvegicus*). Lygaeidae occur almost exclusively in the oldest wildflower strips; however, only two species develop locally high abundances: *Platyplax salviae* in strips where the host plant *Salvia pratensis* grows, and *Rhyparochromus pini* which was abundant in 2 strips for unknown reasons. Since many Lygaeidae, but not *Platyplax salviae* and *Kleidocerys resedae*, live mostly on the soil surface, they are easily missed by sweep-netting, and they may be under-represented in our samples (Wagner E. 1966; Wachmann E. 1989; Péricart J. 1998). For example Simon (1998) shows, that unsprayed crop edges resembling wildflower strips in their first year can be rich in epigaeic Lygaeidae, which mostly require warm and dry sites with open soil. However, some species may be slow to colonize wildflower strips because of their low mobility or special habitat requirements such as the presence of seeds as food, which first have to accumulate. The numbers and abundance of most Pentatomidae species remained constant during succession, apart from *Eurydema oleraceum* and *Palomena viridissima*, which declined and are both known to feed on crops. The numbers of Pentatomidae also respond positively to grass cover, which is more difficult to explain because, except for *Aelia acuminata*, none of the species are specialized on grass or are typical for grassland, although some others are polyphagous, also feed on grass and are common in cereal fields (Tischler W. 1937). Two species of Nabidae, *Nabis pseudoferus* and *Nabis ferus*, both highly mobile generalist predators, are abundant and present in most wildflower strips. Both species live in various agricultural habitats and react positively to grass cover. While *N. pseudoferus*, a species typical of grassland and crops, is evenly distributed among strips of different age, *N. ferus*, a species typical of young ephemeral habitats, decreases in abundance during succession (Remane R. 1958; Southwood T.R.E. & Leston D. 1959; Péricart J. 1987; Hattwig F. 1997). Of the Coreidae, only *Coreus marginatus*, the single mesophilic species, reaches some abundance. Although it occurs in most strips, it tends to be most abundant in 1st year sites. The Rhopalidae are all generalist species and thus are distributed more or less evenly between wildflower strips of different age, although abundances vary greatly between individual strips. The Anthocoridae, represented by three species of the genus *Orius*, are highly mobile generalist predators and accordingly showed no response to age or grass cover (Southwood T.R.E. 1960; Péricart J. 1972). Species of other families, which are mono- or oligophagous and require warm and dry habitats, are too few and scarce to show any general trends.

Patterns in species traits

The majority of species found in wildflower strips are known to be quite mobile, and some are strong fliers. Species which mostly occur as brachypterous to submacropterous forms, i.e. are little mobile, such as *Nabis brevis*, *Aptus mirmicoides*, *Scolopostethus affinis*, *Raglius alboacuminatus*, *Tropistethus holosericus*, *Chlamydatus pulicarius*, *C. pullus*, *Catoplatus fabricii*, and females of *Leptopterna dolobrata*, showed a tendency to increase in species number and abundance with increasing age of the strips. However, because these species were generally rare and occurred only locally at low abundance, no statistical analysis of their distribution pattern was possible. Their scarcity is not surprising, as the arable landscape consists mainly of temporally and to a certain degree spatially unstable habitats, that have to be recolonized regularly. This is no problem for mobile insect species, while less mobile ones only have a chance to occur in the vicinity of stable habitat islands and require time and connecting habitat elements to colonize new habitats. Although wildflower strips are persistent for up to six years, the pool of bug species present is largely limited by their mobility, independent of other species traits. For a longer successional period of up to 60 years Brown (1985) found a similar, but also not significant, trend.

Species traits, like the feeding specificity, the number of generations per year or the overwintering stage, respond to the age or the grass cover of wildflower strips. The response occurs either in the number of species or in the number of individuals present. For a quantitative analysis, the latter has the advantage of avoiding any bias caused by rare species (Brown V.K. 1986). On the other hand, the reaction of the number of individuals has to be interpreted with caution because it can be strongly influenced by one or a few dominating species. There is also a problem if abundances of species fluctuate strongly from year to year and thus warp the responses (Schowalter T.D. 1996). In our study, this seems not to be a serious problem since a comparison of the data presented here with a second data set from the subsequent year yields similar patterns of species distribution. Possible phylogenetical influences on trait dispersion cannot be controlled, because of small and varying numbers of species in different bug families (Felsenstein J. 1985).

A higher proportion of zoophagous individuals in 1st year wildflower strips is mainly a result of lower numbers of phytophagous species in young strips. The zoophagous Nabidae and Anthocoridae species recorded are all highly mobile, unspecific predators, that are generally common in arable land although they do show habitat preferences. The early abundance of these species runs contrary to the trend found in other studies for predators to increase during succession; however, in most cases this is because of the accumulation of more specialist species (Brown V.K. & Southwood T.R.E. 1987; Southwood T.R.E. 1988; Russell E.P. 1989; Price P.W. 1991; Greiler H.-J. 1994).

Among the phytophagous bugs, there were few monophagous species and their numbers were mainly low, though they tended to increase with age. For monophagous species living on host plants that are not abundant everywhere, i.e. occur in patches, the patch size and frequency as well as the durational stability of the host plant are of major importance (Southwood T.R.E. 1987; Zabel J. & Tscharntke T. 1998). Dispersal is always associated with a cost in terms of energy and time, and a high risk of not finding a host plant (Southwood T.R.E. 1977; Rankin M.A. & Burchsted J.C.A. 1992). For these reasons, monophagous bugs are rarely specialized on annual plant species typical of ephemeral habitats and early successional stages, but are more frequently associated with persistent plants of more advanced successional stages (Southwood T.R.E. 1987; Novotny V. 1994; Novotny V. 1995). They are usually not specialized on single grass species, either; indeed, their numbers tend to decrease with increasing grass cover, because high grass cover leads to the accumulation of plant litter, a subsequent decrease in vegetation cover, and thus low numbers and abundances of potential herbal host plants (Chapter 2).

For oligophagous and polyphagous bugs, the numbers of species are similar in all ages of wildflower strips, but the abundances of oligophagous species increase with age while those of polyphagous species decrease. Polyphagous species are the only phytophagous bugs abundant in the first year, reflecting the fact that they do not depend on the presence of special host plants and accordingly are mostly common in the surroundings. While their proportion of all individuals decreases with age, absolute numbers remain relatively constant in older strips. They show a slight maximum in the second year, which is due to a high abundance of *Adelphocoris lineolatus*. The other abundant polyphagous species are all known to occur in crops, and some may even be responsible for economic damage (Tischler W. 1937; Afscharpour F. 1960; Hattwig F. 1997). In wildflower strips they show differing trends. While *Calocoris norvegicus* gains in abundance, *Lygus rugulipennis*, *L. pratensis* and *Palomena viridissima* all decrease in abundance. This is supposedly due to generalists not being able to cope with the reduced palatability of plants in vegetation of increasing successional age, which is based on better defences of perennial plants against herbivory and lower nitrogen contents in older plant material (Coley P.D. 1980; Reader P.M. & Southwood T.R.E. 1981). The trends observed in relative abundances are supported by similar trends in species numbers of Heteroptera found by Brown (1985). For other insect groups, i.e. sap feeding insects in general (Thysanoptera, Homoptera, most phytophagous Heteroptera) and Curculionidae, a similar decrease of the niche breadth has been observed in advancing succession, at least in pre-forest stages (Brown V.K. & Southwood T.R.E. 1983; Brown V.K. & Hyman P.S. 1986; Novotny V. 1994; Novotny V. 1995).

Abundances of oligophagous species are dominated by *Megalocoleus molliculus* and to a lesser degree *Leptopterna dolobrata*, which have a maximum in the oldest strips, and by *Dicyphus globulifer*, which is commonest in the second year. The low abundance of oligophagous species in the first year is partly due to host plants still being scarce, as the abundance of these species corresponds with that of their host plants. The rate of colonization may also play a role, although we could show for *D. globulifer* and *M. molliculus* that colonization of isolated patches of their host plants by a few individuals occurred within a period of six weeks in spring to early summer up to a distance of at least 140 m from a source. *M. molliculus* is generally known to be a mobile species (Southwood T.R.E. 1960; Ullrich K.S. & Edwards P.J.E. 1999). The female of *L. dolobrata*, on the other hand, is mostly brachypterous and of low mobility, which slows colonization, although the species is frequent in pathway verges (Southwood T.R.E. & Leston D. 1959; Afscharpour F. 1960; Uehlinger G. 2000). The fact that the numbers of oligophagous species reacted positively to grass cover is because about one third of the species recorded feed on grass.

The number of generations produced per year is the only life history trait considered here directly related to the reproduction rate of a species. In terms of species numbers, the proportion of species with only 1 generation per year increases slightly, but not significantly, with age. In terms of abundance, there is a huge increase from roughly one quarter of individuals in the first year to three quarters in the second year. This shows that many species with 1 generation per year are able to colonize wildflower strips within the first season, but that reproduction is relatively slow and they do not reach high abundances. This is achieved only by species with

> 1 generation per year, which is an important characteristic generally found in many pioneer species (Southwood T.R.E. 1977; Brown V.K. 1985; Brown V.K. & Southwood T.R.E. 1987; Novotny V. 1995). Their decline in older strips is probably connected with other species traits; for example, Brown (1986) suggests that they require high food quality throughout the season, and that this is more available in more open, ruderal plant communities. A similar decline of species with > 1 generation per year in advancing succession has been found in various other groups of insects (Brown V.K. & Southwood T.R.E. 1983; Brown V.K. 1985; Brown V.K. & Southwood T.R.E. 1987; Novotny V. 1995).

Although grass cover is mostly high in old wildflower strips, abundances of species with > 1 generation per year respond positively to grass cover; this is because some typical pioneer species with > 1 generation per year are abundant in grassy strips. The only other dominant species is *Notostira erratica*, which together with the less abundant *N. elongata*, are the only grass specialists we recorded producing > 1 generation per year. These species feed on grass leaves which are available all season, whereas the other species found all feed on the ovules and seeds of grasses (McNeill S. 1973; Gibson C.W.D. 1976). These resources are predominantly available for only a restricted period, which might be a cause for most of these species being limited to 1 generation per year. As grass cover also increases the numbers of species also found in pathway verges, we conclude that grassy verges probably serve as a source for the colonization of wildflower strips, at least of grassy ones. Pathway verges in the region usually underlie frequent cutting, which these species must tolerate. This is favoured by a short generation time, which is a precondition for multivoltinism but can also occur in univoltine species (Southwood T.R.E. 1960; Morris M.G. 1979).

The proportion of bug species overwintering in the egg stage increases significantly from the first to the second year. The total number of individuals increases even more strongly, and the increase continues in older strips. Species overwintering as adults have an advantage in ephemeral habitats because they can disperse directly after overwintering and thus are independent of persistent host plants. Species overwintering as eggs, on the other hand, depend on food plants in their overwintering site for development in spring, and thus cannot use annual host plants. In addition, their dispersal occurs later in the season. Accordingly, they colonize wildflower strips later and particularly when the abundance of perennial plant species has increased. After successful colonization, a new generation will only be present in the subsequent year, which accounts for the low numbers of individuals in the first year. The survival rate of insects overwintering as eggs is mostly higher than that of adults, which gives an advantage to those overwintering as eggs in older successional stages, once favourable conditions exist (Leather S.R. et al. 1993). In wildflower strips, all bug species overwintering in the egg stage belong to the Miridae, although this trait does occur occasionally in other bug families (Fauvel G. 1999). Within the Miridae, the majority of species overwinter in the egg stage. Those overwintering as adults are mainly the extreme pioneer species (*Lygus* spp.) or some common species feeding on grass leaves (*Notostira* spp.). We were able to show changes in overwintering strategy during succession in one taxon – the Miridae. Although such trends have rarely been investigated, our results are similar to those found for a successional sere in a wider range of insects by Brown (1986), for a neighbouring disturbed versus undisturbed site in spiders by Maelfait & De Keer (1990), and as a characteristic of common versus rare species in British butterflies by Hodgson (1993).

The presence of a species in the surroundings of wildflower strips appears to have no influence on the rate of colonization. In addition, wildflower strips of different ages and thus habitat characteristics are not colonized selectively by species occurring in the surroundings. This may be the case for individual species, though, especially for comparatively rare and specialized ones, with low statistical impact. A high grass cover, on the other hand, enhances species that also occur in pathway verges.

Common species increase in numbers from the first to the second year, effecting a slight increase in total species numbers, while medium common species only increase in numbers from the third year on. The decrease in medium common species with increasing grass cover can be explained by medium common species probably requiring more specific habitat features, which decrease with increasing grass cover.

Strategies of bug species

Although the proportions of species exhibiting particular traits change during early succession in wildflower strips, the combinations of traits vary widely between species, rendering a clear definition of strategies difficult. Nevertheless, it is clear that species with certain combinations are characteristic for particular stages in the succession. This is the case for monophagous species, which all have only 1 generation per year and mostly overwinter as eggs (only Miridae) or at various stages. Such species are typical 'competitors' of late successional stages, which are rare in the surroundings. Species overwintering in the egg stage tend to colonize wildflower strips late. Other traits may not inhibit the early arrival of species in wildflower strips but have a strong influence on shifts in the relative abundances of species. Species abundant in the first year are mostly typical colonizers, which are highly mobile phyto- and zoophagous generalist species with > 1 generation per year, overwintering as adults, and present elsewhere in the surroundings (Brown V.K. 1985). These are soon followed by other polyphagous and oligophagous species possessing various combinations of species traits, which gain abundance either with time or depending on the abundance of their host plants. Among these, species feeding on grass (on the infructescences, see above) found in wildflower strips stand out as a type with distinct characteristics, i.e. only 1 generation per year, overwintering as egg (Miridae), and inhabiting pathway verges. These features can be related to the typical phenology and management of grasses, and to their abundance in the agricultural landscape.

Implications for the management of wildflower strips

This study has shown that wildflower strips provide the habitat for a high diversity and abundance of heteropteran bugs. In general, species that are present in the surroundings reach high abundances in many wildflower strips. Species that depend on less common, dispersed host plants, tend to be very mobile. As a consequence, a basic set of rather common bug species is easily enhanced in wildflower strips. In contrast, it is more difficult to promote rare bug species requiring specific habitat characteristics with scarce patchy distributions, as these bug species tend to be less mobile (Southwood T.R.E. 1960). Our results suggest ways in which the wildflower strips can be managed to enhance the diversity.

• To create habitats for a diverse bug fauna the development of the vegetation in wildflower strips is decisive. As colonization takes time, and the composition of perennial plant species has a strong impact on the bug community, wildflower strips should be managed for a species rich and structurally diverse perennial flora (Lawton J.H. 1978; Brown V.K. & Southwood T.R.E. 1983; Southwood T.R.E. et al. 1983). This can be optimized by choosing plant species which have a rich associated insect fauna. According to Southwood (1985) these are usually species which have been common in the region for a long time, belong to a large group of related species, and have a complex structure.

• As Simon (1998) shows, unsprayed crop edges can have a very diverse bug fauna rich in epigaeic Lygaeidae and Scutelleridae requiring sites with open soil. Although we did not specifically sample for this component of the bug fauna, it seems probable that the initial stages of wildflower strips are a valuable habitat for epigaeic species, especially where habitat conditions are otherwise favourable, e.g. on calcareous sands, in sites with a rich spontaneous flora and a diverse landscape structure. For other insect groups, e.g. beetles, monophagous species living on annual plants have been found in early succession (Greiler H.-J. 1994). Many of these species are rare, but can probably be promoted by the establishment of wildflower strips.

• For many bug species, colonization does not seem to be a problem. However, some species of the epigaeic fauna are relatively immobile. It is important that when new sites are established, some are located adjacent to existing or previous sites, thus augmenting the temporal and spatial constancy of favourable habitat conditions (Southwood T.R.E. et al. 1983; Southwood T.R.E. 1987; Simon H. 1998).

• Wildflower strips should be managed to avoid the development of a dense grass cover, as a high grass cover is unfavourable for most non-generalist species, but enhances a set of species feeding on grasses and other common meadow species. These are scarce in other wildflower strips but mostly also occur in grassy pathway verges and other grassy sites. Since these species are well represented in the surroundings, they contribute comparatively little to the enhancement of a rich bug diversity on a landscape level.

• As wildflower strips of different age yield similar numbers of species and dominance distributions, except in the first year, but vary in bug species composition, on a landscape level bug diversity is maximized by the creation of a high diversity of strips differing in age, vegetation composition and structure. These ideally should be located in sites varying in habitat conditions, i.e. widely dispersed across the landscape.

References

Achtziger, R. 1991. Zur Wanzen- und Zikadenfauna von Saumbiotopen - Eine ökologisch-faunistische Analyse als Grundlage für eine naturschutzfachliche Bewertung. Berichte ANL 15: 37-68.

Achtziger, R. 1995. Die Struktur von Insektengemeinschaften an Gehölzen: Die Hemipteren-Fauna als Beispiel für die Biodiversität von Hecken- und Waldrandökosystemen. Bayreuther Forum Ökologie 20: 183.

Achtziger, R., Scholze, W. & Schuster, G. 1992. Rote Liste gefährdeter Landwanzen (Heteroptera, Geocorisae) Bayerns. Schriftenreihe Bayerisches Landesamt für Umweltschutz 111: 87-95.

Afscharpour, F. 1960. Ökologische Untersuchungen über Wanzen und Zikaden auf Kulturfeldern in Schleswig-Holstein. Zeitschrift für angewandte Zoologie 47: 257-301.

Belyea, L.R. & Lancaster, J. 1999. Assembly rules within contingent ecology. Oikos 86: 402-416.

Bernhardt, K.-G. 1988. Faunistisch-ökologische Untersuchungen auf Brachflächen in Baden-Württemberg. Wanzen. Arbeitsberichte Lehrstuhl Landschaftsökologie Münster 8: 163-169.

Borcard, D., Legendre, P. & Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology 73: 1045-1055.

Bornholdt, G. 1991. Auswirkungen der Pflegemaßnahmen Mahd, Mulchen, Beweidung und Gehölzrückschnitt auf die Insektenordnungen Orthoptera, Heteroptera, Auchenorrhyncha und Coleoptera der Halbtrockenrasen im Raum Schlüchtern. Marburger Entomologische Publikationen 2: 1-330.

Brown, J. 1984. On the relationship between abundance and distribution of species. The American Naturalist 124: 255-279.

Brown, V.K. 1985. Insect herbivores and plant succession. Oikos 44: 17-22.

Brown, V.K. 1986. Life cycle strategies and plant succession. In: Taylor, F. & Karban, R. (eds.) The evolution of insect life cycles, pp. 105-124. Springer-Verlag, New York.

Brown, V.K. & Hyman, P.S. 1986. Successional communities of plants and phytophagous Coleoptera. Journal of Ecology 74: 963-975.

Brown, V.K. & Southwood, T.R.E. 1983. Trophic diversity, niche breadth and generation times of exopterygote insects in a secondary succession. Oecologia 56: 220-225.

Brown, V.K. & Southwood, T.R.E. 1987. Secondary succession: Patterns and strategies. In: Gray, A.J., Crawley, M.J. & Edwards, P.J. (eds.) Colonisation, succession and stability, pp. 315-337. Blackwell Scientific Publications, Oxford.

Burghardt, G. 1977. Faunistisch-ökologische Studien über Heteropteren im Vogelsberg. Beiträge zur Naturkunde in Hessen 9/10: 1-166.

Coley, P.D. 1980. Effects of leaf age and plant life history patterns on herbivory. Nature 284: 545-546.

Dolling, W.R. 1991. The Hemiptera. Oxford University Press.

Duelli, P. & Obrist, M. 1998. In search of the best correlates for local biodiversity in cultivated areas. Biodiversity and Conservation 7: 297-309.

Duffey, E. 1978. Ecological strategies in spieders including some characteristics of species in pioneer and mature habitats. Symposium of the Zoological Society London 42: 109-123.

Fauvel, G. 1999. Diversity of Heteroptera in agroecosystems: role of sustainability and bioindication. Agriculture, Ecosystems and Environment 74: 275-303.

Felsenstein, J. 1985. Phylogenies and the comparative method. The American Naturalist 125: 1-15.

Gibson, C.W.D. 1976. The Importance of Foodplants for the Distribution and Abundance of some Stenodemini (Heteroptera: Miridae) of Limestone Grassland. Oecologica 47: 352-364.

Greiler, H.-J. 1994. Insektengesellschaften auf selbstbegrünten und eingesäten Ackerbrachen. Agrarökologie 11.

Günther, H., Hoffmann, H.-J., Remane, R., Rieger, C., Simon, H. & Winkelmann, H. 1998. Rote Liste der Wanzen Rote Liste gefährdeter Tiere Deutschlands, pp. 235-242. Bundesamt für Naturschutz, Bonn-Bad Godesberg.

Günther, H. & Schuster, G. 1990. Verzeichnis der Wanzen Mitteleuropas. Deutsche Entomologische Zeitschrift Neue Folge 37: 361-396.

Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. Oikos 38: 210-211.

Hattwig, F. 1997. Wanzen (Heteroptera) in Getreidekulturen unterschiedlicher Bewirtschaftung bei Braunschweig. Braunschweiger Naturkundliche Schriften 5: 353-358.

Hodgson, J.G. 1993. Commonness and rarity in British butterflies. Journal of Applied Ecology 30: 407-427.

Jenny, M. & Weibel, U. 1999. Qualität und Quantität des ökologischen Ausgleichs in drei intensiv genutzten Ackerbauflächen des Klettgaus. Mitteilungen der Naturforschenden Gesellschaft Schaffhausen 44: 107-116.

Jenny, M., Weibel, U. & Buner, F. 1999. Der ökologische Ausgleich in intensiv genutzten Ackerbaugebieten des Klettgaus und seine Auswirkungen auf die Brutvogelfauna. Mitteilungen der Naturforschenden Gesellschaft Schaffhausen 44: 203-221.

Keddy, P.A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3: 157-164.

Kullenberg, B. 1944. Studien über die Biologie der Capsiden. Dissertation. Universität Uppsala, Uppsala.

Lawton, J.H. 1978. Host-plant influences on insect diversity: the effects of time and space. In: Diversity of insect faunas. Symposium of the Royal Entomological Society of London. Mound, L.A. & Waloff, N., (eds.). 105-125.

Leather, S.R., Walters, K.F.A. & Bale, J.S. 1993. The ecology of insect overwintering. Cambridge University Press, Cambridge.

Leston, D. & Scudder, G.G.E. 1956. A key to larvae of the families of British Hemiptera-Heteroptera. The Entomologist 89: 223-231.

Maelfait, J.-P. & De Keer, R. 1990. The border zone of an intensively grazed pasture as a corridor for spiders Araneae. Biological Conservation 54: 223-238.

McNeill, S. 1973. The dynamics of a population of Leptopterna dolobrata (Heteroptera: Miridae) in relation to its food resources. Journ. animal ecology 42: 495-507.

Morris, M.G. 1969. Differences between the invertebrate faunas of grazed and ungrazed chalk grassland. III. The heteropterous fauna. Journal of Applied Ecology 6: 475-487.

Morris, M.G. 1979. Responses of grassland invertebrates to management by cutting. II. Heteroptera. Journal of Applied Ecology 16: 417-432.

Moulet, P. 1995. Hémiptères Coreoidea, Pyrrhocoridae, et Stenocephalidae Euro-méditerranéens. Faune de France 81. Fédération Francaise des Sociétés de Sciences Naturelles, Paris.

Novotny, V. 1994. Association of polyphagy in leafhoppers (Auchenorrhyncha, Hemiptera) with unpredictable environments. Oikos 70: 223-232.

Novotny, V. 1995. Relationships between life histories of leafhoppers (Auchenorrhyncha - Hemiptera) and their host plants (Juncaceae, Cyperaceae, Poaceae). Oikos 73: 33-42.

Økland, R.H. & Eilertsen, O. 1994. Canonical correspondence analysis with variation partitioning: some comments and an application. Journal of Vegetation Science 5: 117–126.

Otto, A. 1994. Für die Schweiz neue oder selten gesammelte Wanzen-Arten (Heteroptera). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 67: 189-197.

Otto, A. 1995. Für die Schweiz neue oder selten gesammelte Wanzen-Arten (Heteroptera) - Zweiter Beitrag. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 68: 137-142.

Otto, A. 1996. Die Wanzenfauna montaner Magerwiesen und Grünbrachen im Kanton Tessin (Insecta: Heteroptera) - Eine faunistisch ökologische Untersuchung. Dissertation. ETH Zürich, Zürich.

Péricart, J. 1972. Hémiptères Anthocoridae, Cimicidae et Microphysidae de l' ouest-palearctiques. Faune de l'Europe et du Bassin Méditerranéen 7, Paris.

Péricart, J. 1983. Hémiptères Tingidae euro-méditerranéens. Faune de France 69. Fédération Francaise des Sociétés de Sciences Naturelles, Paris.

Péricart, J. 1984. Hémiptères Berytidae euro-méditerranéens. Faune de France 70. Fédération Francaise des Sociétés de Sciences Naturelles, Paris.

Péricart, J. 1987. Hémiptères Nabidae d' Europe occidentale et du Maghreb. Faune de France 71. Fédération Francaise des Sociétés de Sciences Naturelles, Paris.

Péricart, J. 1998. Hémiptères Lygaeidae d' Europe occidentale et du Maghreb. Vol. 1, 2 & 3 . Faune de France 84 A, B, C. Fédération Francaise des Sociétés de Sciences Naturelles, Paris.

Price, P.W. 1991. Insect Ecology. 2nd ed. John Wiley & Sons, New York.

Rankin, M.A. & Burchsted, J.C.A. 1992. The cost of migration in insects. Annual Review of Entomology 37: 533-559.

Reader, P.M. & Southwood, T.R.E. 1981. The relationship between palatability to invertebrates and the successional status of a plant. Oecologia 51: 271-275.

Remane, R. 1958. Die Besiedlung von Grünflächen verschiedener Herkunft durch Wanzen und Zikaden im Weser-Ems-Gebiet. Zeitschrift für angewandte Entomologie 42: 353-464.

Rieger, C. 1979. Vorschlag für eine Rote Liste der Wanzen in Baden Württemberg (Heteroptera). Veröffentlichungen für Naturschutz und Landschaftspflege Baden-Württemberg 49/50: 259-269.

Rieger, C. 1984. Zur Systematik und Faunistik der Weichwanzen Orthops kalmi Linné und Orthops basalis Cost (het. Miridae). Veröffentlichungen für Naturschutz und Landschaftspflege Baden-Württemberg 59/60: 457-465.

Russell, E.P. 1989. Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. Environmental Entomology 18: 590-599.

Sanderson, R.A. 1992. Diversity and eveness of Hemiptera communities on naturally vegetated derelict land in NW England. Ecography 15: 154-160.

Schowalter, T.D. 1996. Insect Ecology - An Ecosystem Approach. Academic Press, San Diego.

Schwörbel, W. 1966. Ökologie und Faunistik der Wanzen und Zikaden auf dem Tübinger Spitzberg Der Spitzberg bei Tübingen. Die Natur- und Landschaftsgebiete Baden-Württembergs, pp. 759-854. , Ludwigsburg.

Simon, H. 1998. Vergleichende Untersuchungen zur Wanzenfauna (Heteroptera) von Ackerrandstreifen im südlichen Rheinland-Pfalz. Schriftenreihe der Landesanstalt für Pflanzenbau und Pflanzenschutz 6: 237-242.

Southwood, T.R.E. 1960. The flight activity of Heteroptera. Transaction of the Royal Entomological Society London 112: 173-220.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 46: 337-365.

Southwood, T.R.E. 1985. Interactions of plants and animals: patterns and processes. Oikos 44: 5-11.

Southwood, T.R.E. 1987. Plant variety and its interaction with herbivorous insects. In: Insect-Plants - Proc. 6th Intern. Symp. Insect-Plant Relationship. Labeyrie, V., Fabres, G. & Lachaise, D., (eds.) Dr. W. Junk Publishers, Pau 1986. 61-69.

Southwood, T.R.E. 1988. Tactics, strategies and templets. Oikos 52: 3-18.

Southwood, T.R.E., Brown, V.K. & Reader, P.M. 1979. The relationship of plant and insect diversities in succession. Biological Journal of the Linnean Society 12: 327-348.

Southwood, T.R.E., Brown, V.K. & Reader, P.M. 1983. Continuity of vegetation in space and time: a comparison of insects' habitat templet in different successional stages. Researches in Populations Ecology Supplement 3: 61-74.

Southwood, T.R.E. & Leston, D. 1959. Land and water bugs of the British Isles. Warne & Co. Ltd., London.

ter Braak, C.J.F. & Smilauer, P. 1998. Canoco reference manual and user´s guide to Canoco for Windows. Centre for Biometry, Wageningen.

Tischler, W. 1937. Untersuchungen über Wanzen an Getreide. Arbeiten über physiologische und angewandte Entomologie aus Berlin-Dahlem 4: 193-231.

Uehlinger, G. 2000. Einfluß von Buntbrachen auf die Diversität der Wanzenfauna und des Samenvorrats im Boden einer Ackerlandschaft. Diplomarbeit. ETH Zürich.

Ullrich, K.S. & Edwards, P.J.E. 1999. The colonization of wild flower-strips by insects (Heteroptera). In: Maudsley, M. & Marshall, J. (eds.) Heterogeneity in Landscape Ecology, Proceedings of the 1999 IALE(UK) conference, IACR-Long Ashton Research Station, Bristol. 131-138.

Vietmeier, A., Haumes, M. & Plate, H.-P. 1996. Einige wichtige Vertreter der räuberischen Blumenwanzen (Heteroptera: Anthocoride) und ihre Eignung zur biologischen Schädlingsbekämpfung. Mitteilungen aus der biologischen Bundesanstalt für Land- und Forstwirtschaft Berlin-Dahlem 325.

Wachmann, E. 1989. Wanzen beobachten - kennenlernen. Neumann-Neudamm, Melsungen.

Wagner, E. 1952. Blindwanzen oder Miriden. Fisher, Jena.

Wagner, E. 1966. Wanzen oder Heteropteren. 1. Pentatomorpha. G. Fischer, Jena.

Wagner, E. 1967. Wanzen oder Heteropteren. 2. Cimicomorpha. G. Fischer, Jena.

Wagner, E. 1970/71. Die Miridae Hahn, 1831, des Mittelmeerraumes und der Makronesischen Inseln (Hemiptera, Heteroptera). Teil 1. Entomologische Abhandlungen Supplement zu Band 37.

Wagner, E. 1973. Die Miridae Hahn, 1831, des Mittelmeerraumes und der Makronesischen Inseln (Hemiptera, Heteroptera). Teil 2. Entomologische Abhandlungen Supplement zu Band 39.

Wagner, E. 1975. Die Miridae Hahn, 1831, des Mittelmeerraumes und der Makronesischen Inseln (Hemiptera, Heteroptera). Teil 3. Entomologische Abhandlungen Supplement zu Band 40.

Wagner, E. & Weber, H.-H. 1964. Hétéroptères Miridae. Faune de France 67. Fédération Francaise des Sociétés des Sciences Naturelles, Paris.

Wagner, E. & Weber, H.-H. 1978. Die Miridae Hahn, 1831, des Mittelmeerraumes und der Makronesischen Inseln (Hemiptera, Heteroptera). Teil 4. Entomologische Abhandlungen Supplement zu Band 42.

Weiher, E. & Keddy, P.A. 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. Oikos 74: 159-164.

Zabel, J. & Tscharntke, T. 1998. Does fragmentation of Urtica habitats affect phytophagous and predatory insects differentially? Oecolgia 116: 419-425.

Chapter 4. The colonization of wildflower strips by insects (Heteroptera)

Karin S. Ullrich and Peter J. Edwards

In: Maudsley, M. & Marshall, J. (eds.) Heterogeneity in Landscape Ecology, Proceedings of the 1999 IALE(UK) conference. IACR-Long Ashton Research Station, Bristol 131-138.

Abstract

In a project to investigate the contribution of wildflower strips to general plant and insect diversity in intensive arable landscapes more than 200 flowering plant and 100 Heteroptera species have been found. The most abundant bug species are mainly generalists, including many polyphagous and oligophagous species with several host plant species. Because dispersal abilities are of major importance for the colonization of these strips we studied bug dispersal experimentally by setting up small patches of host plants at different distances from a wildflower strip. The results show 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. None of the species caught in this experiment was found only in the wildflower strip; all species moved at least some distance into the crop, and individuals of some species reached a distance of 138 m within a few weeks or one generation. However, species differ in dispersal speeds, distances and patterns.

Introduction

In the early 1980's the first wildflower strips were introduced experimentally in Switzerland in an attempt to enhance general biodiversity in intensively used arable land. These wildflower strips are mostly sown with arable weeds and some ruderal plant species, but many other plant species recruit spontaneously. More than 200 plant species have been found in wildflower strips in the research area, the Klettgau. Plant species composition can vary considerably depending on the age of the strip, soil conditions and other environmental factors. Since 1993 farmers have been paid to maintain wildflower strips and other ecological compensation areas, and they must now allocate seven percent of their land to such use as a condition for receiving other subsidies. As a result wildflower strips have been introduced into the landscape on a large scale. The effects of these schemes on biodiversity are the subject of various research projects including the one described here.

The Klettgau is an area of intensively used arable land in the north of Switzerland. The region is relatively dry and warm , and the soils are gravelly, being derived from floodplain deposits, which are locally covered by loam. In 1991 the Swiss Ornithological Institute started a project to promote the grey partridge and the European hare in the Klettgau; together with the Canton of Schaffhausen office for Nature Conservation they sponsored the creation of a large number of wildflower strips, which are the subject of this study.

We are interested in how effectively wildflower strips contribute to the enhancement of biodiversity at a landscape level. This leads to some more concrete questions about which plant and insect species live in the strips, where they come from, and over what distances they can disperse. We hope that the answers will allow us to address more practical questions such as how far apart wildflower strips should be placed to ensure adequate colonization.

We chose the Heteroptera (Insecta: Hemiptera) as indicator group of overall insect diversity. The reason for this choice is that the true bugs are an ecologically very diverse group and it has been shown that bug diversity correlates closely with insect diversity in general (Duelli P. & Obrist M. 1998). Besides a survey of the vegetation and the Heteropteran fauna in wildflower strips, the dispersal of bugs was investigated in an experiment which we called the 'flower-window experiment', in which we set up small patches of the host plants of various bug species within fields.

Materials and methods

Flower-window experiment

We chose three common plant species of wildflower strips, *Silene alba*, *Achillea millefolium* and *Centaurea jacea*, on which we had formerly found rather host-specific bug species (Wagner E. 1952; 1966; 1967; 1970/71; 1973; 1975). At the beginning of April small individuals of these species were planted in separate plots (1 x 2 m^2) at seven distances from a wildflower strip (up to 138 m) in a soybean and a wheat field. Since the fields in the area are rather small, the plots were spread out over two different crops: soya adjacent to the wildflower strip and wheat at distances beyond 68 m from the strip.

The wildflower strip was isolated within the landscape, with no other wildflower strips or other possible sources of specialist bugs nearby. The plots were sprayed twice with pyrethrum within ten days to remove any bugs which may have been imported with the plants. By randomising the arrangement of the plots we tried to minimise any 'stepping stone' effect. We monitored the colonization of the plots by bugs by sampling them every two weeks from mid-May to mid-July. On each occasion we placed a sampling tent over an area of $1m^2$ in the centre of the plot and collected the insects for an 8 minute period with a suction sampler. We did the same in control areas within the crop and the wildflower strip.

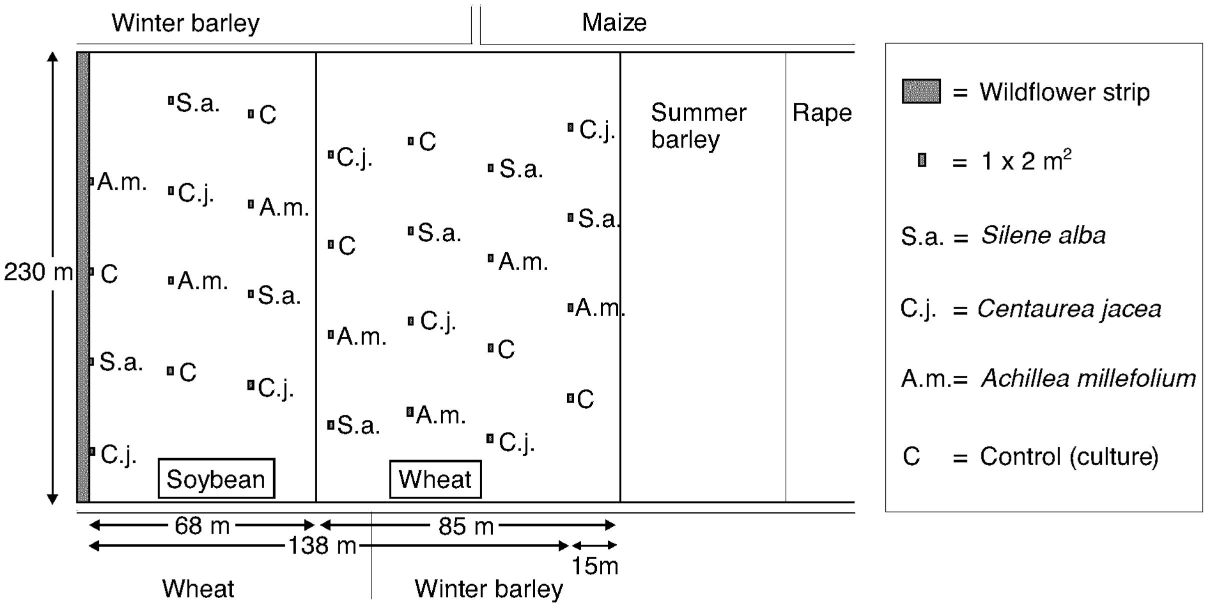


Fig. 1. Site plan of the flower-window experiment.

Results and Discussion

Altogether more than 100 bug species occur in wildflower strips in the Klettgau. Most of these are generalists. Among these are many oligophagous species as well as polyphagous species, which have host plants common in wildflower strips or elsewhere in the surroundings. A few rarer species also occur locally.

The three plant species in the experiment differed in their growth, *Achillea* producing the largest biomass and *Silene* the smallest. There were also differences in the structure of the two crops, soya and wheat, which may have affected the results. The soybean crop had a lower stature than the wheat. This certainly affected the microclimate of the plots, and also the growth and conspicuousness of the plants they contained.

Preferences

In general, the specialist bug species showed the expected preferences for their host plant, and were only found in the plots containing that species (Table 1). Interestingly, some polyphagous species like *Adelphocoris lineolatus* and *Lygus* species also showed preferences for particular plant species. Even the predatory *Orius* species, which were found on all plant species, showed preferences in the order *Achillea* > *Centaurea* > *Silene* > crop plants.

Table 1. Preferences for host plants

	Achillea millefolium	*Centaurea jacea*	*Silene alba*	Soybean	Wheat
phytophagous species					
oligophagous species					
Dicyphus globulifer			●		
Megalocoleus molliculus	●	•	•		
Chlamydatus pulicarius	●	•	•		
Carpocoris fuscispinus		●			
Dolycoris baccarum		●			
polyphagous species					
Adelphocoris lineolatus	●	•	•		
Lygus species	●	●	•	•	•
zoophagous species					
Orius species	●	●	•	•	•

The greater numbers of individuals collected on *Achillea* may have several different causes:

- a true preference
- an indirect preference due to the greater visual and olfactorial apparency (conspicuous inflorescences, aromatic foliage and flowers)
- an artefact due to the fine leaf structure offering less protection for the bugs during suction which thus might be more complete
- a bias due to the greater biomass of *Achillea*

Dispersal

Wildflower strips serve as a dispersal source for at least some bug species. Indeed, none of the bug species found in this experiment was found only in the wildflower strip. It seems that all of them are mobile and moved away from the flower strips. At least some individuals of most bug species reached the maximum distance (138 m) within a few weeks. Thus it is clear that arable land is no insuperable barrier for these species, which can fly over it or may even be present within it. However, the various bug species show different types of dispersal patterns as well as different dispersal speeds and distances of movement, as the following examples show.

Dicyphus globulifer

95% of all individuals of *Dicyphus globulifer* were found within about 100 m of the wildflower strip. The development of the population during the season can be clearly seen by the initially increasing and then decreasing numbers. In spite of the differences in numbers of individuals, the shape of the curve remains very similar. Beyond a distance of 23 m the number of individuals declines exponentially (Fig. 2).

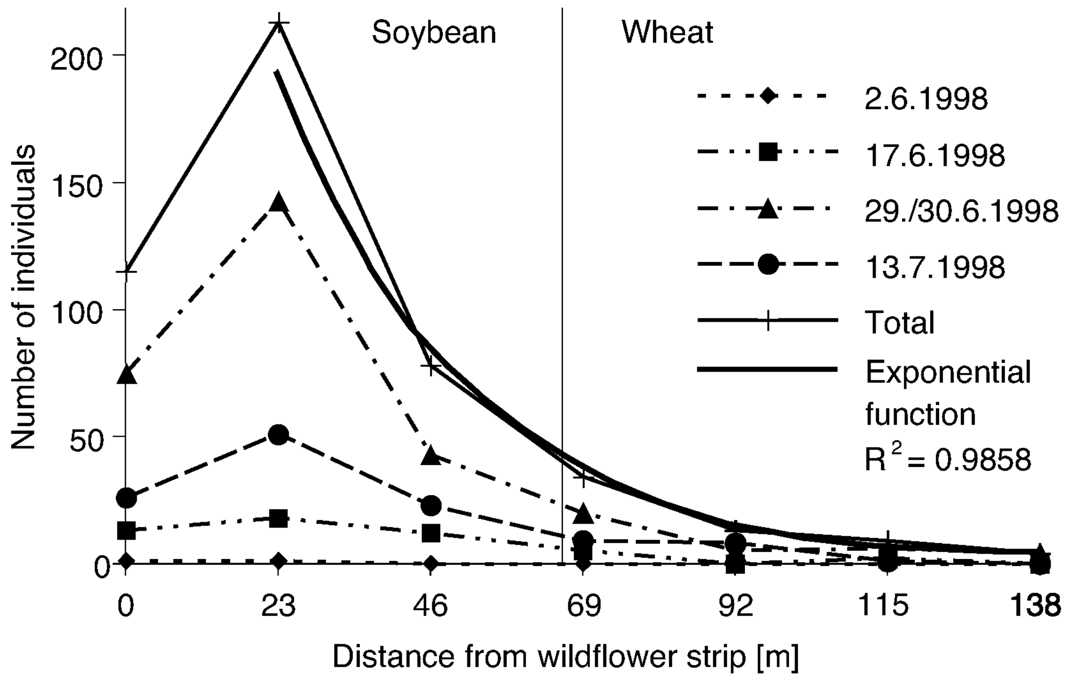


Fig. 2. *Dicyphus globulifer* on *Silene alba*

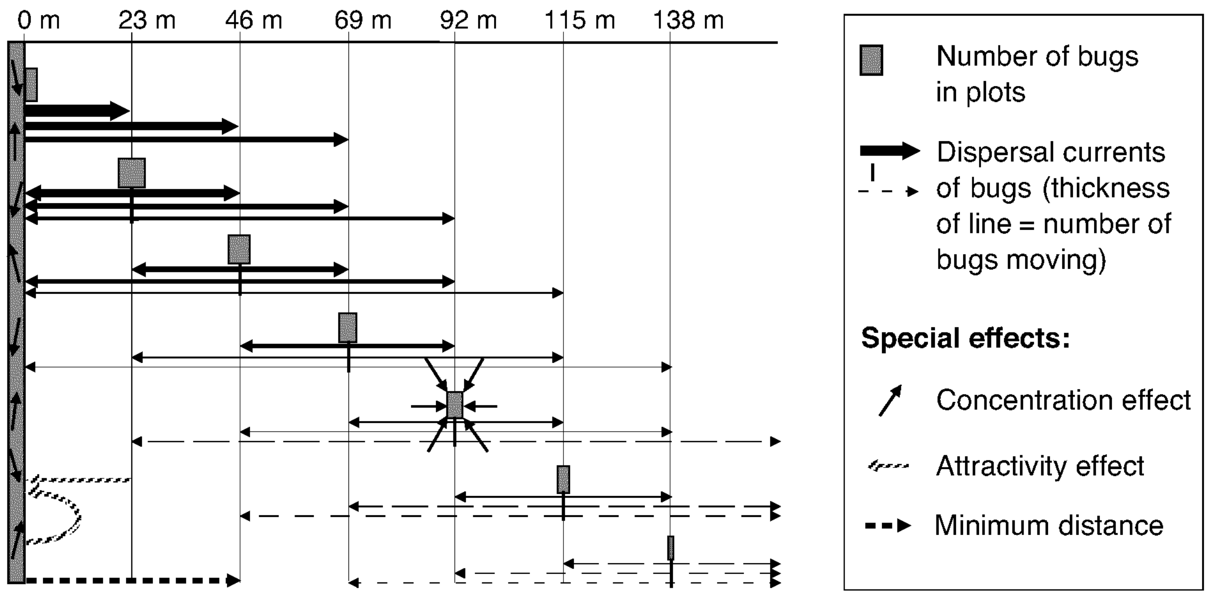


Fig. 3. Dispersal pattern of *Dicyphus globulifer*

This represents the theoretically simplest case of a regular decrease, which can be explained by a dispersal pattern shown in Fig. 3. According to Southwood (1960) species with a large number of host plants fly more than closely allied ones with a single host plant and species with a high level of flight activity are mainly associated with temporary habitats. Of all bug species found in the experiment *D. globulifer* is allied closest to its host plant, *Silene alba*, a perennial species. This might be a reason for the ideal dispersal pattern shown by *D. globulifer*.

The smaller numbers of individuals in the plot directly adjacent to the wildflower strip can be explained by one or several interacting effects (Fig. 3).

- Concentration effect – in the wildflower strip and the directly adjacent plot the bugs distribute over the whole length while they concentrate on the short sections of the plots within the field.
- Attractivity effect – the big area of the wildflower strip is more attractive for the bugs than the small plots, which has an effect over a certain distance depending on the species.
- Minimum distance – after taking off the bugs fly for a minimum distance.

Megalocoleus molliculus

The numbers of this species decrease in a more or less linear fashion with increasing distance and there is no tendency for reduced numbers in plots immediately adjacent to the wildflower strips. *Megalocoleus molliculus* reaches a distance of about 80m within less than four weeks; only a few individuals get further.

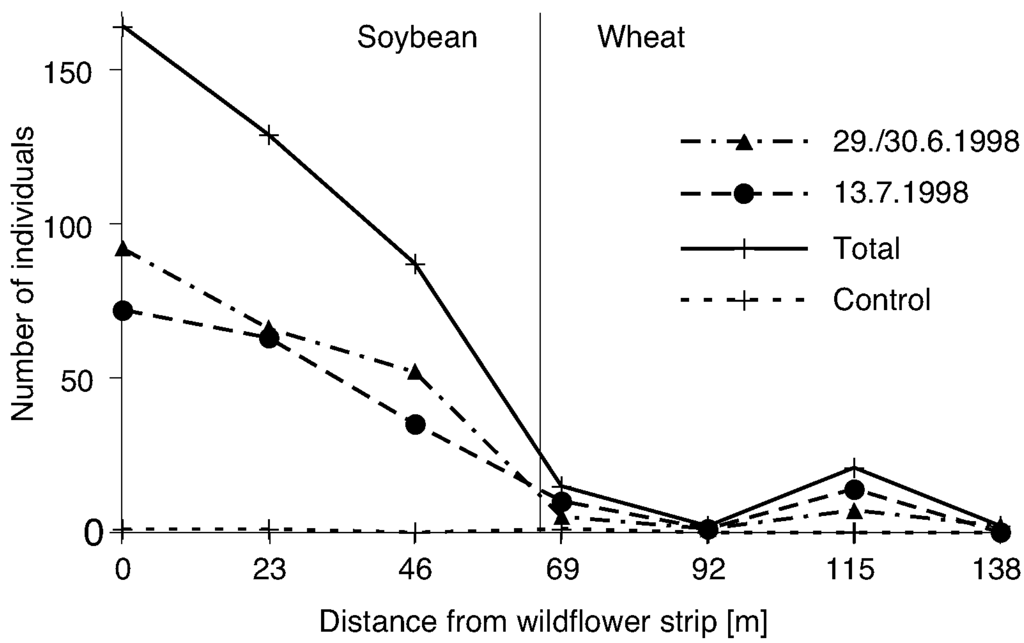


Fig. 4. *Megalocoleus molliculus* on *Achillea millefolium*

There are again several possible explanations for the linear to slightly convex shape of the curve. For example, it may be that this species only moves short distances at a time. However, it is also possible that the results reflect an effect of the change in crop from soya to wheat. In previous studies *M. molliculus* has been caught in great numbers by light traps and suction traps, which indicates a high flight activity of the species (Southwood T.R.E. 1960).

Other species, *Chlamydatus pulicarius*, *Carpocoris fuscispinus* and *Dolycoris baccarum*, show distribution patterns similar to those for *Megalocoleus molliculus* and *Dicyphus globulifer* but with fewer individuals.

Adelphocoris lineolatus and Lygus species

The dispersal patterns of some of the more ubiquitous species are more difficult to interpret. These patterns vary considerably with time but are similar for all plant species, which suggests that the same processes are at work in each case. The dispersal patterns of *Adelphocoris lineolatus* and the *Lygus* species developed in a similar way. At the beginning, these species were only found close to the wildflower strip in the soybean field. Later their numbers increased, but mainly in the soybean field with only few individuals in the wheat field; finally their numbers increased even more and at the same time they were found more evenly spread over all distances.

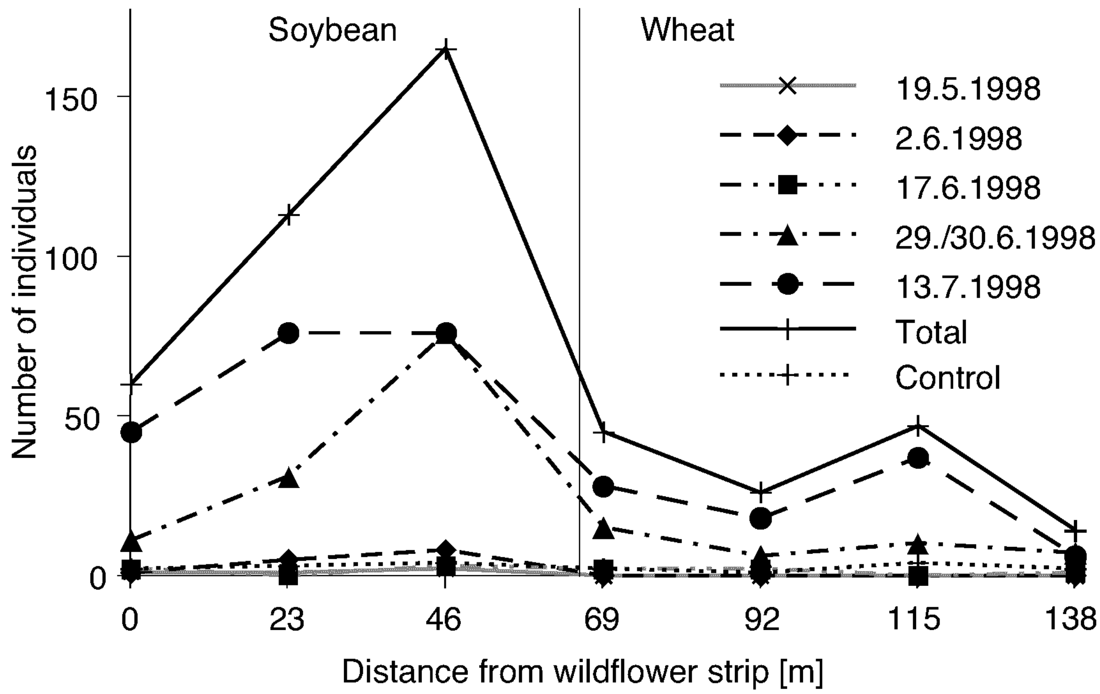


Fig. 5. *Lygus* species on all plant species

In this case it is impossible to differentiate between the potential effects of the distance and the crops. Thus it remains an open question whether the observed pattern has been caused by waves of immigration from the wildflower strip or the surroundings in general, or whether it merely reflects differences between the crops. *Lygus rugulipennis*, a species living on many annual plant species of temporary habitats, is known to be very mobile and even to migrate (Southwood T.R.E. 1960; 1962).

Orius species

The predatory *Orius* and *Nabis* species as well as *Stictopleurus punctatonervosus* show a more or less even distribution over all distances (Fig. 6).

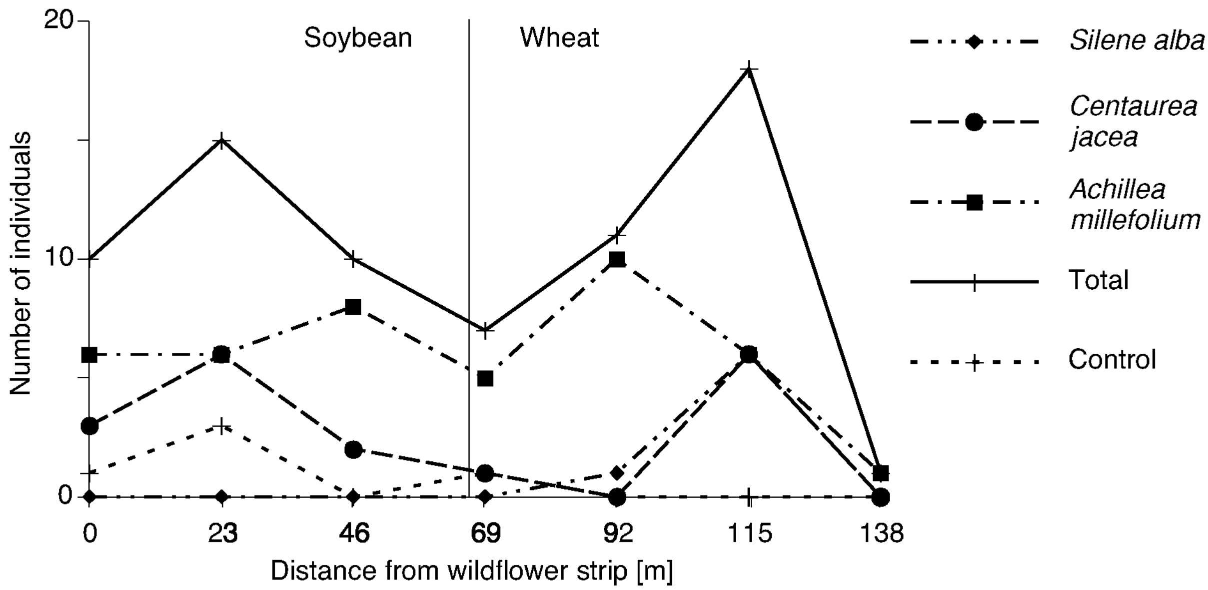


Fig. 6. *Orius* species on all plant species.

Thus these animals are either present everywhere in the fields or they cover long distances in a short time; the latter seems possible since *Orius* is a predatory species living on flowers, which are temporary habitats, and must search for its prey. Previous work has shown that species of *Orius* are, indeed, very mobile (Southwood T.R.E. 1960).

Conclusion

Although arable land seems not to be a significant barrier for some rather common Heteroptera species, the distance to a potential source of dispersal still plays a role for the speed and quality of colonization. The rarer species tend to occur rather locally and thus are either more stenotopic or are less successful in dispersal. We hope to be able to verify this causality with the help of bug data from a wide range of wildflower strips with different characteristics and at varying distances from older wildflower strips.

References

Duelli, P. & Obrist, M. 1998. In search of the best correlates for local biodiversity in cultivated areas. Biodiversity and Conservation 7: 297-309.

Southwood, T.R.E. 1960. The flight activity of Heteroptera. Transaction of the Royal Entomological Society London 112: 173-220.

Southwood, T.R.E. 1962. Migration of terrestrial arthropods in relation to habitat. Biological Revue 37: 171-214.

Wagner, E. 1952. Blindwanzen oder Miriden. Fisher, Jena.

Wagner, E. 1966. Wanzen oder Heteropteren. 1. Pentatomorpha. G. Fischer, Jena.

Wagner, E. 1967. Wanzen oder Heteropteren. 2. Cimicomorpha. G. Fischer, Jena.

Wagner, E. 1970/71. Die Miridae Hahn, 1831, des Mittelmeerraumes und der Makronesischen Inseln (Hemiptera, Heteroptera). Teil 1. Entomologische Abhandlungen Supplement zu Band 37.

Wagner, E. 1973. Die Miridae Hahn, 1831, des Mittelmeerraumes und der Makronesischen Inseln (Hemiptera, Heteroptera). Teil 2. Entomologische Abhandlungen Supplement zu Band 39.

Wagner, E. 1975. Die Miridae Hahn, 1831, des Mittelmeerraumes und der Makronesischen Inseln (Hemiptera, Heteroptera). Teil 3. Entomologische Abhandlungen Supplement zu Band 40.

Conclusions

This thesis has shown that wildflower strips can support a high diversity of plant and insect species. While plant diversity is highest in strips in their first year, and these also contain most rare plant species, bug diversity is highest in strips in their second year and older, which also contain most specialized bug species. Each taxon usually requires special habitat conditions, which may create conflicts in nature conservation with regard to management and the creation of new habitats. According to the overall results of this study, however, no trade-off between the vegetation and bug fauna of wildflower strips is necessary. This conclusion can probably be extended to insects in general. The high floristic diversity found in wildflower strips in their first year is mainly due to a large number of annual species, including the majority of rare species. Annual plant species, however, are more efficiently promoted in arable flora reserves, unsprayed crop edges and wildflower rotation fallows, which thus should be established as complementary landscape elements in addition to wildflower strips.

In contrast to total species numbers, trends in the diversity and composition of plant and bug communities are similar in many ways and are closely linked. In both plant and bug communities, species composition is very variable and responds more strongly to environmental factors than does species number. In both cases, succession is the most important differentiating factor, especially in the inital phase. From the second year on, site and management factors also have a considerable influence on the vegetation, while the resulting vegetation in turn strongly affects the bug species composition. This is evident in the positive correlations found between the numbers of bug species and perennial plant species, and between the abundances of some bug species and their host plants. In addition, according to other sources, bug diversity is enhanced by a high structural diversity of the vegetation. A high grass cover has a negative effect on the species composition of plant and bug communities, enhancing common species at the cost of others. Comparatively rare plant and bug species tend to be present only locally, although dispersal is no problem for the majority of bug species.

Single wildflower strips should be managed to maximize long-term floristic and structural diversity by a careful choice of sites and the use of suitable seed mixtures. Sites with a high initial pressure of grasses or other problem weeds should be avoided. However, in order to achieve the maximum biodiversity from wildflower strips, it is even more important to have a large number of heterogeneously managed strips, which are well dispersed across the landscape.

Acknowledgements

Without the help of many people I would not have been able to carry out this project. First of all I would like to thank Prof. Peter J. Edwards for the initiation of the project, his plentiful ideas, the polish he gave to the text and his always kind support.

My thanks are addressed to:

- Prof. Peter Duelli, for his advice in experimental planning and his comments on the manuscript.
- Dr. Sabine Güsewell, for her always ready and competent advice in statistical questions and other valuable input.
- Dr. Johannes Kollmann and Sophie Karrenberg, for comments on early versions of manuscripts.
- Barbara Köhler for her persistence and input during evening discussions of results.
- Markus Jenny, Urs Weibel and Martin Bolliger, who introduced me to the Klettgau project and provided me with valuable information.
- Fritz Uehlinger, who also provided me with important local information and let me use his barn for the storage of material.
- many farmers in the Klettgau, who allowed me to work in their wildflower strips and crops. Among these I owe special thanks to Reiner Gysel and Ernst Külling-Elmer for their cooperation in the flower-window experiment.
- Gabriela Uehlinger, for her engaged and independent work for her diploma thesis, which contributed to this study.
- Manuela Di Giulio and Sibylle Studer, my project fellows, for their practical support, helpful discussions and comments, and the nice time we shared in the Klettgau.
- Kirsten Edelkraut and Marzio Fattorini, for their engaged help in the field even under very adverse conditions.
- a whole staff of assistants helping with the tedious sorting of insect samples: Pia Baumann, Enrico Bellini, Barbara Fassnacht, Christine Fehr, Fernande Gächter, Gabi Jakobs.
- Ralf Heckmann for the determination of vast amounts of bugs.
- Dieter Ramseier, for practical tips and the permission to take plants for the flower-window experiment from a wildflower strip under his charge.

- my office fellows Holger Buschmann, Michael Keller, Matthias Meier and Stefan Wahl for support of many kinds.
- Kaspar Pflugshaupt, Karsten Rohweder and Hans-Heini Vogel for help in computer matters.
- Rene Graf and Anita Hegi for the provision of technical equipment.
- the Swiss Science Foundation for the funding of the project.

Many other kind people contributed to my enjoying the time I spent at the Geobotanical Institute. Last but not least I want to thank my parents, flat mates and other friends for their support and consideration, throughout, and especially towards the end of this study.

Curriculum Vitae

Surname	Ullrich
First names	Karin Susanne
Date of birth	7 October 1966
Place of birth	Freiburg i. Brsg., Germany
Nationality	German

Education

School	Kreisgymnasium Kirchzarten A-levels, June 1985
University	Studies in biology at the Albert-Ludwigs-Universität Freiburg (Germany) and the Trent University Peterborough (Canada), 1986-1995 Specialization in Geobotany, Zoology, Limnology and Soil science Diploma thesis: "Stillwasservegetation in der südlichen Oberrheinebene: Pflanzengesellschaften – Synökologie und Besiedlung durch *Somatochlora flavomaculata* und *Sympetrum sanguineum* (Odonata)", supervised by Dr. R. Buchwald and Prof. O. Wilmanns Diploma obtained in 1995
Dissertation	Assistant at the Geobotanical Institute, ETH Zürich, research project under the direction of Prof. P. J. Edwards, 1996-2001 "The influence of wildflower strips on plant and insect (Heteroptera) diversity in an arable landscape"

Teaching assistant in practical courses in ecology (1992-2000)

Project in commission, 1985-1986 (Werkvertrag Schutzgemeinschaft Libellen Baden-Württemberg): "*Somatochlora flavomaculata* (Odonata): Verbreitung, Biologie, Habitat, Schutz- und Pflegemaßnahmen"