INVASION AND BIODIVERSITY IN GRASSLANDS AND FIELD BORDERS

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INVASION AND BIODIVERSITY IN GRASSLANDS AND FIELD BORDERS

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Invasion and Biodiversity in Grasslands and Field Borders

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1 ABSTRACT

The aim of the current project was to investigate both the mechanistic background of biological invasions and the implications for biodiversity in grasslands and field borders. It consists of an *ex situ* experimental part which focuses on the underlying ecological mechanisms of invasion, and a more practical oriented *in situ* part concerning invasion and biodiversity in field borders.

For the ***ex situ*** part, three experiments were performed with synthesized grass communities. The first and the second experiment were aimed at examining how the performance of grass species, inserted as invaders in the gaps of synthesized grassland communities, was affected by invader and community traits. In the first experiment, eight perennial grass species were used both as invasible monocultures and as potential invaders in gaps in these monocultures. Invader traits and ecosystem characteristics were examined, as well as their relative importance in determining invasion success. In the second experiment, three grass species were inserted as invaders in communities of different species richness (1, 2, 4, 8 species). In this study, the focus was on how species richness, light transmittance, and productivity of the communities affected invader performance during two successive years. The objective of the third experiment was to elucidate interspecific differences in survival of grass species subjected to an extreme climatic event. This, in order to understand how extreme events will eventually change the structure, species composition, and the invasibility of plant communities. Therefore, eight grass species were exposed to a simulated heat wave in the field (‘free air’ temperature increase at 11 °C above ambient) combined with drought. Ecophysiological responses to the increasing stress were studied besides morphological and ecophysiological characteristics of the same species growing in unstressed conditions.

Invasion success expressed as germination correlated significantly with germination time, light penetration in the gaps, and N acquisition by the edge plants. Success expressed as leaf length correlated with seed mass, germination time, and light availability. Variation in germination was best explained by invader identity, whereas variation in leaf length was equally attributed to invader and monoculture identity. The results suggest that invasion success depends on a match between invader characteristics and ecosystem properties, and that species traits alone are not very good predictors.

The second study showed that in both the first and the second season following invader establishment, realized growth (invader leaf length) was positively related to percentage light transmittance (which was the best predictor for invasibility) and negatively related to neighbour biomass, in all species examined. The richness-invasibility relationship became significant only in Year 2, where increasing neighbourhood richness enhanced complementarity (demonstrated by means of I_{max},

an index for assessing the degree of complementary resource use), which in turn negatively affected invader leaf length. In the first year, such a relationship had not yet developed, probably because the communities were still young and plant interactions limited. However, even in Year 2, the richness effect saturated at low richness, with no mixture overyielding the best two-species mixture. The data suggest that invader growth might be suppressed most in gaps with low light penetration and low availability of other resources. This might e.g. be achieved by moderately productive, species-rich communities, with preferably some broad-leaved species.

The third study indicated that species with a greater leaf area survived significantly longer under the climatic extreme, whereas there was no effect of specific leaf area on survival time. High quantum yield of photosystem II (F_v/F_m) and low intercellular CO_2 concentrations (C_i) throughout the stress period were also related to long survival. However, the strongest determinants of species survival time were the amounts of variance (r^2) in light-saturated stomatal conductance (g_s) and photosynthetic CO_2 uptake rate (A_{max}) that were explained by stress duration. These results suggest that species of which the stomata react strongly to daily fluctuations in temperature, vapour pressure deficit and irradiation, despite increasing stress, are more vulnerable during extreme events and might disappear as first if severe heat waves occur more often in the future.

The ***in situ*** study investigated agro-ecological functions (nature conservation, agriculture, environment) and implications of newly created, mown sown and unsown field margin strips installed on ex-arable land to increase biodiversity.

From **conservational concern**, the development of species rich field margin strips was not strongly affected by the installed type of margin strip since species diversity converged over time, whether strips were sown or not. Convergence between unsown and sown margin strips occurred also in terms of species composition: unsown and sown strips became similar over time. Mowing without removal of cuttings significantly reduced species richness, yielded grassier margin strips and delayed similarity in species composition between sown and unsown margin strips. Species richness on the longer term was not significantly affected by sun or shade conditions nor by disturbance despite significant temporary effects shortly after the disturbance event. On the contrary, vegetation composition in terms of importance of functional groups changed after disturbance: the share of spontaneous species increased resulting in higher similarity between the sown and unsown vegetation. Furthermore, risk of invasion was highest in the disturbed unsown community on the unshaded side of a tree lane. A positive effect of botanical diversity on insect number and diversity was found. However, the effects of botanical diversity on insect number were mediated by light regime. At high light availability differences between plant communities were more pronounced compared to low light availability. The abundance of some insect families was dependent on the vegetation composition. Furthermore light availability significantly influenced insect diversity as well as the spatial distribution of families.

From **agricultural concern**, installing margin strips by sowing a species mixture, and the use of a mowing regime with removal of cuttings are good practices to diminish the risk of species ingrowth into adjacent crops by creeping roots and rhizomes. Seed dispersal was only problematic one year after the installation of the field margin strips, particularly nearby the unsown margin strip. Wind-borne seeds were dispersed over limited distances, mainly within 4 m of field margins.

Annual herbage yield was not affected by mowing management. Dry mass (DM) yield of sown/unsown communities converged over time. Compared to herbage from an intensively managed fertilized grassland, field margin herbage revealed a low feeding value, owing to a low crude protein content, a low digestibility and a high crude fibre content. The unsown community had a higher forage quality than communities sown to breed commercially available grass varieties. Both digestibility and crude protein content decreased over time irrespective of plant community or location. Mid June cuts were more productive than mid September cuts, but digestibility and crude protein content were lower. The use of herbage from field margins as hay for horses or as a component in farmland compost are good alternatives.

A strong relation was found between the distribution of pest insects and their antagonist families along field margin strips, indicating a status of biological equilibrium.

From **environmental concern**, field margin strips buffered boundary vegetation and watercourses against cropped areas loaded with high levels of mineral nitrogen. Margin strips reduced the mineral nitrogen content of the soil in the margin and mineral nitrogen loss during winter months. Mineral nitrogen loss was not affected by field margin type but by distance from the field crop. A minimal width of 5 m is necessary to reach an optimal reduction in mineral soil N and N losses.

Keywords: Biodiversity, Complementarity, Disturbance, Drought, Extremes, FATI, Field margin, Grass, Herbage quality, Insects, Invasibility, Invasion, Invasiveness, Leaching, Mowing regime, Weeds infestation.

2 INTRODUCTION

2.1 Invasiveness and invasibility

Understanding why some plant species establish as invaders while others do not, or why some habitats, regions or biomes seem more prone to invasions than others, is still limited (Prieur-Richard & Lavorel 2000), mainly because much effort has been invested in observational studies yielding little generality or predictive power. Progress is hampered primarily by the multitude of factors involved: the success of an exotic species in a new habitat is not only the resultant of the capacity of the alien to invade (*invasiveness*) and the susceptibility of the system to being invaded (*invasibility*), both of which seem to be associated to specific attributes, it is also determined by propagule influx density (Kolar & Lodge 2001), and by the time elapsed since the invader was introduced (Kowarik 1995; Thompson *et al.* 2001). These factors make the linkage of invasion success to common attributes of either species or ecosystems a hazardous enterprise. Many studies also tend to generalize from examples of successful invasions, and rarely include observations of non-invaded communities. Further complication arises from the fact that neither invasiveness nor invasibility can be measured directly. Invasiveness can only be derived by comparing the success of an alien species with that of others invading in the same habitats. Similarly, invasibility can only be derived by comparing the degree to which a system is invaded with the degree to which other systems are invaded by the same invaders. Studies on the common attributes of the most successful invaders or the most invaded habitats frequently ignore this complexity by focusing on invasion success, rather than on its components invasiveness and invasibility.

Important determinants of invasibility on a broad scale are disturbance regime, climate, level of environmental stress, the abundance of natural enemies, competitors and mutualists, propagule pressure, resource availability, community structure, and ecosystem type (Alpert *et al.* 2000; Levine 2000; Kolar & Lodge 2001). However, these factors do not explain variation in invader performance observed at the local scale, which probably arises from small-scale differences in invasibility, interacting with invader traits. Elucidating these small-scale processes may have important implications for management, in particular if feasible techniques can be devised (e.g. altering nutrient input or mowing regime) to locally reduce community invasibility. Because in natural invasion events, the combined influence of species traits, community or ecosystem traits, and (uncontrolled or unidentified) environmental and anthropogenic factors blurs the underlying pattern, manipulation experiments with simulated invasion in synthesized communities might be very useful.

2.2 The role of species richness

A possible driver for microsite differences in invasibility might be local variation in species richness. The hypothesis that more diverse communities are less susceptible to invasion (Elton 1958; review by Levine & D'Antonio 1999) has attracted much attention and has recently been tested both with experimental studies on synthesized communities (Levine 2000; Naeem *et al.* 2000; Hector *et al.* 2001) and with studies on large-scale natural invasion patterns (Stohlgren *et al.* 1999; Foster *et al.* 2002). In studies of the second type, the most diverse areas are usually the most invaded, contrary to experimental studies that tend to support the hypothesis that diversity enhances invasion resistance. This controversy between the different types of studies can be resolved by distinguishing the causal effects of diversity on invasion resistance from the effects of factors associated with diversity across communities, such as disturbance, water and nutrient levels, percent open canopy or bare ground and climate (Levine *et al.* 2002). Despite the support by theoretical models (Kokkoris *et al.* 1999), the results of the experimental approach are debated by several authors (Hodgson *et al*. 1998; Wardle 2001). This is because the observed negative relationship between richness and invasibility can be explained by two different mechanisms: one based on complementary resource use, which is a true biological mechanism, and the other based on the so called "sampling effect". According to the mechanism of "resource use complementarity", increasing species richness results in more complete utilisation of resources and consequently fewer available resources for possible invaders. The "sampling effect" model involves a greater probability of including the most competitive species in the assembled community as species richness is increased, which also reduces invasibility.

Also little is known about the mechanistic pathway by which species richness, through complementary resource use, affects invasion resistance. Some studies indicate that the effect of richness on invasibility is mediated by reduced resource availability (e.g. nutrients, light, or water; Hector *et al.* 2001), which implies it is indirect. As a consequence, it might be weak compared to the effects of variation in resource availability in the environment on invasibility, such that manipulation of richness would only have little potential. On the other hand, because richness might influence several above- and below-ground resources at the same time, it could be strongly associated with invasibility, and consequently a good management tool.

2.3 Interactions with climate change

A factor increasing the susceptibility of ecosystems to being invaded are extreme climatic events. Increasing atmospheric concentrations of greenhouse gases are projected to change the frequency, intensity, and duration of extreme events, yielding more hot days and heat waves, and associated increased summer drying over nearly all land areas in the course of the 21st century (IPCC 2001). Such extremes will exert major effects on the distribution of plant species and the composition of plant communities. In perennial grasslands, severe droughts may debilitate established plants or may open gaps by causing mortality, by which communities become more susceptible to invasion by alien species (Buckland *et al.* 2001). Extreme events will not affect all species alike. Plants have adopted different strategies to cope with drought, often involving a mixture of stress avoidance and tolerance that varies with genotype. Such mixed strategies are predominantly found in trees and shrubs, while herbs and annuals rely mostly on pure avoidance (Chaves *et al.* 2002). In a more extreme future climate, stress-avoiding species that lack special adaptations to overcome severe drought and heat seem most at risk. To help predict future changes in global vegetation patterns, it would be interesting to know which species are most sensitive to excessive drought and heat, and which are able to survive such extremes. Generalizing beyond the responses of given species requires knowledge on the mechanisms underlying interspecific differences in survivorship and the ecophysiological basis of the sensitivity to extremes of individual species. However, until now only a handful of studies on extreme events and plants have been done (Van Peer *et al.* 2001; Van Peer *et al.* 2004), most of which have focused on community processes, rather than on the factors responsible for the different responses of individual species. Also the combination of heat and drought stress has thus far hardly been studied at the leaf and plant level, while water deficits in the field rarely act alone (Chaves *et al.* 2002).

2.4 Biodiversity and invasion in field borders

During the last decades, biodiversity in agricultural landscapes in Northern and Western Europe has declined considerably owing to the intensification of agriculture in Northern and Western Europe from the 1950's on. Species composition of animals and plants in different areas has become more similar and is characterized by a few dominant species (Joenje & Kleijn 1994). Next to the impact on plant species (Marshall & Arnold 1995), the impact of modern agriculture on animal species has been significant. Regular mechanical disturbance, increased chemical weed control and pesticide use, drift of agrochemicals into remnant field boundary habitats, field enlargement and the general simplification of crop rotations have contributed to the impoverishment of many insect groups on arable land (Sotherton & Self 2000; Morris & Webb 1987). Consequently organisms downstream the food web are affected, as e.g. the chicks of farmland birds like the partridge (*Perdix perdix*) (Campbell et al. 1997).

As a result of modern agronomical operations, field boundaries have become the dominant refugia for biodiversity in agricultural landscapes. Nowadays these semi-natural habitats survive as remnants, most often as linear features, of which field margins are the commonest structures. Despite an ongoing reduction in field boundary habitats (Chapman & Sheail 1994), a range of public initiatives has resulted in the creation of new field margin features on ex-arable land in Northern and Western Europe, notably conservation headlands and margin strips. Support mechanisms exist to encourage farmers to create new habitats, to restore old ones or expand existing boundaries by means of margin strips, to restore the landscape connectivity, to care for small landscape elements. Expanding existing field boundaries is generally done by taking the outer metres of an arable field out of production and allowing it to regenerate naturally or sowing it to grass or a grass/forbs mixture, usually under a mowing regime (e.g. Marshall & Nowakowski 1992; Dunkley & Boatman 1994; Hart *et al.* 1994). Despite the growing interest in field margin strips fundamental knowledge is lacking concerning the maximisation of biodiversity of margin strips and their agro-ecological functions and implications. The following study concentrates on newly created, mown sown and unsown field margin strips on ex-arable land installed between the pre-existing boundary and the arable crop. Some of the experiments investigate the susceptibility of field margins to being colonized or invaded by alien species.

2.5 Objectives

(1) Identify factors critical to invasion, in order to *a priori* monitor highly invasive species, to characterise ecosystems most susceptible to and conditions most conducive to invasion, and to develop protective strategies. Study how diversity in plant communities acts as promoter or resistance to invasion, and how diversity itself is modified by invasive species.

(2) Identify interactions with climate change, by studying the impact of climatic extremes on mortality in grassland vegetation, as a basis for gap creation and subsequent invasion. Explain the underlying mechanisms of the sensitivity to climatic extremes in different species, to predict which grasslands will be most susceptible.

(3) Evaluate techniques to locally regulate (maximize) diversity in plant communities, in casu field borders. Assess effects of realized diversity in field borders on neighbouring crops. Devise management options to minimise risks of invasion into field borders, and from field borders into arable land.

3 MATERIALS AND METHODS

3.1 Invasiveness and invasibility

3.1.1 Plant material and experimental design

An experiment was set up to identify plant and community characteristics associated with invasion success in the gaps of dense grassland. A design was developed with the same species acting both as invaders and as invaded systems, to distinguish between influences of invasiveness and invasibility within the same experiment. In order not to limit the range of invasiveness to high values, we used a series of native species of unknown invasion potential (Thompson *et al.* 2001), covering a range of productivities: *Agrostis tenuis* Sibth. (*At*), *Arrhenatherum elatius* L. (*Ae*), *Dactylis glomerata* L. (*Dg*), *Festuca arundinacea* Schreb. (*Fa*), *Festuca rubra* L. (*Fr*), *Holcus lanatus* L. (*Hl*), *Lolium perenne* L. (*Lp*) and *Poa trivialis* L. (*Pt*). Grass species were chosen because grasses have been responsible for some of the world's most destructive invasions (D'Antonio & Vitousek 1992), grassland cultivation is a key activity in Western European agriculture, and invasions are often cause for concern in grassland management (Watkinson & Ormerod 2001).

The monocultures were sown between 23 April and 4 May 2001 in plastic containers placed outdoors (75 cm x 55 cm and 20 cm deep), filled with steam-sterilized sandy loam on a bottom layer (2 cm) of course-grained sand to improve drainage. The seeds were planted in a hexagonal design 3.5 cm from each other, yielding 328 seeds per container. In each container, eight predefined positions were kept bare in order to create a 'gap' in which the invaders were inserted later. Before the invader seeds were inserted, the monocultures were cut twice (29 June and 26-27 July 2001) to simulate mowing in extensively managed grassland. A final cut took place on 10 and 11 October. In keeping with the extensive management, low amounts of fertilizer were supplied after sowing and after the harvests in June and July (total: 50 kg N ha^{-1} yr^{-1}, 50 kg K ha^{-1} yr^{-1} and 80 kg P ha^{-1} yr^{-1}, supplied in three equal fractions). In addition to the natural rainfall, water was supplied by capillary rise, by placing the containers in 3 cm of water. Regular weeding removed all natural colonization.

On 6 August 2001, 10 days after the second harvest of the monocultures, in each of the eight gaps per monoculture, 10 seeds of each time a different invader species were inserted. Only the first germinating seed in each gap was kept. In this way all possible combinations of invader species and invaded monoculture species were achieved, including species invading their own monoculture. The set of eight different monocultures was replicated three times (24 containers in total). Timing of seed insertion was chosen in the month of maximum seed fall in the field (August), and was aimed at having closed-canopy conditions shortly after germination of the invaders, to have high resistance to invasion.

3.1.2 Measurements

An analysis of invasiveness and invasibility requires assessment of the success of the invaders; this was quantified by a variety of measurements. Cumulative germination percentage was determined until germination was complete. Survival was monitored weekly during September and October 2001, two-weekly in November and December, and monthly afterwards until May 2002. Realized growth was measured as total leaf length per invader (laminae only, all leaves combined) on 1 October 2001. The fate of the invaders after 10 months of growth in the monocultures was assessed with an additional measurement of total leaf length (leaf length 2002) around the peak of next year's growing season, on 28 May 2002.

The measured invader characteristics were average seed mass, calculated from 200 seeds per species, and average germination time by species, expressed as days from insertion to germination. Also characteristics of the invaded monocultures were determined. The extent to which monocultures shaded the invaders was estimated non-destructively by measuring PFD above the canopy and in each gap at 2 cm above the soil surface, yielding percentage light penetration ($PFD_{intercepted}$). A small quantum sensor with a gallium arsenide photodiode (Pontailler 1990) was used, attached to a thin metal rod. Light penetration was measured approximately every 10 d (on cloudy days because instantaneous interception under diffuse light is a good estimator of average daily interception) until the October harvest. Average $PFD_{intercepted}$ was calculated for three important life stages of the invaders: (1) '$PFD_{intercepted}$ germination', (average of 7 and 18 August); (2) '$PFD_{intercepted}$ start of growth' (average of 18 and 23 August); (3) '$PFD_{intercepted}$ growth' (average of five measurements from 18 August until 25 September). At the end of the 2001 growing season (2 and 3 October), the height of the 6 plants bordering each gap was measured to assess competitive pressure from neighbour plants. On 5, 8 and 9 October these plants were harvested (> 3.5 cm to allow regrowth), oven-dried for 48 h at 75 °C, weighed, ground, and analysed for total N (organic + inorganic) and C content (NC-2100 analyser; Carlo Erba Instruments, Milan, Italy).

Statistical analyses were performed with SPSS 10.0 (SPSS, Chicago, IL, USA). Leaf length was log-transformed and germination percentage arcsine transformed to improve normality.

3.1.3 Research questions

(1) Do the selected species vary in invasiveness and do their monocultures vary in invasibility? (2) Are the differences in invasiveness associated with specific traits of the invaders? (3) Are the differences in invasibility associated with specific properties of the monocultures? (4) Is there a relationship between the invasiveness of a species and the invasibility of its monoculture? (5) What is the relative importance of invasiveness and invasibility in invasion events?

3.2 The role of species richness

3.2.1 Plant material and experimental design

A second experiment was set up to find out whether and how species richness, % light transmittance, and plant productivity affect invader performance, and whether these effects depend on invader identity or change through time. To this end, mixtures varying in species richness (1, 2, 4, 8) were created experimentally from a series of native perennial grass species. The selected species, varying in productivity, were: *Agrostis tenuis* Sibth. (*At*), *Arrhenatherum elatius* L. (*Ae*), *Cynosurus cristatus* L. (*Cc*), *Dactylis glomerata* L. (*Dg*), *Festuca pratensis* Huds. (*Fp*), *Festuca rubra* L. (*Fr*), *Holcus lanatus* L. (*Hl*) and *Phleum pratense* L. (*Pp*). The species were sown in trays between 11 and 14 March 2002 and seedlings were transplanted between 6 and 15 May 2002 into plastic containers placed outdoors (30 cm x 20 cm x 14.5 cm deep). The latter were filled with steam-sterilized sandy loam on a bottom layer (2 cm) of course-grained sand and were embedded in the soil to be level with the surrounding grassland vegetation. Following a substitutive design (40 plants per container), 24 different species mixtures were created, including monocultures of all species, eight bicultures, four mixtures of four species, and four mixtures of eight species. In each container, two predefined positions were kept bare to form ‘gaps’ in which invaders were inserted later on. The set of 24 mixtures was replicated three times and in each replicate an other species was inserted as invader: *Festuca arundinacea* Schreb., *Lolium perenne* L. and *Poa trivialis* L., which were the three most invasive grass species from a previous experiment (Milbau *et al.* 2003). Weekly rotation of the containers diminished influences of position and height of adjacent communities on plant growth.

The communities were assembled according to following rules: (1) each species composition is unique (to include as many combinations as possible) (2) all species occur in equal proportions both within each level of species richness and within each mixture (maximum evenness) (3) species assemblages at a given diversity level differ maximally in composition (minimal number of species in common). In each mixture the plants were positioned as follows: (1) the eight neighbour plants surrounding each gap contain equal proportions of every species present in the mixture, (2) the spatial arrangement of these neighbours is different for the two gaps within each container, with a maximum number of different interactions, (3) clumping is avoided in the mixtures to maximize interspecific interaction, and (4) each of the four replicas of the eight-species mixture has a different internal arrangement (denoted as N = 8 (1), N = 8 (2), N = 8 (3) and N = 8 (4), with N species number).

Before the invader seeds were inserted (10 in each gap), the vegetation was cut twice (4 July and 2 August 2002). In keeping with extensive management, low amounts of fertilizer were supplied at planting and after the July and August harvests (total: 50 kg N ha^{-1} yr^{-1}, 50 kg K ha^{-1} yr^{-1} and 80 kg P ha^{-1} yr^{-1}, supplied in three equal fractions). In addition to natural rainfall, water was added by capillary rise during drier periods. Regular weeding removed all natural colonization.

3.2.2 Measurements

After inserting the invader seeds on 12 August 2002, we determined germination time and cumulative germination percentage until germination was complete. Only the first (out of 10) germinating seed in each gap was kept. Realized invader growth was measured as total leaf length per plant (laminae only, all leaves combined) and aboveground biomass (cut to 2 cm above ground level and oven-dried for 48 h at 75°C) at the end of the first growing season on 9 October 2002, and as total leaf length in the middle of the second season on 7 July 2003. Survival was monitored weekly during September and October 2002, two-weekly in November and December, and monthly afterwards until July 2003. On 9 October 2002 and 8 July 2003, the invaded communities were cut to 3.5 cm above ground level and the eight neighbour plants bordering each gap were dried and weighed together ('biomass of neighbour plants'). Shading of the invaders was estimated by measuring photosynthetic photon flux density above the canopy and in each gap at 2 cm above the soil surface, on 20 August 2002 and on 10 September 2002, two weeks and five weeks after the August harvest, respectively, in order to have data on a more open (% PAR transmittance O) and a more closed (% PAR transmittance C) vegetation. A small quantum sensor with a gallium arsenide photodiode (Pontailler 1990) was used, attached to a thin metal rod.

The index I_{max} (after Trenbath 1976 and Garnier *et al*. 1997) was used to analyse the effect of species richness on productivity in each mixture and was calculated as

$$I_{\max} = \left(\sum_{i=1}^{n} Pi \right) / \max(M_i)$$

with P_i biomass produced by species *i* in the mixture, and max (*Mi*) biomass produced by the component species that was most productive in monoculture. Applied to our experiment, I_{max} = *P/*max (*M*), with *P* biomass of the eight neighbour plants surrounding a gap and max (*M*) biomass of the 8 neighbour plants of the most productive monoculture among the component species. When I_{max} > 1, the mixture "transgressively overyields" the monocultures (transgressive indicates that mixture productivity is compared to the most productive monoculture, and not to average monoculture productivity), which indicates positive complementarity (Garnier *et al.* 1997), and allows one to reject the "sampling effect" hypothesis as the sole explanation of positive richness-biomass relationships (Spehn *et al*. 2000).

Statistical analyses were performed with SPSS 10.0 (SPSS, Chicago, IL, USA). Invader leaf length was log-transformed and germination percentage arcsine transformed to improve normality.

3.2.3 Research questions

(1) Do species richness, % light transmittance and neighbour plant productivity influence invader performance, and how are they related? (2) Does richness affect the invaders through complementary resource use? (3) Which of the above parameters is the best predictor of invader growth? (4) Are the observed patterns the same in different invader species? (5) Concerning management, how can invasibility locally be reduced?

3.3 Interactions with climate change

3.3.1 Plant Material

To understand how extreme events will eventually change the structure, species composition, and even the invasibility of plant communities, parameters linked to interspecific differences in survival time of the extreme need to be identified. We therefore monitored eight perennial grass species, known to differ in drought sensitivity, for various morphological and ecophysiological parameters in non-stress conditions and during exposure to a simulated heat wave: *Agrostis tenuis* Sibth. (*At*), *Arrhenatherum elatius* L. (*Ae*), *Cynosurus cristatus* L. (*Cc*), *Dactylis glomerata* L. (*Dg*), *Festuca arundinacea* Schreb. (*Fa*), *Festuca rubra* L. (*Fr*), *Lolium perenne* L. (*Lp*) and *Poa trivialis* L. (*Pt*). From 1 to 4 April 2003, seeds of the selected species were planted at 2.5 cm interspaces in plastic pots (20 cm x 15 cm x 14.5 cm deep), to form monocultures (18 replicates per species) of 30 plants each. Monocultures were used instead of individual plants in pots in order to avoid unrealistic radiation profiles. At every plant position the first germinating seed out of five was kept.

Before sowing, the pots were weighed empty and then filled with a fixed amount of air-dried steam-sterilized sandy loam. Three samples of this air-dried soil were oven-dried at 60 °C for ten days and weighed. Based on the mean ratio of the oven-dried to air-dried mass of these samples, the oven-dried mass of the soil added to the pots was calculated, as a basis for monitoring soil water content (see below). After sowing, the pots were placed in a greenhouse until 27 May, and outdoors afterwards. They were well watered until the start of the experiment and were supplied with low amounts of fertilizer (total: 50 kg N ha^{-1}, 50 kg K ha^{-1} and 80 kg P ha^{-1}) in two equal fractions on 13 June and 31 July. At the start of the experiment (11 August 2003), the pots were randomly assigned to four identical sets: one unheated set, and three heated sets in which the plants were exposed to a simulated heat wave in combination with drought stress. Each set contained six replicate pots of each monoculture species, or 48 pots in total. Daily rotation of the pots between the heated sets and within all sets minimized possible effects of set and position. The pots assigned to the unheated set were kept close to field capacity, while irrigation of the pots in the heated sets was arrested on 11 August. Soil relative water content (RWC_{soil}) in these heated pots was calculated daily on nine randomly chosen pots per species by dividing the actual amount of water in the soil (soil mass including water minus mass of oven-dried soil) by the potential amount of water in the soil (mass of fully wet soil after drainage minus that of oven-dried soil).

3.3.2 Microclimate

A heat wave ('free air' temperature increase and drought) was simulated by irradiating three replicate sets of 48 pots, placed level with the surrounding grassland vegetation, with additional infrared radiation (IR) (0.8-3 µm) using the FATI system (Nijs *et al.* 1996). Three second-generation prototypes of this device (Van Peer *et al.* 2004) were used to individually irradiate the three sets that were exposed. Each FATI module consisted of a frame with six 1500-W IR lamps, suspended 1.2 m above the ground, which homogeneously irradiated an area of 1.2 x 1.2 m. On a fourth set of 48 communities, which were not exposed to drought and heat and served to measure plant characteristics in non-stress conditions, a dummy construction was placed, with lamp enclosures but no IR lamps. The heated sets were covered with a transparent shelter suspended at 2.5 m height, which eliminated precipitation but did not obstruct direct solar radiation. The experiment lasted until 8 September, when the plants in the heated sets had died. Because a natural heat wave occurred during the stress period, heating was switched off for three days (ambient maximum $T_a > 32$ °C) to avoid unrealistic stress levels in the heated sets.

Average daily maximum, minimum and mean temperatures (air, canopy and soil) during the stress period are shown in Table 1, for both the unheated and heated sets. The average instantaneous increase in temperature owing to the heating (days when the heating was switched off excluded) equalled 11.27 ± SD 2.15 °C, 12.73 ± SD 2.43 °C, and 11.79 ± SD 2.15 °C for T_{air}, T_{canopy}, and T_{soil}, respectively (n = 600 in all cases).

Table 1 Average values ± SD of daily maximum, minimum, and mean temperatures (air, canopy, and soil at 5 cm depth) during a simulated heat wave (11 August – 6 September 2003) for unheated and heated plants.

	Air temperature (°C)			Canopy temperature (°C)			Soil Temperature (°C)		
Treatment	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean
Unheated (*n* = 27)	25.4 ± 3.6	13.3 ± 2.7	18.5 ± 2.5	25.7 ± 4.1	11.7 ± 3.0	17.8 ± 2.9	20.7 ± 2.3	16.0 ± 2.4	18.4 ± 2.2
Heated (*n* = 27)	35.8 ± 3.6	23.7 ± 2.1	28.8 ± 2.2	36.5 ± 3.6	23.9 ± 2.8	29.3 ± 2.5	32.6 ± 2.5	26.0 ± 2.2	29.2 ± 2.0

3.3.3 Measurements

Morphological characteristics and productivity. At the beginning of the experiment, six plants per species (one per pot) were harvested from the unheated set to determine total leaf area per plant, number of leaves per plant, total plant leaf mass and specific leaf area (SLA, leaf area: leaf dry mass, $m^2\ kg^{-1}$). Productivity of the monocultures during summer was estimated by cutting two pots (30 plants) per species to 2.5 cm on 5 August, and harvesting them again after one month of regrowth. Biomass was dried 48 h at 70 °C.

Ecophysiological characteristics. Ecophysiological measurements on the unheated plants were taken at the start of the heat wave (11 August 2003) and were repeated on 22 August 2003. The plants in the heated sets were measured daily during the stress period (except predawn leaf water potential (Ψ_l, MPa), which was measured every two days) until the leaves were desiccated and ecophysiological measurements were no longer possible (after about ten days of stress). For all measurements, each day the plants were randomly chosen, with the constraint of taking an equal number of plants per set, each from a different pot. Plants near the pot edge were avoided. All measurements were done on recently expanded leaves.

Ψ_l was measured on six excised leaves per species with a Scholander pressure chamber (ARIMAD-2, ARI Kfar Charuv Water Supply Accessories, Tel Aviv, Israel). Leaves were enclosed in plastic bags during transport and petioles were recut just before measurement. Instantaneous determinations of light-saturated photosynthetic CO_2 uptake rate (A_{max}, µmol CO_2 $m^{-2}\ s^{-1}$), stomatal conductance (g_s, mol $m^{-2}\ s^{-1}$), transpiration rate (TR, mmol H_2O $m^{-2}\ s^{-1}$), and intercellular CO_2 concentration (C_i, µmol mol^{-1}) at saturating photosynthetic photon flux density (PPFD = 1500 µmol photons $m^{-2}\ s^{-1}$) were done around midday with a portable gas exchange system (LI-6400, Li-Cor, Lincoln, Nebraska, USA) in six leaves per species. CO_2 concentration, air temperature, and humidity during the measurements approximated the ambient conditions. Instantaneous water-use efficiency of photosynthesis (WUE, mmol mol^{-1}) was calculated as A_{max} / TR. Chlorophyll fluorescence parameters (nine replicates per species) were measured using a portable chlorophyll fluorometer (PEA, Plant Efficiency Analyser, Hansatech Instruments Ltd., Norfolk, England). The background fluorescence signal (F_0) and the maximum fluorescence (F_m) were measured following dark adaptation for one hour to determine the maximum quantum efficiency of photosystem (PS) II (F_v/F_m; $F_v = F_m - F_0$).

Plant survival time. Survival time of the stressed plants was measured by removing each time two pots per species (= 60 plants) from below the FATI constructions, after different exposure times to the heat wave (6, 11, 15, 17, 19, 22, 24, 26, and 29 days of stress). At each removal, pots were re-watered and the number of growing individuals counted. The drought periods required to reduce survivorship to 50% and 25% (T_{50} and T_{25}, respectively) were used as measures of survival time.

3.3.4 Research questions

(1) Are interspecific differences in survival time under climatic extremes related to the species responses to the imposed stress? (2) Are differences in survival time related to ecophysiological of morphological characteristics in unstressed conditions?

3.4 Biodiversity and invasion in field borders

3.4.1 Field trials

***Trial 1 (all research questions except 6, 7, 8 and 16; see 3.4.10 for questions*)**

In June 2001, a field margin experiment was established on nutrient rich arable land in a split plot design with four plant communities (main plot), three mowing regimes (subplot) and three blocks. The plant communities were randomized within three blocks and the three mowing regimes were randomized within the plant communities. The split plot design was installed on two contrasting soil types in Belgium, province of West Flanders, namely at Poperinge (SITE1: 50°52′N, 2°45′E, drained sandy loam soil, pH-KCl 6.8, 1.5% C) and at Beernem (SITE2: 51°09′N, 3°20′E, sandy soil, pH-KCl 5.7, 3.3% C). Analysis of top soil (0-30 cm) of SITE1 showed that extractable P and K were 27 mg/100 g soil and 31 mg/100 g soil, respectively, and total mineral N was 43 kg ha^{-1}. Analysis of top soil (0-30 cm) (June 2001) of SITE2 showed that extractable P and K were 75 mg/100 g soil and 31 mg/100 g soil, respectively, and total mineral N was 113 kg ha^{-1}. The experimental sites (360 x 10 m) were ploughed from 7 months old Italian ryegrass in May 2001 and divided in 36 plots (10 x 10 m) arranged along a east-west oriented watercourse at SITE1 or an east-west oriented tree row along a ditch at SITE2. The pre-existing boundary was constituted by a watercourse bank with irregular pattern of shrubs, pollarded trees, and young trees at SITE1, and a small ditch bank along a tree row of 50 years old oaks at SITE2. SITE2 was situated on an organic farm, so no agrochemicals were used in the adjacent crops.

Apart from an unsown spontaneously evolving plant community (CONTR), three different sown communities were studied (MIXT1, MIXT2, MIXT3). MIXT1 was established with a seed mixture of 63 species comprising native seeds of local provenance. For MIXT2 a commercially available seed mixture of 77 species comprising species completely unrelated to the sowing region was used. The initial composition of MIXT3 was identical to that of MIXT2, but once a year seed rich herbage originating from neighbouring roadsides was added in order to enhance species diversity. Roadsides were cut around the end of September. Plant species in MIXT1 and MIXT2 were selected from a wide range of vegetation types: annual and perennial forbs from dry to moist grassland and perennial forbs thriving in nutrient rich soils. Nitrogen-fixing dicotyledons were incorporated to improve the nutritional value of the biomass.

In the installation year 2001, the field margin plots were cut once on 15 September with removal of the cuttings. During the subsequent years (2002, 2003, 2004) the experimental plots were cut twice per year with cuttings either left or removed resulting in three different mowing regimes: REMOV0, no removal of cuttings; REMOV1, removal of first cutting; REMOV2, removal of both cuttings. The cutting height was 5 cm. To allow the seed set of a major part of the species and to allow the establishment of young seedlings, the first mowing date was postponed till 15 June (first cut). The vegetation was mown a second time around 15 September (regrowth cut). Care was taken to reduce seed dispersal due to removal of the cuttings. Neither fertilisers nor other agrochemicals were applied to the experimental margin plots.

Trial 2 (research question, 6, 7, 8, 16)

In September 2001, a field margin experiment was established on nutrient rich arable land in a strip split plot design with two light regimes (the vertical treatments), four plant communities (the horizontal treatments), and two levels of disturbance (subplot treatments) in three replicates. The two light regimes were established by installing a field margin strip along the southern and the northern side of a tree lane consisting of two rows of very uniform 50-year-old beeches, perfectly east west oriented, offering a sunny and a shady side. Consequently, the vegetation development in the field margin plots occurred under a high light regime on the sunny southern side and a low light regime on the northern shady side. Within each margin strip (240 m x 10 m each), all plots (10 m x 10 m) were arranged in a split plot design with four plant communities and two levels of disturbance in three replicates.

The strip split plot design was installed in Belgium, province of West Flanders on humous sandy soil (pH-KCl 5.7, 2.9%) at Beernem (51°09′N, 3°20′E) after ploughing from temporary grassland. Analysis of top soil (0-30 cm) in September 2001 showed that extractable P and K were 65 mg/100 g soil and 25 mg/100 g soil, respectively, and total mineral N was 98 kg ha^{-1}.

The same plant communities as in trial 1 were installed. Each plant community evolved by two disturbance levels: half of the subplot vegetations were undisturbed and half were disturbed once, on 19 September 2002 (i.e. the disturbance event), shortly after the September cutting, by a rotor cultivator, harrowing superficially (to a depth of 4 cm) the whole plot. This artificial disturbance, causing severe gap formation, was aimed to simulate multiple tractor passage on margin strips. Immediately after the disturbance event, disturbed as well as undisturbed subplots were oversown with a 1:1:1:1: mixture of four potential invader grass species (called hereafter, ‘invaders’), namely: *Lolium perenne* L., *Arrhenatherium elatius* J. & C. Presl , *Dactylis glomerata* L. and *Festuca arundinacea* Schreber at a total density of 500 viable seeds per m² in order to study the susceptibility of the plant communities for being invaded (invasibility) under different levels of light and disturbance.

In the installation year 2001, the field margin plots were not cut. During the subsequent years (2002, 2003), the experimental plots were cut twice per year with removal of cuttings similar to REMOV2 in trial 1. Vegetation succession occurred under zero fertilisation and no herbicide and pesticide use.

3.4.2 Seed bank analysis

The persistent seed bank of the uppermost soil profile (0-8 cm) of trial 1 was analysed to assess the risk of having problem weeds within the adjacent crops and/or the margin strip itself. The persistent seed bank was sampled within the central 4 x 4 m area of each subplot, after ploughing (end of May 2001) and prior to installation (June 2001) of the trial. Samples were analysed with the seedling emergence method according to the recommendations of Thompson *et al.* (1997). The seed density of each species in soil seed banks was expressed as the number of seedlings in an area of 1 m² to a depth of 8 cm.

3.4.3 Vegetation analysis

Prior to each cutting, abundance of plant species was measured on a Tansley (1954) scale within the central 4 x 4 m area of each 10 x 10 m subplot. Thirty days after every mowing date, species presence and importance was studied in 16 randomly placed quadrates (13 x 13 cm) within the central 4 x 4 m area of each plot according to the combined frequency-rank method of De Vries (De Vries & de Boer 1959). Species presence was expressed in terms of importance (I%) based on the ranking of biomass contributed by the various plant species within each quadrate. The I% of a functional group was calculated by adding the I% of all contributing species of that group. Both the total number of species (species diversity) and the number of sown wildflower species, all expressed as spp/16 m², were determined by recording the presence or absence of each individual species within the central 4 x 4 m area of each 10 x 10 m plot.

Furthermore, percentage uncovered area (i.e. exposed mineral soil including litter) was estimated in eight randomly placed 80 x 80 cm quadrates within the central 4 x 4 m area of each 10 x 10 m subplot. Similarity of vegetation development between sown and unsown plant communities within cutting treatment (trial1) or light regime (trial2) was compared using Sorenson's quantitative measure C_N (Magurran 1988). Index C_N incorporated both species occurrence and species importance. Aside from the vegetation analysis in the margin strips, species richness and abundance of the pre-existing boundary vegetation was yearly recorded in June on a Tansley (1954) scale. Species nomenclature and habitats followed Van Der Meijden (1990).

3.4.4 Seed rain monitoring

To determine the maximum contamination level by specialized anemochorous species (SPAN), seed dispersal into adjacent crop was monitored periodically around critical seed dispersal periods between 10 May and 10 June (hereafter May-June) and between 14 August and 9 September (hereafter August-September). At both locations, seed rain was sampled on the southern side of the east-west oriented margin strips. Prevailing wind direction during all monitoring periods was north-northeast. So, wind-born seeds were transported into the adjacent crop area. All captured wind-born seeds in the adjacent crop were attributed to the field margins since there was no contamination originating in the surrounding perennial grassy verges or fields. Seed rain nearby each main plot was monitored along 12 sampling axes (tree blocks x four main plots) perpendicular centred to the east-west oriented main plots using blue biosignal traps (BUGSCAN-BIOBEST), sized 20 x 40 cm with a sticky surface of 0.08 m² faced northward. Sticky seed traps were placed vertically 30 cm above the crop canopy (50 cm above ground level) at six positions (0, 2, 4, 8, 16 and 32 m from the field margin strip) in the adjacent crop. Only filled seeds were counted. The number of captured seeds per species was expressed as seeds per m² sticky surface.

3.4.5 Herbage yield and quality

Herbage yields were determined twice per year around 15 June and 15 September by cutting the central 4 x 4 m quadrate of each plot using an Agria motor cutter at a cutting height of 5 cm. Herbage was weighed on the field to determine fresh herbage yield. Per plot, herbage samples were taken and dried for 12h at 75°C to calculate dry matter (DM) yield. DM yield of both the first and the regrowth cut were added to determine annual DM yield. Mean DM yield over the period 2002-2004 was then calculated by averaging DM yield of the three subsequent years.

Per year, herbage quality parameters of each plot under REMOV2 were determined. Dried herbage samples were ground in a RETSCH mill and analysed for crude protein (CP, %), crude ash (ASH, %), crude fibre (CF, %) and organic matter digestibility (OMD, %). ASH content was determined gravimetrically after calcination during 4 h at 550 °C. Crude fibre content was analysed gravimetrically after calcination of the non-soluble residues that remained after heating in 0.26 mol l^{-1} H_2SO_4 and 0.23 mol l^{-1} NaOH, successively. CP content was determined as 6.25 x Kjeldahl-N content. OMD (%) was determined *in vitro* according to the pepsine-cellulase method (De Boever *et al.* 1988). The energy value of margin herbage was calculated according to formulas of CVB (1999) and was expressed as Dutch Feed Units (VEM, Voedereenheid Melk; De Boer & Bickel 1988). Herbage quality parameters were determined per individual cut. Herbage quality of the annual yield was calculated as the weighted average of herbage quality of the first cut and regrowth cut. Mean herbage quality over the period 2002-2004 was then calculated by averaging herbage quality of three subsequent years.

3.4.6 Mineral nitrogen auguring

During the winter period 2003-2004, mineral N content at SITE1 and SITE2 was determined separately in three soil horizons (0-30, 30-60 and 60-90 cm). Mineral N analysis was performed on soil samples taken at the end of the growing season (29 October 2003) and before the start of the next growing season (1 March 2004). Soil auguring was performed at six auguring positions along nine transects perpendicular centred to MIXT1, MIXT2 and CONTR managed under REMOV2. Auguring positions for both sites were: one position in the field crop area (position 2.5 m) one position at the margin edge (position 0 m) and four positions in the margin strip (positions -1.25, -2.5, -5 and -7.5 m at 1.25, 2.5, 5 and 7.5 m, respectively, from the margin edge). Samples were immediately deep frozen prior to determination of nitrate N (NO_3-N) and ammonium N (NH_4-N) using continuous flow spectroscopy performed on oven-dried soil. Mineral nitrogen (N_{min}, kg ha^{-1}) in each soil horizon was calculated by adding amounts of NO_3-N and NH_4-N. Amounts of N_{min}, NO_3-N and NH_4-N in the soil horizon 0-90 cm (hereafter called total N_{min}, total NO_3-N and total NH_4-N, respectively) were calculated by adding individual amounts in each soil horizon. N_{min} loss (kg N ha^{-1}) during winter was estimated by subtracting the residual N_{min} at the end of October from N_{min} at the end of February of the next year.

3.4.7 Abiotic conditions

Abiotic conditions at the shaded and unshaded side of trial 2 were characterized by measurement of the soil water status and light availability. During the period from 27 June to 6 September 2002, soil moisture content of 3 soil profiles (0-10 cm; 10-20 cm; 20-30 cm) was assessed every two weeks within the center of every plot. Undisturbed soil samples were taken in soil sample rings of known volume (100 cm^3). After drying the samples for 24h at 105 °C, the volumetric moisture content (vol%) was calculated. On two complete sunny days (9 August and 3 September 2002) photosynthetic active radiation (PAR, μmol photons m^{-2} s^{-1}) above the field margin canopy (i.e. incident PAR) and PAR within the field margin canopy (i.e. transmitted PAR) was measured at both the unshaded and shaded side with the Sunscan Canopy Analysis System SS1 (Delta-T Devices). This system also calculated the canopy leaf area index (LAI) of the plant communities on 3 September 2002.

3.4.8 Monitoring mobile flying insects nearby field margin strips

The insect fauna was monitored during a four week period from 7 August to 3 September 2002 using yellow biosignal sticky traps (BUGSCAN-BIOBEST) sized 20 cm x 40 cm. The yellow color is highly attractive to insects due to its high reflection properties (Bernays & Chapman 1994). Traps were installed on both shaded and unshaded side along twelve transects perpendicular centered to the field margin community plots. Along each transect, traps were placed vertically 30 cm above the crop canopy (at both sides: unsprayed unfertilized mixture of red clover and Italian ryegrass) at five monitoring positions: 4 m inside the margin strip, upon the edge between margin strip and crop and at three positions in the crop: 4, 8 and 16 m away from the margin edge. These positions are further indicated as –4 m, 0 m, 4m, 8m and 16 m. The traps were replaced weekly. Prior to determination of trapped insects, collected traps were temporarily stored in a refrigerator at 2 °C. Captured insects were determined according to Elseviers insect Guide (Chinery 1982) using a trinocular microscope (120X). Per trap, all insects were determined to family level, some to superfamily or order level and counted per family, superfamily or order. Total number of insects (hereafter insect number) in the period from 7 August to 3 September 2002 was calculated by adding the weekly counts per position. Family richness was expressed as the number of occurring insect families. Shannon diversity index (Magurran 1988) was used to determine biological diversity of insects in the margin strips. Insect families were classified according to their feeding habit and divided into crop damaging insects (pests), pest antagonists (predators and parasitoids) and flower visiting insects (pollinators). This classification is of limited value since both antagonists as well as plant damaging species may occur within some families.

3.4.9 Statistical computations

In general, S-plus 2000 for Windows was used to carry out the statistical computations for analysis of variance of a strip split plot design (Trial1:vertical factor, location; horizontal factor or main plot factor, plant community; subplot factor, cutting treatment; Trial2:vertical factor, light regime; horizontal factor or main plot factor, plant community; subplot factor, disturbance level). Independent t-tests (P = 0.05) were used to compare differences in seed bank, vegetation and insect composition. To determine changes of parameters over time, linear regression analysis was used. To determine the pattern of succession over time in terms of functional groups, a principal component analysis on a variance-covariance matrix was performed on data of I% of following functional groups: annual non N fixing dicotyledons (ANDIC), annual monocotyledons (ANMON), annual legumes (ANLEG), perennial non fixing dicotyledons (PERDIC), perennial monocotyledons (PERMON) and perennial legumes (PERLEG).

Family richness and insect numbers were statistically analyzed with S-plus 2000 for Windows according to a strip split plot design (Gomez & Gomez 1984) with three factors (light regime, plant community and monitoring position). Abiotic factors were analyzed according to a strip plot design with two factors (light regime and plant community). ANOVA (SPSS10 for Windows) was used for statistical calculations of N_{min}, NO_3-N, and NH_4-N amounts.

3.4.10 Research questions

3.4.10.1 Nature

Maximisation of biodiversity in margin strips:

(1) Is there any potential for naturally regenerated strips to develop into floristic diverse plant communities or are they pauperised of species? (2) Which mowing regime of the newly created communities maximizes species richness and how does the cutting regime direct biodiversity and vegetation succession? (3) What is the success of introducing seed mixtures differing in seed provenance to recreate a diverse semi-natural community? (4) Is the application of species rich roadside herbage useful to enhance botanical diversity? (5) Is there any similarity in the vegetation between unsown and sown communities?

Effects of disturbance and/or light intensity:

(6) What is the effect of disturbance and light regime on biological invasion? (7) How does a single disturbance affect species richness, early botanical succession and vegetation similarity at high and low light regime? (8) What is the effect of light regime and plant community on insect number, insect composition and insect diversity both in the margin strip and in the adjacent field crop?

3.4.10.2 Agriculture

Potential weed problems in the margin strip and the adjacent crop:

(9) What is the best field margin strip management (field margin type and cutting regime) to reduce the abundance of ingrowing and/or specialized anemochorous weeds? (10) How deep do airborne seeds from margin species penetrate into adjacent crops? (11) Is a soil seed bank analysis a useful tool to predict the risk of problem weeds in the margin strip and in the adjacent crop?

Agricultural valorisation of margin herbage:

(12) Does the mowing regime and/or field margin type affect dry matter yield over time? (13) What is the impact of field margin type and associated vegetation composition on herbage quality? (14) Is herbage quality affected by cutting time? (15) How useful is herbage from field margin as an animal feed?

Pests:

(16) Is there a relation between pest insects and their generalist predators and parasitoids?

3.4.10.3 Environment

Soil mineral N content and loss during winter:

(17) How do sown/unsown margin strips bordering arable crops reduce mineral N residues and loss during winter? (18) Is mineral N content and loss affected by plant community or location? (19) Which margin width is advisable to minimize soil mineral N content and loss nearby the pre-existing boundary? (20) Is species richness and botanical composition of boundary vegetation positively affected by the presence of the margin strip?

4 RESULTS

The research questions, methods, and experiments in this section refer to the corresponding parts of section 3 (e.g. 4.1 refers to 3.1; 4.2 to 3.2, etc.)

4.1 Invasiveness and invasibility

We first investigated whether the success of the simulated invasions varied with the identity of the invader and/or the identity of the invaded monoculture (question 1). Two measures of success, germination percentage and total leaf length, were significantly affected by invader species and monoculture species (ANOVA, significant invader effect: $F_{7,63}$ = 25.750 for germination and 5.306 for leaf length; significant monoculture effect: $F_{7,63}$ = 4.460 for germination and 6.167 for leaf length; $P < 0.0001$ in all cases, Fig. 1). Interactions between invader identity and monoculture identity were not significant, neither for germination nor for growth (same analysis; for germination: $F_{49,63}$ = 1.080 and $P = 0.359$; for leaf length: $F_{49,63}$ = 1.095 and $P = 0.344$). The third measure of success, survival until next spring, was not significantly affected by invader or monoculture identity (contingency tables; for invader identity, $\chi^2_{7,0.05}$ = 11.556 and $P = 0.116$; for monoculture identity, $\chi^2_{7,0.05}$ = 12.000 and $P = 0.101$). Most invaders (75 %) survived their first winter.

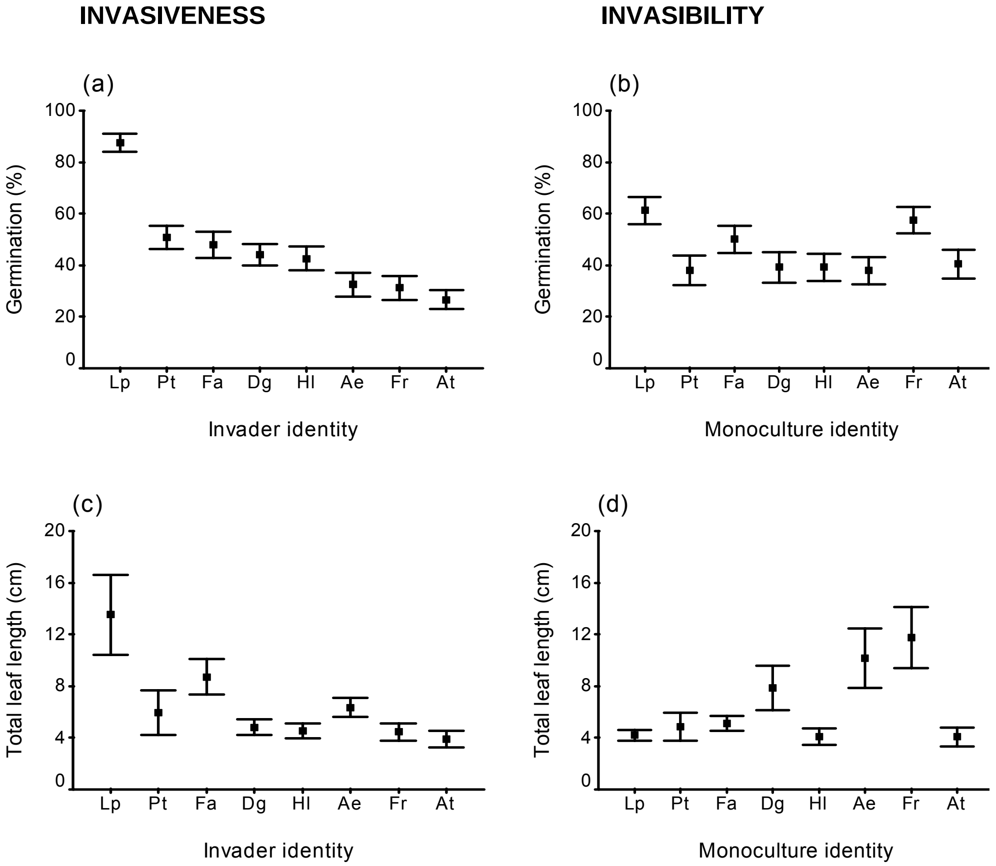

Fig. 1 (a) Mean percentage germination of the different invader species. **(b)** Mean percentage germination of invader seeds in the different monoculture species. **(c)** Mean total leaf length per plant of the different invader species at the end of the first growing season. **(d)** Mean invader total leaf length per plant in the different monoculture species. Bars represent ± 1 SE; (**a,c)** refer to invasiveness (means by invader species); (**b,d)** refer to invasibility (means by invaded monoculture species). Ae, *Arrhenatherum elatius*, At, *Agrostis tenuis*, Dg, *Dactylis glomerata*, Fa, Festuca arundinacea, Fr, *Festuca rubra*, Hl, *Holcus lanatus*, Lp, *Lolium perenne*, Pt, *Poa trivialis*.

Table 2 shows the Spearman correlation coefficients between the different measures of invasion success, averaged either by invader or by monoculture identity. For invasion success by invader (invasiveness), percentage germination, leaf length, and percentage survival (until spring 2002) were all positively correlated. In other words, the species with the best germinating seeds also had the highest growth rates and survived the longest. Surprisingly, calculated by monoculture (invasibility), none of the correlations were significant. This implies that suitable conditions for germination are not *per se* suitable conditions for growth and survival.

We next investigated whether the differences in success between the eight invader species correlated with the traits they possessed (question 2, invasiveness). Invader leaf length was negatively correlated with germination time and positively correlated with seed mass, which varied from 0.10 mg for *At* to 2.53 mg for *Ae.* Germination percentage correlated negatively with germination time (Table 3a). Differences in invasiveness between the species were thus partly due to interspecific variation in seed mass and germination rate.

Table 2 Spearman rank correlation coefficients (two-tailed; $n = 8$) between different measures of invasion success.

	(a) by invader	**(b)** by monoculture
leaf length * % germination	0.810^{*}	-0.060 ns
% survival * % germination	0.824^{*}	0.305 ns
leaf length * % survival	0.909^{**}	0.494 ns

*,** $P < 0.05$ and $P < 0.01$, respectively; ns, not significant. Correlations were calculated between (a) average values by invader species (i.e. for each invader species the success was averaged across all invaded monocultures), and (b) average values by monoculture species (i.e. for each monoculture species the success was averaged across all invader species inserted).

To test whether differences in invasion success among monocultures were associated with traits of these monocultures (question 3, invasibility), correlations were calculated between the various measures of success and the gap attributes, averaged by monoculture identity (Table 3b). Leaf length correlated significantly with '$\text{PFD}_{\text{intercepted}}$ start of growth', but correlations with amount of nitrogen, height and biomass of the neighbour plants were not significant. Percentage germination of the invaders correlated positively with the amount of nitrogen in the bordering plants and negatively with '$\text{PFD}_{\text{intercepted}}$ germination'. Thus, invasibility of the monocultures was governed by the light penetrating the gaps, especially shortly after insertion of the invader seeds, and by the nitrogen acquisition of competitors surrounding the gaps.

To verify whether the significant correlations found at the end of the first growing season still held after 10 months of invader growth, they were recalculated for leaf length measured on 28 May 2002. For germination time and '$\text{PFD}_{\text{intercepted}}$ start of growth', there was still a significant correlation with invader leaf length ($r = -0.21$ and $r = 0.38$ respectively, $P < 0.05$ in both cases). The correlation between seed mass and leaf length, however, had disappeared ($P > 0.05$).

Table 3 Spearman rank correlation coefficients (two-tailed) between invasion success (leaf length or percentage germination) and **(a)** invader characteristics (averaged by invader species) and **(b)** monoculture characteristics (averaged by monoculture species).

(a) Invasiveness

	Seed mass	Germination time
Leaf length (n = 168)	0.348**	-0.199**
Germination % (n = 192)	0.127 ns	-0.406**

(b) Invasibility

	$PFD_{intercepted}$ germination	$PFD_{intercepted}$ start of growth	$PFD_{intercepted}$ growth	N in neighbour plants	Height of neighbour plants	Biomass of neighbour plants
Leaf length (n = 168)	/	0.234**	0.399 ns	-0.129 ns	-0.031 ns	-0.141 ns
Germination % (n = 192)	-0.220**	/	/	0.187**	/	/

*,** $P < 0.05$ and $P < 0.01$, respectively; ns, not significant; /, correlation is meaningless, PFD, photon flux density.

Question 4 concerns possible relationships between invasiveness and invasibility. Are good invaders highly invasible when grown in monoculture, or do they instead offer much resistance? Or is there no relationship at all? We plotted the average invasion success in every species of monoculture (invasibility), expressed either as percentage germination of the invader seeds or as total invader leaf length at the end of the first growing season, against the average invasiveness of the different invader species, expressed as leaf length (not shown). For none of the invasion success measures, invasiveness and invasibility were significantly related ($P > 0.05$). The capacity to invade, therefore, seems unrelated to the capacity to offering resistance to invasion. Nevertheless, none of the most invasible monocultures (*Fr* and *Ae*) were themselves good invaders, whereas none of the best invaders (*Lp* and *Fa*) had high invasibility.

With the results of the ANOVA used for question 1 we further compared the relative importance of invasiveness and invasibility (question 5). For leaf length, the total sum of squares (SS_T) was 21.5, while the invader sum of squares (SS_I) was 3.2 and the monoculture sum of squares (SS_M) was 3.8. This means that invader identity explained 15% of the total variation and monoculture identity 18% of the total variation in leaf length. However, for invasion success expressed as germination (SS_T = 79943.7, SS_I = 36721.8 and SS_M = 6360.3), invader identity explained 46% of the total variation and monoculture identity only 8%.

4.2 The role of species richness

4.2.1 Germination

For the three invader species, in the second experiment in synthesized ecosystems, we examined if there was a relationship between percentage germination, or germination time (days after seed insertion in the gaps), and species richness, % light transmittance or neighbour biomass. Percentage germination decreased significantly with species richness in *F. arundinacea* (linear regression, $y = 70.608 - 2.243x$, $P = 0.048$, $r^2 = 0.08$), while in *L. perenne* a negative relationship was found between germination percentage and biomass of the neighbour plants (linear regression, $y = 106.355 - 50.984x$, $P = 0.016$, $r^2 = 0.12$). The influence of light on germination percentage was not significant, nor were there significant regressions for germination time ($P > 0.05$ for all species).

Seed mass (averaged per invader species) could not explain the observed variation in germination percentage (all invaded gaps; linear regression, $P > 0.05$), but had a significant effect on germination time, with longer germination times in bigger seeds (linear regression, $y = 5.043 + 0.316x$, $P = 0.038$, $r^2 = 0.03$).

4.2.2 Invader growth

Because several invaders were smaller than the harvesting height, total leaf length per plant rather than biomass was used as measure for invader growth. Invader leaf length at the end of the first growing season did not depend on the species richness of its neighbours, but increased significantly with increasing % PAR transmittance and was negatively related to the biomass of its neighbour plants at the end of the first growing season (linear regressions, Fig. 2). This pattern was observed for the three invader species (except for biomass in *L. perenne*), with % PAR transmittance O being the best predictor in *F. arundinacea* and *L. perenne* ($r^2 = 0.21$ and $r^2 = 0.23$, respectively), and neighbour plant biomass the best predictor in *P. trivialis* ($r^2 = 0.18$). In the second growing season, on the contrary, invader leaf length declined significantly towards the higher richness levels (linear regression, Fig. 3). As in the first year, leaf length was positively associated with % PAR transmittance (in Year 2, % PAR transmittance C, measured in more closed gaps, was a better predictor for leaf length than % PAR transmittance O) and negatively with biomass of the neighbour plants (measured in Year 2), but this time the regression slopes were steeper (except for neighbour biomass in *P. trivialis*). In *F. arundinacea* and *L. perenne* percentage PAR penetrating in the closed gaps was the best predictor of leaf length in the second season ($r^2 = 0.24$ and $r^2 = 0.45$, respectively), while in *P. trivialis* leaf length was associated most strongly with species richness ($r^2 = 0.30$). For *P. trivialis*, the relative importance of biomass and light in affecting leaf length changed over time, with light becoming more important in Year 2. Neighbour plant biomass and % PAR transmittance were correlated, with the strongest correlations between % PAR transmittance O and neighbour biomass Year 1 (Pearson correlation: n = 143, r = -0.458, $P < 0.001$) and between % PAR transmittance C and neighbour biomass Year 2 (Pearson correlation: $n = 143$, r = -0.217, $P = 0.009$).

To explain why the effect of richness on invader growth was different between the two years, we determined whether and how species richness modified % PAR transmittance, biomass of the neighbour plants or I_{max} for both times of measurement. Since community traits were not affected by invader identity (ANOVA with factors invader species and richness, invader effect: for PAR O: $F_{2,131} = 0.236$, $P = 0.790$; for PAR C: $F_{2,131} = 0.406$, $P = 0.667$; for biomass Year 1: $F_{2,131} = 0.786$, $P = 0.458$; for biomass Year 2: $F_{2,131} = 1.202$, $P = 0.304$), correlations were calculated with all invaders combined. Species richness correlated negatively with % PAR transmittance and positively with the biomass of the plants surrounding the gaps in both harvesting years (Table 4).

Table 4 Spearman's rank correlations between species richness of communities and percentage light transmittance in gaps, biomass of neighbour plants surrounding the gaps, and I_{max} (index for assessing degree of transgressive overyielding). PAR transmittance was measured when the vegetation around the gaps was recently mown in more open gaps (% PAR transmittance O) and after prolonged regrowth of the neighbour plants in more closed gaps (% PAR transmittance C).

	Percentage PAR transmittance O	Percentage PAR transmittance C	Biomass neighbours year 1	Biomass neighbours year 2	I_{max} year 1	I_{max} year 2
Species richness						
Correlation coefficient	**- 0.273**	**- 0.373**	**0.438**	**0.367**	- 0.124	**0.514**
P	0.001	< 0.001	< 0.001	< 0.001	0.140	< 0.001
N	143	143	143	143	143	143

Significant values ($P < 0.05$) are in bold.

For I_{max}, however, a different result was found between the two years. When I_{max} was calculated with the biomass data of the first growing season, no relationship with species richness was observed, whereas I_{max} increased with richness in Year 2. Regressions of invader leaf length on I_{max} show that I_{max} negatively affected invader growth in the second growing season, while leaf length in the first year was not associated with I_{max} (Fig. 4).

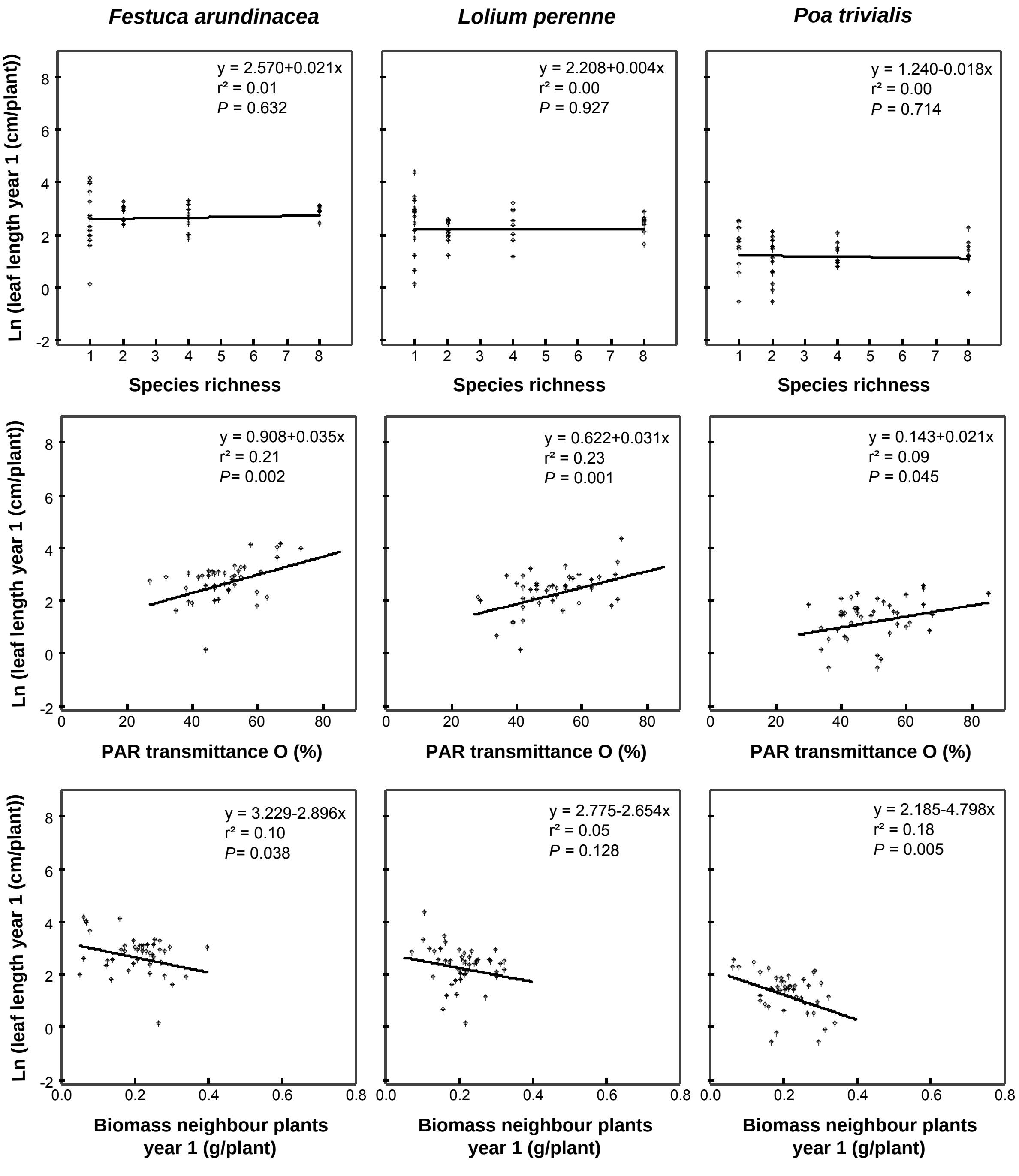

Fig. 2 Effect of species richness, % transmittance of photosynthetically active radiation (PAR transmittance O, measured when the vegetation around the gaps was recently mown and the invaders rather young), and biomass of the neighbour plants in Year 1 on invader performance, expressed as total leaf length per plant at the end of the first growing season, for the three different invader species.

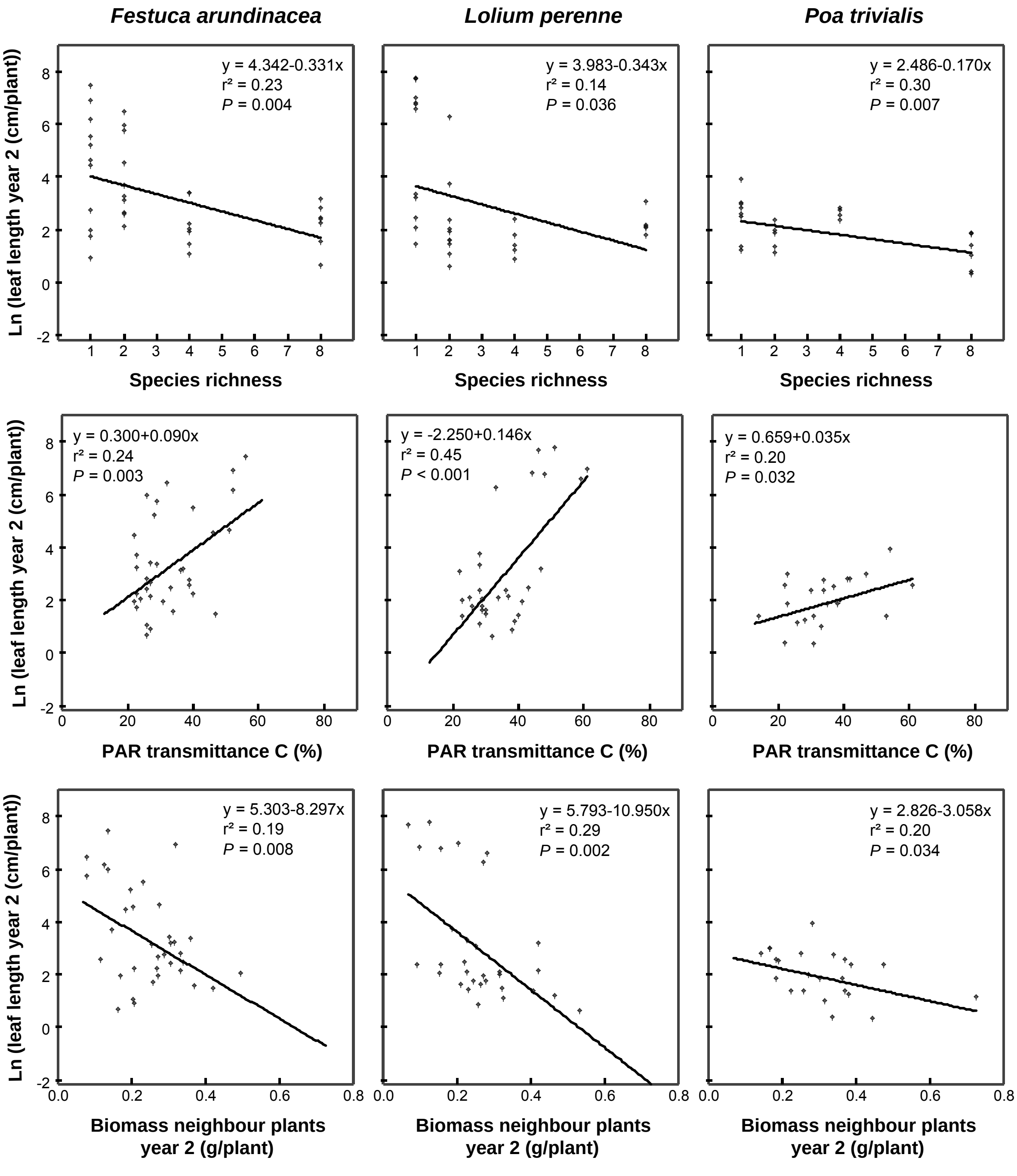

Fig. 3 Effect of species richness, % transmittance of photosynthetically active radiation (PAR transmittance C, measured after prolonged regrowth of the neighbour plants), and biomass of the neighbour plants in Year 2 on invader performance, expressed as total leaf length per plant in the second growing season, for the three different invader species.

Values of I_{max} were also higher in the second year than in the first one (ANOVA, factor = year, $F_{1,283} = 23.568$; $P < 0.001$), with transgressive overyielding ($I_{max} > 1$)

occurring in 80% of the mixtures in Year 2 versus only in 55% of the mixtures in Year 1. To summarize, in Year 1 species richness did not affect the level of complementarity, and differences in complementarity did not affect invader growth. In contrast, in Year 2, species richness did increase complementarity, which in its turn suppressed the invaders.

Invaders had a significantly higher leaf length in Year 2 compared to Year 1 (Figs. 2 and 3; ANOVA with factors invader and year, for year: $F_{1,\ 216} = 15.302$, $P < 0.001$). Especially in the monocultures and the two-species mixtures invader leaf length had increased. Community age also affected neighbour plant productivity, though not alike in all richness levels (Fig. 5). At the end of the first growing season, a wide range in monoculture productivity was observed, while the two-species mixtures all had very similar biomass. Also in the four- and eight-species mixtures the range was small (Fig. 5a). However, in the second year, the monoculture biomasses converged (especially through elevated productivity of the mixtures that were least productive in Year 1), while a wide range in productivity had developed in the mixtures (Fig. 5b). Whereas monoculture biomass increased only little in the second year, most of the two-, four- and eight-species mixtures became much more productive.

Further, a positive relationship between invader leaf length in all the gaps and invader seed mass (averaged per invader species) was found in both Year 1 (linear regression, $y = 0.990 + 0.750x$, $P < 0.001$, $r^2 = 0.41$) and Year 2 (linear regression, $y = 1.718 + 0.724x$, $P = 0.005$, $r^2 = 0.089$).

4.2.3 Survival

Survival of the invaders was highest in *F. arundinacea* (78%), while in *L. perenne* 65% and in *P. trivialis* only 53% of the plants survived until the second year. A logistic regression showed that neighbour biomass was a significant predictor of survival for the invader *F. arundinacea*, with more surviving individuals as neighbour biomass decreased (df = 1, Wald = 5.350, $P = 0.021$). For *P. trivialis* and *L. perenne* no significant relationships were found.

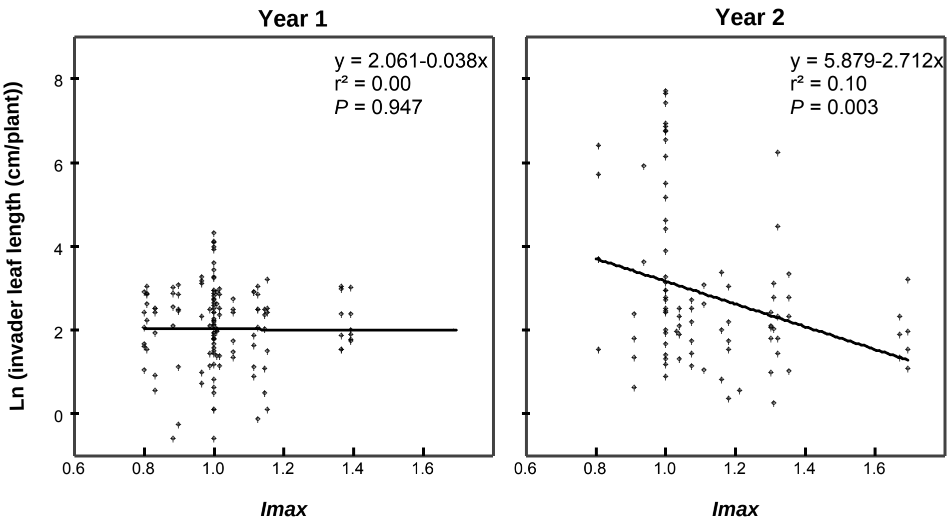

Fig. 4 Relationship between invader leaf length and I_{max} (index indicating complementary resource use if $I_{max} > 1$) in the first and the second growing seasons with all richness levels combined.

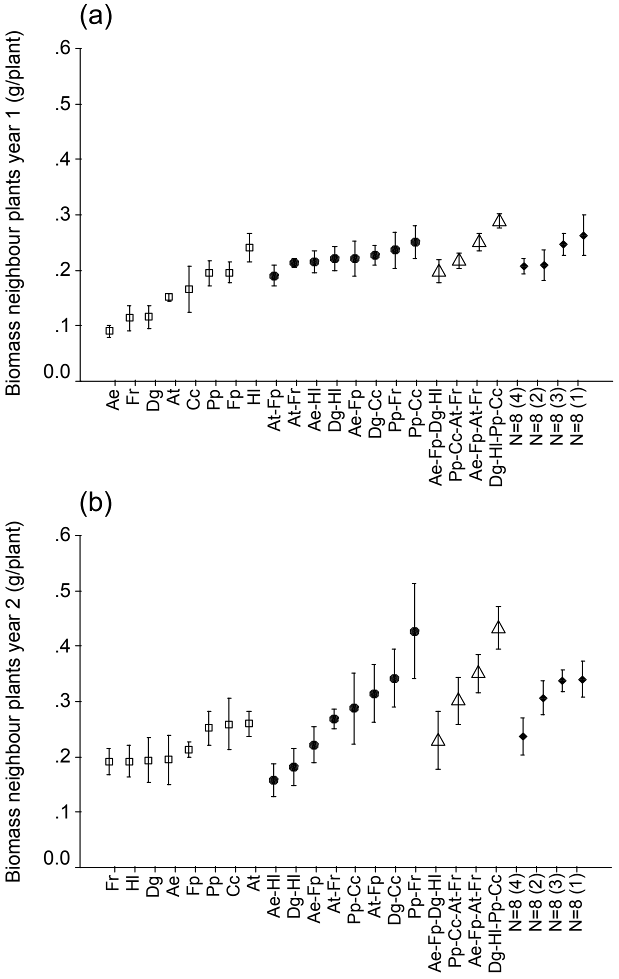

Fig. 5 Neighbour plant biomass in (a) the first growing season and (b) the second growing season for the different species compositions. Open squares are monocultures, closed circles bicultures, open triangles four-species mixtures and closed rhombs eight-species mixtures. Ae, *Arrhenatherum elatius*; At, *Agrostis tenuis*; Cc, *Cynosurus cristatus*; Dg, *Dactylis glomerata*; Fp, *Festuca pratensis*; Fr, *Festuca rubra*; Hl, *Holcus lanatus*; Pp, *Phleum pratense*. Symbols represent means of cumulative biomass of the eight neighbours for each composition ± 1 SE (*n* = 6).

4.3 Interactions with climate change

4.3.1 Survival

In the third experiment, the survival curves of the eight species were significantly different (survival analysis, Wilcoxon test, $\chi^2_{7,0.05} = 165.95$, $P < 0.001$). Percentage survival decreased sharply after around 8 days of stress in the species *At* and *Cc*, and between day 10 and 14 in the others (Fig. 6a). Species *Ae* and *Dg* survived the longest, with live individuals still being found after 19 and 22 days of stress, respectively. The ranking according to decreasing T_{50} was: *Dg*, *Fa* & *Fr*, *Ae*, *Lp*, *Pt*, *Cc*, *At*. According to decreasing T_{25} only the position of *Ae* changed: *Ae*, *Dg*, *Fa* & *Fr*, *Lp*, *Pt*, *Cc*, *At*.

4.3.2 Variations of the parameters during progressive heat and drought

RWC_{soil} decreased progressively during the stress period, and reached a minimum after eight to ten days, depending on species (Fig. 6b). *At* depleted the water supply fastest, whereas *Ae* and *Fr* were the most conservative consumers. Ψ_l declined sharply in all species after about three days (not shown). After seven days, the values had dropped below the maximum range of the equipment of –3 MPa. *Ae* had the highest average Ψ_l during the first seven days and *At* the lowest, but interspecific differences were limited. In all species, F_v/F_m fluctuated around 0.8 at the beginning of the stress and then decreased, indicating photoinhibition (not shown). F_v/F_m declined earlier in *At* (from day 4 on) than in the other species (after 6 to 8 days), whereas in *Ae*, there was little decline throughout. Most species were able to recover partially at around days 6-7, which were overcast.

Fig. 7 shows the progressive effect of drought and heat on g_s and A_{max}, which followed a similar pattern and approximated zero after ten days of stress. In most species the trend was decreasing, though fluctuating, except in the species with low values (*Ae* and *Dg*), which were more stable. These fluctuations were most probably due to variations in irradiance, temperature, and atmospheric vapour pressure deficit (VPD) between different days. The peak values in A_{max} and g_s on day 3 and day 6, for example, coincided with a significant drop in VPD and leaf temperature (not shown). Transpiration rate significantly correlated with g_s in all species (Pearson correlations, $P < 0.05$ in all cases). Values of C_i approximated 260 µmol CO_2 mol^{-1} during the first six days of stress in all species, but thereafter started to increase (not shown). *Ae*, *Dg* and *Fa* maintained the initial values longer than the other species. The g_s value at which C_i started to increase, the so called C_i inflexion point which indicates permanent photoinhibition (Flexas & Medrano 2002), equalled approximately 50 mmol m^{-2} s^{-1} in all species.

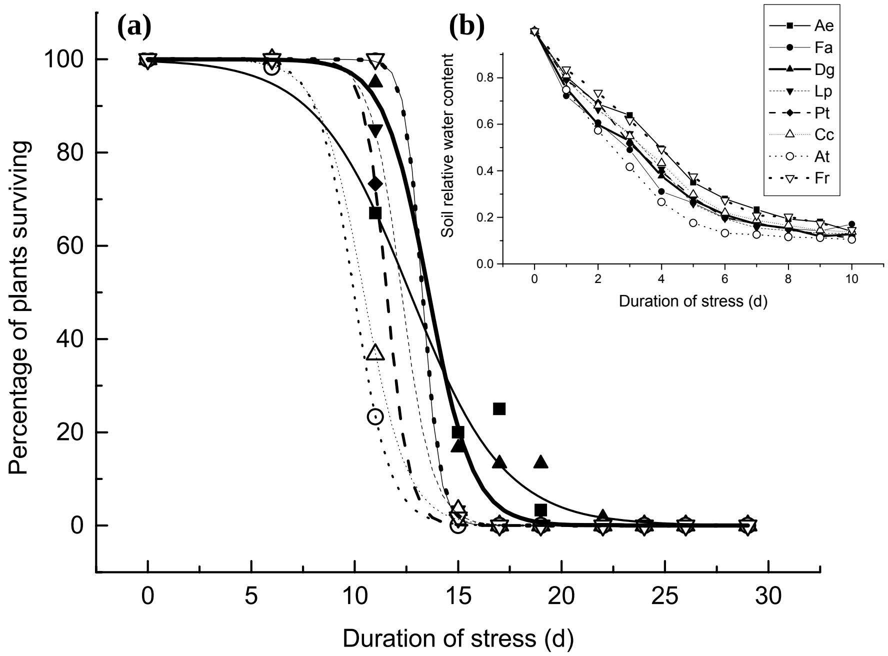

Fig. 6 **(a)** Species survival percentage measured after different exposure times to a simulated heat wave. Data are fitted with dose response curves: $y = A\big/\left(1+10^{(\log x_0 - x)p}\right)$. Each symbol is based on 60 plants in two pots. **(b)** Decrease of soil relative water content (RWC_{soil}) during the first 10 days of exposure to the heat wave. Data are means of nine pots. Species codes: Ae, *Arrhenatherum elatius*; At, *Agrostis tenuis*; Cc, *Cynosurus cristatus*; Dg, *Dactylis glomerata*; Fa, *Festuca arundinacea*; Fr, *Festuca rubra*; Lp, *Lolium perenne*; Pt, *Poa trivialis*

4.3.3 Relationship between survival time and ecophysiological responses

We first investigated whether the survival time of the species was related to the course of their ecophysiological parameters during the stress (question 1). For each parameter, we calculated the average value by species during the first ten days of exposure and tested whether these averages explained a significant fraction of the interspecific variation in survival time (linear regressions).

Survival time (T_{25}) increased significantly with increasing F_v/F_m ($y = -1.108 + 21.607x$, $P = 0.028$, $r^2 = 0.58$, not shown), and decreased significantly when the species had higher C_i ($y = 19.923 - 0.019x$, $P = 0.018$, $r^2 = 0.63$, not shown). The fraction of explained variance increased when F_v/F_m and C_i were both included in the model (multiple regression, $T_{25} = 9.948 + 11.519 \times (F_v/F_m) - 0.013 \times C_i$, $P = 0.041$, $r^2 = 0.72$). Survival time was not related to the average values of A_{max}, g_s, TR, WUE, or RWC_{soil}.

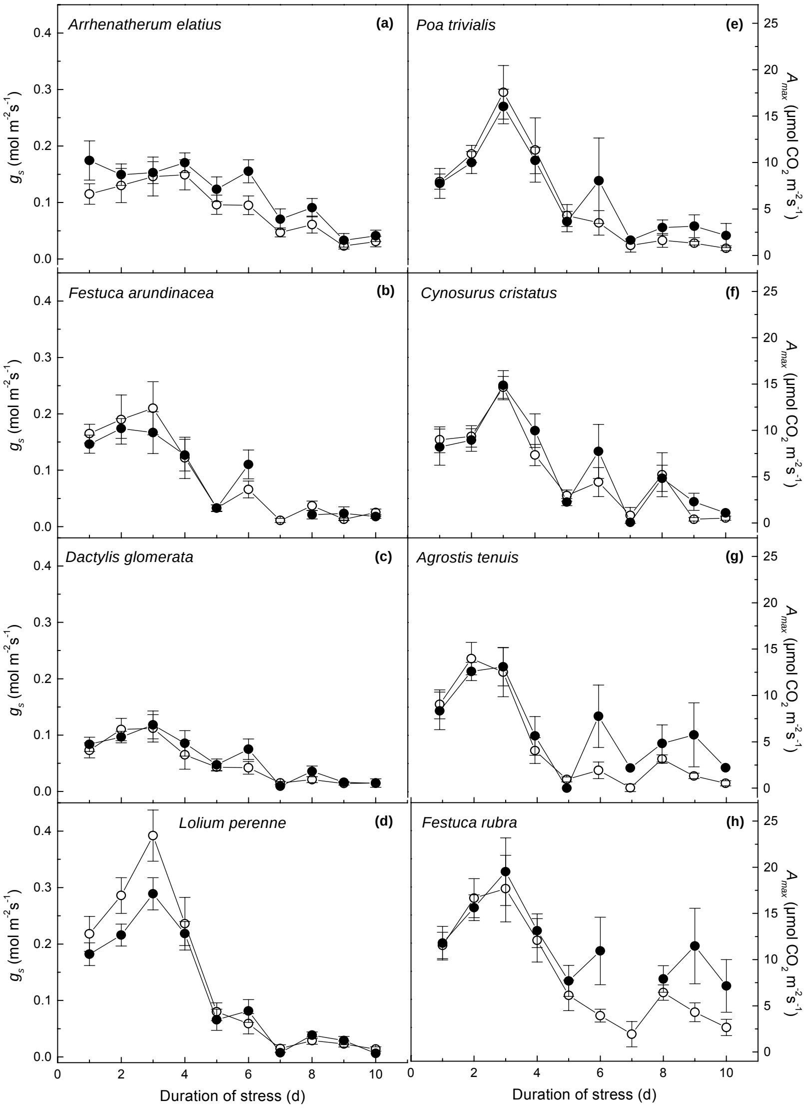

Fig. 7 Time course of stomatal conductance (g_s) (open circles) and light-saturated photosynthetic CO_2 uptake rate (A_{max}) (solid circles) during the heat wave. Means ± SE of six replicates.

In a second analysis, A_{max}, g_s, TR, F_v/F_m, and $\log_{10}$ (RWC_{soil}) were linearly regressed against time, for each species separately. This enabled us to quantify how much of the variation in these parameters could be explained by stress duration (by means of r^2), and how much variation was due to daily fluctuations in temperature, vapour pressure deficit, irradiation, etc. ($1-r^2$). Because linear regressions require at least six data points and there were only four measurements of Ψ_l during the stress, this parameter was not considered. All regressions were significant, except A_{max} against time for species *Fr* ($P = 0.066$). The obtained r^2-values and regression slopes of the significant regressions were then used to investigate whether species survival time was related to the amount of variation in the parameters that could be explained by stress duration (r^2), or to the gradient of the regression line. Significant relationships were found between survival time (T_{25}) and the r^2 of the relationship between g_s or A_{max} and stress duration ($y = 1.750 + 21.410x$, $P = 0.004$, $r^2 = 0.78$, Fig. 8a, and $y = 4.582 + 12.766x$, $P = 0.009$, $r^2 = 0.78$, Fig. 8b, respectively). The slopes of the regressions by species of F_v/F_m against time also explained survival time ($y = 15.451 + 57.679x$, $P = 0.042$, $r^2 = 0.52$).

Subsequently, regressions per species were calculated for A_{max}, g_s, TR, and F_v/F_m against RWC_{soil}, to quantify how much of the variability in these parameters was accounted for by the water availability in the soil. The regressions were significant for A_{max} (except for *Fr*), g_s, and TR, but not for F_v/F_m (only three out of the eight species gave a significant result). Again, the r^2 values and the slopes of these relationships (only for A_{max}, g_s, and TR) were used to explain species survival time. A significant relationship was found only between survival time (T_{50}) and the r^2 of A_{max} against RWC_{soil} ($y = 4.393 + 13.026x$, $P = 0.006$, $r^2 = 0.81$).

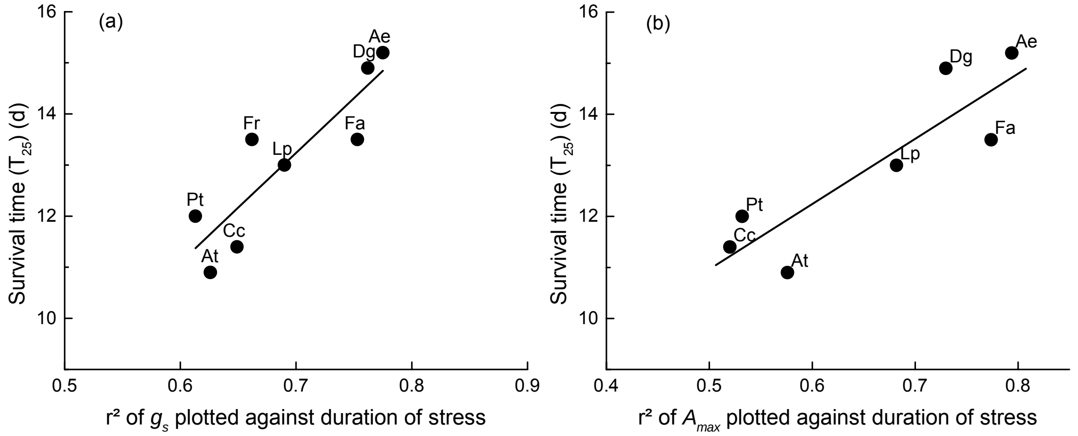

Fig. 8 (a) Relationship between survival time and the amount of variation in light-saturated stomatal conductance (g_s) explained by stress duration, the latter being expressed per species as the r^2 of the regression of g_s against time. (b) Relationship between survival time and the amount of variation in light-saturated photosynthetic CO_2 uptake rate (A_{max}) explained by stress duration, the latter being expressed per species as the r^2 of the regression of A_{max} against time. Survival times T_{50} and T_{25} are the drought periods required to reduce survivorship to 50% and 25%, respectively. See Fig. 6 for species codes.

Beside simple regressions also multiple regressions were calculated with non-correlated parameters as predictors. A multiple regression with as predictors both the r^2 of the relationship between A_{max} and RWC_{soil}, and the slope of the regression of TR against RWC_{soil}, explained 95% of the variance in species survival time ($T_{50} = 6 + 12.969 \times$ (r^2 of A_{max} against RWC_{soil}) $- 0.212 \times$ (slope of TR against RWC_{soil}), $P = 0.002$, $r^2 = 0.95$). None of the other multiple regressions (all possible combinations) were significant.

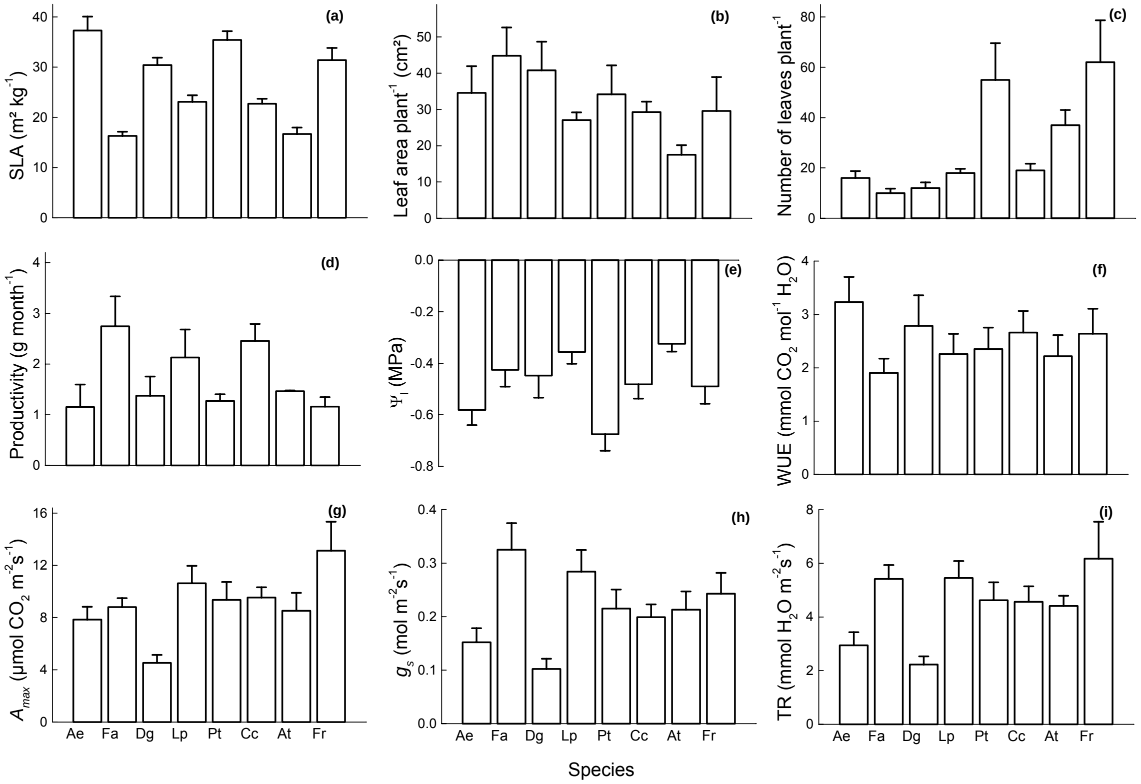

Fig. 9 Plant characteristics of the grass species measured in unstressed conditions (not exposed to the heat wave and well watered). Means ± SE of six replicates for specific leaf area (SLA), leaf area per plant, and number of leaves per plant, and means ± SE of 12 replicates for water use efficiency (WUE), predawn leaf water potential (Ψ_l), light-saturated photosynthetic CO_2 uptake rate (A_{max}), stomatal conductance (g_s), and transpiration rate (TR). Productivity was measured on two pots per species. See Fig. 6 for species codes.

4.3.4 Relationship between survival time and plant characteristics in non-stress conditions

Fig. 9 shows the interspecific variation in morphological and ecophysiological parameters in non-stress conditions. As there was a clear range in most parameters (except in F_v/F_m, not shown), we investigated whether species survival time could be predicted from them (question 2). Linear regressions with survival time (T_{25} or T_{50}) as dependent variable and the average values of the species characteristics (measured on unheated plants) as independent variables, revealed a significant relationship for leaf area per plant: T_{50} was longer in plants with a greater total leaf area (y = 8.265 + 0.120x, $P = 0.033$, $r^2 = 0.56$, Fig. 10). None of the other parameters were related to survival time, although the species surviving longest, *Ae* and *Dg*, tended to have low A_{max}, g_s, TR and high WUE compared with the other species. The results were not improved (i.e. no new relationships were found) by using multiple regressions with non-correlated parameters as predictors.

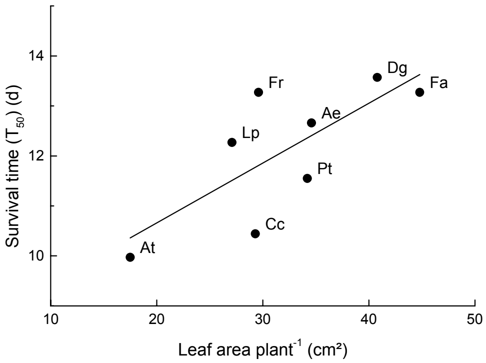

Fig. 10 Relationship between species survival time and average leaf area per plant (*n* = 6). Survival time T_{50} is the drought period required to reduce survivorship to 50%. See Fig. 6 for species codes.

4.3.5 Probabilistic model

In order to validate the probabilistic model of Nijs & Impens (2000), a series of grass communities differing in species composition were exposed to a simulated heat wave. For every species, we calculated, based on the monoculture data, the probability that an individual survives (p'). From this data the probabilities of survival of the species in the different plant mixtures could be calculated (expected probability of survival; e.g. p'^{40} for a monoculture, as there were 40 individuals per container). We compared these data with the proportion of communities in which at least one individual survived after the heat and drought stress (Fig. 11). We found that the survival values increased with increasing species number, but saturated at four species. Our data support the probabilistic model, which predicts an asymptotic relationship between number of functionally analogous species and probability of functioning.

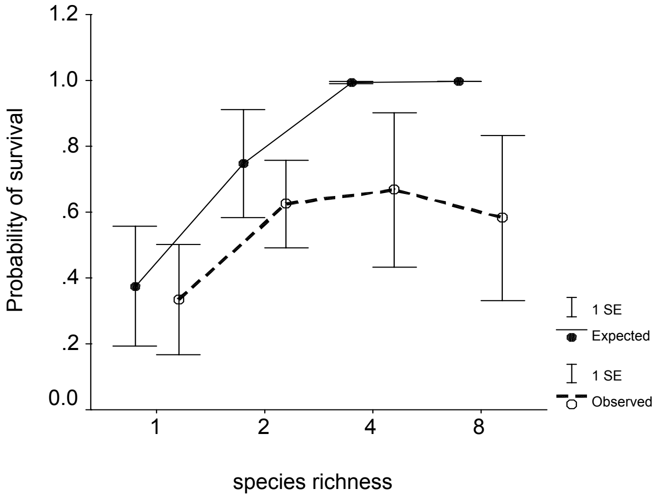

Fig. 11 Relationship between probability of community survival and number of species. Calculated and observed data are shown.

4.4 Biodiversity and invasion in field borders

4.4.1 Nature Conservation

4.4.1.1 Maximisation of biodiversity

This paragraph gives an answer to research questions 1 to 5 (see 3.4.10).

After three years of succession total species diversity was significantly altered by the plant community (*P* = 0.03) and the cutting treatment (*P* = 0.001) but not by the location. However a significant interaction between location and plant community occurred (*P* = 0.03). At SITE1, CONTR (16.1 spp.) was more species rich than MIXT2 (14.9 spp.) and MIXT1 (14.3 spp) (lsd=1.9 spp.). At SITE2, the highest species-richness was observed in MIXT1 (18.7 spp.) followed by CONTR (18.2 spp.) and MIXT2 (12.8 spp.) (lsd=1.9 spp.). The addition of roadside herbage significantly increased species richness with approximately 2 spp./16 m² on both locations (SITE2: MIXT3, 14.6 spp. versus MIXT2, 12.8 spp.; SITE1: MIXT3, 16.8 spp. versus MIXT2, 14.9 spp.). The species richness was significantly higher for REMOV2 (17.2 spp.) than for REMOV0 (14.4 spp.) (lsd=0.7 spp.). REMOV1 responded intermediary with 15.8 spp.

Since initially species diversity was significantly higher for the sown communities and since the unsown community revealed a higher increase (SITE2) or lower decrease (SITE1) in species diversity, species diversity of sown and unsown communities converged during the first three successional years, irrespective of mowing regime or location (Table 5).

Upon establishment 72% of the sown wildflower species emerged in MIXT3 and MIXT2, and 42% in MIXT1. During the following years the number of sown wildflowers decreased significantly, irrespective of plant community, mowing regime or location. Diversity of sown wildflower species (except for SITE1 and MIXT3 at SITE2) decreased at higher rate under REMOV0 since all slopes of regression equations were more negative under REMOV0 than under REMOV2, irrespective of plant community. In October 2003, the cutting treatment (*P* = 0.005) significantly determined the total number of surviving sown wildflower species. The highest number of sown wildflower species was recorded under REMOV2 (4.1 spp.), which significantly differed from REMOV1 (3.2 spp.) and REMOV0 (2.8 spp.) (lsd=0.4 spp.).

In the installation year prior to the first mowing, vegetations at SITE2 were choked by the nitrophylous species *Solanum nigrum* L., *Chenopodium album* L. and *Urtica urens* L., which were dominant or highly abundant. The presence of these species was attributed to their high seed densities in the soil seed bank. Soil seed bank at SITE2 was unbalanced due to high seed densities of only a few plant species: compared to SITE1, the soil seed bank at SITE2 revealed significant threefold higher seed densities of arable nitrophylous competitive annuals *S. nigrum*, *U. urens* and *C. album*.

Table 5 Species diversity (spp./16m^2) during succession (2001-2003). See 3.4.1 for abbreviations.

Location	Cutting Treatment	Plant Community	Before Mowing Sept 2001	After mowing[1]					Slopes[2]
				M1 Oct 2001	M2 July 2002	M3 Oct 2002	M4 July 2003	M5 Oct 2003	
SITE1	**REMOV0**	**CONTR.**	34.3	8.3	24.7	21.0	17.0	16.3	-0.82
		MIXT1	33.7	17.3	15.7	17.7	15.3	14.0	-3.99
		MIXT2	49.7	18.0	15.7	14.3	17.0	12.7	-4.55
		MIXT3	48.7	16.7	19.0	16.3	23.3	17.7	4.73
	REMOV2	**CONTR.**	34.3	10.0	24.7	26.7	16.0	16.0	-1.18
		MIXT1	33.7	18.0	18.7	19.7	18.0	15.0	-3.30
		MIXT2	49.7	19.0	17.7	18.3	15.7	15.0	-5.57
		MIXT3	48.7	19.0	27.3	15.7	21.3	18.3	-1.79
SITE2	**REMOV0**	**CONTR.**	13.7	14.0	19.3	18.0	15.7	16.0	0.65
		MIXT1	33.0	21.3	20.7	17.3	18.7	15.3	-6.92 *
		MIXT2	42.0	25.3	14.0	11.7	12.0	11.3	-17.00 ***
		MIXT3	42.0	23.0	19.3	12.3	18.3	12.0	-11.30 *
	REMOV2	**CONTR.**	13.7	10.3	17.0	20.7	15.3	19.0	8.18
		MIXT1	33.3	18.3	24.7	25.7	23.0	20.3	2.00
		MIXT2	42.0	24.3	22.7	17.3	17.0	14.7	-13.00 *
		MIXT3	42.0	24.0	28.0	13.7	26.6	19.0	-3.36

[1] M…, number of subsequent cutting and associated monitoring date

[2] Slopes (10^{-3} spp.day^{-1}) of regression of species diversity (spp.) on time (days, Oct 2001-Oct 2003):
*, **, *** p<0.05, p<0.01, and p<0.001 respectively

In Fig. 12 succession patterns of plant communities under REMOV2 (Fig. 12A) and REMOV0 (Fig. 12B) are shown: time-trajectories (2002-2004) of plant communities at SITE1 and SITE2 were plotted against the first two principal components Z1 and Z2. Principal components analysis revealed that the principal components (Z) explained 56.4% (Z1); 36.9% (Z2), 6.1% (Z3), 0.6% (Z4), 0.1% (Z5) and 0.0% (Z6) of the total variance. Since the first two components accounted for 93.3% of the total variance, all other components were ignored further on. The first component was 0.815(ANDIC)+0.506(PERDIC)+0.275(ANLEG)-0.070(PERLEG)+0.720(ANMON)-0.952(PERMON) (ANDIC, annual dicotyledons; PERDIC, perennial dicotyledons; ANLEG, annual legumes; PERLEG, perennial legumes; ANMON, annual monocotyledons; PERMON, perennial monocotyledons). The coefficients of Z1 primarily contrasted on the one hand I% of PERMON and on the other hand I% of ANDIC, PERDIC and ANMON. The second component (Z2) was 0.516(ANDIC) +0.172(PERDIC)-0.228(ANLEG)-0.990(PERLEG)+0.362(ANMON)+0.303(PERMON) which primarily contrasted I% of PERLEG and I% of other functional groups.

Vegetation succession in the period 2002-2003 was characterized by a steady increase in I% of perennials at the expense of annuals since values of Z1 decreased over time. Furthermore plant communities became more grassy over time since values of Z2 increased while values of Z1 decreased over time. The I% of legumes decreased over time irrespective of mowing regime, location or plant community except for CONTR under REMOV2 revealing an increase over time at SITE1 or a stable I% at SITE2.

Vegetation succession differed considerably between locations irrespective of mowing regime or plant community: At SITE1, legumes were more abundant than at SITE2 since succession patterns revealed lower values of Z2. Under REMOV0, the I% of monocotyledons increased at higher rate than under REMOV2 since values of Z1 were more negative under REMOV0. Similarly, the decease in I% of legumes occurred at higher rate under REMOV0 since values of Z2 were less negative for REMOV0 compared to values of REMOV2. Furthermore time-trajectories of CONTR and sown communities converged over time, irrespective of mowing regime or location. So similarity in vegetation composition in terms of functional groups occurred between sown and unsown communities.

Similarity of species importance as assessed by C_N, increased significantly between 2001-2003 at SITE1 with the slope of all linear equations of C_N over time being positive with *P*-values between 0.05 and 0.006. MIXT2 revealed higher rates of convergence than MIXT1 at SITE1. Similarly, rate of convergence was faster under REMOV2 than under REMOV0. Three years after installation C_N was significantly determined by the mowing regime ($P = 0.02$) and location ($P = 0.001$) but not by the plant community. C_N was significantly lower at SITE2 than at SITE1 (0.18 versus 0.39) (lsd=0.04). C_N was significantly higher for REMOV2 (0.32) than for REMOV0 (0.23) (lsd=0.03). At the end of 2003, C_N showed significant interaction between plant community and location ($P = 0.05$). At SITE2, C_N was not influenced by the plant community (MIXT2, 0.21; MIXT1, 0.21) whereas at SITE1, C_N was significantly higher for MIXT2 (0.45) than for MIXT1 (0.28) (lsd 0.06).

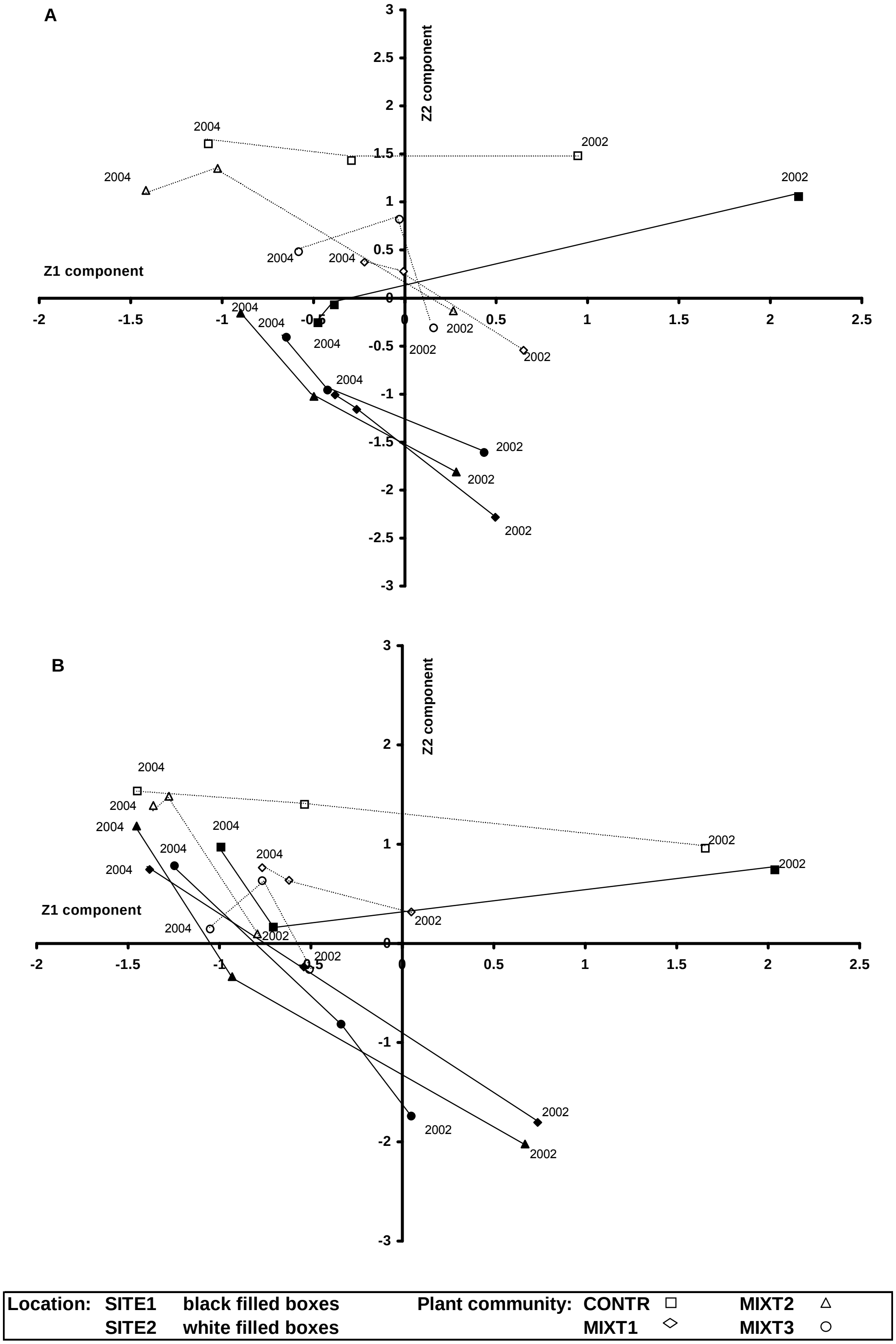

Fig. 12 Time-trajectories of sown and unsown plant communities under REMOV0 (B) and REMOV2 (A), plotted against the first two principal components Z1 and Z2.

4.4.1.2 Effect of light and disturbance on floristic diversity

This paragraph gives an answer to research questions 6 and 7 (see 3.4.10).

Prior to disturbance (June 2002), the total species diversity was significantly determined by plant community but not by light regime. The unsown community had a significant lower species diversity than the sown communities (CONTR, 11.9 spp versus MIXT1, 23.0 spp.; MIXT2, 22.7 spp. and MIXT3, 21.6 spp.; lsd=3.6 spp). However, one month after the disturbance event (October 2002), significant interactions between light regime and plant community and between light regime and disturbance occurred. On the unshaded side, total species diversity in CONTR (13.0 spp.) was significantly lower than species diversity in MIXT2 (16.7 spp) and MIXT1 (19.2 spp.) but not on the shaded side (MIXT1, 20.3 spp.; MIXT2, 17.8 spp.; CONTR, 19.8 spp.). Disturbance caused a significant higher species diversity on the unshaded side (undisturbed, 15.3 spp. versus disturbed, 16.9 spp.) but a significant lower diversity on the shaded side (undisturbed, 19.0 spp. versus disturbed, 16.7 spp.) (lsd=1.5 spp.) (Fig. 13). However, one year after the disturbance event (October 2003) species diversity was no longer influenced by the disturbance level.

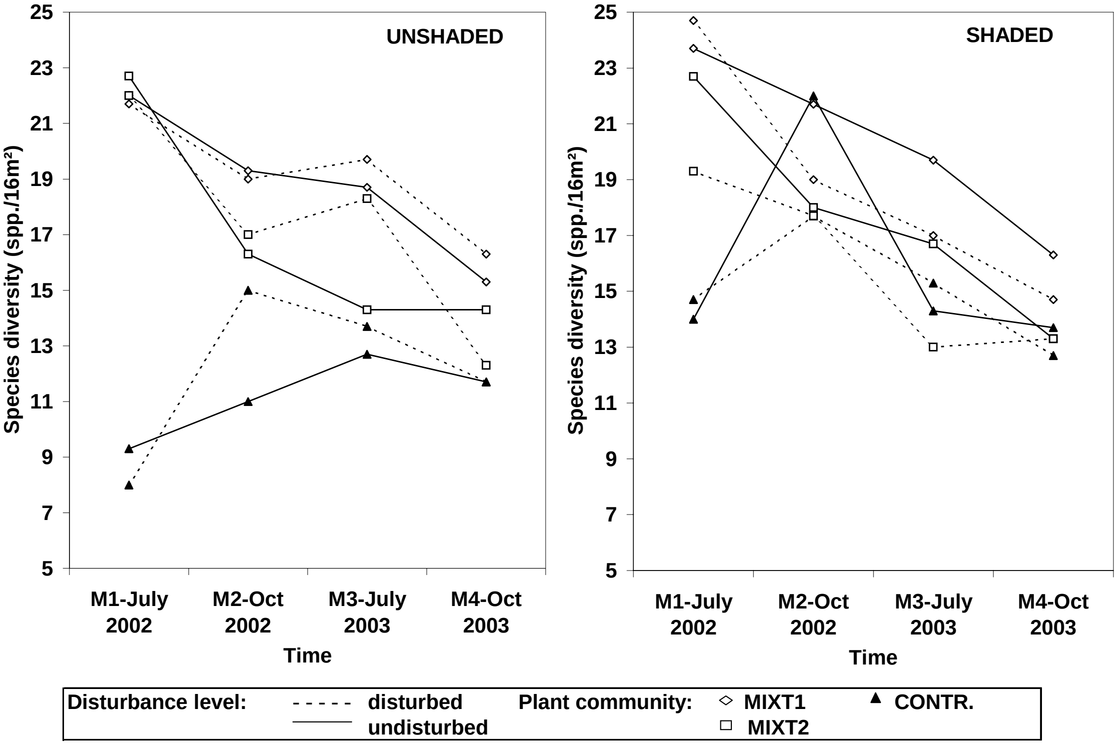

Fig. 13 Species diversity (spp. 16m^{-2}) during succession (2001-2003) with or without disturbance on 19 September 2002. See 3.4.1 for abbreviations.

Disturbance caused a significantly higher number of annual species on the unshaded side (undisturbed 1.8 spp. versus disturbed 3.4 spp.; lsd=0.7 spp.) but not on the shaded side (undisturbed 3.0 spp. versus disturbed, 2.8 spp.). Furthermore a significantly higher number of annual species was found in disturbed MIXT3 (undisturbed, 0.67 spp.; disturbed, 2.5 spp.; lsd=1.3 spp.) and disturbed MIXT2 (undisturbed, 2.0 spp.versus disturbed 3.5 spp.; lsd =1.3 spp.).

In general, during the first 3 successional years, species diversity of sown communities significantly declined over time on both the shaded and unshaded side of the tree lane irrespective of disturbance level. The species diversity of CONTR increased on the unshaded side and decreased (but at lower rate than sown communities) on the shaded side (Fig. 13).

Similar succession patterns were found as reported before, irrespective of plant community, light regime or disturbance level. One year after the disturbance event, the I% of perennials or annuals was not significantly determined by light regime or disturbance level. Similar results were found for I% of monocotyledons and legumes. However within monocotyledons, the I% of spontaneous perennial monocotyledons was significantly determined by the disturbance level (P = 0.03). The I% was significantly higher in disturbed plots (undisturbed, 25.5% versus disturbed, 29.1%; lsd=3.1%). There was also a significant interaction between plant community and light regime (P = 0.001). Sown communities showed higher I% on the shaded side than on the unshaded side (MIXT2: unshaded, 7.6% versus shaded, 9.3%; MIXT1, unshaded, 14.9% versus shaded, 28.3%; MIXT3, unshaded, 5.3% versus shaded, 6.5%) (lsd=13.6%). CONTR however showed significantly higher I% on the unshaded side (unshaded, 85.3% versus shaded, 61.2%) (lsd=13.6%).

Disturbance caused also some temporary effects: shortly after disturbance, disturbance caused a significant higher I% of annual spontaneous dicotyledons (disturbed, 11.8% versus undisturbed, 4.7%; lsd=3.3%) probably due to a significantly higher percentage uncovered area shortly after disturbance (disturbed, 54.0%, undisturbed, 19.3%; lsd=3.7%). But 10 months after the disturbance event, the I% of annual spontaneous dicotyledons decreased again predominately at the expense of perennial sown and spontaneous monocotyledons and to a lesser extent of perennial spontaneous dicotyledons. One year after the disturbance event, the I% of annual spontaneous dicotyledons was no longer significantly determined by the disturbance level. Next to the similarity in succession pattern, vegetations in sown and unsown communities became increasingly similar over time as indicated by increasing C_N over time. One year after the disturbance event, C_N was significantly determined by light regime and disturbance level. C_N was significantly higher on the shaded side (shaded 0.46 versus unshaded 0.34 (lsd=0.12). C_N within disturbance level was significantly higher in disturbed plots (disturbance, 0.46 versus undisturbed, 0.34 lsd=0.08).

The I% of invader grasses increased over time irrespective of plant community, light regime or disturbance level except for the shaded disturbed MIXT2. One year after the disturbance event, the I% of invaders was significantly determined by light regime (p=0.001). Furthermore, there was a significant interaction between plant community and disturbance level (P = 0.01). The I% of invaders was significantly higher on the unshaded side than on the shaded side (unshaded, 39.3 versus shaded 20.6; lsd=7.7). The I% of invaders was lower (not significant) in sown disturbed communities MIXT1 (undisturbed, 36.5% versus disturbed, 34.8%) and MIXT2 (undisturbed, 44.0% versus disturbed, 31.2%) but was higher in unsown CONTR (undisturbed, 4.7% versus disturbed, 19.5%; lsd=11.6%). However, in sown communities care should be taken in the interpretation since the invader grasses were already present in the pre-disturbance vegetation (part of the initial sowing mixture). Nevertheless in disturbed sown communities, the increase in importance of invader grasses over time was not an invasion effect since no new propagules were found shortly after the disturbance event contrary to the undisturbed unsown community. This also means that the unsown community was more susceptible to being invaded.

4.4.1.3 Effect of light and disturbance on invertebrate diversity

This paragraph gives an answer to research questions 8 and 16 (see 3.4.10).

The insect orders with the highest number of trapped insects were the order of *Diptera*, order of *Thysanoptera* and *Hymenoptera*. The order of *Diptera* accounted for half the total number of trapped insects (185 288 insects). Within this order 32 insect families were represented.

Some families were exclusively trapped on either the unshaded or shaded side. However, most families occurred on both sides. Aside from 45 indifferent families (not shown) and with the exception of the families of *Cecidomyiidae* and *Ectopsocidae*, all the other insect families were trapped in significantly higher numbers on the shaded side. Among the insect families showing preference to the shaded side, many families are generally associated to water or moist conditions such as *Haliplidae*, *Dolichopodidae*, *Dryomyzidae*, *Empididae*, *Lauxaniidae* and superfamily of *Dascilloidea* or to decaying materials such as *Asilidae*, *Calliphoridae*, *Otitidae, Sepsidae.* Over the screening period from 27 June to 6 September 2002 the unshaded side revealed a significantly higher average soil moisture content in the profile (unshaded, 32.3 vol% versus shaded, 37.3 vol%; lsd = 2.4 vol%).

A small number of insect families occurred exclusively in either the field margin strip or in the adjacent field crop. However, most occurring families were trapped in both areas. At the shaded side, aside from indifferent families, 13 families were preferentially trapped above the field crop whilst the family of *Phoridae* and order of *Mecoptera* were preferentially trapped above the field margin strip. At the unshaded side, 8 families showed preference to the field margin strip whilst 5 families showed preference to the field crop. Families preferring the field margin strip differed on both side of the tree lane indicating different habitat preferences. Some families such as *Empididae*, *Chironomidae* and *Cicadellidae* preferred the field crop independently of light regime. Others like the family of *Phoridae* showed preference to the field crop at the unshaded side but preferred the field margin strip at the shaded side. The order of *Thysanoptera* showed preference to the field margin at the unshaded side but was indifferent at the shaded side.

Within the field margin strip at monitoring position –4 m, insect composition differed between sown and unsown communities at both unshaded and shaded side. At both light regimes, CONTR showed higher insect number of *Bibionidae*, *Aphidoidea*, *Proctotrupoidea* (significant at both light regimes) and of *Dolichopodidae, Lauxaniidae*, *Mycetophilidae, Oestridae*, *Scatopsidae* and *Psyllidae* (significant at one side). At both light regimes, sown communities showed higher insect number of *Cicadellidae*, *Chalcidoidea*, order of *Thysanoptera* (significant at both light regimes) and of *Ichneumonoidea*, *Caecillidae*, *Aleyrodidae* and *Berytinidae* (significant at one side).

The Shannon diversity index was significantly determined by plant community (P = 0.02) and revealed a significant interaction between light regime and monitoring position (P = 0.03). The Shannon index nearby CONTR (2.57) was significantly higher than nearby sown communities (2.49 for both MIXT2 and MIXT1) (lsd=0.06). This corresponds with the significantly higher floristic diversity (CONTR, 20.6 spp. versus MIXT2, 15.2 and MIXT1, 14.1 spp.; lsd= 3.6 spp.) and lower LAI (CONTR, 2.3; sown communities 7.6-7.7; lsd=0.7) in August 2002. Furthermore, transmitted PAR under the canopy on 9 August 2002 was significantly higher in CONTR (unshaded, 460.7 μmol m^{-2} s^{-1}; shaded, 301.5 μmol m^{-2} s^{-1}) than in sown communities (unshaded 235.9-253.7 μmol m^{-2} s^{-1}; shaded 222.9-226.6 μmol m^{-2} s^{-1}) irrespective of light regime (lsd within light regime=55.1μmol m^{-2} s^{-1}). At the shaded side, Shannon indices of all monitoring positions were not significantly different (2.59, 2.59, 2.66, 2.61, 2.70 for position –4, 0, 4, 8, 16 m respectively; lsd within side =0.12); At the unshaded side Shannon index of position 0 m was significantly lower than all other positions (2.46, 2.21, 2.48, 2.46, 2.45 for position –4, 0, 4, 8, 16 respectively; lsd within light regime =0.12). Within each monitoring position, Shannon index was significantly higher at the shaded side than at the unshaded side (data above; lsd otherwise=0.13).

Family richness was significantly determined by light regime (P = 0.007) and not by plant community or monitoring position. At the shaded side a significant higher number of insect families occurred (shaded, 43.5 families versus unshaded, 37.9 families; lsd=1.9 families). At position –4 m within the field margin strip, CONTR showed the highest family richness compared to sown communities irrespective of light regime. The insect number showed a significant interaction between light regime and position (P < 0.001), between light regime and plant community (P = 0.049) and between plant community and monitoring position (*P* = 0.047). At the unshaded side, significantly higher numbers of insects occurred nearby CONTR than nearby sown communities (CONTR, 1746 insects per trap versus 1349 in MIXT1 and 1505 in MIXT2, lsd=239). At the shaded side, the numbers nearby sown/unsown communities were comparable (CONTR 1531 insects per trap, 1580 in MIXT1 and 1614 in MIXT2, lsd=239). Within plant community, the insect number was not significantly altered by light regime, although nearby CONTR a higher number was found at the unshaded side (unshaded side, 1746 insects per trap versus 1531 insects at the shaded side; lsd=327).

Compared to sown communities, CONTR revealed a higher insect number both in the margin strip (position –4 m: CONTR, 1362 insects per trap versus 1143 in MIXT1 and 1267 in MIXT2) as well as at the field margin edge (position 0 m: CONTR, 1952 insects per trap versus 1387 in MIXT1 and 1506 in MIXT2, lsd=295). So, in the field margin strip, CONTR showed both the highest diversity and the highest numbers of insects. The similarity in the distribution pattern of numbers of pest insects and antagonists clearly indicates that a higher number of pest insects corresponds with a higher number of their antagonists resulting in significant positive correlation coefficients irrespective of light regime (unshaded side, 0.61; shaded side, 0.65; $P < 0.01$).

4.4.2 Agriculture

4.4.2.1 Weed infestations nearby margin strips

This paragraph gives an answer to research questions 9 to 11 (see 3.4.10).

Ingrowing margin weeds. Three years after installation in October 2004, the I% of ingrowing species was significantly determined by location, plant community and cutting treatment. The I% was significantly higher at SITE2 (10.8%) than at SITE1 (2.9%) (lsd=7.8%). CONTR revealed significant higher I% than sown communities (CONTR, 14.5% versus 3.1-5.4% for sown communities; lsd= 6.6%). REMOV0 revealed significant higher I% than REMOV1 and REMOV2 (REMOV0, 12.4% versus REMOV1, 5.0% and REMOV2, 3.2%; lsd=3.8%). The I% significantly increased over time under REMOV0 with 6.75 I% per year. The I% significantly increased over time at SITE2 with 8.26 I% per year but significantly decreased at SITE1 with 3.98 I% per year.

Within ingrowing margin species, no significant factors were found for *Elymus repens* (L.) Gould, *Cirsium arvense* (L.) Scop. and *Urtica dioica* L. one year after installation in October 2002 (Table 6). However three years after installation, in October 2004, the situation had changed completely. The I% of *C. arvense* was significantly determined by cutting treatment with significantly lower I% under REMOV2 than under REMOV1 and REMOV0. The I% of *E. repens* was significantly determined by cutting treatment with significantly lower I% under REMOV1 and REMOV2 than under REMOV0. CONTR revealed a significantly higher I% of *E. repens* than sown communities at SITE2 while no significant differences were found at SITE1. The I% of *U. dioica* was significantly determined by plant community and cutting treatment: the I% was significantly lower under REMOV2 than under REMOV0 and REMOV1; CONTR and MIXT1 showed significantly higher I% than MIXT2 and MIXT3.

Table 6 Importance (I%) of rhizomatous margin species during succession (2001-2004). See 3.4.1 for abbreviations.

			Cirsium arvense				***Elymus repens***				***Urtica dioica***			
			Time[2]			**Slope[3]**	**Time**			**Slope**	**Time**			**Slope**
LOC[1]	**COM[1]**	**CT[1]**	**M2**	**M4**	**M6**		**M2**	**M4**	**M6**		**M2**	**M4**	**M6**	
	CONTR.		0.3	1.0	2.9		5.5	9.3	8.2		0.2	0.7	3.1	1.88 **
	MIXT1		0.0	0.2	0.8		1.8	4.1	2.2		0.2	0.8	2.4	1.54 *
	MIXT2		0.0	0.0	0.0		1.2	1.3	4.1		0.0	0.0	0.2	0.21 *
	MIXT3		0.1	0.0	0.0		1.7	1.4	2.7		0.0	0.0	0.4	0.37 *
		REMOV0	0.0	0.1	1.2	0.94 **	2.6	5.7	7.9	7.56 ***	0.1	0.7	3.0	2.03 ***
		REMOV1	0.0	0.2	1.1	1.21 **	2.8	3.3	2.9	2.20 *	0.1	0.4	1.0	0.77 *
		REMOV2	0.3	0.5	0.5	0.35	2.2	3.2	2.1	1.63	0.0	0.0	0.5	0.20
SITE1	CONTR.		0.6	1.9	5.8	5.52 **	0.0	0.0	0.3		0.0	0.0	0.7	
	MIXT1		0.0	0.0	0.0		0.0	0.0	0.9		0.0	0.0	0.7	
	MIXT2		0.0	0.0	0.0		0.0	0.0	1.0		0.0	0.0	0.0	
	MIXT3		0.0	0.0	0.0		0.0	0.0	1.4		0.0	0.0	0.0	
SITE2	CONTR.		0.0	0.0	0.0		10.9	18.6	16.0	14.33 **	0.4	1.4	5.4	
	MIXT1		0.0	0.4	1.7	1.28 *	3.7	8.3	3.5	4.66	0.4	1.7	4.1	
	MIXT2		0.0	0.0	0.0		2.3	2.7	7.3	5.16 *	0.0	0.0	0.3	
	MIXT3		0.3	0.0	0.0	-0.12	3.4	2.8	4.0	3.48	0.0	0.0	0.9	
Anova[4]:														
LOC			NS	NS	NS		NS	NS	NS		NS	NS	NS	
COM			NS	NS	NS		NS	**	NS		NS	NS	*	
LSD													2.2	
CT			NS	NS	*		NS	*	*		NS	NS	*	
LSD					0.6				4.1				2.1	
LOC*COM			NS	*	*		NS	**	*		NS	NS	NS	
LSD within loc				1.2	3.6			2.8	7.2					
LSD otherwise				1.4	3.9			5.2	13.1					
LOC*CT			NS	NS	NS		NS	*	NS		NS	NS	NS	
LSD within loc								3.3						
LSD otherwise								19.6						
COM* CT			NS	NS	NS		NS	NS	NS		NS	NS	NS	
LOC*COM*CT			NS	NS	NS		NS	NS	NS		NS	NS	NS	

[1] LOC, Location; COM, Community, CT, cutting treatment

[2] M2, October 2002; M4, October 2003; M6, October 2004

[3] Slope (%.10^{-3}.day^{-1}) of linear regression equation of I% on time (days)

[4] Significance: NS, not significant; *, **, *** Sign. at $p<0.05$, $p<0.01$ and $p<0.001$; LSD, Least Sign.Difference

Seed dispersal into adjacent crops. In August-September 2002, seed rain (expressed as seeds per m² sticky surface) into the adjacent crop was a factor 4 to 8 times higher perpendicular to CONTR than perpendicular to sown communities (3565 seeds/m² for CONTR versus 400-821 seeds/m² for sown communities). One year after installation, in August-September 2002, the number of captured seeds of SPAN at 0 m from the field margin was significantly higher nearby CONTR than nearby sown communities (1531 seeds/m² for CONTR versus 17-92 seeds/m² for sown communities; lsd=519 seeds/m²). Two years after installation (2003) seed dispersal of SPAN into adjacent crops in the same period was similar for all plant communities (from 0 to 23 seeds/m²). Compared to the preceding year, seed dispersal at 0 m from the margin strip was low. Three years after installation in May-June 2004 only seeds of *Taraxacum officinale* Wiggers were captured at 0 m from the margin strip. Number of captured seeds was significantly higher nearby CONTR than nearby sown communities (73 seeds/m² for CONTR versus 2-6 seeds/m² for sown communities; lsd=29 seeds/m²).

Seed dispersal decreased exponentially with increasing distance into the field. Averaged over all plant communities, the total number of captured seeds was significantly higher at 0 m (536 seeds/m²) than at further distances from the field margin, at which the results were similar (at 2 m, 358; at 4 m, 295; at 8 m, 129; at 16 m, 54 and at 32 m, 13 seeds/m²). Nearby sown communities from 90% to 99% of all captured seeds were disseminated within 4 m from the field margin; nearby CONTR, 81.3% was disseminated within 4 m from the field margin.

Seed dispersal distance was determined by plant species (seed density between brackets): seeds of *Echinochloa crus-galli* (L.) Beauv. (3.75 seeds/m²), *Galinsoga parviflora* Cav. (2.5 seeds/m²) and *Arrhenaterium elatius* J. & C. Presl. (2.5 seeds/m²) were disseminated within 4 m adjacent to the field margin; *Sonchus oleraceus* L. (3.75 seeds/m²) and *Sonchus arvensis* L. var. *arvensis* (2.5 seeds/m²) were detected within 16 m from the field margin. *Erigeron canadensis* L. showed the highest seed dispersal distance (32 m) at a seed density of 33.7 seeds/m².

4.4.2.2 Herbage quantity and quality

This paragraph gives an answer to research questions 12 to 15 (see 3.4.10).

Annual yield. Mean annual DM yield showed significant interaction between location and plant community; it was not significantly affected by mowing regime. The sown plant communities outyielded CONTR both at SITE1 (7551, 14523, 15599, 13659 kg DM ha^{-1} for CONTR, MIXT1, MIXT2 and MIXT3 respectively) as well as at SITE2 (7167, 9343, 9680, 10267 kg DM ha^{-1} for CONTR, MIXT1, MIXT2 and MIXT3 respectively) (lsd within location=904 kg DM ha^{-1}). Within plant communities mean annual DM yield was significantly higher at SITE1 than at SITE2 except for CONTR (data above; lsd otherwise=2398 kg DM ha^{-1}).

Despite zero fertilization, annual DM yield at SITE1, averaged over mowing regimes, increased significantly over time as shown by the positive slopes of linear regression equations (3083, 1055, 951, 692 kg DM year^{-1} for CONTR, MIXT1, MIXT2, MIXT3 respectively). A similar trend was seen at SITE2. The difference in DM yield between

CONTR and sown communities decreased over time since CONTR showed higher rates of increase than sown communities.

Mean CF, CP, ASH, OMD and VEM are shown in Table 7. The average values of CF showed a significant interaction between plant community and location. Mean CF was significantly lower for herbage from CONTR than for herbage from sown communities irrespective of location. Within sown communities, SITE2 revealed a significantly lower mean CF for herbage from MIXT1 than herbage from MIXT2 and MIXT3 contrary to SITE1 revealing no significant differences in mean CF. At SITE1 linear regression of annual CF over time revealed positive slopes (significant for MIXT1 and MIXT2) irrespective of plant community. At SITE2, annual CF increased for MIXT1 and MIXT3 but remained stable (CONTR) or decreased for MIXT1. Slopes were higher at SITE1 than at SITE2. Furthermore, slopes were higher for MIXT1 and MIXT2 than for CONTR irrespective of location. Mean CP was not significantly affected by location or plant community. Generally, annual CP significantly decreased over time except for CONTR at SITE1, the decrease being higher at SITE1 than at SITE2 since slopes of linear regression equation were more negative at SITE1.

Table 7 Mean CF, CP, ASH (% on DM), OMD (% on DM) and VEM units of annual DM yield from sown/unsown plant communities at two locations See 3.4.1 for abbreviations.

		CF		CP		ASH		OMD		VEM	
Location	**Community**	**Mean**	**Slope[3]**	**Mean**	**Slope[3]**	**Mean**	**Slope[3]**	**Mean**	**Slope[3]**	**Mean**	**Slope[4]**
SITE1	CONTR	30.9	0.4	9.0	0.5	8.7	-0.9 *	59.2	-1.6 *	660	-10
	MIXT1	37.5	1.4 *	9.6	-0.8 *	7.6	-0.6 *	55.2	-3.8 **	611	-42 **
	MIXT2	35.9	0.9 *	9.9	-1.3 **	8.4	-0.8 ***	56.5	-3.2 ***	622	-33 ***
	MIXT3	35.8	0.8	9.9	-1.3 **	8.3	-0.4	57.0	-2.3 *	629	-25 *
SITE2	CONTR	31.8	0.0	10.5	-1.2 *	8.4	-0.9 *	61.4	-0.3	689	3
	MIXT1	34.8	0.4	10.4	-0.6 *	8.8	-1.3 ***	57.6	-3.1 **	633	-29 *
	MIXT2	37.3	-0.6	9.6	-0.7 *	8.2	-1.0 ***	57.6	-1.6 *	638	-12
	MIXT3	35.8	0.3	10.1	-0.6	8.7	-0.9 *	58.4	-2.4 **	644	-23 *
Mean											
SITE1		35.0		9.6		8.3		57.0		631	
SITE2		34.9		10.1		8.5		58.8		651	
	CONTR	31.4		9.8		8.5		60.3		674	
	MIXT1	36.1		10.0		8.2		56.4		622	
	MIXT2	36.6		9.7		8.3		57.1		630	
	MIXT3	35.8		10.0		8.5		57.7		637	
		Sign.[1]/ LSD[2]		Sign./ LSD		Sign./ LSD		Sign./ LSD		Sign./ LSD	
Location		NS/1.0		NS/0.7		NS/0.4		**/1.1		**/14	
Community		***/1.4		NS/1.0		NS/0.5		***/1.5		***/20	
Location x Community		*/2.0		NS/1.4		*/0.7		NS/2.2		NS/29	

[1] Significance: NS, not significant; *= p<0.05; **=p<0.01; ***=p<0.001

[2] LSD, least significant difference (p<0.05)

[3] Slope (%. year^{-1}) of linear regression of CF (%), CP (%), ASH (%) and OMD (%) on time (year)

[4] Slope (units VEM. Year^{-1}) of linear regression of VEM (units) on time (year)

At SITE1 mean ASH of herbage from MIXT1 was significantly lower than mean ASH of herbage from MIXT2, MIXT3 and CONTR. At SITE2 no differences in mean ASH were found between plant communities. Annual ASH significantly decreased over time irrespective of location or plant community. Mean OMD of herbage was significantly affected by plant community and location. Mean OMD was significantly higher at SITE2 than at SITE1 and OMD significantly higher in CONTR than in sown communities showing no significant differences. Generally, annual OMD decreased over time as indicated by the significant negative slopes of linear regression equations. The decrease in annual OMD occurred at highest rate in the herbage from MIXT1 and at lowest rate in the herbage from CONTR irrespective of location. Generally the decrease in annual OMD occurred at higher rate at SITE1.

Similarly mean VEM was significantly affected by location and plant community. Herbage from SITE2 revealed a significantly higher mean VEM than herbage from SITE1. Herbage from CONTR revealed significantly higher mean VEM than herbage from sown communities that did not differ significantly. At SITE2, annual VEM of herbage from sown communities significantly decreased over time irrespective of location except for MIXT2 at SITE2.

Per cut. Mean DM yield and quality differed between mid-June cut and the regrowth cut at mid September. The first cut significantly outyielded the second cut with 77-122% depending on the site. This was due to the higher grass growth rate in springtime compared to growth rates in summertime. Dissimilar to the mean DM yield, the first cut had a lower mean digestibility than the regrowth cut, reflected in a higher mean crude fibre and significantly lower crude protein contents of the first cut compared to the regrowth cut. Compared to quality parameters in grassland produced on intensively managed dairy farms the forage quality harvested in the field margin strips was inferior (Table 8).

Table 8 Mean ASH, CP, CF (% on DM), OMD (% on DM) and VEM units per cut compared to quality parameters of cuts from intensively managed grassland See 3.4.1 for abbreviations.

		Margin strips			
	Intensively managed	SITE1		SITE2	
Quality parameter	**grassland[1]**	**Mid-June cut**	**Regrowth cut**	**Mid-June cut**	**Regrowth cut**
ASH	9.7	6.6-7.5	8.2-9.2	7.3-7.7	9.1-10.1
CP	22.5	6.6-7.4	11.4-13.4	8.5-9.3	12.0-13.1
CF	20.0	30.7-39.4	32.3-36.6	31.8-36.7	29.5-37.8
OMD	80.0	51.8-60.2	55.4-58.2	53.3-59.8	62.5-64.8
VEM	997	574-680	613-642	588-673	691-733

[1] According to CVB (1999)

4.4.3 Environment

4.4.3.1 Soil N_{min} nearby margin strips

This paragraph gives an answer to research questions 17 to 19 (see 3.4.10).

Presented results deal with N_{min} analysis at SITE2 during the winter period 2003-2004. Similar results were found at SITE1 and for winter period 2002-2003. At the end of October 2003 residual total N_{min} (Fig. 14A) was significantly determined by auguring position and not by plant community. Total N_{min} under the crop area were extremely high. Total N_{min} was significantly higher at positions 2.5 and 0 m than at positions inside the field margin strip. Total N_{min} in the field margin strip decreased asymptotically from position 0 m up to position –7.5 m except for a slight increase at position –7.5 m. Total N_{min} averaged over all positions perpendicular to MIXT1 was significantly higher than total N_{min} perpendicular to MIXT2 or CONTR.

Residual total NH_4-N (Fig. 14B) at the end of October 2003 was significantly determined by auguring position at SITE2. Total NH_4-N inside the margin strip increased with increasing distance away from the edge with the crop area. The closer to the tree lane, the higher total NH_4-N. Similar to total N_{min}, residual total NO_3-N (Fig. 14C) at the end of October 2003 was significantly determined by auguring position. Total NO_3-N of position 2.5 m and 0 m far exceeded the Flemish legal prescription of 90 kg NO_3-N ha^{-1} in the horizon 0-90 cm. Inside the field margin strip, NO_3-N was lower than 90 kg ha^{-1}. No exceedings occurred. Similar to N_{min}, total NO_3-N in the field margin strip decreased asymptotically from 0 m up to position –7.5 m except for a slight increase at position –7.5 m at SITE2. N_{min} reduction in the field margin strip occurred mainly in the soil horizons 30-60 and 60-90 cm (Fig. 14A). Compared to the field crop area, N_{min} in the horizon 30-90 cm was eightfold higher than N_{min} at position –5 m. In the field crop area, 70% of total N_{min} was found in the horizon 30-90 cm. In the margin strip, percentile contribution of the horizon 30-90 cm in total N_{min} was only 50%. Half of total NH_4-N was found in the uppermost horizon irrespective of position (Fig. 14B). Contrary to positions inside the margin strip, approximately 70% of total NO_3-N in the field crop area was found in deeper soil horizons 30-60 and 60-90 cm (Fig. 14C). The reduction in NO_3-N inside the margin strip was higher in the deeper soil horizons 30-60 and 60-90 cm than in the uppermost soil horizon.

On 1 March 2004 total N_{min} was significantly determined by auguring position. Total N_{min} amounts in the crop area (135.9 and 145.2 kg N ha^{-1} for position 2.5 and 0 m respectively) were significantly higher than at positions inside the field margin strip (103.4, 87.7, 88.6, 106.4 kg N ha^{-1} for position –1.25, -2.5, -5, -7.5 m respectively; lsd=32.3 kg N ha^{-1}) except for the outermost position –7.5 m. Total NH_4-N on 1 March 2004 was significantly determined by auguring position: total NH_4-N increased from the crop area to the edge with the pre-existing boundary: 52.8, 57.2, 60.4, 60.9, 63.1, 76.3 NH_4-N for position 2.5, 0, –1.25, -2.5, -5, -7.5 m respectively (lsd=11.8. kg NH_4-N ha^{-1}). On 1 March 2004, total NO_3-N was significantly higher in field crop area than inside the margin strip: 83.1, 88.0, 43.1, 26.8, 25.5, 30.1 kg NO_3-N ha^{-1} for positions 0, -1.25, -2.5, -5, -7.5 m, respectively (lsd=27.8 kg NO_3-N ha^{-1}). In the margin strip total NO_3-N decreased from position 0 to –5 m and increased again closer to the pre boundary. Patterns of total NO_3-N followed at best patterns of total N_{min}. N_{min} loss over the winter period 2003-2004 was solely significantly determined by position.

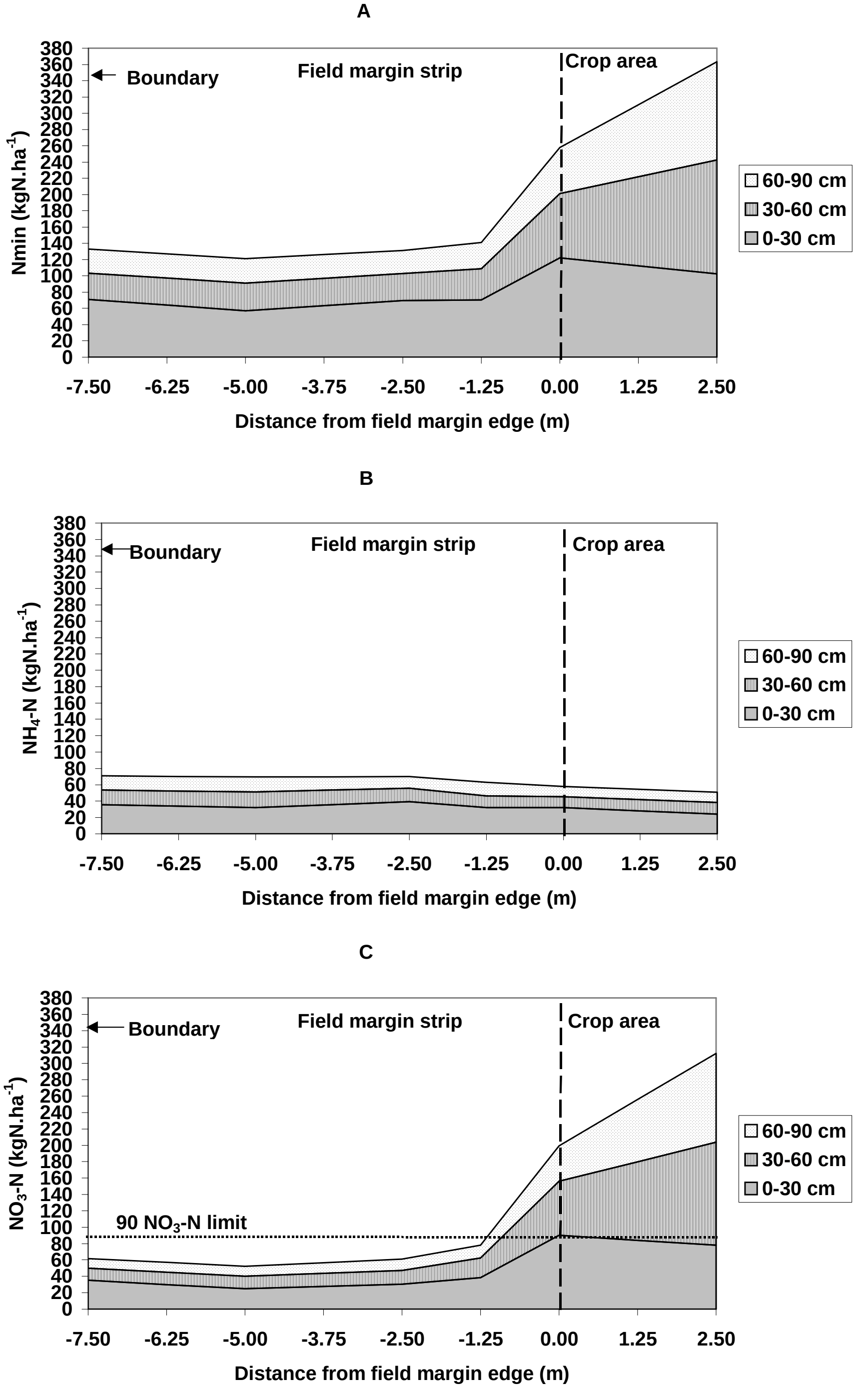

Fig. 14 Distribution of total N_{min} (A), NH_4-N (B) and NO_3-N (C) in soil horizons related to distance from the crop edge. SITE2, 29 October 2003.

Inside the field margin strip N_{min} loss decreased with increasing distance from the edge with the field crop area:112.5, 43.3, 32.9, 26.4 kg N ha^{-1} for positions 0, -2.5, -5, -7.5 m respectively (lsd=95.3 kg N ha^{-1}). Inside the field margin N_{min} loss was minimal at 7.5 m from the edge with the field crop. Under the field crop area, extremely high N_{min} losses (227.4 kg N ha^{-1} at position 2.5 m) were found.

4.4.3.2 Species richness and composition of boundary

This paragraph gives an answer to research question 20 (see 3.4.10).

Three years after installation of the margin strip, species diversity was higher compared to the species diversity prior to installation: 42 spp. in 2001 versus 49 spp. in 2004. Slow growing non nitrophilous species such as *Geranium molle* L., *Stellaria graminea* L., *Veronica chamaedrys* L., *Viola arvensis* Murray, *Cerastium fontanum* Baumg., *Hypericum dubium* Leers and more in particular leguminous species such as *Ornithopus perpusillus* L., *Medicago lupulina* L. and *Vicia hirsuta* S.F. Gray did not occur prior to installation of the margins strip but were present after installation. None of these species originated from sowing mixtures of the margin strip. Aside from changes in species composition, also changes in species abundance occurred over the 4-year period. Some species preferring low soil fertility such as *Calluna vulgaris* (L.) Hull, *Anthoxanthum odoratum* L., *Rumex acetosella* L., *Festuca rubra* L. and *Cytisus scoparius* (L.) Link that were already present prior to installation became more abundant after installation.

5 DISCUSSION

All the objectives of the project (see 2.5) were achieved. The results of the different experiments, which were conducted to meet these objectives, will be discussed in the following section.

5.1 Invasiveness and invasibility

5.1.1 Invasiveness

By inserting different invader species in the same series of monocultures, we were able to compare the invasion success of these species in identical conditions (surrounding vegetation and nutrient supply, weather, distance to neighbouring plants, etc.), which is difficult to achieve in natural invasion studies. Some species proved more 'invasive' than others in terms of germination (*Lp* and *Pt*) and growth (*Lp*), while some proved very poor invaders (e.g. *At*, which had poorer germination than most other species). Once germinated, however, survival until next spring was the same for all species. Some invaders, nevertheless, remained very tiny, just surviving, but not growing, so this extremely poor invasiveness was clearly not reflected in the survival data. We therefore recommend also using data on growth and spread, in addition to survival, to assess whether invaders are successful or not. In our data, germination, growth, and survival were positively correlated. If this is confirmed for other species and in other conditions, germination might be used to predict invasion success (for example by inserting invader seeds in potentially sensitive systems).

Leaf length and seed mass were positively correlated during the first growing season, but not in the second. It is known that larger seeds yield larger seedlings, enabling better access to light and/or a more reliable water supply, and consequently superior establishment in dense vegetation (Westoby *et al.* 1996). However, later in seedling life, after reserves have been fully deployed into seedling structures, larger seed size no longer confers any direct advantage, with variation in growth rate becoming the major determinant of plant size, and thereby of the outcome of competitive interactions among individuals (Dalling & Hubbell 2002). This is probably why in the second year correlation with leaf length was no longer significant.

Our experiment showed that early germination following a disturbance (clipping of the vegetation) was critical to seedling establishment. This time window is illustrated by the fact that, even in the second growing season, invader leaf length correlated negatively with species germination time. All plants that were still doing well in the second growing season had germinated within 6 d after sowing (not shown), whereas the invaders from later-germinating seeds had all remained very small or died. Early germination is thus not only an important feature in the case of competitive interactions between seedlings, but also helps invaders to escape from light competition with fast-growing established plants.

In trying to explain why, in our experiment, the species *Lp* and *Fa* were the best invaders in terms of total leaf length, we checked whether they had the shortest germination time or the largest seed mass. We found that *Ae* had the largest seeds, followed by *Fa* and *Lp*. Germination was fastest in *Lp*, followed by *Hl* and *Fa*. This suggests that both conditions have to be fulfilled. Only the species with a high score for both traits (*Lp* and *Fa*) were good invaders, while species with high seed mass but slow germination (*Ae*) or with fast germination but small seeds (*Hl*) were not very invasive.

5.1.2 Invasibility

Unlike invader success by species, invasion success in the monocultures differed according to the way it was expressed. In some monocultures germination was good, but invader growth low (e.g. *Lp*); in others it was opposite (*Dg* and *Ae*) and only the *Fr* monoculture had high scores for both. This implies that the monocultures varied in multiple traits, some affecting growth, and others affecting germination of invaders.

Seed germination requires the availability of water, air, light, the right temperature and chemical soil constituents (e.g. nitrate) (Hilhorst & Karssen 2000). By affecting light penetration, temperature, and humidity at the soil surface, canopy structure is an important determinant of the onset of germination and the subsequent fate of seedlings. This is reflected in the negative response of the germination of our grasses to '$\text{PFD}_{\text{intercepted}}$ germination'. This is in agreement with the high-irradiance response (HIR), the inhibiting effect of continuous, moderate illumination (or light interrupted by a period of dark) on germination (Pons 2000). Seeds in more open gaps with a higher irradiance might therefore have germinated less well. The alternative of seeds in the more open gaps desiccating sooner can be excluded because the seeds were watered regularly. A third possibility is that seeds are more likely to be washed away by heavy rainfall in more open vegetation. Nitrate has been known for a long time to stimulate seed germination, in general within the range of 0-0.05 M (Hilhorst & Karssen 2000). We expected that high N accumulation by gap-bordering plants would reflect low N availability for the invaders. Surprisingly, invader germination correlated positively with total edge-plant N. Possibly, soil N-concentrations remaining high (> 0.05 M) for longer in slow-growing monocultures were responsible for this.

In our experiment especially the amount of light penetrating in the gaps during the first weeks of seedling development was important for later invader success, which implies that success is partly determined by what happens in the most vulnerable juvenile state. From this we deduce that grasslands that re-close the canopy more quickly after mowing should offer higher resistance against invaders. This also implies that invasion in dense vegetation that is scarcely mowed strongly depends on the timing of invader seedfall and/or germination (Milberg *et al.* 2000), in addition to the height, growth rate and growth form (more or less lateral spread) of the resident plants. The role of light transmittance in determining the invasibility of the different monocultures is confirmed by the data on '$\text{PFD}_{\text{intercepted}}$ start of growth'. The monocultures *Fr* and *Ae*, in which invader leaf length was significantly higher than in the others, were also the monocultures with the greatest amount of light penetrating in their gaps.

5.1.3 Relationship between and relative importance of invasiveness and invasibility

Overall, invasibility of the monocultures, expressed as average invader germination or leaf length in these monocultures, was not correlated with the invasiveness of the species these monocultures were composed of. Silvertown *et al.* (1994) reported similar results, with species ranks on invasiveness that were fairly consistent in different grazing treatments, but with a much less consistent rank order of invasibility. The sum of squares breakdown reported with regard to question 5, demonstrates that the germination of seeds of possible invaders largely depended on the identity of these species (in other words, on their seed quality, germinability, etc.), while monoculture identity had little impact on this. By contrast, invader growth depended on both invader and monoculture identity in almost the same proportion. This suggests that species characteristics may largely determine the extent of an invasion event (number of propagules and seedlings), while the establishment success (growth and survival of the invaders) is more likely to be determined by both species and ecosystem characteristics. This is in accordance with many studies that argue that invasion success depends on a match between invader characteristics and habitat and that species traits alone are not a significant predictor (Alpert *et al.* 2000).

5.2 The role of species richness

5.2.1 Invader germination and survival

Species richness of the communities was negatively related to percentage germination in *F. arundinacea*, and germination of *L. perenne* decreased with increasing neighbour biomass (which was correlated with species richness). A negative relationship between germination and species richness was also found in an experiment of Levine (2000), who attributed it to greater species cover in the more diverse treatments. In our experiment, the decrease in germination with increasing richness could not be attributed to decreasing light availability, but probably arose from co-variation of species richness with other factors affecting seed germination, such as temperature in the gaps or the availability of water or chemical soil constituents (e.g. nitrate, Hilhorst & Karssen 2000). Higher richness might, by way of increased productivity, result in higher water and nutrient use, leaving less of these essential resources available to the invader to germinate and establish well.

Similar to other studies, no direct relationship between species richness and invader survival was found (e.g. Lavorel *et al.* 1999). However, in this study, biomass of the neighbour plants significantly predicted survival of *F. arundinacea*. Decreased resource availability and root space for the invaders growing in more productive communities are possible explanations for the lower survival in these cases (Aarssen & Epp 1990; cf. effects on germination).

5.2.2 Invader growth: the role of light transmittance and neighbour biomass

Our first question was whether invader growth was influenced by the species richness of the neighbour plants, the % light transmittance in the gaps or neighbour plant biomass. A positive relationship with % PAR transmittance was observed for leaf length measured both in the first and in the second year, in all the invader species examined. Leaf length in the first growing season was associated most strongly with PAR transmittance O (measured when the vegetation around the gaps was recently mown), while invader leaf length in Year 2 showed higher correlation with PAR transmittance C (measured after prolonged regrowth of the neighbour plants, but still in Year 1). This implies that light availability played an important role in stimulating growth, both in young and older invaders. The significant relationship between leaf length in Year 1 and % light transmittance during the seedling stage indicates that seedling growth was an important determinant of plant size at the end of the first season. In the second year, however, realized growth seemed to depend more on the light conditions during the adult stage. The regression slopes were steeper in the second year than in the first, probably because the invaders did not yet have the opportunity to fully expand in Year 1, contrary to Year 2, in which especially some of the invaders growing in the more open gaps became huge. This indicates that mowing, and thus increasing available light, will more strongly promote large/adult invaders because they can grow much faster due to their higher light interception and nutrient capture compared with smaller or younger plants. The exponential growth phase after cutting might therefore be important to focus on in future work.

Except for *L. perenne* in Year 1, invader leaf length decreased significantly with increasing biomass of the neighbour plants. Also in other experiments, standing biomass explained a significant part of the variation in community invasibility (Hector *et al*. 2001, Foster *et al.* 2002). Similar to light transmittance, the regression slopes were steeper in Year 2, mostly because leaf length had increased strongly in cases with unproductive neighbours.

5.2.3 Invader growth: the role of species richness

In this section we discuss the richness effects on invader growth and how these effects were mediated by light, neighbour biomass and I_{max} (Questions 1 and 2). Different results were found for the richness-invasibility relationship between the first and the second years. At the end of the first growing season, invader leaf length was independent of the number of neighbour species, while in the second growing season it decreased with increasing species richness. This discrepancy might be due to a stronger diversity effect on resource availability as the invaded communities became older. This is strongly supported by the different relationships between richness and I_{max} in both years. In Year 1, I_{max} was not related to species richness, whereas in Year 2 a significant positive relationship was found. This suggests that invader growth in Year 2 was partly suppressed by more complete resource use (e.g. nutrients) at the higher richness levels, which was confirmed by the negative relationship between I_{max} and invader leaf length in Year 2. In Year 1, on the other hand, overyielding occurred in fewer mixtures than in Year 2, and there was no relationship between species richness and I_{max}, or between I_{max} and invader leaf length, which explains the lack of a richness-invasibility relationship. Although some overyielding occurred in the first year ($I_{max} > 1$), it did not affect invader growth, suggesting sufficient resources were available for the invaders. This might be due to the relatively low productivity of the neighbour plants in the first year and indicates that transgressive overyielding does not per se result in shortage of an essential resource.

The biomass data of the neighbour plants for each of the species mixtures show more clearly the differences between both years. In Year 1, biomass in the two-, four- and eight-species mixtures was fairly similar for all species combinations and rarely exceeded the most productive monocultures. The observed gradient in monoculture productivity probably reflects slower and faster growing species, and the similar biomass for the mixtures indicates that the communities were not yet fully developed and species interactions (e.g. competition, facilitation, complementary resource use) still limited. In Year 2, however, neighbour plant biomass was much higher than in Year 1, and the mixtures were much more productive than the monocultures, indicating interactions between the composing plant species. In addition, a range in productivities within the species-rich communities had developed, which, together with the larger number of mixtures that were much more productive than the most productive of their component species, yielded the positive relationship between I_{max} and species richness in Year 2.

To summarize, in the second season increasing neighbourhood richness resulted in higher complementarity, which in turn negatively affected invader leaf length. In the first year, such a relationship had not yet developed, probably because the communities were still young and interactions limited. The steeper regression slopes between leaf length and PAR or leaf length and biomass in the second growing season compared to the first, made the decrease in leaf length with richness more pronounced.

5.2.4 Invader growth: prediction and management

The three invader species showed similar relationships with all the measured gap parameters (answer to Question 4), but the relative importance of the parameters in explaining invader leaf length differed among species and between years. With both years and all species taken into account, species richness was the poorest predictor of invader leaf length, mostly because its relationship with invader performance was not consistent between years. The difficulty in predicting invasibility by means of species richness probably arises from the fact that the effects of richness on invader growth are indirect, and because the relationships between richness and the factors affecting the invaders depend on many variables, e.g. resource supply, substrate heterogeneity, the size of the local and regional species pools, and the scale at which the experiment is carried out (Moore *et al*. 2001). In this experiment, richness seemed to influence the invaders through its co-variation with productivity and resource availability, and these relationships depended on community age (see previous section; Levine 2000; Naeem *et al.* 2000). Also in other studies richness affected invaders indirectly, e.g. through influencing levels of extractable soil nitrate or light penetration (Hector *et al*. 2001). Additionally, in this study the diversity-productivity relationship saturated at low richness levels, with no further increase in productivity beyond two- or four-species mixtures. This implies that raising the richness of moderately diverse communities possibly has little effect on productivity (Wardle 2001) or invasibility. Invader establishment in grassland gaps might be easiest at very low richness levels and become harder (but not impossible) in more species-rich mixtures. However, above a certain species number, further increase of species richness might not further increase the resistance to invader establishment. Therefore, we conjecture that attempts to reduce invasibility solely by increasing local species richness will not always guarantee success, and that establishing species-rich mixtures might reduce invasibility only when coincided by high productivity and reduced availability of limiting resources.

Contrary to richness, % light transmittance and neighbour biomass were significant predictors of growth for all invader species in this experiment, both in young and older communities, with light availability explaining the largest proportion of the variation in leaf length, except for *P. trivialis* in Year 1 (Question 3).

5.3 Interactions with climate change

5.3.1 Relationship between ecophysiological responses during the stress and survival time

Species that maintained high values of F_v/F_m (around 0.8), and low values of C_i (around 260 µmol CO_2 mol^{-1}) during the stress, survived longer. This was not surprising, since both these parameters are related to the condition of the photosynthetic apparatus (electron transport capacity, reflected in F_v/F_m, and carboxylation capacity, reflected in C_i), which is a good proxy for overall stress level. An increase in C_i when stress becomes severe often indicates non-stomatal limitations to photosynthesis, involving progressive down-regulation or inhibition of metabolic processes (Lawlor 1995; Flexas & Medrano 2002). However, caution must be taken since C_i calculation under drought might be inaccurate because patchy stomatal closure, and changes in mesophyll conductance to CO_2 often tend to overestimate C_i (Bota *et al.* 2004).

Although high averages of A_{max}, g_s, and TR during the stress might indicate high water use, these values were not related to survival time. The reason for this might be that these averages do not distinguish whether, for example, a high photosynthetic rate at the beginning of the stress was sharply decreased when water became scarce, or rather whether a moderate initial photosynthetic rate was maintained throughout the stress period. Therefore, information on how rapidly physiological parameters react to developing stress, or on the magnitude of these responses, might be more relevant. This was confirmed by our study of the relationship between the ecophysiological parameters and the imposed stress. By quantifying how much of the daily variation in the parameters was accounted for by the progressive drought (r^2 of the regression), we could explain 78% (r^2 of g_s or A_{max} against duration of stress) to 81% (r^2 of A_{max} against RWC_{soil}) of the variance in survival time. This revealed that especially the extent to which g_s and A_{max} were coupled with stress duration (or RWC_{soil}) was strongly related to survival time. Stomatal conductance depends simultaneously on multiple factors such as light, temperature, atmospheric water vapour pressure deficit, intercellular CO_2 concentration, guard cell and epidermal turgor, and water flow through the soil and plant (Netting 2000; Franks *et al.* 2001; Tuzet *et al.* 2003). The degree to which these factors influence g_s varies between species (Tardieu & Simonneau 1998). For example, stomata of different species vary in their sensitivity to leaf water potential (Henson *et al.* 1989; Leuning *et al.* 2003; Tuzet *et al.* 2003), which in turn is a function of soil water potential, the rate of flow through the soil and plant, and the xylem hydraulic resistance. In our data, we found interspecific differences in the amounts of daily variation in g_s and A_{max} that were explained by stress duration or RWC_{soil}, which were indicators for water availability of the soil. In the best surviving species (*Ae* and *Dg*), g_s and A_{max} correlated strongly with the decreasing soil water supply, while only little daily variation in these parameters could be attributed to other factors. In the other species, the dependence of g_s and A_{max} on stress duration was lower, which suggests that the stomata in these species were more influenced by the aforementioned microclimatic factors. Much higher peaks in the values of g_s and A_{max} in these species compared to *Ae* and *Dg* at days 3 and 6, on which there was a significant drop in PPFD, air temperature, and VPD, support this. We therefore hypothesize that interspecific differences in survival time might be related to the extent to which stomata react to changes in soil water conditions relatively to changes in other environmental and physiological factors. The reason why this had an effect on survival time was that the peak values of g_s and A_{max} were not immediately compensated by equally large drops in these parameters, such that after a few days of stress the consumed amount of water was greater in the species with higher fluctuations. A similar division of stomatal responses is mentioned in a study of Gutschick & Simonneau (2002), who state that stomatal conductance responds to two distinct environments: (1) the local and aerial environment of the leaf, defined by irradiance, temperature, humidity, CO_2 concentration and boundary-layer condition, and (2) the distal environment, particularly that of the roots, which generates root-sourced signals of water stress (abscisic acid, ABA) and contributes to determining leaf water potential. However, more research on the relative importance of aerial versus root signals (ABA) for reducing g_s, with respect to survival of extremes, is needed.

Although only eight grass species were used, a range in survival times and different responses to the stress were observed. When more species and functional types are considered, the diversity of plant responses, special adaptations, and specific defence mechanisms against extreme heat and drought is likely to further increase (Chaves *et al.* 2002). The use of species belonging to the same functional type, however, has the advantage that underlying mechanisms might be easier to detect because interference of different mechanisms is limited. Even though our results apply only to the studied grass species, we think that the detected relationships might also be relevant for other species, because increasing water loss due to fluctuations in g_s might adversely affect all species under progressive drought stress. As the plants in this study had no stress history, acclimation to stress as a result of previous exposure was not considered. Exposure to subsequent stress episodes can influence the stomatal reaction to Ψ_l, VPD, irradiance, etc. in a way that water loss is scaled down (Bohnert & Sheveleva 1998; Tabaei-Aghdaei *et al.* 2000), hence the survival times recorded in the current study may well represent a lower limit for the stress levels used.

5.3.2 Relationship between survival time and plant characteristics in non-stress conditions

Total leaf area per plant was the only morphological characteristic related to survival time, with longer survival in species with more foliage. This was surprising because a greater transpiring surface evidently enhances water loss, and many plant species react to drought by partial or complete abscission of the leaves (Clifton-Brown *et al.* 2002; San Jose *et al.* 2003; Rascher *et al.* 2004). The above finding is also in contradiction with the idea that slow growth enhances resistance to moderate drought (Tardieu & Simonneau 1998; Polley *et al.* 2002).

However, when due to extreme conditions the stomata are almost entirely closed, plants with a large leaf area might have a greater water reserve, which will be depleted first before the basal meristem desiccates and the plant eventually dies. This might explain the longer survival time in the grasses with a larger leaf area. Whether this mechanism occurs also in other life forms remains to be seen, although it would not be unexpected to find it in other hemicryptofytes than grasses. There was no correlation between SLA and survival, although a low SLA is often associated with plants developed under conditions of poor water supply (Fernández *et al.* 2002). Resistance to extremes thus seems to be governed by other mechanisms than resistance to moderate drought.

None of the ecophysiological plant characteristics measured on the unheated plants were related to stress survival time; the main reason for this being that the behaviour in unheated conditions was a poor predictor of the behaviour during the heat wave. For example, while most species reduced g_s by a factor of two in response to the stress, the most ‘water wasting’ species in non-limiting conditions (*Fa*) reduced g_s by a factor of four, which made it the second most economic species when water was scarce.

5.4 Biodiversity and invasion in field borders

5.4.1 Conservational concerns

5.4.1.1 Maximisation of biodiversity

Species diversity of unsown and sown communities converged during the first three successional years after establishment on ex-arable land. So, species diversity on the long term seemed unaffected by the type of plant community that was installed. Initially, species diversity was significantly increased by sowing species-rich mixtures. However, in the subsequent years, floristic diversity of sown communities decreased (commercial community) or remained stable (native community). Meanwhile, the unsown community became species richer.

The decrease in species diversity in sown communities was hastened under a mowing regime without the removal of cuttings and/or when the plant community was based on a commercial seed mixture of foreign provenance instead of a native seed mixture. Three years after installation, species diversity was significantly higher under a mowing regime with complete removal of cuttings than under a regime with no or partial removal of the biomass. Indeed the non-removed biomass hampered the growth in the aftermath and prevented the introgression of species. Also Persson (1995) found that yearly mowing with removal of cuttings was necessary to keep high numbers of species in roadsides, especially the low-growing ones. The annual addition of seed-rich roadside herbage significantly increased the floristic diversity with approximately 2 spp/16 m².

The number of occurring sown wildflower species decreased over time in sown communities, irrespective of plant community, location or mowing regime. However, the decrease was hastened under a mowing regime without the removal of cuttings and/or when the plant community was based on a commercial seed mixture of foreign provenance instead of a native seed mixture.

Annuals, although initially highly present (even dominant in unsown plots), steadily decreased in importance whilst perennials steadily increased in importance. These changes occurred at higher rate when cuttings were not removed and/or in vegetations based on commercial seed mixtures. Convergence in species importance between pairs of sown and unsown communities within mowing treatments occurred at SITE1.

5.4.1.2 Effect of light and disturbance on floristic diversity and invasion

Disturbance caused only a temporary effect (one year after the disturbance event), significantly influenced by light regime. The temporary increase in species richness on the unshaded side of the tree lane could be explained by the higher light penetration in disturbed communities on the unshaded side, favouring spontaneous introgression of temporary gaps created by disturbance. Predominately annual species introgressed shortly after the disturbance event. On the shaded side spontaneous introgressing species apparently could not compensate for the loss of species by the detrimental effect of disturbance on plant survival because of restricted light availability. This dual disturbance effect on species diversity reflects findings of Begon *et al.* (1990) who stated that disturbance induces plant mortality that might decrease species diversity, and opens up space for colonisers from elsewhere, which might increase species diversity.

Installing species rich mixtures in field margins strips, offered no surplus value in maximizing species richness since species diversity converged during the first three successional years irrespective of light regime, disturbance level or plant community.

Disturbance caused a temporary significant increase of the importance of annual spontaneous dicotyledons one month after the disturbance event. This was due to the temporary increase of uncovered area after disturbance. The facilitation of spontaneous annual dicotyledons by disturbance was also reported by several authors (Grime 1979; Wilson & Tilman 1991). Later on, the annual spontaneous dicotyledons were quickly replaced by predominantly perennial spontaneous monocotyledons and to a lesser extent perennial spontaneous dicotyledons. Similar succession patterns were reported by Hodgson (1989).

As a result of the successional changes within and between functional groups, communities became increasingly similar as indicated by Sorenson's quantitative index. However, the index was significantly higher for disturbed plots. This means that sown and unsown communities became more similar after disturbance owing to the increase in proportional importance of spontaneous species within the functional groups in disturbed plots. Furthermore, Sorenson's quantitative index was significantly higher on the shaded side of the tree lane. Probably this could be explained by the significant higher percentage uncovered area on the shaded side during early succession offering more opportunities for spontaneous species to colonize.

The invasive success of invaders was significantly higher at higher light intensity because of higher light availability in prevailing gaps. The effect of plant community on the importance of invader grasses was significantly influenced by disturbance level. The unsown community showed highest invasibility under disturbance contrary to sown communities. Biological invasions are often cause for concern in grassland management (Watkinson & Ormerod 2001), and invasive species might further spread into the adjacent crop causing pernicious weed problems. The minimalisation of the risk of biological invasion is also of concern for nature conservation: biological invasions are considered an increasing threat to biodiversity (D'Antonio & Vitousek 1992; Watkinson & Ormerod 2001). Therefore it is recommended to install field margins by sowing, especially at unshaded field sites.

5.4.1.3. Effect of light and disturbance on faunistic diversity

During the monitoring period from 7 August to 2 September 2002, 78 insect families were trapped at the shady and sunny side of a tree lane. Half the number of trapped insects belong to the order of *Diptera*. The order of *Diptera* was also the most important order in grassy field margin strips according to findings of Canters & Tamis (1999). This huge diversity might be partly attributed to the structural diversity of the woody landscape at Beernem. Bommarco (1999) accentuated the beneficial effects of structural diverse surroundings on family richness. However spatial presence and distribution of insect families was significantly affected by light regime, monitoring position and plant community. Families associated with moist conditions or decaying material were caught in larger numbers on the shaded side since soil moisture content was significantly higher at the shaded side of the tree lane. Some insect families preferred the field margin strip whilst others preferred the adjacent crop. Some insect families were more abundant in the unsown margin strip whilst others preferred the sown margin strips. This different distribution pattern between margin types might be explained by the difference in structural diversity and composition of the vegetation.

Besides the composition, Shannon diversity index, family richness as well as insect number were also greatly affected by light regime. The shaded side was significantly more diverse than the unshaded side as reflected by the significant higher Shannon diversity indices irrespective of monitoring position. Similarly significantly more insect families were found at the shaded side. Apparently the moist conditions at the shaded side were more attractive to a lot of insect families either directly or indirectly by the impact of shading on the botanical composition of the margin strip.

The diversity and abundance of insects was also clearly affected by the plant community type of the field margin strip. The unsown community was significantly more diverse than the sown communities as reflected by the significant higher Shannon diversity index. Compared to sown communities, the unsown community showed a significant higher insect number at the unshaded side but not at the shaded side. Probably both insect number and diversity was affected by the botanical diversity of the plant community since highest family richness and number was found in the species richest community (i.e. the unsown community). Also Thomas & Marshall (1999) and Lagerlöf & Wallin (1993) found a positive correlation between botanical diversity and invertebrate diversity. In addition to the botanical diversity, insects might show a preference to the open vegetation structure of the unsown community characterized by a low LAI, an abundance of low growing plant species and a higher PAR transmittance in the canopy offering better opportunities to warm up, fly, feed and hunt. The higher soil moisture content in the unsown communities might have attracted some specific families.

The effect of plant community on the number of pest and antagonist families was mediated by light regime. In general, the number of pest families and antagonist families was significantly higher in the unsown community (data not shown). Several authors (Marino & Landis 1996; Samu 2003) reported beneficial effects of structural and floristic diverse plant communities on diversity and presence of predator insects directly by the availability of niches, nectar and pollen and indirectly by the higher availability of prey insects. Distribution patterns of plant damaging insects ran parallel to distribution patterns of pest antagonist indicating a status of biological equilibrium along field margin strips. Probably the higher availability of prey insects contributed to a higher family richness of their antagonists as also reported by Marino & Landis (1996) and Samu (2003).

5.4.2 Agricultural concerns

5.4.2.1 Potential risk of weed infestations nearby margin strips

Farmers are reluctant to install margin strips because they fear weed invasion and seed dispersal into adjacent crops. According to Naylor (2002) the worst perennial weed species which have the largest impact on crop yields of many crops in northern Europe are the nitrophylous ingrowing species *Elymus repens* and *Cirsium arvense* which were found actively adjusting root and shoot growth into locally resource-rich zones (Campbell *et al.* 1991; Kleijn 1997) such as the crop area. In our study, importance of ingrowing species significantly increased over time under cutting regime without removal of cuttings. Three years after installation, the importance of ingrowing species in field margin strips significantly quadrupled when cuttings were not removed and tripled or were multiplied by five in the unsown margin strip. Mowing with removal of cuttings enhanced mineral depletion of soil thus taking away optimal growing conditions for ingrowing species. Mowing with removal of cuttings also reduced the percentage uncovered area over time significantly, thus reducing gaps prone to colonization by ingrowing species. So, mowing with removal of cuttings is a good practice to diminish the risk of species ingrowth into adjacent crops by creeping roots and rhizomes. The low species competitiveness of unproductive low-growing species in the unsown community is likely to be responsible for the increase of the ingrowing species. So, ingrowing species are better suppressed by sown margin strips than by unsown margin strips.

Besides the potential risk of ingrowth of rhizomatous species into the adjacent crop, weed problems might be increased by seed rain from anemochorous margin species into the adjacent crop. Seed monitoring from 14 August to 9 September at SITE2 revealed that 4 to 8 times more wind-born seeds of specialized anemochorous species, mainly disseminated by annuals, were captured nearby the unsown community than nearby sown communities. So unsown field margin strips, contrary to sown communities, were hot spots for specialized anemochorous species. This might be explained by the higher percentage uncovered area and importance of anemochorous annuals in the unsown vegetation during the first two successional years compared to sown communities. Seed dispersal was only problematic one year after installation of the field margin strips particularly nearby the unsown margin strip. Knowing this, one might tighten the management during the first year after installation in order to prevent plants from flowering during this first year. The decrease in seed dispersal over years might be explained by the significant decrease in importance of annual and perennial specialized anemochorous species during succession and the decrease in invasible gaps over time.

Wind-borne seeds were dispersed over limited distances, mainly within 4 m of field margins: 82-99% of all dispersed seeds were disseminated within 4 m from the field margin strip. However, seed dispersal distance depended on plant species with highest dispersal distance for *Erigeron canadensis* (32 m). Furthermore, high summed seed densities of *Solanum nigrum*, *Urtica urens* and *Chenopodium album* were significantly correlated with high percentages uncovered area in the vegetation after the first cutting. So, the analysis of the soil seed bank offers opportunities to predict the potential risk of weed invasion into adjacent crops.

5.4.2.2 Herbage yield and quality

Despite zero fertilization, mean annual DM yield of sown/unsown unfertilised field margin strips over their first three successional years was high (between 7 360 and 12 470 kg ha^{-1}) compared to agriculturally managed intensive grasslands, reflecting a high nutrient richness of the soil in these plots, formerly used as arable land. Moreover, annual DM yield increased significantly over time irrespective of plant community, mowing regime or location. Apparently the nutrient stocks were high enough to prevent limitation of the yield potential during the studied period, despite an ongoing mineral depletion owing to the removal of cuttings, as reflected by significantly decreasing ash contents over time. Marrs (1993) reports very high nutrient levels on arable land in Western Europe as a result of the application of large amounts of inorganic fertilizers over the last 50 years. According to Oomes (1992) DM production must drop to 5 000 to 7 000 kg ha^{-1} year^{-1} before successful establishment of species-rich vegetation becomes possible.

Surprisingly, annual DM yield was not significantly affected by mowing regime. Although the removal of the cuttings took away quite a lot of nitrogen, potential DM yield losses due to the depletion of nitrogen were probably compensated by the yield stimulating effect of nitrogen fixing legumes (Jefferies *et al.* 1981), which were more important when cuttings were removed than when cuttings remained on the field.

Annual DM yield of the unsown community was significantly lower than of sown communities irrespective of location. However, the discrepancy in annual DM yield between sown and unsown community decreased over time. Initially the unsown community showed higher importance of low productive annuals, which were quickly replaced by more productive perennial grasses and to a lesser degree by perennial legumes stimulating the grasses to grow.

Mean digestibility of the forage was extremely low (below 60%), irrespective of plant community or location. At mid-June most of the grasses and legumes are at an advanced stage of phenological maturity, characterized by a high proportion of lignin and structural carbohydrates in the dry matter, thus reducing digestibility (Chesson *et al.* 1995). The digestibility of herbage from sown communities, containing a high proportion of bred grass and legume varieties, was significantly lower than the digestibility of herbage from the unsown community, which was also reflected in the significantly lower crude fibre content in the unsown community. Differences in digestibility between sown and unsown community were attributable to differences in species composition during succession. Under delayed cutting, early flowering species are less digestible than late flowering species. Compared to sown communities, unsown communities revealed a significantly higher importance of late flowering grasses particularly of *Agrostis stolonifera* and dicotyledons.

Annual digestibility of the forage significantly decreased over time at a faster rate in the sown plant communities than in the unsown community, irrespective of location. This was also reflected by the significant increase of annual crude fibre content over time. Changes in digestibility over time might be attributed to the varying species composition of sown and unsown plant communities over time. A late first cut around mid June probably provoked a species shift towards more early flowering grasses, which set viable seed before harvesting. Compared to the mid-June cut, the regrowth cut revealed lower DM yield but higher digestibility. Nevertheless, digestibility of the regrowth cut remained below 65%.

Here we have a contradiction between good agronomic practices and practices to stimulate botanical diversity. As long as management agreements for field margins prescribe not to mow before mid-June, it might be beneficial to compose initial sowing mixtures with forage species with a delayed maturity or with species which show a slow decrease in digestibility when ageing such as *Phleum pratense* or *Agrostis stolonifera*, with stem elongation around half June, rather than *Dactylis glomerata*, *Lolium multiflorum* or *Festuca pratensis*, with stem elongation starting in the second half of May. Nevertheless, it might be beneficial both for agriculture as well as for species diversity to take the first cut early in the season, e.g. around half May. Herbage harvested at this developmental stage of maturity will be more digestible compared to herbage harvested at mid June. Additionally a series of wildflower species might be enabled to grow and to reproduce more successfully during summertime when grass growth is much lower than in springtime. Simultaneously the mineral depletion of soil will be maximized since Nevens & Reheul (2002) found that mineral export by removal of herbage was maximized around the end of May, well before the flowering stage of many grasses and dicotyledones. From the same viewpoint, sowing productive legume-rich perennial margins are preferable to unsown field margins in order to accelerate mineral depletion of the soil provoked by the extra nitrogen input by the legumes: the extra nitrogen input provokes initially the development of a high biomass volume, extracting a lot of P and K, potentially enhancing botanical diversity in the long run.

According to in vitro analyses, herbage mass harvested in field margins is of low quality when used as animal forage, owing to sub optimal values of crude protein, digestibility and VEM.

5.4.3 Environmental concerns

The installation of a field margin strip, separating pre-existing boundary and crop area, decreased residual N_{min} significantly close to the boundary. This reduction occurred in the deeper soil horizons (30-60 and 60-90 cm), which are more prone to mineral leaching. At 5 m inside the field margin strip, N_{min} was reduced by approximately 50% to 70% compared to N_{min} under the crop area. At the end of the growing season, NO_3-N in the field margin strip never exceeded Flemish legal prescription of 90 kg residual NO_3-N ha^{-1} in the horizon 0-90 cm (Vlaamse Regering 2000), contrary to the field crop area. Within the margin strip, NO_3-N significantly decreased with increasing distance away from the crop edge, irrespective of location or auguring year.

Contrary to NO_3-N, NH_4-N in the margin strip at SITE2 increased with increasing distance from the crop edge, owing to the presence of a row of fifty years old oaks in the boundary. Close by tree rows, soil pH is often low due to the acidifying effect of nitrification of leaf litter (Van Breemen *et al.* 1982). Consequently, during litter decomposition, the organic matter input nearby tree rows was mainly ammonified instead of nitrified under conditions of low pH since the activity of nitrifying bacteria is reduced at pH-KCl below 6.0 (Fenchel *et al*. 1998). So, aside from the adjacent crop area, soil N_{min} in the field margin strips was also influenced by the semi-natural vegetation of the boundary.

In the margin strips, N_{min} losses during winter were significantly lower than in the crop area. So, a perennial vegetation at the edges of fields might reduce nitrogen leaching into watercourses. Field margin type did not significantly determine N_{min} loss.

Taken into account the asymptotically decreasing pattern of N_{min} and NO_3-N, a field margin of 5 m width sufficiently reduced soil N_{min} and N_{min} losses. At greater width offered no extra reduction in losses of nitrogen. A margin width of 5 m corresponds with margin widths recommended by Marrs *et al.* (1989), De Snoo & de Wit (1993) and Tsiouris & Marshall (1998) for drift of herbicides, pesticides and granular fertilizers (deposited by disk spinners), respectively.

Species richness and composition of boundary vegetation evolved positively after installation of a margin strip between boundary and field crop. Prior to the installation, slow growing or small plant species were poorly present. Three years after installation of the margin strip species diversity was enriched at SITE2 by plant species of conservation interest in particular slow growing wildflower species. Furthermore these forbs, and more in particular leguminous species, became more abundant after installation of the margin strip.

6 CONCLUSIONS AND RECOMMENDATIONS

6.1 Invasiveness and invasibility

We created a framework gathering the results of the two experiments on invasion in grassland gaps (Fig. 15). It shows us that grassland ecosystems are more invasible if the availability of nitrogen and light is high, whereas high aboveground biomass and high species richness reduce their invasibility. Concerning invader traits, large seeded species that are able to germinate shortly after gap creation, might establish better than other species, and thus need special attention.

The most successful invasions in our experiments occurred when both the invader and the ecosystem showed traits that were related to invader success. Introduction of a successful invader into a less invasible ecosystem or introduction of a less invasive species in a highly invasible ecosystem, was not very successful, on the other hand. This stresses the importance of studying both invader and community traits and confirms that invasion success depends more upon the interaction between characteristics of non-native species and their potential new habitats than on species traits alone (Alpert *et al*. 2000).

6.2 Prevention of invasion in grassland gaps

To derive strategies to control/prevent invasions, we propose to concentrate on community productivity and light availability, and to a lesser extent on species richness. Our results indicate that invader growth might be suppressed most in gaps with low light penetration and low availability of other resources (reflected in high neighbour biomass and high values of I_{max}). Low light transmittance might be achieved by vegetation dominated by broad-leaved species or by high and dense vegetations (small gaps). Low resource availability requires low nutrient input and/or almost complete use of the available resources by the resident plants, which can be obtained through complementary resource use in a species-rich community. Reducing soil fertility by adding carbon is another possibility (Baer *et al.* 2004). Also highly productive communities might limit invasions through increased competition for space and nutrients, but they mostly occur on nutrient-rich soils, which in turn might benefit invasions. However, because light availability, productivity, and nutrient availability are correlated, we must keep in mind that part of the variation explained by one of these variables must be attributed to the other co-varying variables. This implies that the impact on invasibility of decreasing the availability of light or increasing the neighbour productivity might be smaller or larger than expected, dependent on the absolute amount of photosynthetically active radiation reaching the communities and on the nutrient and water availability in the ecosystem.

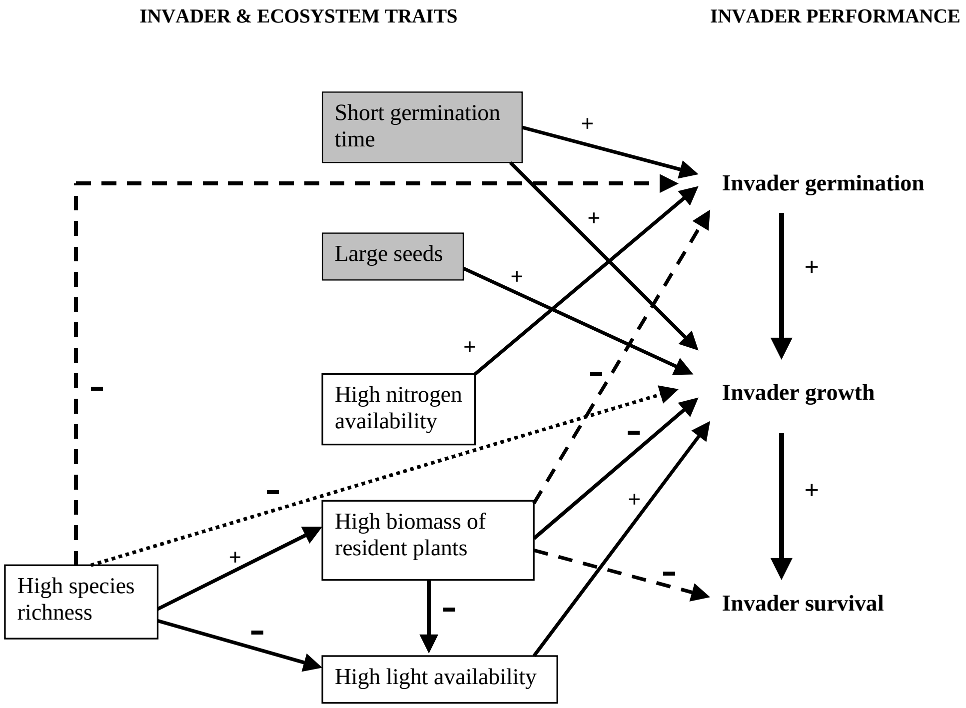

Fig. 15 A framework, indicating species traits and ecosystem traits that determine invader success on local scale, derived from experiments on synthesized grassland communities. Invader traits are shown in grey rectangles, ecosystem traits in white rectangles. Arrows show significant relationships, which can be positive ("+") or negative ("-"). Dotted lines indicate that a significant relationship was only found for some of the species (------), or that the relationship was only valid from the 2^{nd} growing season onward (………).

Increasing the species richness of grasslands might also be a good management practice to restrict invasions, but it depends on the circumstances and the scale. When environmental conditions allow for resource partitioning, higher species richness may lead to greater use of limiting resources (e.g. nitrogen) and greater productivity (Fridley 2003), which both reduce invader success. Additionally, diverse ecosystems absorb more light within their closed canopies through better three-dimensional space filling and greater biomass (Spehn *et al*. 2000), and therefore reduce invader growth, because of lower light availability. So, moderately productive, species-rich communities, with preferable some broad-leaved species, and a low nutrient input, could suppress the growth of invasive species.

6.3 Ecophysiological and morphological basis for the sensitivity of individual grass species to climatic extremes

To understand how extreme events will eventually alter the invasibility of multi-species communities, requires besides a comprehension of the role of diversity also knowledge of the ecophysiological basis of the sensitivity to climatic extremes of individual species. In our experiment, grass species with a greater leaf area survived significantly longer, probably because they contained a higher absolute amount of water per plant, which delayed the desiccation of the basal meristem. Surprisingly, there was no effect of specific leaf area, and fast growers (high water consumption) were not significantly more sensitive to the imposed stress.

High quantum yield of photosystem II (F_v/F_m) and low intercellular CO_2 concentration (C_i) throughout the stress period indicated long survival, but the strongest determinants of species survival time were the amounts of variance (r^2) in light-saturated stomatal conductance (g_s) and photosynthetic CO_2 uptake rate (A_{max}) that were explained by stress duration. Species in which g_s responded strongly to the imposed heat wave and only little to the daily fluctuations in temperature, vapour pressure deficit and irradiation, were able to survive longer (best survivors: *Dactylis glomerata*, *Arrhenatherum elatius*, *Festuca arundinacea*, *F. rubra*). On the contrary, species of which the stomata reacted strongly to the fluctuating abiotic environment of the leaf (e.g. *Cynosurus* cristatus, *Agrostis tenuis*) were more vulnerable during the extreme, and might disappear as first if severe heat waves occur more often in the future.

6.4 Biodiversity and invasion in field borders

As farmers are afraid of the development of weedy annual and rhizomatous species, they prefer a sown above a spontaneously emerging vegetation (Van der Meulen *et al.* 1996). A cutting management fits into their perception of ‘clean’ fields. Hence the promotion of field margins might be more successful if farmers are advised to use a seed mixture upon installation of the margin and if they are advised to cut the margin twice a year. Furthermore, a cutting management of a productive vegetation with removal of the cuttings will accelerate mineral depletion of the soil, promoting the development of a botanically diverse vegetation.

Field margin strips are likely to be disturbed by wheeled or tracked machinery, which increases their invasibility. Therefore, it is advisable, especially at unshaded field sites, to install field margins by sowing in order to minimize the risk of invasion. Furthermore, sown field margins do not conflict with nature conservation purpose: our results show that shortly after installation, the perennial sown vegetation became increasingly look-alike to the spontaneous vegetation leaving opportunities for spontaneous introgression thus encouraging nature conservation on the long-term. At shaded field sites, the installation of new field margins by sowing has no surplus value compared to spontaneous re-vegetation since there is little risk of biological invasion under low light availability.

Field margins strips installed to enhance floristic diversity might be beneficial to overall insect diversity and insect densities. In common agricultural practice many field margin strips are preferentially installed along the shady sides of tree rows and hedges because this area is less productive. From the viewpoint of nature conservation this practice is no obstacle since faunistic diversity might benefit. Unsown margin strips might be preferred to sown communities, particularly at the unshaded side, because of its open vegetation structure and/or higher botanical diversity. However, this might conflict with the agricultural viewpoint that unsown field margin strips might increase the potential risk of weed infestations in both the field margin and adjacent crops (West *et al.* 1997; Smith *et al.* 1999). An argument in favor of the unsown strips is the conclusion that a higher family richness entrains a higher number of antagonist families, which may be useful in biological control of emerging pests in adjacent crops. We have demonstrated that the potential risk of weed infestation is low in case of a pauperized seed bank and in case of the absence of aggressive weeds nearby. Under these circumstances it is highly recommendable to install spontaneously developing field margin strips.

Mowing with removal of cuttings is a good practice to diminish the risk of species ingrowth into adjacent crops by creeping roots and rhizomes. Furthermore, ingrowing species are better suppressed by sown margin strips than by unsown margin strips. Seed dispersal was only problematic one year after installation of the field margin strips, particularly nearby the unsown margin strip. Knowing this, one might tighten the management during the first year after installation in order to prevent plants from flowering during this first year.

Analysis of the soil seed bank offers opportunities to predict the potential risk of weed invasion into adjacent crops. If this risk is substantial, it is recommended to avoid a spontaneous development and to install the margin strip by sowing. According to the seed species present in the seed bank, one may choose a spring or an autumn sowing. Sowing in autumn might avoid germination of thermophile competitive annuals like *S. nigrum* and *C. album* (Chancellor 1985). This avoids choking of vegetation in the installation year, and hence leaves little space for autumn-germinating annual weeds to introgress, or leaves a more competitive vegetation to compete with ingrowing species.

Concerning the time of mowing, there is a contradiction between good agronomic practices and practices to stimulate botanical diversity. It might be beneficial both for agriculture as well as for species diversity to take the first cut early in the season, e.g. around half May, instead of the prescription not to mow before mid June. Herbage harvested at this developmental stage of maturity will be more digestible compared to herbage harvested at mid June. Additionally a series of wildflower species might be enabled to grow and to reproduce more successfully, and the mineral depletion of the soil will be maximized. When, after several years of mineral depletion biomass yields have dropped substantially, the first cut might be delayed again in order to allow seed set of early flowering species. Sowing productive, legume-rich perennial margins is preferable to unsown field margins in order to accelerate mineral depletion of the soil.

Herbage mass and hay from field margins might be used as food for horses, requiring a tasteful hay, low in energy and proteins. An alternative destination is its use as a component in farmland compost. The proposed width of a field margin to sufficiently reduce soil mineral nitrogen and mineral nitrogen losses is 5 m.

To conclude, the results suggest that both biotic factors (species richness and productivity of the resident plants) and abiotic factors (availability of light and nitrogen; disturbance) are related to invader performance (germination, growth and survival) in grassland communities. The best procedure for the installation and management of field borders depends on the goals that need to be achieved (increase of botanical biodiversity; increase of insect diversity; minimization of the risk of invasion, etc.).

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