Species richness and weed abundance in the vegetation of arable field boundaries

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Abstract

Kleijn, D. 1997. Species richness and weed abundance in the vegetation of arable field boundaries. PhD thesis, Wageningen Agricultural University, Wageningen, 177 pp.

In the modern arable landscape, the vegetation of perennial field boundaries have important ecological functions such as providing a habitat for farmland wildlife, providing overwintering sites for predatory insects, providing movement corridors, reducing soil erosion and acting as an agrochemical buffer. In recent decades, plant diversity in these linear landscape structures has declined severely. The present study aims at identifying the most important factors that control botanical species richness in herbaceous arable field boundaries. The field boundary vegetation is usually managed by farmers who consider the boundary to be a source of weeds. Therefore, research concentrated on factors that simultaneously increase species richness and reduce weed abundance in the boundary vegetation.

Species richness was primarily affected by an accumulation of nutrients in the field boundary. Nutrients may reach the boundary in two ways: (i) by misplacement of fertilizer and (ii) by capture of arable nutrient resources (through root growth into the field) by plants in field boundaries. The high nutrient levels in the boundary resulted in an increased productivity of the vegetation and a dominance of tall, competitive species. Subsequently, low statured species disappeared from the habitat and species richness declined. The most common type of boundary management practiced by farmers did not include removal of the cut material after mowing which strengthens the eutrophication of arable field boundaries. Herbicide drift had adverse effects on species richness but the effects were less severe and consistent compared to the effects of nutrients.

The main factor promoting weed growth (in the study area primarily the clonal weeds *Cirsium arvense* and *Elymus repens*) was the presence of bare soil in the boundary. Bare soil may be created by cultivation activities of the farmer or by the smothering effects of cut material left lying in the boundary after mowing. Bare soil generally promotes the establishment of annual weed species. Furthermore, the perennial weed *Elymus repens* was found to be able to concentrate its biomass selectiveley in bare patches within the perennial vegetation. Additionally, bare soil was found to favour the establishment of tall competitive (early successional) species compared to later successional species which are indicative of more species rich plant communities.

The results of this study suggest that boundaries that are not regularly disturbed and low to moderately productive combine species richness with low weed abundance. This may be achieved by a regular and consistent mowing regime of the boundary vegetation that includes removal of the cuttings. A boundary management approach is suggested which may be combined easily with other farming activities.

Key words: Agricultural landscape, field boundary, field margin, crop edge, conservation headlands, vegetation composition, species richness, weeds, *Elymus repens*, herbicide drift, eutrophication.

"I thought of the long ages of the past, during which the successive generations of this little creature had run their course - year by year being born, and living and dying amid these dark and gloomy woods, with no intelligent eye to gaze upon their loveliness - to all appearance such a wanton waste of beauty. Such ideas excite a feeling of melancholy. It seems sad that on the one hand such exquisite creatures should live out their lives and exhibit their charms only in these wild inhospitable regions, doomed for ages yet to come to hopeless barbarism; while on the other hand, should civilized man ever reach these distant lands, and bring moral, intellectual, and physical light into the recesses of these virgin forests, we may be sure that he will so disturb the nicely-balanced relations of organic and inorganic nature as to cause the disappearance, and finally the extinction, of these very beings whose wonderful structure and beauty he alone is fitted to appreciate and enjoy. This consideration must surely tell us that all living things were *not* made for man."

Alfred Russel Wallace, 'The Malay Archipelago', 1869

Voorwoord

Ruim vijf jaar geleden was ik na mijn afstuderen op deeltijdbasis werkzaam bij de toenmalige vakgroep VPO. Op mijn fietsje verzamelde ik op grote schaal zaden van graslandsoorten in de omgeving van Wageningen. De uit deze zaden ontsproten planten hebben me in de tussenliggende periode aardig bezig weten te houden en onderzoek hieraan vormt een groot deel van dit proefschrift. Bij dit onderzoek zijn een groot aantal mensen behulpzaam geweest en hebben mij het werk lichter en leuker gemaakt. Bij deze wil ik al deze mensen bedanken. Voor een aantal mensen kom ik er niet zo makkelijk vanaf. Wouter Joenje is grotendeels verantwoordelijk voor het fenomeen 'plantenecoloog Kleijn'. Wouter, bedankt dat je een afgestudeerde plantenveredelaar de kans gaf zich te verdiepen in een nieuw, uitdagend vakgebied. Martin Kropff erfde in 1995, als kersverse Prof Onkruidkunde en Toegepaste Plantenoecologie in Agro-ecosystemen, een bende eigenwijze aio's met vrijwel afgeronde onderzoeken en het hart op de tong. Met inzet en groot enthousiasme behartigde hij sinds die tijd mijn belangen en managede hij me door de tweede fase van de promotie. Dank! Frank Berendse, als promotor op iets grotere afstand (250m), zag toe op de meer fundamenteel ecologische kant van het onderzoek en zorgde ervoor dat ik altijd kritisch naar de natuurkwaliteit van 'mijn' akkerzomen bleef kijken. De vele inhoudelijke overleggen met Jan van Groenendael over proefopzetten, resultaten en conceptartikelen waren zeer stimulerend en dit proefschrift is er beduidend beter door geworden. Zonder Ineke Snoeijing was een groot deel van dit werk nooit uitgevoerd en het feit dat ik tijdens mijn vakanties het werk volledig kon vergeten was grotendeels te danken aan de wetenschap dat zij alles onder controle had. Bedankt! Marein Verbeek fietste achterwielen aan gort, versleet telefoontoestellen en sleet de knieën uit menig spijkerbroek bij zijn geslaagde poging om de vegetaties van de hedendaagse akkerzomen in kaart te brengen en gegevens los te peuteren bij boeren die haast niet te traceren waren. Leonie van der Voort nam gedurende een lange zomer zeldzame akkeronkruiden onder het mes. Mijn kamergenoot Peter Schippers wil ik bedanken voor het onverstoorbaar aanhoren van mijn tirades tegen computer soft- en hardware in het bijzonder, en meer in het algemeen tegen alle personen die weigerden de, mijns inziens toch duidelijk aanwezige, genialiteit van mijn werk in te zien. De keren zijn niet te tellen dat ik bij Eddie Kremer ben binnengelopen vanwege niets, wissewasjes, software problemen, GENSTAT vraagjes, ransuilen kijken of het bespreken van de gang van zaken op de Vakgroep of Universiteit. Hopelijk vond hij dat ook leuk. De morele steun van mijn huisgenoten gedurende mijn promotie moet zeker niet onderschat worden. Casper Vroemen ("Artikel geaccepteerd? Tja, dat gaat je een avondje kroeg kosten"), Lia van den broek ("Mooi, zullen we het nu dan weer over iets interessants hebben?") en Ivo Raemakers ("Hoezo natuur?"), dankzij jullie was relativeren gelukkig bijzonder eenvoudig. Met Rob van Tol heb ik heel wat frustaties weggefietst, gezwommen en gedronken. Proost! Pap en Mam, de wetenschap dat jullie er altijd voor me zijn, vormt een fantastische basis in mijn leven. Geerdien, met jou aan m'n zij durf ik nog wel drie promoties aan.

Hulde!!   David

Stellingen behorende bij het proefschrift '*Species richness and weed abundance in the vegetation of arable field boundaries*', door David Kleijn.

1. Als men in Nederland op korte termijn de soortenrijkdom van akkerzoomvegetaties substantieel wil verhogen zal men, naast het invoeren van het juiste beheer, niet kunnen ontkomen aan het introduceren van soorten.

Dit proefschrift.

2. Maatregelen gericht op het tegengaan van drift van herbiciden zullen weinig effectief zijn in het behouden van botanische diversiteit zolang de voedselrijkdom van de akkerzoom niet wordt teruggebracht.

Dit proefschrift.

3. Het gebruik van herbiciden in akkerzoom-vegetaties bevoordeelt de akkeronkruid-soorten in deze habitat.

Dit proefschrift.

4. Het bekritiseren van andermans natuurbeleid gaat ons nog het beste af.

5. Natuurbeheerders laten concurreren (Programma Beheer 1997) leidt tot optimalisering van het behalen van marginale natuurdoeltypen.

6. Het is nutteloos te discussiëren over de beste onderzoeksmethode zonder deze in de context van een duidelijke vraagstelling te plaatsen.

7. De moeilijkste opgave van onze tijd ligt in het overtuigd zijn van de betrekkelijkheid van de eigen mening maar er desalniettemin voor staan.

André Klukhuhn, Volkskrant 23 december 1995.

8. Een vegetatie is als een taal: dynamisch en zich continu aanpassend aan zijn omgeving maar toch blijvend herkenbaar.

9. Gezien het feit dat zo'n 10 procent van het totaal aantal soorten vaatplanten op aarde epiphytisch groeit, wordt er te weinig onderzoek verricht aan de taxonomie en ecologie van epiphyten.

10. Ecologisch onderzoek is als tekenen: alleen de belangrijkste lijnen eruitlichten anders wordt het chaos.

11. Fieldwork surely tempers any arrogance bred by higher education.

Mark W. Moffet, 1993. The high frontier.
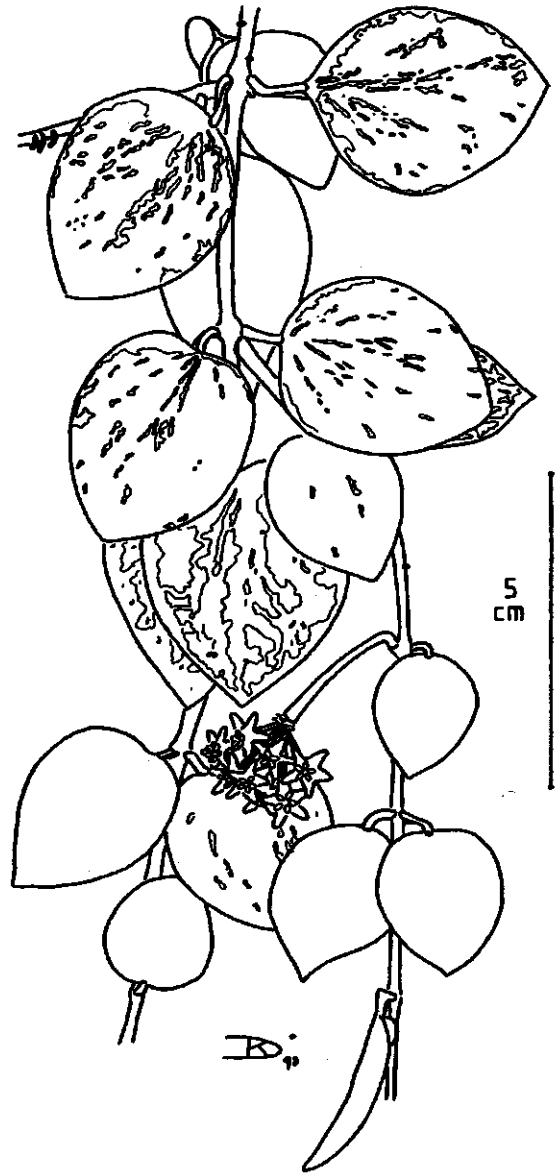
Vrijwel alle soorten uit het Zuid-Oost Aziatische planten-geslacht Hoya *groeien epiphytisch. Vele soorten vertonen specta-culaire aanpassingen aan de extreme groeiomstandigheden in boomkruinen. Weergegeven is een nog onbeschreven soort welke endemisch is op het Oost-Indonesische eiland Biak. De planten groeien daar veelal in het organisch materiaal van mierennesten (*Crematogaster spec.*).*

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General introduction

The rise and fall of arable field boundaries

Standing in the agricultural landscape, one may be surrounded by arable fields in every direction. As far as the eye can see neat rows of wheat, sugar beets or maize blend together to form huge blankets that cover the earth. In contrast to ancient agriculture, in the late twentieth century the crops grown by the farmers do not tell much about the people that grow it or the area in which it grows. Looking at a maize field one may be in Africa, Indonesia or in the Netherlands notwithstanding the species being originally restricted to Mexico. Likewise, rice cultivation started about 8000 years ago along the Yangtze River in South China (Smith 1994), but rice fields can now be encountered in a variety of countries including Italy, Senegal and the United States of America. More than the crop, it is the way the fields are embedded in the countryside that helps a twentieth century spectator to pin down the whereabouts of a location. The shape and size of the fields in combination with the shape, structure and floristic and faunistic composition of the landscape elements surrounding the fields still are characteristic to countries or even districts.

The most important characteristic of arable agriculture is the regular disturbance of large areas of soil. Given sufficient rainfall in a region, the natural vegetation will usually be dominated by perennial plant species, while agriculture throughout the world predominantly relies on annual cropping systems. The transition area from the cropped area, or the arable field, to the surrounding natural vegetation is called the field margin. Within the field margin we can distinguish on one side the outer meters of the arable field which is called the crop edge, and on the other side the first meters of permanent vegetation bordering the arable field: the field boundary.

During the many centuries since the adoption of agriculture, the once natural field boundary vegetation has been influenced and managed increasingly by man according to specific needs. Different needs in different areas have resulted in a multitude of field boundary types. For instance, the grassy bunds characteristic of the sawah landscape in South-East Asia emerged out of the need to flood the rice fields and/or to control soil erosion. In England, the need for cattle fencing after abandonment of village pastures led individual farmers to plant and prune trees, ultimately formalized in the Enclosure Acts: in the period 1750-1850 hedges were planted at an average rate of 3200 km per year creating extensive hedgerow landscapes (Muir & Muir 1987). In areas with excess water during one or more seasons, ditches facilitated timely drainage of the fields. Not seldomly field boundaries served more than one purpose and the shape or composition may have changed as the needs of the owners changed. In the province of Friesland, in the Netherlands, hedgerows were initially constructed to mark the borders of fields of different owners and to fence the cattle.

Additionally it functioned as a windbreak (in the first year after pruning the hedgerow, potato's were planted instead of the more vulnerable cereals) and as a source of wood with a variety of purposes: firewood for domestic use or sold to bakers, poles and stalks for fencing, bean stalks, twigs to make birch-brooms or to be used in dike construction and oak-bark sold to tanners (Alleijn 1980). In Northern Italy, first the Etruscans and later the Romans planted trees and shrubs to separate fields of different owners. Vines (*Vitis vinifera*) grew upon these trees for grape production and this kind of cultivation was called 'vite maritata', or promiscuous vine growing. This kind of cultivation lasted for more than two millennia but in the 18th and 19th century was replaced by cultivation of pollarded white mulberry (*Morus alba*) whose leaves were fed to silkworm larvae when silk production proved to be more profitable economically (Groppali 1993).

Some plant species, but especially animal species have adapted to these new habitats. One of the largest farmland animals, the hare (*Lepus europaeus*), uses field boundaries for shelter in daytime while feeding in the crops at night (Tapper & Barnes 1986). For the grey partridge (*Perdix perdix*) it is extremely important as breeding site (Potts 1986).

As the human population increased, the demand for food increased and the area occupied by arable land increased as well. Nowadays, huge uninterrupted areas of cultivated land can be found around the world (Central-France, the North-American Mid-West, the Indonesian island of Java and the Dutch Flevopolders to mention just a few). In these areas field boundaries are one of the last refuges for (semi-) natural vegetation and all the organisms relying on it. In other regions natural habitats have been fragmented by agriculture and field boundaries may, besides being a habitat, also play an important role in the dispersal of organisms between fragments (Bennet *et al.* 1994, Fry 1989).

During the twentieth century, agriculture specialized, especially in Western Europe and North America. Most mixed farms specialized on either arable or livestock farming. Arable farmers increasingly concentrated their efforts on growing a small number of crops for the market and formerly profitable by-products were abandoned. Labour-cost rose rapidly and field boundary management had to be time-efficient, were they not to be abandoned. As a consequence, the perennial field boundary vegetation lost part or all of its original functions. The introduction of barbed wire soon made the laborious and time consuming hedgerow management for fencing superfluous. Additionally, wood production for domestic use became unnecessary since most households changed from stoves fuelled by wood to gas or oil fuelled stoves or cooked electrically. Synthetic brooms replaced birch-brooms; cheap, imported bamboo sticks were used as bean stalks and so on. In fact, with the increased mechanization of agriculture, the costs of field boundaries were considered to be greater than the benefits as will be elucidated in the next section, and the number of field boundaries in Western Europe and North-America decreased drastically (Alleijn 1980, Baltensperger 1987, Chapman & Sheail 1994). Additional factors contributing to the decrease in field boundary habitats were urban expansion and construction or improvement of roads (Baltensperger 1987).

Negative and positive aspects of contemporary arable field boundaries.

In the highly mechanized and labour-efficient twentieth century agricultural systems, field boundaries may interfere with crop production or reduce revenues in several ways:

(1) Field boundaries reduce the cropping area. Two fields of 400 x 400 m, including the boundary structures, have less area that can be cultivated than one field of 400 x 800 m. Furthermore, the area occupied by headlands, which are generally less productive because of soil compaction or poor seedbed preparation caused by the regular turning of farming machinery, increases as well.

(2) Field boundaries reduce the efficiency of cultivation. Analogous to (1), a farmer has to turn his plough or spray boom twice as often on the two 400 x 400 m fields compared to the 400 x 800 m field.

(3) Field boundary vegetation may compete with the crop for light, water and nutrients. Especially shading by tall, unmanaged hedgerows and woodlots may have serious effects on crop yields. Naturally, the consequences of these effects are more serious when fields are small than when fields are large. Mainly because of point 1 to 3, large scale re-allotment schemes have taken place in various West-European countries in recent decades. These have been one of the most important causes for the decrease in field boundary habitats (Alleijn 1980, Muir & Muir 1987).

(4) Farmers presently consider field boundaries as a source of weeds, pests and diseases (Boatman 1992, de Snoo & Wegener Sleeswijk 1993, Marshall & Smith 1987). In modern field boundaries certain weed species have been found to occur in both the field boundary and the arable field (Marshall 1989) and to infest the field from the field boundary (Theaker *et al.* 1995). Interestingly, although several studies have reported an increased abundance of weeds near the field boundary (e.g. Marshall 1989, Wilson & Aebischer 1995) no estimates are available with respect to the amount of yield losses they cause. Indeed, Wilson & Aebischer (1995) suggest that the abundance of weeds in the crop edge is the result rather than the cause of the poor crop performance. Many virus, fungi, bacteria and insect species overwinter outside the floral desert that an arable field often is in winter time (Thresh 1981). For instance, 42% of the aphid species which are regularly target of control measures use secondary non-crop hosts (van Emden 1965). Common West-European genera used as alternative host in addition to crops are *Cirsium, Crepis, Lathyrus, Lotus, Rubus, Salix, Viola*, and many species of the families *Caryophyllaceae, Gramineae* and *Umbelliferae* (Eastop 1981). Another example is the fungus powdery mildew on pea (*Erysiphe pisi*) which has alternative hosts in *Heracleum sphondylium, Lathyrus pratensis, Ranunculus acris* and *R. repens* (Wheeler 1981), all common field boundary species.

(5) The maintenance of most field boundary types is costly (see also Semple *et al.* 1994) and time consuming and even if cheap and efficient management is possible, such as in road-side verges, arable farmers usually do not have the proper machinery.

(6) Field boundaries can be a habitat for wild relatives of crop plants. Producers of carrot seed (*Daucus carota*) for example, have to take care that their commercial varieties do not inter-breed with wild varieties (also *Daucus carota*).

On the other hand, field boundaries also have positive effects on crop growth. The most important (or best studied) effects are:

(1) Field boundaries may function as a windbreak. Wind speed downwind a hedgerow is reduced over a considerable distance (Forman & Baudry 1984). Especially the taller and more vulnerable crops, such as cereals, may be protected from wind damage. Furthermore, partly as a result of reduced wind speed, water losses are reduced as well in a broad zone near hedges. In Niger, Long *et al.* (1986, in Nair 1993) found a 23% yield increase of millet in windbreak protected areas compared to areas where no windbreaks had been planted on a gross area

basis, i.e. including the area occupied by the windbreaks. However, net effects of windbreaks on crop yields are variable and seem to depend on climatological conditions. Kowalchuck and de Jong (1995) found reduced yields up to 10 m into the crop and slightly increased yields from 10-20 m into the field in a dry year. In the next, more moist year the competition effect was smaller and the zones of improved crop growth was absent.

(2) Field boundaries reduce soil and wind erosion. 15 Per cent of the total world soil surface suffers from soil degradation (World Resources 1991-92, 1992-93 in Parlevliet 1993). Most of it is caused by runoff or wind erosion. It is quite obvious that in mountainous or hilly areas soil erosion is a potent danger and that most farmers have terraced their fields with the boundaries solidly vegetated to prevent the collapse of the steep terrace sides. However also in flat areas soil erosion may pose problems in agriculture since the soil remains bare for large portions of the year. In the United States of America soil erosion caused and still causes an enormous loss of fertile topsoil. Field boundary-like structures of permanent grassy vegetation (filter strips) interspersing arable fields were found to reduce soil erosion by at least 41% (Robinson *et al.* 1996, Tim & Jolly 1994).

(3) Field boundaries are a source of natural enemies of crop pests. For a large number of predatory insects field boundaries are essential since they do not overwinter in cultivated soils (Dennis *et al.* 1994, Sotherton 1984) and they use the habitat to build up their population before moving out into the crop (van Emden 1990). Although numerous studies have shown that predatory insects can have considerable suppressing effects on pest insects in the crop (Altieri & Letourneau 1982) assessment of economic benefits due to the presence of predatory insects from field boundaries still lack. However, with pesticide use becoming increasingly restricted (LNV 1990) biological control of crop pests will become more and more important in the near future, making the potential of field boundaries more interesting.

Some of the positive aspects of field boundaries do not relate to crop production. Field boundaries play an important role in improving the environment and nature in the agricultural landscape and may indirectly generate extra income to the farmer. The most important aspects are:

(I) Field boundaries can act as protective buffer strips for agrochemicals. Modern agriculture depends on large external inputs of fertilizer and pesticides. These substances are known to be harmful for a large number of organisms, including humans. The boundary vegetation may function as a filter preventing runoff of agrochemicals to reach nearby habitats with susceptible or vulnerable organisms such as in ditches or nature reserves (Daniels & Gilliam 1996, Frede *et al.* 1994, Jenssen *et al.* 1994). Furthermore, Van de Zande *et al.* (1995) found a vegetated strip to reduce spray drift considerably better than a bare strip.

(II) Field boundaries can serve nature conservation purposes. Some characteristic farmland animals such as the partridge (*Perdix perdix*), the quail (*Coturnix coturnix*), the hamster (*Cricetus cricetus*) and the brown hare (*Lepus europaeus*) have specialized on arable fields (De Vries and De Vries-Smeenk 1967, Potts 1986, Tapper & Barnes 1986). For these species field boundaries are crucial as sites to shelter, forage or breed. The decline of the partridge in the Netherlands has been demonstrated to be linked with the abundance of field boundary habitats (Maris 1996). Other animals, especially bird species, have not specialized on farmland to such a degree but still are rather characteristic for landscapes dominated by arable fields. To name just a few: the corn bunting (*Milaria calandra*), yellowhammer (*Emberiza citrinella*), whitethroat (*Sylvia communis*), yellow wagtail (*Motacilla flava*), skylark (*Alauda arvensis*) (Greenwood 1995). But also mammals like the wood mouse (*Apodemus sylvaticus*),

bank vole (*Microtus agrestis*), and common shrew (*Sorex araneus*) (Tew *et al.* 1994; the literature on the ecology of farmland mammals and birds primarily comes from the United Kingdom and this list might be biased towards animals that specifically prefer hedgerows) and their predators polecat (*Mustela putorius*) and weasel (*Mustela nivalis*). Additionally, many animal species reluctantly cross open areas such as arable land and field boundaries might serve as migratory routes or corridors for animals connecting fragments of habitat (Bennet *et al.* 1994). Due to the decline of natural habitats a range of plant species can now predominantly be found in field boundary structures. In Twente, the Netherlands, the red-list woodland species *Phyteuma spicatum*, *Gagea lutea* and *Mespilis germanica* are mainly found in hedgerows (Alleijn 1980).

(III) Historical and cultural value of field boundaries. Williamson (1968) determined a hedgerow landscape in East Anglia, England, to pre-date the Roman invasion. This indicates that the individual hedgerows, which in part still exist, are over 2000 years old. If it were a building, people would pay entrance fees to watch it. On the Wadden Sea island Texel, the Netherlands, farmers developed a specific type of cattle fences after the common pastures were abandoned in the 17th century. With sand and grass sods they raised steep earthen walls (tuinwallen), which are unique in the Netherlands, possibly in the world. Nowadays, a small part of the island has been declared a 'landscape reserve' to save this cultural heritage from re-allotment schemes and neglect in management.

(IV) Aesthetic and recreational value. In the Netherlands more and more people escape the busy city-life to spend their free time in the rural landscape. Besides an agronomic function, agricultural areas increasingly serve as recreational areas. However, most people prefer areas with a diverse landscape and avoid the large scale agricultural areas like the Flevopolders. Field boundary habitats determine largely the scale and aesthetic appearance of a landscape. In the favoured areas a lot of farmers recently opened mini-campings to supplement their income from agriculture.

The need for diverse field boundaries?

Since the turn of the century diversity in those field boundaries that have escaped removal or replacement by barbed wire has declined steadily. Variation in the shape and structure of field boundaries decreased between different areas (Alleijn 1980). Species composition of animals and plants in different areas became more similar (Joenje & Kleijn 1994) and finally species-richness in individual field boundaries decreased (Boatman 1989, 1992). In recent decades, the reduced diversity in field boundaries has received increased attention. Numerous public initiatives arose to restore old field boundaries and scientists in various countries started to investigate the ecological functionality of field boundaries in the agricultural landscape with respect to nature conservation, environment and crop protection (e.g. Forman & Baudry 1984, Marshall & Birnie 1985, Sotherton 1984, Way & Greig-Smith 1987).

However, the number of rare species that find their exclusive habitat in a perennial field boundary vegetation is rather low (Hooper 1987). Therefore it has been argued that there is no urgent need for increased efforts to raise diversity in these habitats. Instead, it would be much more efficient to allocate financial resources to research and management of rare species, preferably in nature reserves where conservation measures can be taken easily and without debate with a third party (the farmer). Subsequently, in agricultural areas farmers

could concentrate on farming and would not have to bother with nature conservation. *I do not agree with this line of thought.*

The arable landscape is an ecosystem in which plant and animal life are intimately connected. Since most of the area in the agricultural landscape is occupied by crops which are kept free of most wildlife, almost all animals depend on whatever vegetation is left: field boundaries, road verges and farmyards. Animal diversity is closely connected to plant diversity (Brown & Soutwood 1987, Lagerlöf & Wallin 1993, Remund *et al.* 1989, Southwood *et al.* 1979, Sparks & Parish 1995), therefore maintenance of botanically diverse field boundary vegetation is relevant to the diversity of the entire arable ecosystem. With the exception of a considerable number of rare arable weeds, the arable ecosystem does not yet harbour many species that are threatened with extinction. However, extensive research on the grey partridge (Maris 1996, Panek 1997, Potts 1986, Rands 1985) shows that this may be a matter of time. Indeed, in Switzerland the population of grey partridges declined within 30 years from 15000 birds to just a few pairs (Jenny 1995). Restoring the carrying capacity of the arable ecosystem now seems a more sustainable conservation option than creating reserves once the species is really rare.

The diversity of the agro-ecosystem is relevant to crop protection issues. Most crop species have been derived from early successional species. In their natural habitats these species are usually short lived and distributed patchily. As a result, their presence is unpredictable to herbivores specialized on them (Rhoades & Cates 1976). Crops, however, are grown on large areas of land and their presence is predictable which may explain why widespread epidemics occur regularly in agriculture but seldom in nature (Begon *et al.* 1990). Agricultural systems are in many respects similar to an early successional habitat: disturbances create conditions unsuitable for the continued coexistence of plant, herbivore and enemy and colonization by both pest and predator is an important aspect of the system (Price *et al.* 1980). Colonization occurs mainly from the field boundary (Wratten & Thomas 1990). Contemporary, species poor field boundaries are dominated by early successional species (Boatman 1989, 1992) and therefore contribute to the problem. On the other hand, Brown & Southwood (1987) demonstrated that midsuccessional vegetation stages which were most species rich, not only had a high insect diversity, but also had the lowest herbivore/enemy ratio. Maintenance of diverse field boundaries thus may increase the stability of the arable cropping system and reduce the need for large-scale pesticide use. Which brings me to the next reason to aim for botanically rich field boundaries.

Modern agriculture relies heavily on external inputs of agro-chemicals. As a result, considerable amounts of these substances can now be found in soil and surface waters (Breeuwsma *et al.* 1989, Foster *et al.* 1989). Agrochemicals are harmful to humans as well as wildlife. Both pesticides (Freemark & Boutin 1995, Marrs *et al.* 1992) and fertilizers (Bobbink 1991, Mountford *et al.* 1993, Tilman 1993) generally have profound negative effects on the species richness of perennial vegetation. Field boundaries are the semi-natural habitats most exposed to drift of agrochemicals. Therefore a diverse field boundary vegetation may be considered indicative of an ecologically sustainable and environmentally sound way of crop production (Joenje, personal communications).

Furthermore, with an ever increasing population growth, world-wide more and more land is turned into arable land to meet the rising food demand. Especially in densely populated regions most area is occupied by buildings, infrastructure and fields. Any efforts to preserve global biodiversity have to include arable landscapes. Additionally, efforts initiated by the

developed countries (who usually have little natural, undisturbed habitats left) to preserve biodiversity in 'third world' countries (who generally still have large but rapidly in size decreasing undisturbed habitats) may meet scepticism from the latter party if they realize that the majority of the land surface in the 'first world' countries is managed without any regard for wildlife whatsoever. Then there is the fact that not all people have the same definition of an arable field. In one of the worlds most diverse biotopes, the tropical rain forest, many a people practice shifting cultivation. To them the forest is arable field, field boundary and natural habitat at the same time, i.e. whose definition of agriculture do we use when we decide where to conserve diversity and where to 'let farmers farm'.

Finally, the aesthetic value of the arable landscape is at stake when we discuss the diversity of field boundaries. The arable landscape is home to the rural population and additionally harbours an increasing number of recreating urban dwellers. A landscape of arable fields surrounded by structurally, faunistically and floristically diverse field boundaries is generally considered to be more attractive than one of arable fields encompassed by monotonous strips of green vegetation.

Aims and approach.

I want to make clear that, with respect to national or even global biodiversity, nature management in agricultural areas can not replace nature management in reserves or nature development projects. Nature reserves in densely populated areas such as the Netherlands are *essential* for the preservation of our remaining natural heritage. In modern field boundaries, however, even very common plant species with a broad ecological amplitude such as *Daucus carota*, *Galium mollugo* or *Centaurea jacea* have disappeared (Joenje & Kleijn 1994). With the exception of some attractively flowering weeds (e.g. *Cirsium arvense*, *Sonchus arvensis*) most nectar producing species, essential to a range of insect species, have thus disappeared from the arable landscape. Restoring a necessary, basic level of botanical diversity in the agricultural landscape, which secures the existence of a broad range of animal life, is what should be aimed for. Previous experiences in the Netherlands have demonstrated that a subsidized, top-down approach such as the 'Relatienotabeleid' have been little successful in maintaining botanical diversity (Dijkstra 1991, Engelsma & Waardenburg 1994). I therefore propose an approach which elucidates and highlights the benefits farmers may expect from thoughtful boundary management. Such an approach is not based on subsidies and is therefore sustainable, that is, farmers will not stop their newly adopted management regimes once the subsidies are stopped. This is essential, since the restoration of botanically rich vegetation is a matter of maintaining the proper management for a very long time. Boatman (1991) and co-workers first adopted this approach which is based on the farmers' perception that field boundaries are a source of weeds. In other habitats, the natural and semi-natural vegetation harbours very limited numbers of arable weed species which furthermore seldom have high abundances (Schmidt 1993, Sykora *et al.* 1993). Thus, careful use of herbicides in combination with proper boundary management should eliminate weed problems in the boundary vegetation. At the same time this type of boundary management will probably result in an increased species richness in the long run.

There is however only a limited amount of information available on the main factors that affect species richness and the success of arable weeds in field boundary vegetation. What are

the relative effects of drift of herbicides and misplacement of fertilizers? What is the dominant type of boundary management and how does it affect the species richness? How well are species able to disperse to and re-establish in field boundaries when they have gone extinct at a site? *This thesis aims at identifying the main factors that affect both the botanical species richness and the abundance of weeds in arable field boundaries.* The results presented in this thesis may help us understand the causes for the recent decline in species richness of arable field boundaries. It may subsequently give us insight in the perspectives for increased diversity in field boundaries based upon the previously described relationship between the weediness and species richness of a boundary vegetation.

Most experiments in the following chapters are limited to herbaceous vegetation on sandy soils, and are executed in the vicinity of Wageningen, the Netherlands (51°59'N, 5°30'E). The limitation to focus on one type of boundary was made to be able to explore the effects of most of the important factors affecting the species composition of field boundaries, while still being able to complete the work within the available four years. Sandy soils retain nutrients less efficiently compared to loam or clay soils (Foth & Turk 1972), therefore the effects of fertilization are expected to manifest themselves more rapidly on sandy soils. The choice to focus on herbaceous vegetation was inspired by the abundance of grassy ditch banks in the Netherlands. Furthermore, the response of grasslands to fertilization is meticulously documented (e.g. Bakker 1987, Berendse *et al.* 1992, Bobbink 1991, van Strien *et al.* 1989) which make interpretation of the results easier. Research on grass dominated field boundaries will yield results complementary to those from the United Kingdom where extensive research is being done on hedgerow boundaries. Although, three chapters in this thesis deal with extended boundaries, the approach followed in this thesis does not foresee in the introduction of large-scale extensions of field boundaries. Large-scale extensions of field boundaries, however desirable from a nature conservation perspective, are not considered to be optional on economic grounds: neither the farmer nor the government can or will pay for it. Temporary extensions of field boundaries within the framework of the European Set-Aside scheme is, from a botanical point of view, not interesting since botanically rich permanent vegetation does not generally develop within this short period of time.

In conclusion, with respect to the diversity of a habitat, we can make a distinction between α diversity (the number of species in a habitat) and β diversity (structural diversity in a habitat). Although β diversity of the vegetation is extremely important for the abundance and species richness of arthropods (Southwood *et al.* 1979) only α diversity is examined in the present studies. Therefore, when diversity is mentioned in the next chapters this refers to the number of species on a per area basis.

Outline of the thesis

The booklet that lies in front of you starts with an exploration of the current state of the art of Dutch field boundaries. Approximately 100 herbaceous field boundaries on sandy soils are surveyed and the owners/tenants of the arable fields are interviewed with respect to fertilizer and herbicide use, farming equipment and boundary management (Chapter 2). Vegetation composition is analysed both syntaxonomically and by regression analysis. The effects of various cultivation and management activities, such as nitrogen inputs and crop rotation, on vegetation composition are analysed.

In Chapters 3 and 4 vegetation development on extended field boundaries is monitored. Since the management history of existing field boundaries is generally not known, it is difficult to relate vegetation composition, and more specifically the causes for botanical changes in vegetation composition, to management or land use factors. Creating new field boundaries by extending existing boundaries with an extra strip of vegetation may solve this problem since starting conditions of the new boundaries are known. Chapter 3 reports on three years of secondary succession in herbaceous field boundary strips in France, the Netherlands and the United Kingdom, that were created by extending the original field boundary with an extra four meters in early spring 1993. Strip plots are either sown with grass or allowed to regenerate naturally. The developing vegetation in the new boundary plots and the pre-existing boundary is followed for three years and compared between countries, soil types, boundary types and between the grass sown and regeneration plots. Chapter 4 reports on a more detailed analysis of the vegetation composition three years after establishment in the Dutch strips only. Patterns in species composition over the total width of the plots is compared between the grass, the regeneration and an additional forbs plot (an introduced mixture of grassland forbs). Finally, in Chapter 5 the effects of the establishment of an extended boundary on the weed flora and crop yields in the crop edge are determined.

Plants in arable field boundaries may capture nutrient resources applied to the crop by root growth into the crop edge. The most abundant arable weeds that occur both in the boundary vegetation and in the crop, predominantly reproduce vegetatively by means of rhizomes or roots. The success of these clonal plants may be explained by their ability to reallocate limiting resources to their boundary shoots once they have grown into the arable field (see Stuefer *et al.* 1996). In this manner, they may capture arable nutrient resources more efficiently and their boundary shoots may be at a competitive advantage compared to non-clonal boundary plants. The experiments presented in Chapter 6 quantify the effect of capture of arable resources by a grassy boundary vegetation and determine whether clonal species capture resources more efficiently than non-clonal species. Results are discussed in the light of the eutrophication and the persistence of clonal weeds in the boundary habitat.

Chapter 7 examines whether the establishment success of perennial species with a contrasting ecology differs between vegetation types. The establishment rate of species is highly relevant to their chances of (re-)colonization in field boundaries. The species range from tall, ruderal, early successional species to short, late successional species. Three types of vegetation are used to examine the establishment response: a bare fallow arable field and spontaneously vegetated one and two year old fallow arable fields. After initial sowing, establishment of the species is monitored by following emergence, mortality, plant growth and seed production for two years.

Drift of herbicides allegedly is one of the major causes of the decline in species richness in arable field boundaries. However, although numerous papers have discussed drift distribution patterns after field applications and report on bio-assay studies with both plant and insect species, hardly any work has been done in field boundary vegetation (Freemark and Boutin 1995). In existing field boundaries the effects of agrochemical drift are difficult to examine since these vegetation structures have probably been exposed to drift of such compounds in the past. Demonstration of any botanical change within these habitats due to these factors may therefore fail (Marshall 1992). A comparable vegetation not bordering an arable field does not have this disadvantage. In Chapter 8, the effects of herbicide drift are simulated by applying low doses of herbicides to two types of perennial vegetation. In these experiments

the effects of low doses of fertilizer are examined as well. Additionally, the effects of the field study are compared with a glasshouse, herbicide bio-assay with some 20 of the species present in the field experiments. Implications of the results for the diversity in boundary vegetation are discussed.

In Chapter 9 the ecological background of the success of the most common boundary weed in the study area, the clonal species *Elymus repens* is examined. Especially, the effects of open gaps in the vegetation in combination with productivity of the habitat upon clone growth is studied.

Chapter 10 does not deal with the field boundary but with the crop edge. The outer meters of the arable field is a potential refuge for a large number of rare arable weed species. Conservation efforts have focused on these crop edges by determining the effects of cessation of pesticides. In Chapter 10 the effect of fertilization via light penetration on plant growth of both rare and common arable weeds is examined experimentally.

Finally, the general discussion in Chapter 11 focuses on the most important findings of this thesis and aims at integrating the results of the different experimental studies. Furthermore, the relative importance of the various examined factors are discussed and the most important factors determining plant species richness and the abundance of weeds in herbaceous field boundaries on sandy soils are identified. The perspectives for the restoration of diverse boundary vegetation are discussed. Information gaps in current field boundary ecology and directions for future research are given.

2

Factors affecting the species composition
of arable field boundary vegetation

Summary

In recent decades the botanical diversity of arable field boundaries has declined drastically. To determine the most important factors responsible for this decline, the vegetation composition of 105, one metre wide, herbaceous arable field boundaries in the Central and Eastern Netherlands was surveyed. Biomass samples of the boundary were taken at 0-0.33, 0.34-0.66 and 0.67-1.00 m from the adjacent arable field. Furthermore, farmers were interviewed with respect to boundary management and land use on the adjacent arable field. The two datasets were analysed both phytosociologically and by means of multiple linear regression analysis.

The boundary vegetation could be classified into five closely related and species poor frame communities characterized predominantly by species indicative of the *Molinio-Arrhenatheretea*, *Koelerio-Corynephoretea* and *Artemisietea vulgaris*. Due to the large similarity in species composition, the five frame communities were poor indicators of boundary management or land use characteristics.

Multiple linear regression analysis revealed that predominantly nitrogen input and the type of crop rotation on the adjacent arable field affected the composition and biomass production of the field boundary vegetation. Phosphorus inputs and type of boundary management had less effects on the boundary vegetation. Absence of any correlation of boundary management with the species composition probably resulted from the unvarying type of boundary management: most boundaries were cut with cuttings not being removed. The boundary vegetation was furthermore characterized by a peak in biomass production in the zone near the arable field. In this zone the species *Elymus repens* and annual dicot species were significantly more abundant while perennial dicots and monocots were significantly less abundant compared to the zones further from the arable field.

Key words: arable landscape, herbaceous field boundary, land use, vegetation composition, species richness.

Introduction

In recent years there has been an increased attention for the functional ecology of arable field boundaries (e.g. Bennet *et al.* 1994, Boatman 1994, Halley *et al.* 1996, van Emden 1990,

Wiens 1992). Field boundary vegetation may benefit crop growth by serving as windbreaks (Forman & Baudry 1984), by reducing soil erosion (Tim & Jolly 1994) and they may enhance the abundance of the natural enemies of crop pests (Coombes & Sotherton 1986, Sotherton 1984). However their most pronounced impact lies in sustaining farmland wildlife. In the modern agricultural landscape, arable fields are virtual wildlife deserts and most animal and non-crop plant species depend on field boundaries for food, shelter, overwintering sites or simply a place to grow (e.g. Bunce *et al*. 1994, Kaule & Krebs 1989, Potts 1986, Tew *et al*. 1994).

Maintaining a high level of botanical diversity in these structures is essential to many farmland animals. For instance, the abundance and diversity of arthropods, with butterflies being studied most elaborately, is higher in and along botanically rich field boundaries (Feber *et al*. 1996, Lagerlöf & Wallin 1993, Sparks & Parish 1995). Small mammals were found more frequently in boundaries with a high abundance of berry producing species (Poulton 1994). A high diversity of plant species may even benefit crop production since parasitism of crop pests may be enhanced by the presence of nectar-producing plants outside the crop, which provide food for the nectar feeding adults of many parasitoid species (Hickman & Wratten 1996, Powell 1986).

Although regionally the total area occupied by field boundaries may be substantial, these landscape structures generally have a limited width. As a result of the high edge-area ratio, field boundaries may show an increased susceptibility to disturbances. Disturbances may be caused by activities on the adjoining arable fields such as close ploughing, misplacement of fertilizer or drift of herbicides which may seriously suppress species richness in this habitat (Freemark & Boutin 1995, Kleijn & Snoeijing in press, Marshall 1987). Furthermore, field boundaries are usually maintained by the farmers and one of their primary maintenance objectives is weed control. As a result, herbicide use in the hedge bottom or ditch bank is rather common (Boatman 1992, de Snoo & Wegener Sleeswijk 1993, Marshall & Smith 1987) with serious consequences for the floristic diversity of boundaries. Other management activities such as trimming hedges, or different mowing regimes may affect the vegetation composition as well.

This study presents the results of a botanical survey in 105 arable field boundaries. Furthermore, the farmers cultivating the fields bordering these boundaries were interviewed with respect to their agricultural activities and boundary management. The two datasets were linked and analysed to answer the following questions (1) what is the vegetation composition in herbaceous field boundaries on sandy soils? (2) what type of boundary management is performed and what are the cultivation characteristics of the fields bordering the boundaries? and (3) what are the relationships between the boundary management, the land-use on the adjacent arable field and the composition of the boundary vegetation?

Methods

In June and July 1995, 105 field boundaries were surveyed on the sandy soils of the Central and Eastern Netherlands. To facilitate comparisons between sites, only those were selected that had a relatively homogeneous, grass dominated boundary vegetation which was not shaded by trees or shrubs. Boundary vegetation composition may change with decreasing distance from the arable field (Kleijn *et al*. 1997). Therefore relevés were made, following the

ordinal scale of van der Maarel (1979), in 4 m long quadrats at 0-0.33, 0.34-0.66 and 0.67-1.0 m from the field.

Furthermore, in the boundaries biomass samples were taken by cutting all above-ground vegetation from 0.5 x 0.33 m quadrats in each of the three relevés. The samples were separated into four functional groups: (1) Annual dicotyledoneous species (dicots), which are mostly arable weeds. (2) *Elymus repens* (nomenclature following van der Meijden 1990) which is the most important perennial, boundary associated, weed species. These two groups are of interest from a weed control point of view. (3) Perennial dicots which are important for the aesthetic appearance of the boundary and for insect abundance and diversity since they flower abundantly (Frei & Manhart 1992, Weiss & Stettmer 1991). (4) Monocots other than *Elymus repens*. Annual and perennial monocots were combined because of the very small contribution of the annual monocots (nine species with very low abundance). Dry weight of the biomass samples was determined after drying for 48 hours at 80°C.

From winter 1995 to summer 1996 the owners/tenants (hereafter: farmers) of the arable fields adjacent to the surveyed field boundaries were tracked down and interviewed verbally. The questions addressed (1) the preferred boundary type, (2) the approximate age of the boundary, (3) the type of boundary management, (4) the use of herbicides in the boundary, (5) the crop rotation on the adjacent field, (6) the mineral and organic fertilizer inputs per crop (7) the type of fertilizer spreader, (8) the preventative measures taken to reduce fertilizer misplacement, (9) the herbicide inputs per crop and (10) the most problematic arable weeds in the crop. The average nitrogen (N) and phosphorus (P) content per type of organic fertilizer was derived from Anonymous (1993). Subsequently, for each site the N and P inputs per crop were calculated by adding the inputs from the mineral fertilizer and the organic fertilizer and the field average was determined by taking the five-year mean of the crop rotation.

Analysis

Botanical data were collected from all 105 boundaries and analyses using only species data were performed on the complete dataset. The boundaries of nine sites were mown after taking relevés but before biomass samples had been taken, therefore, analyses involving only the productivity (and species richness) of the vegetation were performed on 96 boundaries. Furthermore, since the users of 30 of the 105 adjoining fields could not be found or declined to co-operate, a complete set of vegetation data and environmental variables was obtained for 69 sites (for 3 sites no biomass ánd no interview data were obtained). Relationships between vegetation composition and environmental variables were therefore analysed for these 69 boundaries only.

The data were analysed using two approaches: a phytosociological and a multiple linear regression approach. A phytosociological approach is essential to identify qualitative differences between the vegetation composition of sites. Two relevés may be equally species rich but not have a single species in common. The phytosociological approach is able to distinguish between these relevés while an approach based on regression analysis is not. On the other hand, field boundary vegetation may be characterized by gradients in biomass production and species composition (Kleijn *et al.* 1997), while an optimal phytosociological classification requires homogeneity in the relevés. Multiple linear regression analysis provides a clearer picture of quantitative trends and readily reveals above-mentioned respect gradients. Therefore, in this study both approaches were used and may be compared with

respect to their usefulness in field boundary ecology.

For phytosociological purposes the three relevés in each site were analysed as one 4 x 1 m relevé, to avoid pseudo-replication. Therefore the scores of each species were averaged over the three relevés. Subsequently, the rough table of 105 relevés was structured by means of TWINSPAN (Hill 1979) and the syntaxonomical status of the species was determined using the classification of Schaminée *et al.* (1996) and Westhoff & Den Held (1975). Correlation between the relevés and the set of environmental variables was determined by Canonical Correspondence Analysis (Jongman *et al.* 1987) and depicted in an ordination diagram. Environmental variables used in the analysis were N-inputs, P-inputs, type of boundary management and type of crop rotation.

The average biomass variables (mean of three positions) and total species number per boundary site were used to determine correlations between the above-mentioned environmental and the vegetation variables. For this purpose, multiple regression analysis was used (GENSTAT 1993) involving a stepwise procedure in which, starting with the full regression model including all environmental variables, those variables were removed that did not significantly contribute to the fit of the model (Sokal & Rohlf 1995).

The effect of position in the boundary (distance from the field) on species numbers was analysed on all 105 sites while its effect on biomass production of different functional groups was analysed for the 96 sites of which biomass data were obtained. In case of significant effects of the qualitative variables management, position and rotation, differences between different levels of those variables were tested using t-tests.

Prior to all regression analyses, residuals were plotted vs. fitted values to test for constancy of variance of the errors. If variance increased with increasing values of species numbers or biomass production, ln-transformed data were used in the analyses.

Results

Field boundary and crop cultivation characteristics

The surveyed field boundaries were managed in three, qualitatively different ways. Cutting and removing the boundary vegetation was rather uncommon in the study area: less than 10% of the farmers removed the cuttings after mowing. Cutting the boundary vegetation without removing the mown vegetation was by far the most popular management type while one third of the boundaries was not managed at all (Table 2.1). Approximately half of the field boundaries was not managed by the farmers but by municipalities or other governmental institutions due to the fact that many of the surveyed boundaries bordered public roads or major watercourses. Herbicide use in the field boundary itself was not very common (Table 2.1).

Land use on the arable field could be categorized into four groups of which the (more or less) continuous growing of silage maize and the rotation of cereals, potato, silage maize and sugar beet (not necessarily in that order) were the most common ones (Table 2.1). The 'other' category includes continuous, low input cereal production as well as a fallow-crop rotation in which fallow dominated. Since most maize fields were fertilized organically only, 30 farmers did not have fertilizer spreaders. Single and twin disc spreaders and oscillating spout spreaders were common, while the fairly high numbers of the very accurate (and expensive)

Table 2.1 Characteristics of 74 field boundaries and their adjoining arable fields, based upon a questionnaire survey carried out in 1995-1996. Not all farmers responded to all questions, which account for different numbers at different characteristics. Numbers in bold refer to the levels these variables were given in the Canonical Correspondence Analysis and Multiple Regression Analysis.

Type of boundary management (n=75)	**1.** cutting + removing	**2.** cutting - removing	**3.** no management	
	5	45	25	
Management performed by (n=75)	farmer	municipality	governmental services[1]	
	37	30	8	
Herbicide use in boundary? (n=70)	no yes			
	61 9			
Crop rotation of the arable field (n=75)	**1.** mostly/ only maize	**2.** alternating maize/grass	**3.** potato, cereals, sugar beet, maize	**4.** other
	39	11	20	5

Type of fertilizer spreader (n= 75)	no spreader	single disc	twin disc	oscillating spout	pneumatic
	30	13	7	18	7
Preventative measures taken (n=45)	none[2]	reduced speed	headland deflector	border disc	tilting spreader	other
	23	4	6	6	3	3

Fertilizer inputs on field (organic + mineral, n=75)	minimum	mean	maximum	
Nitrogen (kg.ha^{-1}.y^{-1})	36	222	397	
Phosphate (kg.ha^{-1}.y^{-1})	13	94	178	
Frequency of herbicide application on field (n=75)[3]	0x	1x	2x	3x
	8	64	2	1

Ten worst crop weeds indicated by farmers (n=75)	1. *Chenopodium album* (35) 6. *Cirsium arvense* (8)
	2. *Echinochloa crus-galli* (31) 7. *Capsella bursa-pastoris* (7)
	3. *Elymus repens* (25) 8. *Polygonum convolvulus* (6)
	4. *Solanum nigrum* (24) *Polygonum persicaria* (6)
	5. *Stellaria media* (10) *Viola arvensis* (6)

[1] Rijkswaterstaat and Waterschappen. [2] including the 7 pneumatic spreaders. [3] herbicide frequency data are based upon the crops of 1995 only.

pneumatic fertilizer spreaders may be caused by the inclusion of three fields of agricultural research stations near Wageningen. Half of the farmers that possessed fertilizer spreaders did not take any preventative measures to reduce fertilizer misplacement outside the field, the other half took a variety of measures (Table 2.1) including fertilizing the edge by hand. Average nitrogen and phosphorus inputs were respectively 222 and 94 kg.ha^{-1}.y^{-1}. Herbicides were applied predominantly once a year; the only farmer that applied herbicides three times a year did so as part of a low-dosage weed control strategy in sugar beets. Finally, farmers considered four weed species to be by far the most troublesome: *Chenopodium album*, *Echinochloa crus-galli*, *Elymus repens* and *Solanum nigrum* respectively.

Plant communities

Most of the plant species encountered in the 105 surveyed field boundaries were grassland species, annual and perennial ruderals and species adapted to treading. Well developed and syntaxonomically distinct plant communities could not be recognized in these boundaries, however, the following frame communities were identified (Appendix 2.1).

   1. (HmE) Frame community dominated by *Holcus mollis* and *Elymus repens*. Despite the fact that hardly any species of the *Melampyro-Holcetea mollis* were found, we consider this community to be a transition between *Melampyro-Holcetea mollis* and *Molinio-Arrhenatheretea* because of the dominance of *Holcus mollis*, a character-species of the *Melampyro-Holcetea mollis*. The *Melampyro-Holcetea mollis* comprises communities which can often be found as a narrow band between forest or shrubs on one hand and lower vegetation or bare soil on the other.

   2. (FA) Frame community dominated by *Festuca rubra* ssp *commutata* and *Agrostis capillaris*. This frame community is transitional to the *Molinio-Arrhenatheretea* and the *Koelerio-Corynephoretea*. Communities of the *Koelerio-Corynephoretea* are characeristic of dry sandy and relatively nutrient poor soils. This is confirmed by the mean productivity of this type of boundaries (408 g.m^{-2}, considerably lower than the mean productivity of the other four plant communities). Another typical feature is the low abundance of *Elymus repens* in this community.

   3. (LE) Frame community dominated by *Lolium perenne* and *Elymus repens*. Most probably boundaries which were recently sown with a commercial grassland mixture. This community is relatively poor in *Artemisietea vulgaris* species but rich in *Plantaginetea majoris* species.

   4. (HlE) Frame community with *Holcus lanatus* and *Elymus repens* dominating. This community is distinguished only by the particularly high presence and cover of *Holcus lanatus*.

   5. (ED) Frame community with *Elymus repens* and *Dactylis glomerata* as the major dominants. *Elymus repens*, although very common in the other four communities, reaches its optimum in this community with a characteristic cover of 6.8 (Appendix 2.1). High numbers of species from *Artemisietea vulgaris* and *Chenopodietea* indicate a high productivity in combination with high levels of disturbance.

   Species richness of the different frame communities did not differ substantially and fluctuated between 10.2 and 11.8 (Appendix 2.1).

Effects of land use and management on the boundary vegetation

The different frame communities are only moderately indicative of differences in the environmental conditions. The species composition of relevés grouped in different frame communities largely or entirely overlaps as shown in Fig. 2.1. Around the origin of the axes relevés from all five frame communities can be found. We may learn, however, that FA communities show a bias towards boundaries next to arable fields with low nitrogen and phosphorus inputs (relevés in Fig. 2.1 predominantly depicted in quadrants opposite of the N- and P-arrows), with crop rotations that did not include regular maize cultivation and for boundaries which were not cut (relevés in the same quadrants as the management and rotation arrows). In contrast, the HlE and ED communities show a bias towards fields with high
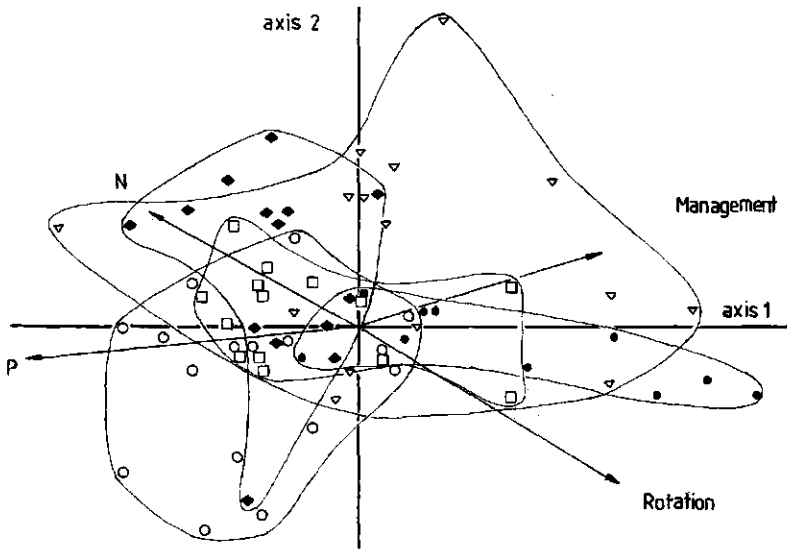
Figure 2.1 *Canonical Correspondence Analysis ordination diagram of the 69 field boundary relevés for which a questionaire was obtained. Environmental variables are represented by arrows. Relevés belonging to the same frame community have been circled. HmE frame community: triangles, FA: filled cicles, LE: squares, HlE: diamonts and ED: open circles. Rotation: 1, continuous maize; 2, maize/grass; 3, potato, cereals, sugar beets, maize; 4, other. Management: 1, cutting + removing; 2, cutting - removing; 3, no cutting. Correlations of axis 1 with P: -0.63, Rotation: 0.48, Management: 0.46, N: -0.39. Correlations of axis 2 with: Rotation: -0.53, N: 0.34, Management: 0.22, P: -0.09.*

fertilizer inputs, with continuous or regular cultivation of silage maize and with the type of boundary management that does include cutting the vegetation. The HmE and LE communities do not show any correlation with the environmental variables.

The results of the multiple regression analysis indicate that all factors were significantly related to (some of) the vegetation variables (Table 2.2). The amount of nitrogen had a pronounced effect on all biomass production variables except on that of the annual dicots.

Table 2.2 *Results of the multiple regression analysis. The factors nitrogen and phosphorus inputs were quantitative variables, management and rotation were qualitative variables. Management: 1 cutting + removing, 2 cutting - removing, 3 no cutting; Rotation: 1 continuous silage maize, 2 maize/grass, 3 potatos-cereals-sugar beets- maize and 4 other.*

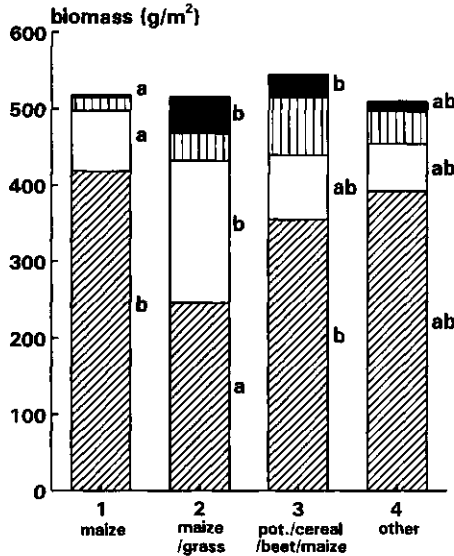|	no. species	biomass $(g.m^{-2})$	monocots (%)	perennial dicots (%)	annual dicots (%)	*Elymus repens* (%)
Nitrogen inputs	ns	***	*	***	ns	*
Phosphorus inputs	ns	ns	*	ns	ns	**
management	ns	**	ns	ns	ns	ns
rotation	***	ns	***	ns	**	**

* $P<0.05$, ** $P<0.01$, *** $P<0.001$

Figure 2.2 Mean biomass production (g dry weight.m^{-2}) and partitioning among different functional groups in the first metre of the field boundary vegetation next to arable fields with different crop rotations. Diagonally hatched bars: monocots, vertically hatched bars: perennial dicots, filled bars: annual dicots, transparent bars: Elymus repens. Different characters indicate significantly differences between rotations only.

Remarkably, boundary vegetation productivity was negatively affected by nitrogen inputs on the bordering arable field. The proportion of both the perennial dicots and *Elymus repens* in the boundary vegetation were negatively related to N-inputs on the field, while the proportion of monocots was positively related. Significant relationships between phosphorus inputs and the boundary vegetation were limited to the monocot fraction of the vegetation (Table 2.2): the contribution of the monocots to the boundary vegetation significantly increased with increasing phosphorus inputs on the field. On the other hand, the contribution of *E. repens* significantly decreased with increasing phosphorus inputs. Species richness was not significantly related to either nitrogen or phosphorus inputs. Furthermore, no significant relationship was found between total vegetation biomass productivity and species richness.

The type of management affected boundary productivity only. Counter-intuitively, boundaries from which the cuttings were being removed had a significantly higher mean biomass production (735 g.m^{-2}) compared to boundaries that were not cut at all: 476 g.m^{-2} (t_{63} = 2.07, $P<0.05$). Boundaries that were cut but from which cuttings were not removed had an intermediate mean productivity of 532 g.m^{-2}.

Crop rotation had a pronounced effect on species numbers in the boundary vegetation. Boundaries next to fields with rotation 1, continuous maize production, were significantly species poorer (6.5 species per 4 m^2) than those next to rotation 3 fields, the potato-cereal-sugar beet-maize rotation (9.2, t_{69} =-3.42, $P=0.001$) or rotation 4 fields, the 'other' category (10.3; t_{69}=-2.82, $P<0.01$). Boundaries next to fields with rotation 2, alternatively maize and
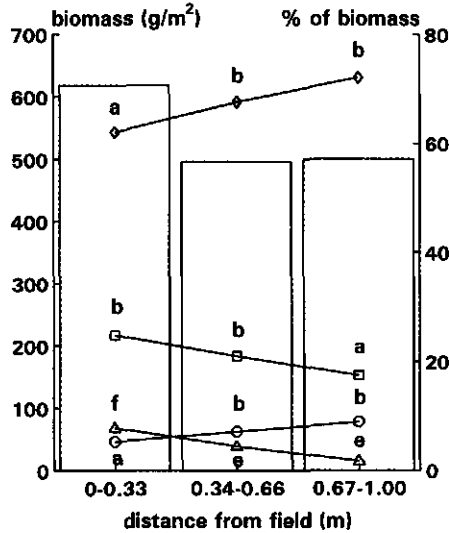
Figure 2.3 Biomass production (g dry weight.m^{-2}) of the boundary vegetation at increasing distance from the arable field and the relative contribution (% of biomass production) of monocots (diamonds), perennial dicots (circles), annual dicots (triangles) and Elymus repens (squares). Different characters indicate significant differences between positions only. For clarity, characters indicating significant differences in biomass production have been omitted, however, 0-0.33 m differs significantly (P<0.01) from 0.34-0.66 and 0.67-1.00 m.

grass, had intermediate numbers of species (7.9 species per 4 m^2). Field boundary productivity was not significantly different between fields with different crop rotations but the partitioning among the functional groups was significantly affected by it (Fig. 2.2). Field boundary vegetation next to rotation 2 fields was made up of significantly less monocots, while it contained significantly more *E. repens*. The percentage of perennial dicot biomass in the boundary vegetation did not differ significantly between fields with different crop rotations, but the percentage annual dicots was significantly higher in boundaries next to fields with crop rotation 2 and 3 compared to 1 (Fig. 2.2).

The vegetation composition at different positions in the field boundary showed some characteristic and statistically significant differences, although the species richness of the 105 arable field boundaries did not change significantly with increasing distance from the arable field. However, the number of perennial species was significantly lower in the first 0.33 m (5.5 species per 1.33 m^2) compared to the positions further from the arable field (6.1, t_{192}=-2.81: *P*<0.01 at 0.34-0.66 m and 6.0, t_{192}=-2.30: *P*<0.05 at 0.67-1.00 m). Annual species showed the opposite pattern, 2.4 species per 1.33 m^2 in the first 0.33 m of the boundary versus 1.8 (t_{192} = 3.31, *P*<0.001) and 1.6 (t_{192} = 4.37, *P*<0.001) at 0.34-0.66 and 0.67-1.00 m respectively. Biomass production in the first 0.33 m was significantly higher than in the sample quadrats further from the arable field (Fig. 2.3).The two functional groups containing arable weeds, the annual dicots and *Elymus repens*, occupied significantly decreasing

proportions of the boundary vegetation biomass with increasing distance from the field. In contrast, monocots other than *E. repens* and perennial dicots increased their relative proportions in the boundary vegetation (Fig. 2.3).

Discussion

Farmers mention a variety of preferred field boundary types, varying from bare soil to 'as colourful as possible', however, the 85% of the responding farmers mentioning weeds in relation to the preferred boundary vegetation point out that they consider weed control to be a very important aspect. Of the species that are considered most troublesome with respect to crop production, only *Elymus repens* is found abundantly in field boundaries. In this respect it is interesting that only 13% of the farmers had used herbicides in their boundaries. Studies in other areas revealed that more than half of the farmers applied herbicides to the boundary vegetation (Boatman 1992, de Snoo & Wegener Sleeswijk 1993, Marshall & Smith 1987). The choice to select only those boundaries that were at least 1 metre wide resulted in a high proportion of boundaries that were not managed by farmers. This suggests that in the arable landscape, wide, grass-dominated boundaries are sparse except where such boundaries are owned by institutions other than farmers.

Since interest in field boundary diversity is of rather recent date, it is not possible to examine changes in time in vegetation composition. In fact, as far as known to the authors, this study is the first to examine field boundary vegetation syntaxonomically, although other linear landscape structures, such as road verges or embankments have been investigated extensively in the Netherlands (Sprangers 1996, Sykora *et al.* 1990, 1993, van der Zee 1992). In contrast to these studies, we could only identify frame communities. Schaminée *et al.* (1995) mention three causes for the existence of associations such as frame communities, which are not fully developed into syntaxonomically distinct entities. First, the communities may be in their primary stages, second, the habitat may be too small or, third, men may have affected the environment adversely, either directly or indirectly. The second and especially the third cause apply to arable field boundaries. Frame communities are in general less indicative of the environmental conditions and the potential species richness of the habitat (Schaminée *et al.* 1995). The gradient in species composition of the selected field boundaries may furthermore have resulted in a less accurate classification. However, the boundaries could not clearly be divided into distinct strips of homogeneous vegetation. Thus we have to conclude that this amount of heterogeneity is inherent to contemporary field boundary vegetation. Accordingly, we may merely conclude that, of the five frame communities (Appendix 2.1), the FA frame community occurs along the least intensively used arable fields while the HIE and especially the ED communities may be found in the most heavily disturbed boundaries along the most intensively used arable fields.

Multiple regression analysis revealed that the activities of farmers on their fields may result in botanical change in the vegetation next to those fields in a number of ways. Increasing nitrogen application levels to the crop was related to reduced productivity of the boundary vegetation. This may be caused by indirect effects such as increased shading of the boundary by the better fertilized crops or by an increased competitiveness of those crops for other limiting resources such as water (the summer of 1995 was rather dry). On the other hand, the relative proportion of the different functional groups responded in a more often

observed fashion (Berendse 1983, Kleijn & Snoeijing in press): monocots increased and perennial dicots decreased significantly with increasing nutrient levels. The effect of phosphate was less pronounced than that of nitrogen, and for the functional groups that were affected significantly, the effects were opposite. The proportion of monocots in the vegetation decreased and that of *Elymus repens* increased significantly with increasing phosphorus levels. A possible explanation may be the phosphorus saturation of many arable fields (but not their boundaries) in the sandy regions of the Netherlands (Breeuwsma *et al.* 1989, Oenema & van Dijk 1994). The boundary vegetation may thus be phosphate limited whereas the crop no longer is.

Crop rotation had a very pronounced effect on the boundary vegetation. Along fields with continuous maize growth, field boundaries were least species rich and almost completely dominated by grasses. The potato-cereals-beets-maize rotation and the 'other' rotations had least adverse effects on species richness. Alternating maize production with grass production resulted in a substantial increase in *Elymus repens* in the boundary. This may be caused by the fact that this is probably the only species that can dominate in both grasslands and arable fields and, in contrast to clonal dicots such as *Cirsium arvense*, is difficult to control in both production systems.

Vegetation composition near the arable field and further from the field differed considerably. Generally, the first 0.33 m of boundary next to the arable field was more productive, had a higher percentage of weedy species and a lower percentage of monocots and perennial dicots. The increased productivity near the field was probably related to the capture of arable nutrient resources by boundary plants (Kleijn 1996). The abundance of arable weeds may be caused by the higher level of disturbances this zone experiences. In an experimental study, the exact position of the field-boundary transition fluctuated from year to year by 0.23 m ($\pm$ 0.16) due to inaccuracies of cultivation activities (Kleijn unpublished results). This high frequency of disturbances, in combination with the high fertility of the habitat, enhances growth of annuals and perennial ruderal species such as *Elymus repens* (Tilman 1987, Wilson & Tilman 1991).

The relationship between management and boundary biomass production illustrates the limitations of the current descriptive approach. Generally, productivity declines as cuttings are being removed annually (Berendse *et al.* 1992) while in this study highest productivity levels were found in boundaries from which cuttings were removed. Therefore, the productivity of the boundary probably determines the type of management a farmer chooses and it is not the management that determines the productivity of the boundary. If productivity is very low, a farmer may decide to do nothing since this saves time and money. To determine the causal relationship between type of management and the botanical boundary composition, an experimental approach is more suitable.

In conclusion, arable field boundaries on sandy soils in the Netherlands are species poor and uniform. The phytosociological analysis demonstrated that the species composition of all studied field boundaries is generally indicative of nutrient rich and disturbed conditions. As a result, environmental conditions like rotation or management are unlikely to correlate with the species composition since most plant communities are similar or too poorly developed to be identified at syntaxonomically meaningful levels. To reveal any relationships in these qualitatively uniform communities, analysis of quantitative data, for instance of functional groups or single species, may be a more appropriate approach.

Acknowledgements

Appendix 2.1 *Synoptic table in which species are grouped according to syntaxonomical status. Species not syntaxonomically differentiating between the grassland communities KOELERIO-CORYNEPHORETEA and MOLINIO-ARRHENATHERETEA but differentiating towards other plant communities have been gouped as KOELERIO-CORYNEPHORETEA + MOLINIO-ARRHENATHERETEA. Numbers in bold indicate species differentiating between frame communities. For each species the presence classes are given: 1 = species found in 0-20% of the relevés in each column; 2 = 21-40%; 3 = 41-60%, 4 = 61-80%, 5 = 81-100%. In brackets the characteristic cover is given, which is calculated as the average cover in those relevés where a species occurs.*

HmE: Holcus mollis-Elymus repens-[Melampyro-Holcetea mollis/Molinio-Arrhenatheretea]

FA: Festuca rubra ssp commutata-Agrostis capillaris-[Molinio-Arrhenatheretea/Koelerio-Corynephoretea]

LE: Lolium perenne- Elymus repens-[Molinio-Arrhenatheretea]

HlE: Holcus lanatus-Elymus repens-[Molinio-Arrhenatheretea]

ED: Elymus repens-Dactylis glomerata-[Molinio-Arrhenatheretea]

Plant community	HmE	FA	LE	HIE	ED
no relevés	19	16	24	21	25
mean no species	10.2	11.8	11.5	10.8	11.2
mean biomass production (g.m^2)	539	408	563	553	589

KOELERIO-CORYNEPHORETEA

Cerastium arvense	1 (0.2)				
Jasione montana		1 (0.1)			
Ornithopus perpusillus		1 (0.3)	1 (0.2)		
Rumex acetosella	2 (0.3)	**4 (1.9)**	1 (0.3)	1 (0.3)	1 (0.2)
Bromus hordeaceus	1 (0.1)	3 (1.6)	2 (0.7)	1 (0.4)	1 (0.2)
Hypericum perforatum	1 (0.2)	1 (0.1)	1 (0.1)	1 (<.1)	1 (<.1)
Veronica arvensis	1 (0.2)	1 (0.2)	1 (<.1)	1 (<.1)	1 (0.1)
Hypochaeris radicata		2 (0.8)	1 (0.1)	1 (0.1)	1 (0.1)

KOELERIO-CORYNEPHORETEA +
MOLINIO-ARRHENATHERETEA

Agrostis capillaris	4 (2.9)	5 (5.9)	4 (4.2)	4 (3.0)	3 (1.3)
Festuca rubra ssp *commutata*	1 (0.1)	**5 (4.6)**	2 (0.8)	2 (1.2)	2 (0.9)
Poa pratensis	2 (0.5)	2 (0.6)	**4 (2.2)**	2 (0.7)	3 (1.0)
Plantago lanceolata	2 (0.3)	1 (0.3)	2 (0.7)	1 (0.1)	1 (0.1)
Achillea millefolium	1 (0.3)	3 (1.3)	3 (1.3)	2 (0.5)	2 (0.3)
Crepis capillaris	1 (0.1)	1 (0.1)	1 (0.2)	1 (0.3)	1 (0.2)
Vicia sativa-nigra	2 (0.6)	1 (0.3)	1 (0.1)	1 (0.1)	1 (0.2)

MOLINIO-ARRHENATHERETEA

Trifolium pratense	1 (0.1)			1 (<.1)	
Cerastium fontanum ssp *vulgare*	1 (0.3)	**3 (1.1)**	1 (<.1)	1 (0.1)	1 (<.1)
Taraxacum officinale	1 (0.1)	1 (0.3)	**4 (0.8)**	2 (0.3)	2 (0.3)
Holcus lanatus	2 (0.9)	2 (0.9)	2 (0.6)	**5 (6.2)**	3 (1.1)
Stellaria graminea	1 (0.1)		1 (<.1)	1 (0.2)	1 (0.3)
Rumex acetosa	1 (0.1)		1 (0.1)	2 (0.4)	1 (0.2)
Ranunculus acris			1 (<.1)	1 (0.1)	1 (<.1)

ARRHENATHERETALIA

Heracleum sphondylium	1 (0.1)			1 (<.1)	
Phleum pratense	1 (0.2)	1 (0.1)	2 (0.7)		
Dactylis glomerata	3 (0.8)	2 (0.3)	4 (2.7)	2 (1.0)	4 (3.3)
Arrhenatherum elatius	2 (0.9)	1 (0.6)	1 (<.1)	2 (1.1)	2 (1.1)
Anthriscus sylvestris					1 (0.2)
Leucanthemum vulgare					1 (0.1)

MELAMPYRO-HOLCETEA MOLLIS

Holcus mollis	**5 (7.1)**	4 (1.8)	1 (0.3)	1 (0.3)	2 (0.8)

Plant community	HmE	FA	LE	HIE	ED
PLANTAGINETEA MAJORIS					
Festuca arundinacea	1 (0.1)				
Leontodon autumnalis		1 (0.1)			
Polygonum aviculare	1 (0.1)		1 (0.3)	1 (0.1)	2 (0.3)
Ranunculus repens	1 (0.2)		1 (0.2)	2 (0.5)	1 (0.2)
Lolium perenne	2 (0.4)	1 (0.1)	**5 (5.4)**	2 (0.5)	2 (0.4)
Elymus repens	5 (3.5)	3 (1.4)	5 (4.5)	5 (4.7)	**5 (6.8)**
Matricaria discoidea		1 (0.1)	1 (0.1)		1 (0.1)
Plantago major			1 (0.3)	1 (<.1)	1 (0.1)
Poa annua			1 (0.1)	1 (<.1)	
ARTEMISIETEAVULGARIS					
Calystegia sepium	1 (0.2)				
Carduus crispus	1 (0.1)	1 (0.1)			
Lapsana communis	1 (0.1)	1 (0.1)			1 (0.1)
Aegopodium podagraria	1 (0.2)	1 (0.2)		1 (0.1)	1 (0.3)
Urtica dioica	1 (0.2)		1 (<.1)	1 (0.6)	2 (0.6)
Galium aparine	1 (0.2)		1 (<.1)	1 (0.5)	1 (0.3)
Bromus sterilis	1 (0.1)		1 (<.1)	1 (0.3)	1 (0.4)
Tanacetum vulgare	2 (0.4)			1 (0.3)	1 (0.4)
Silene dioica	1 (0.1)		1 (<.1)	1 (<.1)	
Artemisia vulgaris	1 (0.2)	1 (0.1)	1 (0.1)	1 (0.2)	1 (0.3)
Rumex obtusifolius ssp *obtusifolius*	1 (0.2)	1 (0.1)	1 (0.2)	1 (0.2)	1 (0.2)
Cirsium arvense	1 (0.1)	1 (0.4)	1 (0.2)	1 (0.5)	1 (0.2)
Cirsium vulgare		1 (0.1)			1 (<.1)
Lamium album			1 (<.1)		1 (<.1)
Silene latifolia ssp *alba*				1 (0.1)	
Glechoma hederacea				1 (0.3)	1 (0.2)
CHENOPODIETEA					
Sonchus oleraceus	1 (0.1)				
Senecio vulgaris	1 (0.1)				1 (<.1)
Chenopodium album	1 (0.2)		2 (0.3)	1 (0.1)	2 (0.5)
Stellaria media	1 (0.2)		2 (0.5)	1 (0.1)	1 (0.1)
POLYGONO-CHENOPODIETALIA					
Oxalis fontana	1 (0.1)				
Sonchus asper	1 (0.1)				
Sonchus arvensis	1 (0.1)	1 (0.1)		1 (0.1)	1 (0.4)
Erodium cicutarium ssp *cicutarium*	1 (0.2)	1 (0.1)	1 (<.1)	1 (<.1)	1 (<.1)
Geranium dissectum		1 (0.2)	1 (0.2)	1 (<.1)	2 (0.3)
Spergula arvensis		1 (0.2)	1 (0.1)	1 (<.1)	
Polygonum persicaria			1 (0.1)	2 (0.3)	1 (0.2)
Lamium purpureum			1 (<.1)		1 (0.1)
Echinochloa crus-galli			1 (0.1)		1 (0.2)
Setaria viridis					1 (0.1)
SISYMBRIETALIA					
Convolvulus arvensis	1 (0.1)				1 (<.1)
Capsella bursa-pastoris	1 (0.1)	1 (0.1)	1 (0.1)		1 (<.1)
Matricaria maritima	1 (0.2)	1 (0.2)	1 (0.1)	1 (<.1)	1 (0.1)
Sisymbrium officinale		1 (0.1)	1 (0.1)		1 (0.2)
Erigeron canadensis		1 (0.2)		1 (<.1)	1 (0.1)
Linaria vulgaris		1 (0.1)		1 (0.2)	
Lactuca serriola		1 (0.1)			

Plant community	HmE	FA	LE	HIE	ED
SECALIETEA					
Scleranthus annuus	1 (0.1)		1 (<.1)		
Matricaria recutita	1 (0.1)	2 (0.4)	1 (0.1)		1 (0.1)
Myosotis arvensis	1 (0.1)	1 (0.2)		1 (0.1)	1 (0.1)
Viola arvensis	2 (0.4)	2 (0.4)	2 (0.4)	2 (0.2)	2 (0.4)
Polygonum convolvulus	1 (0.1)	1 (0.1)	1 (0.1)	1 (<.1)	1 (0.3)
Apera spica-venti	1 (0.3)	2 (0.5)	1 (0.1)	1 (<.1)	1 (0.2)
Vicia hirsuta	1 (0.1)	1 (0.3)	1 (0.1)	1 (<.1)	1 (<.1)
Papaver dubium		1 (0.1)		1 (<.1)	
Anthoxanthum aristatum		1 (0.1)			
Aphanes inexpectata		1 (0.1)			
REMAINING SPECIES					
Senecio viscosus	1 (0.1)				
Rubus caesius	1 (0.2)				
Symphytum officinale	1 (0.1)				
Anthoxanthum odoratum	1 (0.1)				
Potentilla reptans	1 (0.1)				
Galeopsis tetrahit	1 (0.2)	1 (0.1)		1 (<.1)	
Secale cereale	1 (0.1)	1 (0.1)	1 (0.1)	1 (<.1)	
Phragmites australis	1 (0.1)			1 (0.1)	
Atriplex patula	1 (0.2)			1 (<.1)	
Trifolium repens	1 (0.1)		2 (0.6)	1 (0.1)	
Rubus fruticosus	1 (0.2)			2 (0.6)	1 (<.1)
Equisetum arvense	1 (0.3)			1 (0.2)	1 (0.2)
Bromus carinatus	1 (0.1)				1 (0.2)
Senecio sylvaticus		1 (0.1)		1 (<.1)	1 (0.2)
Poa trivialis		1 (0.6)	1 (0.1)		1 (0.3)
Epilobium hirsutum		1 (0.1)			1 (<.1)
Phalaris arundinacea					1 (0.1)
Stellaria holostea				1 (0.2)	
Quercus robur		1 (0.1)		1 (0.1)	
Avena sativa		1 (0.1)	1 (<.1)		
Pinus sylvestris		1 (0.1)			
Prunus serotina		1 (0.1)			
Leontodon hispidus		1 (0.1)			
Amsinckia menziesii		1 (0.1)			
Calluna vulgaris		1 (0.1)			

The following species were found only once with low abundance: *Carex* spec (ED), *Centaurea cyanus* (ED), *Daucus carota* (LE), *Digitalis purpurea* (ED), *Erysimum spec* (ED), *Galeopsis speciosa* (ED), *Galinsoga parviflora* (HE), *Triticum aestivum* (LE), *Robinia pseudo-acacia* (LE), *Polygonum lapathifolia* ssp *pallidum* (HE), *Galium mollugo* (ED), *Hordeum murinum* (HE), *Lotus corniculatus* ssp *corniculatus* (HE), *Malva* spec. (HE), *Quercus rubra* (ED), *Sinapis arvensis* (ED), *Solanum nigrum* (ED), *Trifolium dubium* (HE), *Vicia cracca* (HE).

Similarities in vegetation development of newly established herbaceous strips along contrasting European field boundaries

Summary

In France, the Netherlands and the United Kingdom, arable field boundaries were extended with four metres of crop edge. Plots with perennial, herbaceous vegetation were established by natural regeneration or by sowing grass, both annually cut. Vegetation development was monitored in the first three years after establishment in the original boundary and in the new boundary strip. Species composition, species-richness and biomass production in the new strip were related to those in the original boundary to examine the potential of predicting vegetation development in extended field boundaries from the vegetation composition of the original boundary. Within three years species-richness, biomass production and monocot/dicot ratio in both the grass and regeneration plots converged to the levels of the original boundary in all three countries. Species composition in the new strip was not closely related to the original boundary, however, since only 20-50% of the species encountered in the original boundary at the onset of the experiment had managed to colonize the new boundary strip in the final year. The low similarity was mainly due to low establishment rates of annual and woodland species in the new strip while mobile, perennial grassland species were generally very successful. Sowing grass, which may be preferable with respect to weed control, had adverse effects on species-richness. These relationships, which were found to apply in a broad geographical area and in different boundary types, may aid efforts to restore botanical diversity in arable field boundaries.

Key words: field margin, vegetation composition, species-richness, agricultural landscape

Introduction

The rise of modern agriculture has been accompanied by a fall in the diversity of the agricultural landscape. Next to the impact on arable species, many of whom are threatened with extinction (Kleijn & van der Voort 1997, Wilson 1990), the impact on arable field boundaries has been severe. Field boundaries have been reduced in size or removed, maintenance has been neglected or abandoned and their diversity (in shape, type, structure,

floristic and faunistic composition) has been reduced severely (Muir & Muir 1987).

As of lately there is an increasing understanding and appreciation of the ecological role of field boundaries in the agricultural landscape. They are important overwintering sites and provide alternative host plants for crop pest antagonists, they provide shelter and nesting sites for game (Aebischer *et al.* 1994, Longley & Sotherton 1997), they may function as corridors between natural habitats or may become the last refuge for non-arable species of plants and animals as natural habitats diminish due to human population growth (Kaule & Krebs 1989). The perception of many farmers that field boundaries are a source of weeds (Boatman 1992, Marshall & Smith 1987) may be correct (Theaker *et al.* 1995) but seems to be associated with management practices such as close ploughing, fertilizer misplacement and herbicide use in the boundary, all activities which promote weed growth over growth of the perennial boundary vegetation (Boatman 1992).

Presently, despite an overall ongoing reduction in field boundary habitats (Chapman & Sheail 1994), efforts are being made to restore field boundaries by planting new hedges, restoring old ones or expanding existing boundaries with a strip of perennial herbaceous vegetation (Kaule & Krebs 1989, Feber *et al.* 1996, Maris 1996).

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. Smith & MacDonald 1989, Marshall & Nowakowski 1992, Dunkley & Boatman 1994, Hart *et al.* 1994). Natural regeneration on fallow arable land is characterized by an initial dominance of annuals and other short-lived species, which are, with time, typically replaced by perennial non-woody species and secondly by shrubs and trees (Hodgson 1989). The mowing regime arrests the succession at the perennial non-woody species stage. Species may establish in a regenerating arable field from the soil seed bank or from nearby seed sources. However, as seeds of grassland species, other than the extremely common species, are scarce in an arable field seedbank (Graham & Hutchings 1988, Hutchings & Booth 1996) the potential species-richness of field boundary strips mainly depends on nearby seed sources (Borstel 1974, Smith and MacDonald 1989, Kleijn *et al.* 1997). The existing field boundary is the closest, often the only, source of perennial species in the modern agricultural landscape, consequently, vegetation development may be predicted from the composition of the pre-existing boundary.

The study presented here was aimed at determining (1) whether we can predict vegetational development on extended field boundaries from the species composition in the original boundary, (2) what are the similarities in vegetation development in contrasting boundary types in different countries and (3) whether the vegetation development is different between naturally regenerating and grass sown boundary strips.

Methods

In spring 1993 field boundary plots were established next to existing field boundaries near Rennes (France), Wageningen (the Netherlands) and Bristol (the United Kingdom). Details of the original field boundaries are listed in Table 3.1. The plots were created by taking the outer four metres of the crop edge out of production and either sowing it to *Lolium perenne* or let it regenerate naturally (nomenclature following van der Meijden 1990). Plots were at least 8 m long. Thus in these plots the pre-existing field boundary was broadened by four metre.

Table 3.1 *Soil type, boundary type, boundary management and the number of replicated blocks of the plot types on each field.*

Field	Soil	Boundary type	Management	Replicated blocks
FR				
1	Clay	tall hedge with bank and pollarded trees	no management	6
NL				
2	Sand	ditch bank	flail mown, cuttings not removed	3
3	Sand	ditch bank	flail mown, cuttings not removed	3
4	Sand	verge unpaved road	flail mown, cuttings not removed	3
UK				
5	Clay	tall hedgerow	flail mown, cuttings not removed	3
6	Clay	tall hedgerow	flail mown, cuttings not removed	3
7	Sandy loam	trimmed hedge	flail mown, cuttings not removed	3

Stretches of regular field boundary served as control plots. Management in the original boundary remained as it was before the onset of the experiment (Table 3.1) while the *L. perenne* sown plots (for short: grass plots) and the plots left regenerating naturally (regeneration plots) were mown once a year in autumn with the cuttings being removed. In each field the three boundary types were replicated 3 or 6 times (Table 3.1)

In March 1993, just prior to the establishment of the boundary plots, soil nutrient status was determined in the original boundary, the boundary plots to be and the centre of the arable field. In each replicated block 40 cores, 2.5 cm in diametre and 25 cm deep, were taken at each of the three positions, bulked and mixed. After drying for 24 hours at 40 °C, available nitrate and ammonium, phosphorus and potassium as well as pH were determined on a subsample in 0.01 M $CaCl_2$ (Houba *et al.* 1986, 1990). Total nitrogen, phosphorus and potassium were determined after digestion following Novozamsky *et al.* (1983).

In the original field boundary, 0.5 x 2 m permanent quadrats (PQ) were established next to each plot type. To relate distance from the original boundary to vegetation development in the new strip, each grass or regeneration plot had two PQ's, one near the original field boundary and one near the arable field (Fig. 3.1).

Relevés in the PQ's were made annually in June/July, and peak standing crop was sampled by cutting above-ground biomass of a 0.5 x 0.5 m quadrat on each side of the PQ (Fig. 3.1).
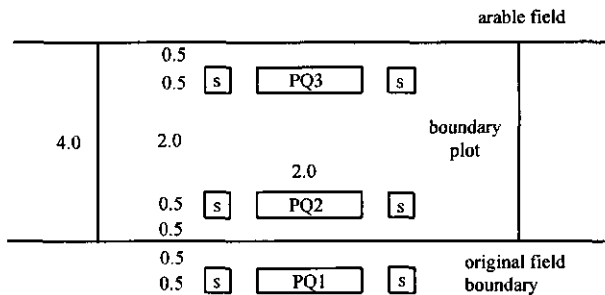

Figure 3.1 *Lay-out of a single boundary plot. Distances in metres. PQ1: Permanent Quadrat at position 1 in the original field boundary. s: biomass sample quadrat.*

The samples were pooled and split into monocotyledoneous species (monocots) and dicotyledoneous species (dicots). Dry weight was determined after 24h at 80°C.

Analysis

To determine the relationship between the vegetation in the original boundary at the onset of the experiment and the vegetation in subsequent years in different PQ's the similarity in species composition with the original field boundary was determined by calculating for each PQ: *(no. species in PQ similar to PQ1(1993)/total no. species in PQ)x100*

Furthermore, species were classified into four functional groups: annual monocots, annual dicots, perennial monocots and perennial dicots. Classification of species is given in Appendix 3.1 and 3.2. Subsequently, for all PQ's in all years, the proportion each functional group contributed to the total number of species was determined.

Data were analysed by means of Analysis Of Variance. Since fields and boundaries in the different countries varied a lot, data from different countries were analysed independently. The PQ's in the original boundary next to the three plot types (grass, regeneration and control) were first analysed to detect changes caused by the presence of the boundary plots. Next, data of the three PQ positions in the grass and regeneration plots were analysed for differences in species similarity, species-richness and biomass production. Percentage data were angular transformed prior to analysis and biomass weights and numbers were ln-transformed if variance was heteroscedastic.

Results

The soil nutrient levels of the original boundary, the boundary plots and the centre of the field did not reveal any obvious trends between the three countries or even within countries (Table 3.2). Only, in the Netherlands, the soil nutrient levels were usually highest in the centre of the field, lowest in the original field boundary and approximately intermediate in the boundary plots. In France, significant differences between the three positions were few and inconsistent. Total nitrogen was highest in the original boundary, significantly lower in the boundary plots and lowest in the centre of the field. Total Phosphorus on the other hand was

Table 3.2 *Soil characteristics (in mg.kg^{-1} dry soil) at the onset of the experiment (March 1993) in the three countries. N_{av}: Nitrogen available to the plant; N_{tot}: total Nitrogen in the soil. Different characters indicate significant differences, no characters: differences were insignificant.*

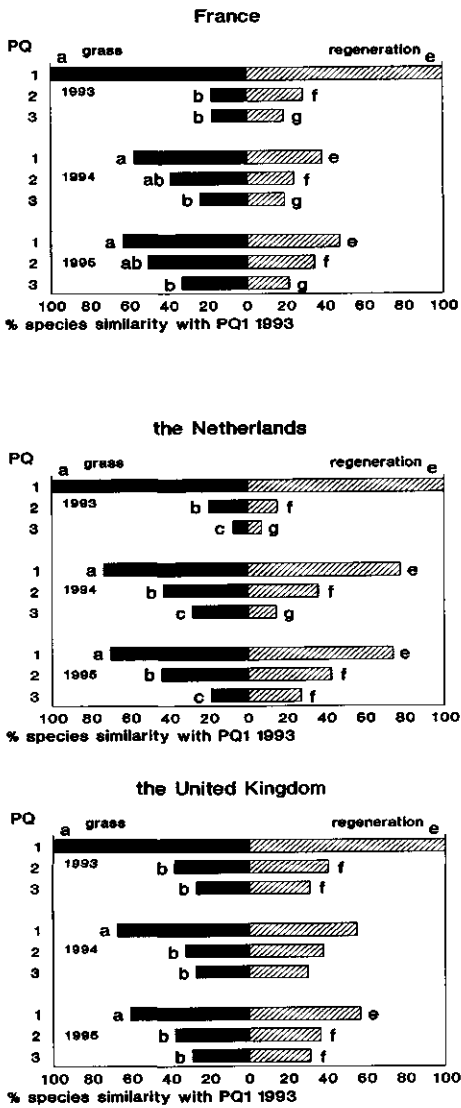|	France			the Netherlands			the United Kingdom		
	original boundary	boundary plots	centre field	original boundary	boundary plots	centre field	original boundary	boundary plots	centre field
pH	3.9[b]	4.6[a]	4.5[a]	4.2[c]	4.8[d]	4.6[de]	6.3	6.3	6.3
N_{av} (as NH$_4$) 1.4		2.2	2.8	2.7	0.9	3.1	4.5	3.1	5.0
N_{av}(as NO$_3$) 6.4		20.8	14.3	5.3[f]	11.9[e]	23.6[d]	13.1[h]	21.4[g]	27.5[g]
K_{av}	58.3	96.5	56.4	36.4[e]	58.9[d]	71.6[d]	148[g]	172[gh]	76[h]
P_{av}	0	0.2	0.3	1.2[e]	2.3[d]	3.2[d]	0.8	0.5	0.8
N_{tot}	1957[a]	1609[b]	1411[c]	1046[e]	1026[e]	1285[d]	3915	3177	3600
K_{tot}	9226	9262	9735	733[de]	667[e]	788[d]	16338[g]	16325[g]	15260[h]
P_{tot}	382[b]	653[ab]	681[a]	49.9[e]	59.9[de]	69.6[d]	674	779	797

France

the Netherlands

the United Kingdom

Figure 3.2 Mean percentage of species in a PQ similar to that in PQ1 in the original boundary in 1993 in France (n = 6), the Netherlands (n = 9) and the United Kingdom (n = 9). Filled bars: grass plots, diagonally hatched bars: regeneration plots. Within years, bars with different characters differed significantly (P<0.05); absence of characters indicate absence of significant effects within years. No significant plot type differences were found.

significantly higher in the centre of the field compared to the original field boundary. In the United Kingdom available nitrogen was significantly lower in the original boundary compared to the other two positions while both total and available potassium were significantly lower in the centre of the field than in the original boundary.

The vegetation in the different original boundaries was characterized by a large number of the same species despite the fact that there were large differences in boundary types, soil types or even geographic latitude (Appendix 3.1). In the French strip 49% of the species were found in one or both other countries while in the Netherlands 59% and the United Kingdom 45% of the species was not unique. None of the species encountered in any of the countries was rare and most species could be classified as common to extremely common.

A comparison between PQ1 next to the control plots and PQ1 next to the grass and regeneration plots (thus buffered from the arable field by a 4 m wide strip of perennial vegetation) did not reveal any significant differences in the similarity index, species numbers or biomass production (data not shown). Therefore, PQ1 next to the grass and regeneration plots can be considered representative for the field boundary in its original state.

The vegetation in the original field boundary was highly dynamic. Species similarity of the vegetation in PQ1 between 1993 and the following two years ranged from some 40 to 80% (Fig. 3.2). In the newly established boundary plots (PQ2 and 3) species similarity with the original field boundary in 1993 increased with time and decreased with distance from that boundary. However, similarity in the boundary plots never rose much above 40% in any country or year. Compared to the vegetation in the grass plots the vegetation in the regeneration plots did not contain a significantly higher or lower
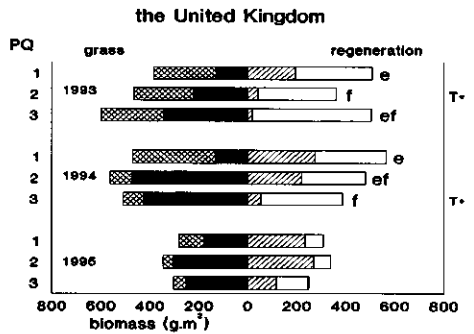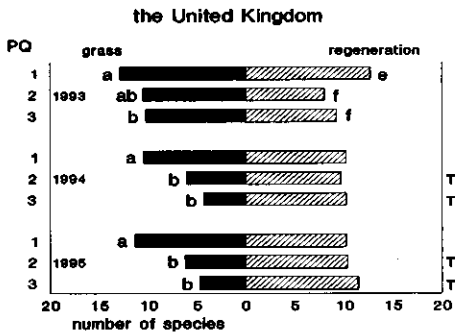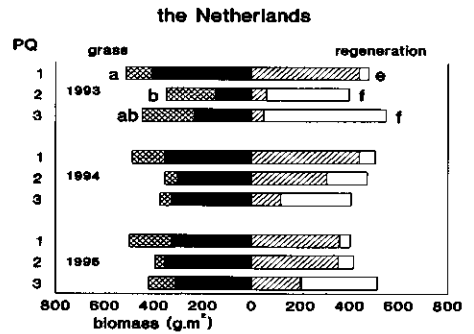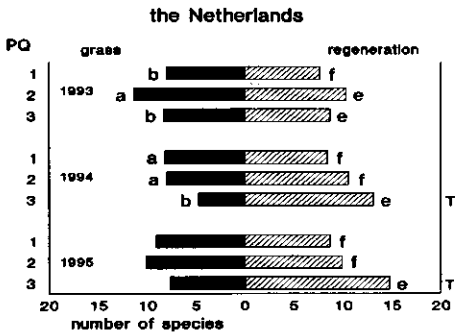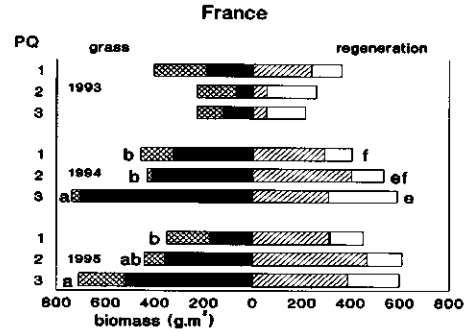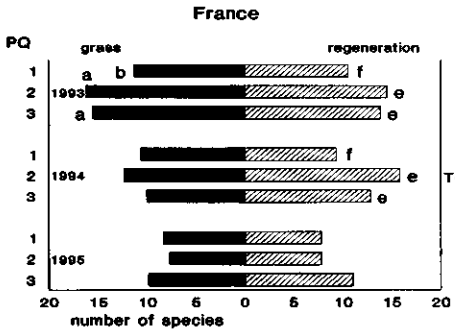
Figure 3.3 *Mean number of species (m⁻²) in the original boundary (PQ1) and the adjoining grass (filled bars) and regeneration plots (diagonally hatched bars) (PQ2 and PQ3) in France (n = 6), the Netherlands (n = 9) and the United Kingdom (n = 9). Within years, bars with different characters differed significantly (P<0.05); absence of characters indicate absence of significant effects within years. T*: Plot type effect, grass and regeneration plots at the same PQ position differed significantly (P<0.05).*

Figure 3.4 *Mean total biomass production (g.m⁻²) in the original boundary (PQ1) and the adjoining regeneration and grass plots (PQ2 and PQ3) in France (n = 6), the Netherlands (n = 9) and the United Kingdom (n = 9). Cross-hatched bars: mean dicot yield in grass plots, filled bars: mean monocot yield in grass plots, diagonally hatched bars: mean monocot yield in regeneration plots, transparent bars: mean dicot yield in regeneration plots. Within years, total biomass bars with different characters differed significantly (P<0.05); absence of characters indicate absence of significant effects within years. T*: Plot type effect, grass and regeneration plots at the same PQ position differed significantly (P<0.05).*

number of species initially found in the original boundary.

The initial species-richness in the pre-existing boundary ranged from a mean of 8 species.m^{-2} in the Netherlands to about 13 in the United Kingdom (Fig. 3.3). In 1995, in France species numbers had become similar in all PQ and plot types after earlier differences between the boundary PQ's on one hand and the plot PQ's on the other. Likewise, in 1995, in the Dutch grass plots and the English regeneration plots, species numbers of all three PQ positions had converged. However, species-richness in PQ3 of the Dutch regeneration plots remained significantly higher than in PQ1 and 2 and in the English grass plots both PQ2 and 3 yielded significantly lower species numbers than the original boundary. In all three countries significant plot type effects were observed; in all cases species-richness in the regeneration plots was significantly higher compared to those in the grass plots (Fig. 3.3).

The long term average biomass production (all PQ's in all years pooled) was very similar in the three countries: 450, 440 and 430 g.m^{-2} for the French, Dutch and English strips respectively. With the exception of the French grass plots, early differences in biomass production between the different PQ positions had disappeared in 1995 (Fig. 3.4). Also, the
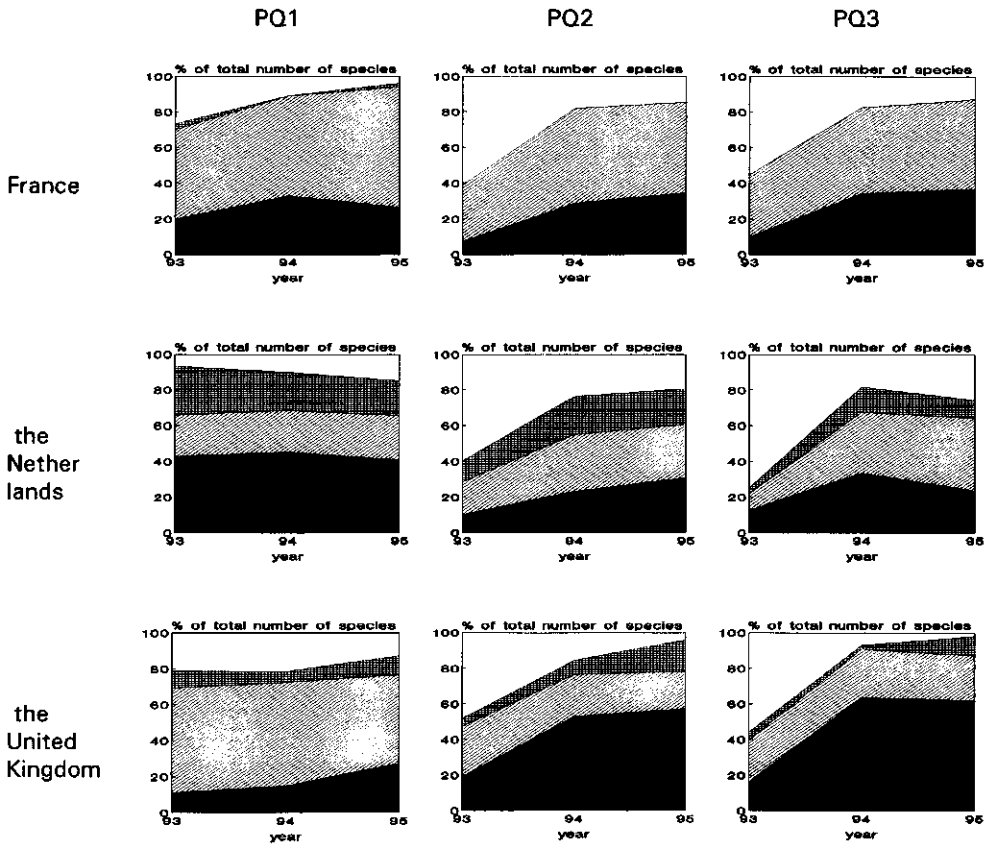

Figure 3.5 *Grass plots: mean changes in time in the percentual contribution of four functional groups to the total number of species in the three PQ's in France, the Netherlands and the United Kingdom. Transparent area: annual dicots; crossed hatched: annual monocots; diagonally hatched: perennial dicots; filled: perennial monocots.*

monocot/dicot ratio had generally converged to the level of PQ1. Exceptions in 1995 were the PQ3 in the Dutch regeneration plots in which monocots contributed significantly ($P<0.05$) less and both PQ's in the English grass plots in which monocots contributed significantly ($P<0.05$) more to total biomass production. Biomass production in the grass and regeneration plots was similar in all years and PQ's in France and the Netherlands. In the United Kingdom PQ2 in 1993 and PQ3 in 1994 yielded significantly higher in the grass plots compared to the regeneration plots but these differences were not found anymore in 1995.

The vegetation in the original boundary in France and the United Kingdom was characterized by a high proportion of annual and perennial dicots (Fig. 3.5 and 3.6) while the Dutch PQ1's were dominated by grassy perennials. In the 1993 established plots vegetation development was characterized by a sharp decrease in annuals and a steady increase in perennial monocots and dicots. The dicotyledoneous species were more rapid in colonizing the plots: their proportion in the initial year was relatively high compared to the monocots. Differences between PQ2 and PQ3 as well as between grass and regeneration plots were small, the only exception being the UK grass plots. In the PQ's in these plots the proportion
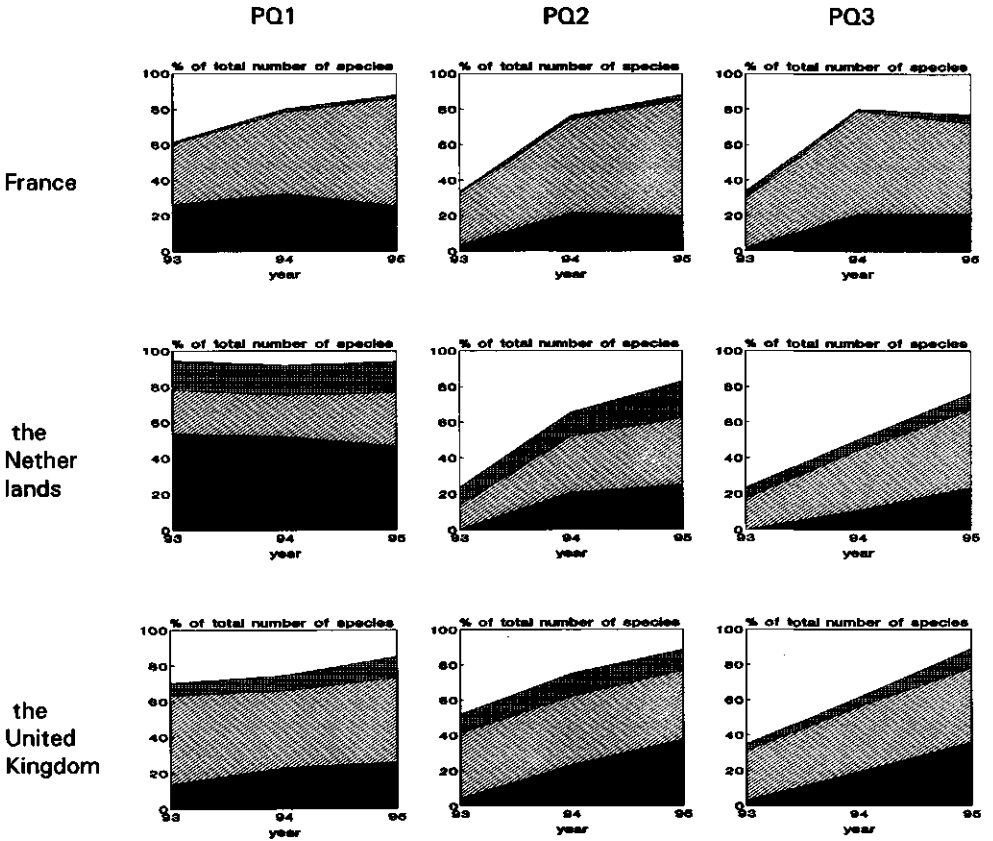

Figure 3.6 Regeneration plots: mean changes in time in the percentual contribution of four functional groups to the total number of species in the three PQ's in France, the Netherlands and the United Kingdom. Transparent area: annual dicots; crossed hatched: annual monocots; diagonally hatched: perennial dicots; filled: perennial monocots.

of grasses was exceptionally high, probably as a result of the low species numbers in these plots which may have resulted in a disproportional contribution of the sown monocot *Lolium perenne*.

Finally, in 1995 an extended perennial field boundary had developed which was primarily composed of a small set of the species found in 1993 in the original boundary (Appendix 3.2). At 0.5 m from the arable field (PQ3) in all three countries a limited number of species (most notably, *Agrostis stolonifera, Poa trivialis, Ranunculus repens* and *Trifolium repens*) had become extremely abundant (compare Appendix 3.1 and 3.2). Total species numbers encountered in the three countries showed a marked decline in France and the United Kingdom and a sharp increase in the Netherlands. The decline in France and the UK was primarily the result of a reduced number of perennial and especially annual dicots: in France, the number of annual dicots had decreased from 25 in 1993 to 6 in 1993. In the Netherlands the increase in total species numbers was almost entirely caused by the increase in annual species both monocots and dicots, 4 in 1993 versus 19 in 1995. Most of the dicots that were not encountered in the new boundary in France and England were woody or woodland species like *Pteridium aquilinium, Stellaria holostea, Crataegus monogyna* or *Ilex aquifolium*.

Discussion

The present study was aimed at determining whether we can relate vegetation development in such strips to the existing boundary and whether some basic rules can be applied for different boundary types or in different areas. The four metre width of the strips in this study was chosen arbitrarily. In practice it may vary according to the needs of the owner.

The analysis of the initial nutrient status of the original boundary, the future boundary plots and the centre of the field revealed large and inconsistent differences for different boundaries and on different soil types. Only the nutrient levels on the Dutch, sandy soils pointed at a consistent trend of increasing nutrient levels from the original field boundary to the centre of the field. Borstel (1974) concluded that changes in soil nutrient levels did not play any major role in steering the first thirty years of succession on fallow arable land. Likewise, Pegtel (1987) found no relationship between the macro-nutrients in the top layer and standing phytomass or species diversity in the first nine years after abandonment of fertilization in grassland. Also in this experiment the large differences in total N, P or K that were observed between the countries did not result in correspondingly large differences in biomass production or species-richness. Therefore, soil nutrient analysis seems of little practical use as a tool to predict vegetation development and the potential species-richness of extended field boundaries.

In fact, mean biomass production was almost equal in all three countries and within two years of establishment productivity levels of the new plots had become similar to the levels of the original boundary in all but the French grass plots, despite the fact that they were established on former (heavily) fertilized arable land. Likewise the monocot/dicot ratio showed a strong tendency towards the levels of the neighbouring original boundary vegetation. In the final year, productivity levels ranged from 250 to 720 $g.m^{-2}$. These levels allow species-richness as high as 30 species per 0.25 m^{-2} in grassland vegetation (Grime 1979). Kleijn *et al.* (1997) found corresponding levels of up to 24 species per 0.25 m^{-2} in

these strips once the dispersal phase was by-passed by means of the experimental introduction of species. However, in this experiment a maximum of 19 species per 1 m^{-2} was found. It suggests that it is a general aspect of modern agriculture that, irrespective of area or country, the agricultural landscape is impoverished and devoid of potential boundary species. Under these circumstances, improved habitat conditions may not lead to the return of diverse field boundaries since most target species have disappeared from the scene.

Similar to the biomass production, the species numbers in the boundary plots seemed to converge to the level of the original boundary in both grass and regeneration plots. Remarkably, significant deviations from the level of the original boundary only occurred in PQ's which had significantly different monocot/dicot ratio's; a high proportion of monocots in the total biomass seemed to depress species numbers. In 1995 the species numbers on a per area basis of the original boundary and the new plots were more or less the same, however, the total number of species encountered in 1993 in the original boundary and in 1995 in the new boundary (PQ3) were much lower in France and the United Kingdom (Appendix 3.1 and 2). This means that in 1995 a smaller set of species was found more often in the quadrats; the quadrats were more uniform. These large differences were predominantly caused by differences in numbers of annual dicots (France) and perennial, mainly woodland dicots (the United Kingdom) while the higher total species numbers in the Netherlands were mainly the result of an increase in all annual species. The apparent selective establishment criteria of the new strips may explain the low similarity in species composition between the original boundary and the new boundary plots: only non-woodland perennial monocots and dicots had high establishment rates in the herbaceous strips in all boundary types.

With respect to the annual species it is important to note that almost all species found are common on arable fields and are considered weeds by farmers. In France and the United Kingdom the number of annual species was much lower in the new boundary plots in 1995 compared to the original boundary in 1993 both in the grass and the regeneration plots. Thus, the establishment of a perennial vegetation strip, either through natural regeneration or by sowing *Lolium perenne*, reduced the number of weed species in field boundaries in these countries. However the number of weed species not necessarily determines the size of the problems caused by weeds. Even a single weed species can cause severe economic damage. In 1995, in the annual-rich Dutch boundary plots, only the perennial weed species *Cirsium arvense* and *Elymus repens* reached a significant abundance, and biomass production of both species was far lower in the grass plots than in the regeneration plots (Kleijn *et al.* 1997). Smith & MacDonald (1989) also found lower weed yields in extended field boundaries sown with grass compared to those left regenerating naturally. Establishment of enlarged field boundaries by sowing grass therefore seems the best option from a weed control point of view. It may, however, have adverse effects on species-richness in the first few years after establishment as was observed in the Netherlands and the United Kingdom. Thus, vegetating extended field margins by means of natural regeneration is the best option for relatively weed-free stretches of boundary while next to seriously weed infested boundaries sowing of grass is preferable.

The presence of a well developed herbaceous vegetation strip next to hedgerows is important for predatory insects, game and other wildlife (Aebischer *et al.* 1994, Stoate & Szczur 1994) while it may also reduce or prevent weed ingress into the arable field (Boatman 1992, Theaker *et al.* 1995). Permanent vegetation on top of ditch banks may prevent the collapse of the bank itself, reduces run-off of soil and pesticides (Tim & Jolly 1994) and

decreases drift of pesticides into surface waters (van de Zande *et al.* 1995). Establishment of narrow strips of herbaceous vegetation along hedges or other field boundaries is now being recommended as part of the restoration of field boundaries (Boatman 1992). These experiments showed that in different areas and boundary types vegetation development in enlarged field boundaries was closely correlated with the original field boundary in terms of species-richness, total biomass production and the dicotyledons/monocotyledons ratio. Species composition was significantly different, however, as common, mobile grassland species most rapidly colonized the enlarged boundary plots whereas many species characteristic to the original boundary were unable to establish themselves. These relationships may help predict the vegetation development in newly established boundary strips as part of the restoration of field boundaries.

Acknowledgements

Appendix 3.1 *Species growing in the original boundary at 0.5 m from the arable field in 1993. Species are ordered in decreaesing frequency of occurrence in the PQ1's (100% in the NL and UK is in all 18 PQ1's next to grass and regeneration plots; 100% in FR is in all 12 such PQ1's). FG : Functional Group, AM = annual monocots, AD = annual dicots, PM = perennial monocots, PD = perennial dicots.*

France	%	FG	the Netherland	%	FG	the United Kingdom	%	FG
Dactylis glomerata	83	PM	Elymus repens	89	PM	Galium aparine	72	AD
Lapsana communis	83	PM	Agrostis stolonifera	78	PM	Rubus fruticosus	67	PD
Rubus fruticosus	83	PD	Holcus mollis	78	PM	Bromus sterilis	56	AM
Holcus mollis	75	PM	Festuca rubra			Epilobium ciliatum	56	PD
Fumaria muralis	67	AD	ssp. commutata	72	PM	Hedera helix	50	PD
Stellaria media	58	AD	Dactylis glomerata	50	PM	Urtica dioica	50	PD
Arrhenatherum elatius	50	PM	Ranunculus repens	44	PD	Poa trivialis	44	PM
Hedera helix	50	PD	Equisetum arvense	39	PD	Epilobium hirsitum	39	PD
Polygonum convolvulus	50	AD	Arrhenatherum elatius	33	PM	Holcus lanatus	33	PM
Conopodium majus	42	PD	Rumex acetosa	33	PD	Lolium perenne	33	PM
Galium aparine	42	AD	Achillea millefolium	28	PD	Prunus spinosa	33	PD
Pteridium aquilinium	42	PD	Cirsium arvense	22	PD	Cirsium arvense	28	PD
Rumex acetosa	42	PD	Holcus lanatus	22	PM	Convolvulus arvensis	28	PD
Achillea millefolium	33	PD	Urtica dioica	22	PD	Geranium dissectum	28	AD
Lamium purpureum	33	AD	Lolium perenne	17	PM	Heracleum sphondylium	28	PD
Polygonum persicaria	33	AD	Plantago lanceolata	17	PD	Veronica persica	28	AD
Digitalis purpurea	25	PD	Polygonum amphibium	17	PD	Anagallis arvensis		
Poa annua	25	AM	Stellaria holostea	17	PD	ssp arvensis	22	AD
Polygonum aviculare	25	AD	Stellaria media	17	AD	Anthriscus sylvestris	22	PD
Teucrium scorodonia	25	PD	Agrostis capillaris	11	PM	Arrhenatherum elatius	22	PM
Anagallis arvensis			Bromus hordeaceus	11	AM	Crataegus monogyna	22	PD
ssp arvensis	17	AD	Poa pratensis	11	PM	Elymus repens	22	PM
Castanea sativa	17	PD	Rumex obtusifolius			Geranium robertianum	22	PD
Crepis capillaris	17	PD	ssp. obtusifolius	11	PD	Glechoma hederacea	22	PD
Juncus bufonius	17	AM	Valeriana officinalis	11	PD	Plantago major	22	PD
Leucanthemum vulgare	17	PD	Angelica sylvestris	6	PD	Ranunculus repens	22	PD
Matricaria maritima	17	AD	Erigeron canadensis	6	AD	Rumex sanguineus	22	PD
Mentha arvensis	17	PD	Lysimachia vulgaris	6	PD	Sinapis arvensis	22	AD
Prunella vulgaris	17	PD	Matricaria recutita	6	AD	Sonchus asper	22	AD
Ranunculus repens	17	PD	Poa trivialis	6	PM	Stachys sylvestris	22	PD
Silene latifolia ssp alba	17	PD	Rumex acetosella	6	PD	Calystegia sepium	17	PD
Stellaria holostea	17	PD	Taraxacum officinale	6	PD	Cirsium vulgare	17	PD
Agrostis stolonifera	8	PM	Trifolium repens	6	PD	Rumex obtusifolius		
Arabidopsis thaliana	8	AD				ssp. obtusifolius	17	PD
Aphanes arvensis	8	AD				Cardamine hirsuta	11	AD
Bryona cretica ssp dioica	8	PD				Corylus avellana	11	PD
Cerastium fontanum						Dactylis glomerata	11	PM
ssp. vulgare	8	AD				Dipsacus fullonum	11	PD
Cirsium arvense	8	PD				Myosotis arvensis	11	AD
Crataegus monogyna	8	PD				Poa annua	11	AM
Elymus repens	8	PM				Tamus communis	11	PD
Galeopsis tetrahit	8	AD				Vicia sativa ssp nigra	11	AD
Geranium molle	8	AD				Acer campestre	6	PD
Helianthus annuus	8	AD				Agrostis gigantea	6	PM
Lonicera periclymenum	8	PD				Arum maculatum	6	PD
Lolium perenne	8	PM				Atriplex patula	6	AD
Myosotis arvensis	8	AD				Bromus hordeaceus	6	AM
Oxalis fontana	8	AD				Chaerophyllum temulum	6	PD
Prunus avium	8	PD				Coronopus didymus	6	AD
Sagina procumbens	8	AD				Crepis capillaris	6	PD
Scrophularia nodosa	8	PD				Daucus carota	6	PD
Solanum nigrum						Fraxinus excelsior	6	PD
ssp. nigrum	8	AD				Geum urbanum	6	PD
Sonchus asper	8	AD				Ilex aquifolium	6	PD
Taraxacum officinale	8	PD				Olearea virgata	6	PD
Triticum aestivum	8	AM				Polygonum aviculare	6	AD

Appendix 3.1 continued

Umbilicus rupestris	8 PD		*Prunus domestica*	6 PD
Urtica dioica	8 PD		*Quercus robur*	6 PD
Veronica arvensis	8 AD		*Rosa canina*	6 PD
Vicia sativa ssp. *nigra*	8 AD		*Rumex crispus*	6 PD
Vicia tetrasperma			*Taraxacum officinale*	6 PD
ssp. *tetrasperma*	8 AD		*Triticum aestivum*	6 AM
Viola riviniana	8 PD		*Vicia sepium*	6 PD

Total

annual monocots (AM):	3	1	4
annual dicots (AD):	23	3	12
perennial monocots (PM):	7	11	7
perennial dicots (PD):	26	16	38
total number of species	65	31	61

Appendix 3.2 Species growing in the new boundary at 0.5 m from the arable field in 1995. Species are ordered in decreasing frequency of occurrence in the PQ3's (grass and regeneration plots pooled, 100% in NL and UK is in all 18 PQ3's; 100% in FR is in all 12 PQ3's). For abbreviations see Appendix 3.1.

France	%	FG	the Netherland	%	FG	the United Kingdom	%	FG
Dactylis glomerata	92	PM	Lolium perenne	72	PM	Holcus lanatus	78	PM
Prunella vulgaris	75	PD	Trifolium repens	56	PD	Lolium perenne	78	PM
Ranunculus repens	75	PD	Cirsium arvense	44	PD	Poa trivialis	72	PM
Poa trivialis	67	PM	Crepis capillaris	44	PD	Ranunculus repens	67	PD
Trifolium repens	67	PD	Epilobium ciliatum	44	PD	Trifolium repens	61	PD
Rumex acetosa	58	PD	Holcus lanatus	44	PM	Agrostis stolonifera	39	PM
Lapsana communis	50	AD	Poa trivialis	44	PM	Rumex obtusifolius		
Agrostis stolonifera	42	PM	Elymus repens	39	PM	ssp obtusifolius	33	PD
Galium aparine	42	AD	Erigeron canadensis	39	AD	Cirsium vulgare	28	PD
Lolium perenne	42	PM	Hypochaeris radicata	39	PD	Poa annua	28	AM
Taraxacum officinale	33	PD	Vicia hirsuta	39	AD	Cynosurus cristatus	17	PM
Achillea millefolium	25	PD	Achillea millefolium	33	PD	Elymus repens	17	PM
Arrhenatherum elatius	25	PM	Poa annua	33	AM	Hordeum vulgare	17	AM
Hedera helix	25	PD	Ranunculus repens	33	PD	Sonchus asper	17	AD
Lolium multiflorum	25	PM	Daucus carota	28	PD	Bromus sterilis	11	AM
Oxalis fontana	25	AD	Geranium dissectum	28	AD	Cardamine hirsuta	11	AD
Plantago major	25	PD	Viola arvensis	28	AD	Cirsium arvense	11	PD
Rubus fruticosus	25	PD	Cerastium fontanum			Galium aparine	11	AD
Bromus sterilis	17	AM	ssp vulgare	22	AD	Geranium dissectum	11	AD
Castanea sativa	17	PD	Festuca rubra			Lamium purpureum	11	AD
Heracleum sphondylium	17	PD	ssp commutatus	22	PM	Plantago major	11	PD
Rumex crispus	17	PD	Rumex acetosa	22	PD	Sinapis arvensis	11	AD
Scrophularia nodosa	17	PD	Rumex obtusifolius			Carex spec	6	PM
Vicia tetrasperma			ssp obtusifolius	22	PD	Cerastium font. ssp vulgare	6	AD
ssp. tetrasperma	17	AD	Vicia sativa ssp nigra	22	AD	Dactylis glomerata	6	PM
Cirsium arvense	8	PD	Apera spica-venti	17	AM	Epilobium ciliatum	6	PD
Crepis capillaris	8	PD	Aphanes inexpectata	17	AD	Epilobium hirsutum	6	PD
Hypochaeris radicata	8	PD	Artemisia vulgare	17	PD	Festuca rubra		
Mentha arvensis	8	PD	Crepis biennis	17	PD	ssp commutata	6	PM
Poa annua	8	AM	Polygonum convolvulus	17	AD	Glechoma hederacea	6	PD
Poa pratensis	8	PM	Stellaria media	17	AD	Heracleum sphondylium	6	PD
Raphanus raphanistrum	8	PD	Taraxacum officinale	17	PD	Juncus effusus	6	PM
Rumex obtusifolius			Agrostis stolonifera	11	PM	Myosotis arvensis	6	AD
ssp. obtusifolius	8	PD	Bromus hordeaceus	11	AM	Petroselinum segetum	6	PD
Salix atrocinerea	8	PD	Carduus crispus	11	PD	Rumex crispus	6	PD
Stachys sylvatica	8	PD	Equisetum arvense	11	PD	Stachys sylvatica	6	PD
Trifolium pratense	8	PD	Erodium cicutarium			Vicia sativa ssp. nigra	6	AD
Urtica dioica	8	PD	ssp cicutarium	11	AD			
Veronica arvensis	8	AD	Juncus effusus	11	PM			
Vicia sativa ssp sativa	8	AD	Leontodon autumnalis	11	PD			
			Linaria vulgaris	11	PD			
			Matricaria recutita	11	AD			
			Picris hieracioides	11	PD			
			Urtica dioica	11	PD			
			Agrostis capillaris	6	PM			
			Arrhenatherum elatius	6	PM			
			Bromus sterilis	6	AM			
			Capsella bursa-pastoris	6	AD			
			Carex ovalis	6	PM			
			Holcus mollis	6	PM			
			Glyceria fluitans	6	PM			
			Lapsana communis	6	AD			
			Plantago lanceolata	6	PD			
			Polygonum amphibium	6	PD			
			Rumex acetosella	6	PD			
			Triticale	6	AM			
			Veronica arvensis	6	AD			

Appendix 3.2 continued

Total

annual monocots (AM):	2	5	3
annual dicots (AD):	6	14	9
perennial monocots (PM):	7	12	10
perennial dicots (PD):	23	22	13
total number of species	38	53	35

4

Patterns in species composition of arable field boundary vegetation

Summary

Vegetation composition in contrasting field boundary plots was analysed by means of transects perpendicular to the arable field three years after establishment. Plots were established on the outer meters of an arable field next to a pre-existing field boundary and sown with 1) a mixture of 30 forbs 2) *Lolium perenne* and 3) plots left regenerating naturally. Tall, competitive species concentrated biomass production in a zone within 1 m from the arable field, while small, stress tolerant species were predominantly found in a zone 3-4 m from the field. The tall species were able to increase total vegetation biomass production significantly in the zone bordering the arable field, probably by means of capturing nutrients from the arable field. The two major arable weeds found in the boundary plots, *Elymus repens* and *Cirsium arvense*, colonized the plots with different strategies but both were seriously reduced in vigour when plots were sown with *Lolium perenne* or with forbs at the onset of the experiment. Species richness in the forbs-plots was relatively high but rather low in the grass- and regeneration-plots caused by a very limited colonization of potential field boundary species; only two species colonizing the boundary plots were new to the original field boundary, while 30% of the species from the original field boundary were not found in the boundary plots after three years. This limited colonization ability may seriously hamper efforts to restore field boundary diversity.

Key-words: field boundary vegetation, species-richness, arable weeds, distribution patterns, biomass gradient

Introduction

Field boundaries have been an important aspect of the human environment since the introduction of agriculture. Arable fields logically end somewhere and people in different areas developed different boundary structures according to specific needs such as fencing, wood for domestic use, drainage of excess water or simply to mark the border between two fields. Before the invention of barbed wire most of the boundaries existed of perennial vegetation like hedgerows, or ditch banks often characterizing the entire landscape. Furthermore, as they usually comprise the largest areas of perennial vegetation amidst annually cultivated fields, they are an important component in the agricultural ecosystem

providing a habitat for many plant species and food, shelter, overwintering sites or corridors between habitats for a multitude of animal species (Bennet *et al.* 1994, Dennis *et al.* 1994, Hooper 1987, Parish *et al.* 1994, 1995).

The intensification of the agriculture since the 1950's has resulted in a dramatic loss of field boundary habitats in Western Europe, while the remaining boundaries in the agricultural landscape have suffered a serious decline in diversity (Boatman 1992, Freemark & Boutin 1995). Since 1985 there has been an increased interest in the functionality of field boundaries in the agricultural ecosystem and in the factors that control diversity in them (e.g., Boatman 1994, Marshall & Birnie 1985, Way & Greig-Smith 1987).

The farmers' perception of field boundaries is pivotal to the condition of field boundaries, as they are primarily involved in the management and maintenance practices. In general, field boundaries are viewed by farmers as sources of pests and weeds (Marshall & Smith 1987) and are managed accordingly. Of the farmers interviewed by Boatman (1992), Marshall & Smith (1987) and De Snoo & Wegener Sleeswijk (1993) 62%, 60% and 59% respectively sprayed their field boundaries, usually with broad spectrum herbicides, in attempts to control perceived weed problems. Indeed, a number of plant species that may seriously hamper crop growth can have populations in both the field boundary and in the crop edge, for instance *Bromus sterilis*, *Cirsium arvense*, *Elymus repens* and *Galium aparine* (Boatman 1989, Marshall 1989, Theaker *et al.* 1995). Therefore, an analysis of the factors affecting field boundary diversity has to include their effects on weed abundance in that boundary.

So far, few studies have tried to relate agricultural practices with the species composition of arable field boundary vegetation. A major difficulty in such attempts is the low level of diversity in most modern field boundaries. Experimental treatments which might have negative effects in botanically rich field boundaries may fail to give any effects in modern species-poor field boundaries (Marshall 1987). Furthermore, since interest in field boundaries is of rather recent date, historical data of the composition of field boundary vegetation, which could have been used as a point of reference, are lacking. Thus there is great need for knowledge of the potential botanical richness and the main factors affecting it in arable field boundaries.

The present study reports on vegetation composition in newly created four meter wide field boundary plots bordering an original boundary three years after establishment. Management regime of the new boundary vegetation was favourable to establishment of a species-rich vegetation so that the results of the present study may function as a point of reference for future studies on this and other experiments. Furthermore, comparisons made between vegetation composition close to and further from the arable field may identify factors related to agriculture that cause botanical change in field boundary vegetation. Thus, data were collected in order to answer the questions:

- Is the composition of arable field boundary vegetation affected by agriculture related factors (e.g. herbicide drift, fertilizer application)?

- Is it possible to restore a high species-richness in a perennial vegetation bordering the arable field?

Table 4.1 *(a) Grassland species occurring in the pre-existing boundaries of three fields at a maximum distance of five meters from the newly created boundary plots. (b) Species sown to the herbs boundary plots. Seeding rate of the mixture was 1 g.m⁻². The percentage of total seed weight is given for each species.*

a. fields:			b.	
Amfoort	Bornsesteeg	Keijenberg	sown species	(%)
Agrostis capillaris	*Agrostis capillaris*	*Achillea millefolium*	*Campanula rotundifolia*	2.6
*Anemona nemorosa***	*Crepis capillaris*	*Agrostis capillaris*	*Centaurea jacea*	8.1
*Angelica sylvestris***	*Dactylis glomerata*	*Arrhenatherum elatius*	*Chaerophyllum temulum*	5.2
*Anthriscus sylvestris***	*Elymus repens*	*Artemisia vulgaris*	*Cichorium intybus*	1.6
Arrhenatherum elatius	*Epilobium ciliatum*	*Bromus hordeaceus*	*Crepis capillaris*	0.1
*Cardamine pratensis***	*Equisetum arvense*	*Carduus crispus*	*Crepis biennis*	1.9
Cerastium fon. ssp *vulgare*	*Erigeron canadensis*	*Chaerophylum temulum*	*Daucus carota*	3.4
Cirsium arvense	*Festuca rub.* ssp *commutata*	*Cirsium arvense*	*Euphrasia stricta*†	0.8
Dactylis glomerata	*Galium aparine*	*Crepis capillaris*	*Galium mollugo*	0.7
Elymus repens	*Holcus lanatus*	*Dactylis glomerata*	*Galium verum* ssp *verum*	0.6
Equisetum arvense	*Holcus mollis*	*Elymus repens*	*Hieracium pilosella*	1.8
Festuca rub. ssp *commutata*	*Juncus effusus*	*Festuca rubra* ssp *commutata*	*Hypericum perforatum*	3.2
Galium aparine	*Lotus uliginosus***	*Holcus lanatus*	*Hypochaeris radicata*	2.1
Holcus lanatus	*Polygonum amphibium*	*Holcus mollis*	*Jasione montana*†	0.3
Holcus mollis	*Ranunculus repens*	*Lamium album***	*Lathyrus pratensis*‡	2.1
Juncus effusus	*Rumex obt.* ssp *obtusifolius*	*Leontodon autumnalis*	*Leontodon autumnalis*	4.0
Lolium perenne	*Urtica dioica*	*Lolium perenne*	*Leonurus cardiaca*	1.6
*Lotus uliginosus***		*Plantago lanceolata*	*Leucanthemum vulgare*	2.0
*Lysimachia vulgaris***		*Plantago major***	*Linaria vulgaris*	0.9
*Poa pratense***		*Poa trivialis*	*Lotus corn.* ssp *corniculatus*	0.7
Poa trivialis		*Potentilla argentea*	*Lysimachia vulgare*‡	1.3
*Ranunculus acris***		*Potentilla reptans***	*Malva moschata*	18.1
Ranunculus repens		*Ranunculus repens*	*Medicago lupulina*†	1.9
*Rubus fruticosus***		*Rumex acetosella*	*Picris hieracioides*	0.4
Rumex acetosa		*Taraxacum officinale*	*Pimpinella saxifraga*	5.2
*Rumex crispus***		*Trifolium pratense***	*Saponaria officinalis*	16.1
Rumex obt. ssp *obtusifolius*		*Trifolium repens*	*Silene latifolia* ssp *alba*	5.4
*Sambucus nigra***		*Vicia hirsuta*	*Tanacetum vulgare*	5.2
Stellaria holostea		*Vicia sativa* ssp *nigra*	*Trifolium arvense*†	0.5
Trifolium repens			*Trifolium dubium*	2.2
Urtica dioica				
Valeriana officinalis				
Vicia hirsuta				
Vicia sativa ssp *nigra*				
*Vicia sepium***				

* Species which were not found in the experimentally established plots after three years; ‡ Sown species that did not establish at all;
† Sown species establishing only in the first year.

Methods

Sites

In April 1993, experimental field boundaries were established on three fields in the vicinity of Wageningen as part of a joint research program with participants in France, The Netherlands and The United Kingdom (Marshall *et al.* 1994). The original boundaries of two of the fields were ditch banks while the third field was bordered by an unpaved road. All pre-existing boundaries were at least 1.5 m wide, had a grassy vegetation on sandy soils which was managed by flail-mower once a year without removing the cuttings. This type of management was maintained throughout the experiment. Species present in the original boundary are given in Table 4.1a. Crop rotation as well as fertilizer and herbicide inputs for the three fields are given in Table 4.2. Fertilizer was applied with a pneumatic fertilizer spreader while pesticides were applied with a tractor-mounted air-assisted hydraulic sprayer.

Table 4.2 Fertilizer and herbicide inputs in three fields bordering the new field boundary plots. Numbers in superscript indicate different applications of herbicides within a season.

Field	Amfoort		Bornsesteeg		Keijenberg	
Crop in 1993:	Spring Wheat		Winter Wheat		Triticale	
herbicides	Certrol Combin (4l/ha)		Starane[1]	(2l/ha)	MCPA	(1.5l/ha)
			MCPA[2]	(1l/ha)	MCPP	(1.5l/ha)
					Starane	(0.5 l/ha)
fertilizer	70 kg N/ha		190 kg N/ha		65 kg N/ha	
	65 kg P/ha		0 kg P/ha		0 kg P/ha	
	165 kg K/ha		0 kg K/ha		75 kg K/ha	
Crop in 1994:	Sugar Beet		Potato		Phacelia (Set Aside)	
herbicides	Betanal[1]	(2l/ha)	Butisan[1]	(1l/ha)	-	
	Goltix[1]	(2kg/ha)	Patoran[1]	(3l/ha)		
	Betanal[2]	(2l/ha)	MCPA[2]	(1l/ha)		
	Tramat[2]	(1.5l/ha)	Gramoxone[3]	(2.5l/ha)		
	Goltix[2]	(1kg/ha)	Reglone[3]	(2.5l/ha)		
fertilizer	150 kg N/ha		195 kg N/ha		65 kg N/ha	
	40 kg P/ha		20 kg P/ha		25 kg P/ha	
	165 kg K/ha		115 kg K/ha		125 kg K/ha	
Crop in 1995:	Potato		Spring Wheat		Silage Maize	
herbicides	Boxer	(3l/ha)	MCPA	(2l/ha)	Lentagran EC (2l/ha)	
	Patoran	(1.5 l/ha)	MCPP	(2l/ha)	Atrazin	(1.5l/ha)
fertilizer	100 kg N/ha		80 kg N/ha		200 kg N/ha	
	40 kg P/ha		0 kg P/ha		55 kg P/ha	
	100 kg K/ha		50 kg K/ha		280 kg K/ha	

Treatments

Three types of experimental field boundary plots were established in the former crop edge, all 8 x 4 m^2 large, parallel to and bordering the pre-existing field boundary. The first type were plots sown with a mixture of 30 species of forbs (Table 4.1b). Species were selected from a range of vegetation types representing possible stages in succession on fallow arable land under a mowing regime (Schmidt, 1993): perennial forbs from open, nutrient rich and more or less disturbed vegetation; perennial forbs from dry, open to closed grasland vegetation; perennial forbs from moist, closed grassland vegetation. Furthermore, these species had to occur on sandy, slightly acid soils, had to flower attractively and sufficient seeds had to be available. Seeds of most of the species were collected around Wageningen in 1992. Some species were purchased at 'de Cruydthoeck' a commercial seed company specialized in wild species of native stock. Aim of this treatment was to establish a boundary type with a high species-richness which, although highly artificially established, may function as a point of reference concerning potential species-richness. For simplicity, this plot will hereafter be referred to as the forbs-plot. The second type were plots sown with *Lolium perenne*. This treatment was included because it is known to be a good weed suppressor in the early stages of arable fallow. The third type were plots allowed to regenerate naturally. On each field three replicates were created with the three treatments randomized within the replicates (resulting in a total of 3 fields x 3 replicates x 3 plot types = 27 plots). All plots were mown once a year in autumn and cuttings were removed. Care was taken to reduce seed

dispersal between plots due to removal of the cuttings.

The effects of agriculture-related factors causing botanical change were expected to diminish with increasing distance from the arable field. Therefore vegetation composition was determined by means of transects perpendicular to the arable field. In August 1995, transects of 4 x 0.5 m^2 (eight 0.5 x 0.5 m^2 subplots) were set out over the total width of each newly created boundary plot. Above-ground biomass of each subplot was cut, separated into species and dry weight was determined after drying for 48 hours at 80°C.

Analysis

Within the field-stratum each plot type was replicated 9 times. Since the performance of a species depends on both its own biomass production and the biomass production of the surrounding vegetation, the performance of a species is expressed proportional to the total biomass production of the subplot. Proportional yields summarize the relative vegetative success of a species and may be considered as the relative ecological performance (Austin & Austin 1980).

Individual species were analysed separately for each treatment plot and, as the biomass data for individual species did not meet the assumptions for ANOVA due to a large number of zero's, a Monte Carlo approach was used to analyse for significant differences caused by subplot position (Sokal & Rohlf 1981). Data of total vegetation biomass and species numbers were analysed by nested ANOVA with the subplot treatment nested within the plot type treatment.

Results

Of the 53 field boundary species listed in Table 4.1a, 16 species did not manage to colonize the experimental plots within the three years of this experiment, while only two species (*Carex ovalis* and *Anthoxanthum odoratum*) encountered in the experimental boundary plots in 1995 had not been found at the onset of the experiment in either the original field boundary or the arable field.

Herbicides were mostly applied once or twice a year (Table 4.2) but visual damage to the field boundary vegetation was not observed in any of the years with the exception of a single occasion when part of the vegetation hanging over the arable field showed curling of leaves and shoots following an application of a MCPA/MCPP mixture.

While the initial conditions of the three plot types did not differ systematically with respect to fertility or soil seed bank (since the plot types were randomized within the nine blocks), the vegetation composition and more surprisingly the vegetation structure, height and biomass production contrasted sharply at the end of the third growing season (Fig. 4.1a-c). Biomass production of the three plot types differed significantly between zero and two meters from the arable field but was not statistically different from two to four meters (Fig. 4.2). From zero to two meters, the forbs-plots always yielded higher than the other plot types while at 0.25 m biomass production of the regeneration-plot was also higher than that of the grass-plots. A comparison of biomass production within plot types showed a significant increase in biomass production at the subplot bordering the arable field for both the forbs- and the regeneration-plots while the grass-plots did not produce any trend in biomass yields (Table 4.3a-c).
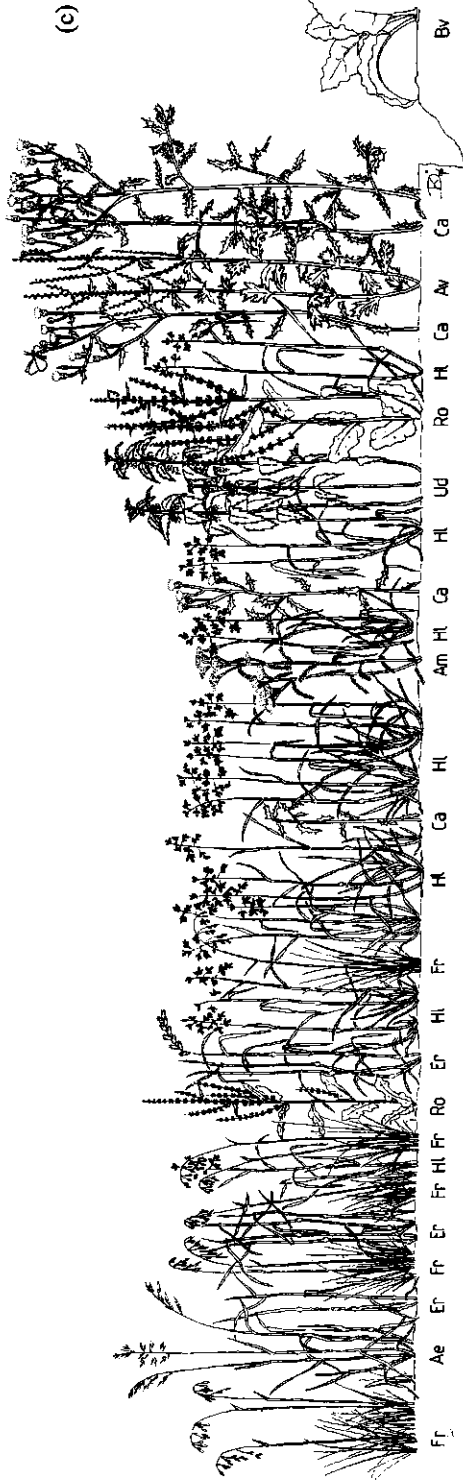
Figure 4.1 *Composition drawing of a cross-section of the boundary vegetation including the most characteristic plant species. Vegetation structure and height is representative and on scale for a vegetation at the end of June. (a) forbs-plot. (b) grass-plot. (c) regeneration-plot. Am = Achillea millefolium, Ae = Arrhenatherum elatius, Av = Artemisia vulgaris, Bv = Beta vulgaris ssp. vulgaris, Ca = Cirsium arvense, Cc = Crepis capillaris, Cj = Centaurea jacea, Dc = Daucus carota, Er = Elymus repens, Fr = Festuca rubra ssp. commutata, Hl = Holcus lanatus, Hpe = Hypericum perforatum, Hpi = Hieracium pilosella, Hr = Hypochaeris radicata, Lp = Lolium perenne, Lv = Leucanthemum vulgare, Ro = Rumex obtusifolius ssp. obtusifolius, Sa = Silene latifolia ssp. alba, So = Saponaria officinalis, Tv = Tanacetum vulgare, Ud = Urtica dioica, Vh = Vicia hirsuta.*
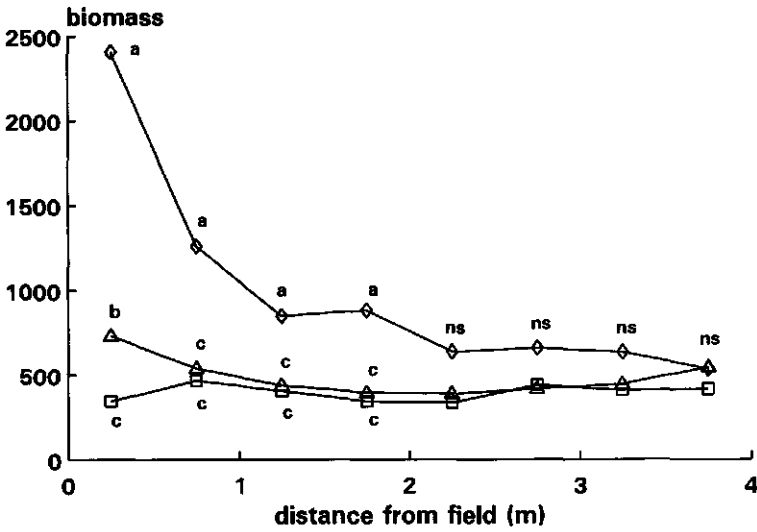
Figure 4.2 *Biomass production of the total vegetation (g.m^{-2}) across experimental field boundary plots sown with forbs (diamants),* Lolium perenne *(squares) or left regenerating (triangles). Different characters indicate significant differences between similar subplots in different plot types (P<0.05).*

Figure 4.3 *Numbers of species (0.25 m^{-2}) across experimental field boundary plots sown with forbs (diamants),* Lolium perenne *(squares) or left regenerating (triangles). Different characters indicate significant differences between similar subplots in different plot types (P<0.05).*
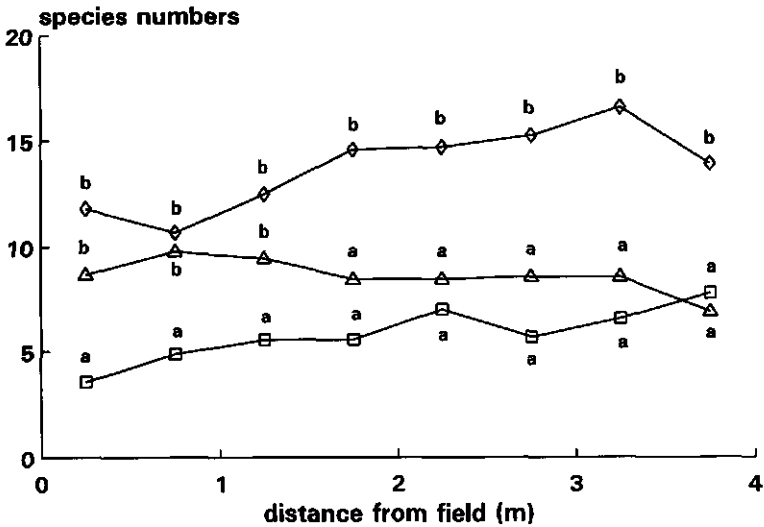
Table 4.3a. The distribution of some of the most common species (in percentage of total biomass) , total biomass production and number of species in relation to distance from the field in plots sown with a forbs mixture (species with an asterisk) in spring 1993. n = frequency, total number of sampled subplots is 72. P-values (Monte-Carlo randomization test) are given for differences between distances. Biomass and species number data were analysed by means of ANOVA, different characters indicate significant differences.

distance	n(%)	0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75	P-value
species										
Agrostis capillaris	(29)	0.3	0.1	0.1	0	0.1	0	1.1	8.0	(0.000)
*Campanula rotundifolia**	(24)	0.02	0.05	0.02	0.06	0.09	0.02	0.47	0.07	(0.981)
*Centaurea jacea**	(93)	12.6	17.8	30.3	21.9	27.1	13.4	15.8	14.1	(0.089)
*Cichorium intybus**	(31)	3.5	1.2	2.0	0.2	0.5	0	0	0.4	(0.243)
Dactylis glomerata	(29)	0	0.2	0.2	0.5	1.0	0.7	3.9	1.1	(0.283)
*Daucus carota**	(36)	0	0	0.01	0.01	0.01	0	0.06	0.25	(0.056)
Elymus repens	(49)	0	0	0.1	0.4	0.5	0.9	1.6	4.2	(0.000)
Festuca rubra ssp. *commutata*	(32)	0	0	0	0.1	0.1	0.3	2.1	12.4	(0.000)
*Galium mollugo**	(83)	1.8	5.7	4.2	3.2	4.8	3.3	1.8	2.2	(0.822)
Galium verum ssp. *verum**	(60)	0.5	0.5	0.4	1.4	1.1	1.0	0.2	0.2	(0.541)
*Hieracium pilosella**	(21)	0	0	0	0.01	0.02	0.01	0.15	0.28	(0.018)
Holcus lanatus	(40)	0.4	0.6	0.3	0.2	3.0	5.2	10.5	9.2	(0.006)
*Hypericum perforatum**	(39)	0.4	0.8	1.8	0.7	3.8	2.3	0.7	0	(0.170)
*Hypochaeris radicata**	(32)	0.1	0.3	0.1	0.5	0.1	0.2	0.7	1.4	(0.108)
*Leucanthemum vulgare**	(90)	1.7	9.8	9.7	16.6	8.9	14.1	8.8	15.9	(0.085)
*Linaria vulgaris**	(25)	0.3	0.1	0.1	0.2	0.1	0.3	0.8	0	(0.945)
*Malva moschata**	(35)	0.3	0.2	0.4	0.7	0.3	0.4	0.4	0	(0.970)
*Picris hieracioides**	(28)	0	0.8	0.3	2.3	0.2	0.4	0.5	0	(0.246)
*Saponaria officinalis**	(99)	8.4	6.3	13.1	7.3	12.8	12.5	4.8	2.9	(0.004)
Silene latifolia ssp. *alba**	(65)	8.7	12.4	7.8	12.3	2.2	8.4	9.1	5.1	(0.743)
*Tanacetum vulgare**	(94)	59.6	40.7	25.9	24.6	26.1	26.4	20.2	3.5	(0.000)
Vicia hirsuta	(28)	0.1	0.2	0.4	0.7	0.2	0.2	0.4	0.7	(0.543)
total biomass (g/m^2)		2408.4^a	1259.6^b	848.4^c	882.0^c	636.0^{cd}	658.0^{cd}	634.0^{cd}	534.8^d	
no. species		11.8^d	10.7^d	12.4^{cd}	14.6^b	14.7^b	15.2^{ab}	16.7^a	13.9^{bc}	

Averaged over the total transect, the mean number of species were, with 5.9 sp./0.25m^2, lowest in the grass-plots, significantly higher in the regeneration-plots (8.6, P<0.05) and highest in the forbs-plots (13.7, P<0.001). Close to the arable field (0-1.25 m), however, species numbers were not significantly different between forbs- and regeneration-plots while in the grass-plots they were significantly lower. Further from the arable field (1.75-3.75 m) species numbers of the forbs-plots became significantly higher than those of the grass- and regeneration-plots (Fig. 4.3). Within plot types species-richness showed a more varied picture (Table 4.3a-c). In general, in the forbs-plots species numbers between 0 and 0.75 m were significantly lower than between 0.75 and 3.75 m from the arable field. In the *Lolium perenne* sown plots a steady and significant increase in species numbers was observed with increasing distance from the field and in the regeneration plots the 0.75 and 1.25 m subplots differed significantly (higher) from the 3.75 subplot only (Table 4.3a-c).

While in the grass- and regeneration-plots no significant relationship existed between total biomass production and species-richness, in the forbs-plots a significant negative regression was found (Fig. 4.4). This relationship was mainly determined by a limited number of plots with very high biomass production and low species numbers, all of them located within 1 meter from the arable field.

Table 4.3b. The distribution of some of the most common species (in percentage of total biomass) , total biomass production and number of species in relation to distance from the field in plots sown to Lolium perenne in spring 1993. Species with an asterisk are species originally sown in the forbs plots. n = frequency, total number of sampled subplots is 72. P-values (Monte-Carlo randomization test) are given for differences between distances. Biomass and species number data were analysed by means of ANOVA, different characters indicate significant differences.

distance	n(%)	0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75	P-value
species										
Achillea millefolium	(25)	0.3	4.8	4.1	0.9	1.1	1.2	0.4	0	(0.211)
Agrostis capillaris	(24)	0	0	0.1	0	1.2	0.8	4.3	8.6	(0.000)
Artemisia vulgaris	(15)	0	4.5	0.1	0	0.4	5.9	5.9	6.8	(0.701)
Cirsium arvense	(15)	4.1	3.0	1.7	3.0	1.6	1.0	0	1.1	(0.939)
Crepis capillaris*	(19)	0	3.5	3.5	2.7	3.0	2.1	0.4	0	(0.302)
Dactylis glomerata	(19)	0	0	0	0	0.1	0	2.8	0.3	(0.182)
Elymus repens	(39)	0	0	0.1	0	0.2	1.9	6.4	8.8	(0.000)
Equisetum arvense	(19)	0	0	0	0.2	0.6	0.4	0.8	1.6	(0.001)
Erigeron canadensis	(25)	0.1	0.1	0.5	0.4	0.1	0	0.1	0	(0.164)
Festuca rubra ssp. commutata	(15)	0	0	0	0	0	0.4	0.2	6.1	(0.000)
Holcus lanatus	(38)	3.4	8.0	5.2	7.4	9.9	17.7	20.6	14.2	(0.093)
Holcus mollis	(13)	0.7	0	0.4	0	0	0.6	4.9	13.5	(0.001)
Lolium perenne	(99)	84.9	71.6	76.7	75.0	69.5	54.9	47.9	27.2	(0.000)
Rumex acetosa	(14)	0.1	0.1	0.4	0.9	0	0.7	1.4	0	(0.530)
Trifolium repens	(17)	0	0.2	0	0	0	0	0.1	0	(0.191)
Vicia hirsuta	(40)	4.0	1.4	4.5	2.7	4.7	1.8	1.4	2.1	(0.882)
Vicia sativa ssp nigra	(18)	0.3	1.1	0.6	1.3	1.3	0	0	0	(0.094)
total biomass (g/m^2)		343.6	466.0	404.8	342.4	334.0	438.4	408.0	414.8	
no. species		3.6^d	4.9^{cd}	5.6^{bc}	5.6^{bc}	7.0^{ab}	5.7^{bc}	6.6^{abc}	7.8^a	

For individual species, four types of distribution patterns could be distinguished (Table 4.3a-c): I. Species showing a random distribution pattern, such as *Galium mollugo* in the forbs-plots, *Vicia hirsuta* in the grass-plots and *Agrostis capillaris* in the regeneration-plots. II. Species significantly increasing in relative abundance with increasing distance from the arable field. Examples are the species *Hieracium pilosella* in the forbs-plots, *Agrostis capillaris* in the grass-plots and *Festuca rubra* ssp. *commutata* in the regeneration-plots. III. Species significantly decreasing in abundance with increasing distance from the arable field. The most striking example was *Tanacetum vulgare* in the forbs-plots which decreased in mean relative performance from 60% of the total biomass at 0.25 m from the arable field to 4% at 3.75 m, despite the fact that it was sown evenly and established accordingly in the first year. *Lolium perenne* and *Cirsium arvense* showed similar patterns in the grass- and regeneration-plots respectively, and especially the pattern of *Cirsium arvense*, which established only by rhizomatous growth, is peculiar since it originated from the pre-existing boundary. Thus in within three years it grew through the four meter wide regeneration-plots and concentrated above-ground biomass production in a zone within 1.5 m from the arable field. IV. Species with a significantly higher abundance in the middle of the plot. In particular, *Holcus lanatus* in the regeneration-plots and *Saponaria officinalis* in forbs-plots.

Although most annual weeds had been able to produce very large quantities of seeds in the first season, these species were virtually absent in the third year. The most common arable weeds that persisted in the boundary plots after two years were *Elymus repens*, followed by *Vicia hirsuta* and *Cirsium arvense* respectively. Based on their mean relative performance, however, *Elymus repens* and *Cirsium arvense* were the only weedy species of significance in

***Table 4.3c.** The distribution of some of the most common species (mean ratio of total biomass) , total biomass production and number of species in relation to distance from the field in plots left **regenerating** since spring 1993. Species with an asterisk are species originally sown in the forbs plots. n = frequency, total number of sampled subplots is 72. P-values (Monte-Carlo randomization test) are given for differences between distances. Biomass and species number data were analysed by means of ANOVA, different characters indicate significant differences.*

distance	n	0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75	P-value
species										
Achillea millefolium	(29)	7.7	10.5	8.3	8.5	6.3	3.7	0.3	0	(0.188)
Agrostis capillaris	(38)	3.4	7.5	0.1	2.0	1.5	3.4	5.2	9.3	(0.742)
Arrhenatherum elatius	(11)	0	0	7.2	8.5	10.5	7.3	10.1	7.9	(0.487)
Artemisia vulgaris	(15)	8.8	0.1	1.3	0.9	0.3	1.6	0.9	1.0	(0.902)
Bromus hordeaceus	(11)	4.6	5.3	5.4	6.1	7.0	3.0	2.5	0.1	(1.000)
Cirsium arvense	(36)	15.1	11.0	10.0	5.7	4.4	2.4	0.8	0.1	(0.001)
*Crepis capillaris**	(19)	0.1	0.1	0.9	0.4	0	0	0.2	0	(0.095)
Dactylis glomerata	(31)	0.1	0.3	0.1	0.1	0.8	1.0	0	2.2	(0.077)
*Daucus carota**	(11)	0.02	0.03	0.02	0	0.65	0	1.09	0	(0.963)
Elymus repens	(69)	3.3	3.4	2.1	1.1	2.4	7.8	11.8	13.1	(0.023)
Epilobium ciliatum	(22)	2.3	3.5	0.3	0.1	0.6	0.2	0.1	0	(0.165)
Equisetum arvense	(13)	0	0.2	0.2	0.4	0.9	1.2	0.8	0.3	(0.892)
Erigeron canadensis	(21)	0.7	0.3	0	0.4	0.4	0.4	0	0	(0.358)
Festuca rubra ssp. *commutata*	(33)	0	0	0.3	0.4	6.1	16.1	18.2	20.7	(0.000)
Holcus lanatus	(64)	14.3	23.1	39.0	56.2	41.2	34.6	27.8	13.7	(0.001)
Holcus mollis	(15)	0	0	0	0	0.1	1.1	7.6	21.2	(0.001)
*Hypochaeris radicata**	(31)	0.1	1.0	3.1	0.2	0.3	0.1	0.1	0.1	(0.059)
Juncus effusus	(19)	0	0.9	1.2	0.2	0	0.1	0	0	(0.177)
Leontodon autumnalis	(11)	4.4	0.05	0.02	0	0	0.02	0.04	0	(0.202)
Ranunculus repens	(49)	2.0	1.5	1.6	0.2	0.1	0	0.1	0	(0.134)
Rumex acetosa	(21)	0	0.1	0.9	0.3	0.7	0.9	0.8	1.4	(0.674)
Rumex obt. ssp. *obtusifolius*	(29)	19.0	11.7	6.2	0.6	3.7	5.8	8.1	6.9	(0.562)
Trifolium repens	(24)	0	0	0	0.2	1.0	0.6	0.4	0.4	(0.003)
Urtica dioica	(14)	2.7	3.1	1.1	0	0	0	0	0	(0.036)
Vicia hirsuta	(31)	0.3	1.6	2.4	1.1	0.7	0.6	0.4	0	(0.025)
Vicia sativa ssp *nigra*	(17)	0.4	0.5	0.5	0.2	0.1	0.1	0.2	0	(0.288)
total biomass (g/m^2)		732.0^a	539.2^{ab}	438.4^b	393.6^b	386.4^b	415.6^b	444.8^b	544.4^{ab}	
no. species		8.7^{ab}	9.8^a	9.4^a	8.4^{ab}	8.4^{ab}	8.6^{ab}	8.6^{ab}	6.9^b	

the boundary plots. On average they remained minor components of the vegetation, never contributing more than *c.* 15 percent of the total vegetation, however, in individual subplots they occasionally dominated the vegetation with mean relative performances of 80 and 79% respectively. Figure 4.5a and b shows that, although the two species displayed opposite distribution patterns, both species had their highest mean relative performance in the regeneration-plots and the lowest in the forbs-plots. Averaged over the transect, biomass production of *Cirsium arvense* declined from 33.4 g/m^2 in the regeneration-plots to 7.5 g/m^2 in the grass-plots (difference significant at P<0.05) and to 0.1 g/m^2 in the forbs-plots (difference between grass- and forbs-plots: P<0.01). Biomass production of *Elymus repens* was with 27.7 g/m^2 significantly higher (P<0.05) in the regeneration plots than in the grass-plots (9.0 g/m^2) and the forbs-plots (5.8 g/m^2). Biomass production of the grass- and the forbs-plots did not differ significantly. The biomass production of *Elymus repens* and *Cirsium arvense* did not differ significantly in the regeneration- and the grass-plots but *Elymus repens* was more successful in the forbs-plots (P<0.001).
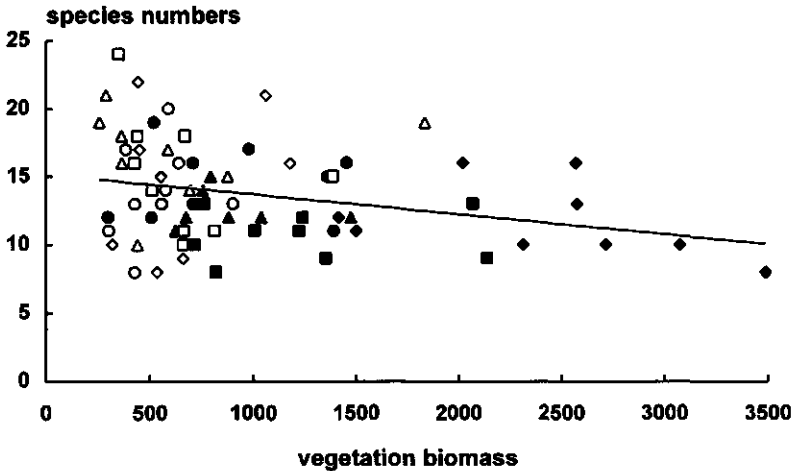
species numbers

Figure 4.4 Relationship between vegetation biomass production (g.m⁻²) and species numbers (0.25 m⁻²) in the forbs-plots. Regression significant (P<0.01). Closed diamants: 0.25 subplot, squares (0.75), triangles (1.25), circles (1.75); open diamants (2.25), squares (2.75), triangles (3.25), circles (3.75).

Discussion

Although the establishment of most of the sown species, including species with low competitive ability, was good, the number of species colonizing the new field boundary plots was low. Only two species were completely new to the field margin and 16, all common to very common species, failed to establish from within 5 meter distance. Similar observations were made by Graham & Hutchings (1988) and Smith & MacDonald (1989) and must be related to the absence of a seed bank and the limited dispersal ability of species characteristic of a perennial grassy vegetation (Hume & Archbold 1986, Van Dorp 1996)

A remarkable result was the increase in biomass production near the arable field in the forbs- and regeneration-plots, which was not found in the grass-plots. Both the regeneration- and the forbs-plots were characterized by a limited number of species with peak mean relative performance close to the arable field which were absent in the grass plots. In the forbs-plots *Tanacetum vulgare* and in the regeneration-plots *Cirsium arvense* and *Urtica dioica* have in common that they are very tall and strong competitors (Grime *et al.* 1988). Kleijn (1996) found that this type of species was able to efficiently capture nutrient resources from the arable field and use it for increased biomass production in the boundary while species of low stature were less able to do so. Campbell *et al.* (1991) and Grime (1994) found species to contrast in their scale of root foraging. Tall, dominant plant species such as *Urtica dioica* were found to actively adjust root and shoot growth into locally resource-rich zones while low-growing species like *Campanula rotundifolia* rather depended on capturing pulses of resources in nutrient-poor environments more efficiently. Thus, it is likely that the success of tall, competitive species in the field boundary plots is related to their ability to use nutrient resources from the arable field for increased biomass production in the boundary. *Tanacetum vulgare* indeed grew roots well over 70 cm into the arable field (Fig. 4.6) while its clonal
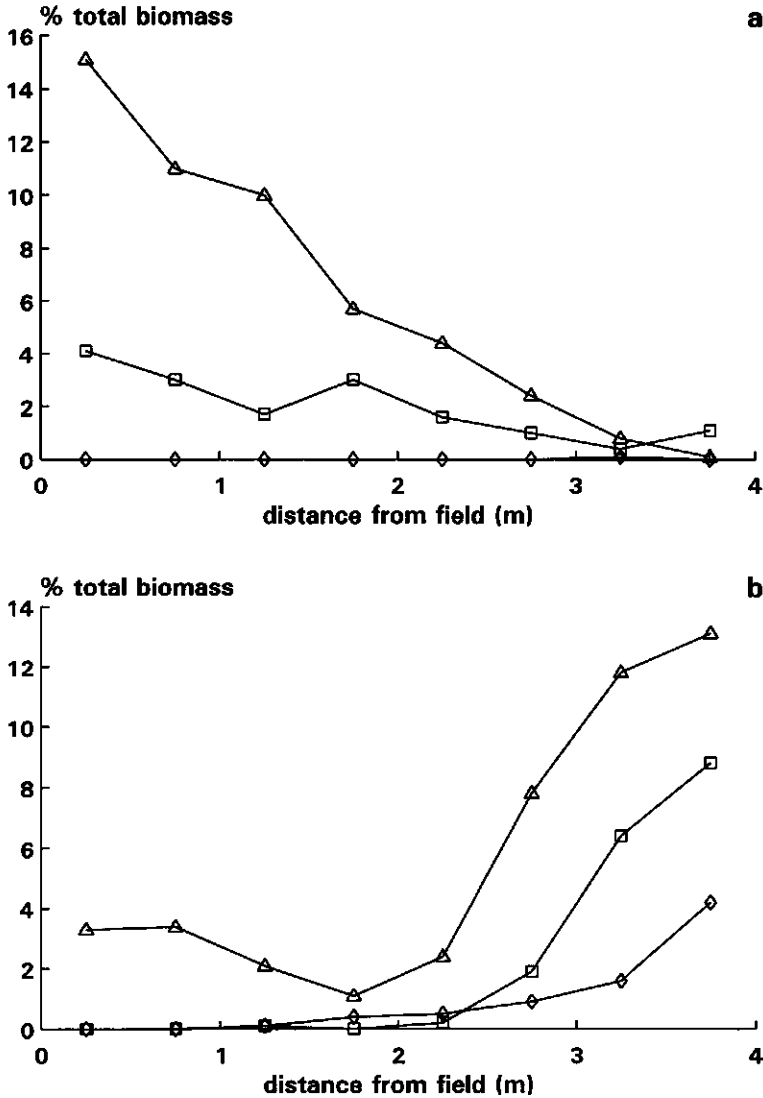
Figure 4.5 *Mean relative ecological performance (biomass species in subplot/total biomass in subplot x 100%) across the experimental field boundary plots for two weedy species: (a)* Cirsium arvense *and (b)* Elymus repens. *Forbs plots: diamants; Lolium perenne plots: squares; regeneration plots: triangles.*

growth habit may explain why the biomass increase was detectable so far from the arable field in the forbs-plots: a single clone can easily cover 1.5 meters with its roots and rhizomes.Presence of these species in the forbs- and regeneration-plots and their absence in the grass-plots is probably the cause for the differential occurrence of the biomass increase in the boundary plots. The distribution pattern displayed by for instance *Hieracium pilosella,* an increasing mean relative performance with increasing distance from the arable field, will be
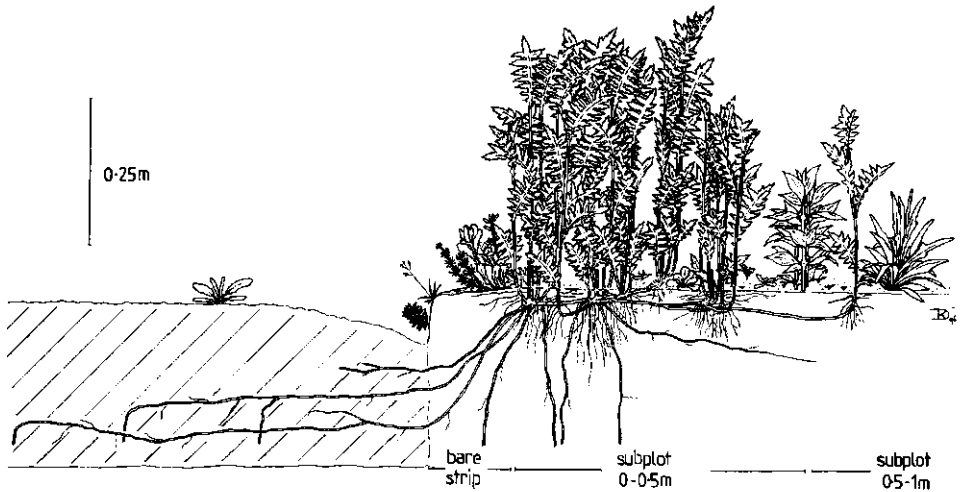
Figure 4.6 *Distribution of shoots, roots and rhizomes of a single* Tanacetum vulgare *plant dug out on 13 May 1996. Total vegetation is depicted above-ground while below-ground only roots and rhizomes of T.* vulgare *are shown. Shaded area is the cultivated soil, ploughed on 7 March 1996.*

the indirect result of the increase in above-ground biomass production in the zone near the arable field. In contrast to the grass species showing similar patterns (the result of the steady but incomplete colonization of the boundary plots from the side of the original boundary) *Hieracium pilosella* , like *Tanacetum vulgare*, was distributed evenly over the forbs-plots at the onset of the experiment. Being a very small and prostrate species, *Hieracium pilosella* must have been shaded out in the zone near the arable field and only survived in the areas with the lowest biomass production.

Interpretation of the species numbers data is difficult since the vegetation within the plots is still far from stable. Species from the original boundary, predominantly grasses, are progressively moving into the boundary plots and may increase species numbers on the one hand (as is most probably the case in the grass-plots) but on the other hand may decrease species numbers as a small number of grasses replace a higher number of forbs and annual species. Thus, predictions about long-term development of species-richness can not yet be made. However, within the forbs-plots with their initially high and uniform species-richness, species numbers after 3 years proved to be related to vegetation biomass production (Fig. 4.4). The high productivity of the vegetation near the arable field caused species numbers to decline. This may be caused by the simple fact that more small than large plants, and thus species, can grow on 0.25 m^{-2} (Oksanen 1996). It was, however, also caused by the incapability of small species like *Hieracium pilosella* to persist in a tall productive vegetation while tall species like *Tanacetum vulgare* wére able to persist in a low productive vegetation. Most normal field boundaries are not wider than 1 m. Therefore, the vegetation biomass increase resulting from the capture of arable nutrients by a small number of dominant species may be very relevant to the low species-richness observed in most modern field boundaries.

The only weedy species with a significant abundance in the boundary plots in this experiment, *Elymus repens* and *Cirsium arvense*, are considered to be the most important

boundary related weed species by farmers (De Snoo & Wegener Sleeswijk 1993). In this experiment, similar to the findings of Smith & MacDonald (1992), abundance of both species was significantly higher in unsown than in sown boundary plots although they had almost opposite distribution patterns across the boundary plots (Fig. 4.5a-b). Abundance of these species is largely related to the absence of competition (Bakker 1960, Marshall 1990, Schmidt & Brübach 1993). Maintaining a competitive perennial vegetation therefore seems to be the best option to control these species in arable field boundaries. The use of herbicides in the field boundary vegetation, presently the most common weed control measure in field boundaries, will probably lead to an increase of either one of the species. Since presently no herbicides exist which control both species without killing the entire vegetation, killing one species will create gaps in the vegetation that benefit the other.

The most important agriculture related factor affecting vegetation composition in this experiment was the abundance of nutrients in the arable field which benefited some species but not others. The biomass increase of a limited number of species resulted in a striking gradient in vegetation height and structure with low numbers of large plants near the arable field and high numbers of small plants near the original boundary (compare Fig. 4.1a and 4.1b). Indirectly species-richness was affected by the gradient in productivity of the vegetation. However, irrespective of any relationship between vegetation productivity and species-richness we could observe that species numbers only reached considerable levels when species were sown. Colonization ability of potential field boundary species was very limited and this might prove to be the most important problem in restoring field boundary diversity. It may take very long indeed before improvement of the habitat results in a more diverse habitat.

Acknowledgements

5

A short note on the effects of newly created herbaceous boundary strips on crop yields and weed pressure in the crop edge

Summary

Three years after establishment, the effects of different types of extended field boundaries on the crop edge of conventionally cultivated fields were examined. In the original crop edge, crop yields, numbers of weed species and weed biomass production were determined at 0.5, 4.5 and 15 m from the boundary. Next, these variables were determined in a new crop edge 0.5 m from four metre wide newly created boundary plots which were established by natural regeneration, sowing with a mixture of grassland forbs or sowing with *Lolium perenne*. Crop yields at 0.5 m from the original boundary were significantly lower than those at 4.5 and 15 m. Furthermore, at this position weeds were more abundant in terms of species numbers and biomass production. Three years after creation of the boundary plots, crop yields next to these plots were significantly lower compared to those obtained under pre-establishment conditions. However, the effects of the forbs and regeneration plots were significantly more severe than those of the grass plots. Boundary vegetation productivity, rather than weed pressure, proved to be the most important correlate of crop yields in the field edge.

Keywords: crop edge, extended field boundary, weeds, crop yield.

Introduction

The outer metres of arable fields are generally characterized by lower crop yields and a more abundant weed flora compared to the centre of the field (Boatman & Sotherton 1988, de Snoo 1994, Kleijn & van der Voort 1997). Poor crop performance in this area is generally contributed to shading, soil compaction from farm machinery, poor seedbed preparation, damage to the growing crop and/or the less efficient fertilizer application (Marshall 1989, Rew *et al.* 1992b, Wilson & Aebischer 1995). Furthermore, competition between crop and weeds may be responsible for suppressed crop yields, although, the results of Kleijn & van der Voort (1997) suggest that the abundance of weeds in the crop edge is in part a result rather than a cause of the poor crop performance.

In recent years, extension of field boundaries has been promoted as a means to increase

field boundary diversity (Boatman 1992, Feber *et al.* 1996, Stoate & Szczur 1994). In addition to the increased area of wildlife habitat, broader and better developed hedgebottoms or ditch banks may also reduce weed ingress from the boundary to the field (Rew *et al.* 1992a, Theaker *et al.* 1995b). Establishment of a well developed perennial vegetation eliminates or reduces the abundance of most annual and perennial arable weeds in the boundary (Boatman *et al.* 1994, Marshall 1990, Rew *et al.* 1995, Smith & MacDonald 1992, Theaker *et al.* 1995a). The way a boundary strip is created may however seriously affect the new crop edge. In boundary strips created by sowing grass or a grass/forbs mixture, weed species have a significantly lower abundance than in naturally regenerating boundary strips (Kleijn *et al.* 1997, Smith & MacDonald 1992). The new crop edge may reflect these differences.

An experiment described by Kleijn *et al.* (1997) facilitated an analysis of the effects of establishing different types of herbaceous boundary strips on crop edge characteristics such as crop yield, weed yield and number of weed species. In particular the following questions were addressed: (1) Do old and new crop edges differ in weed vegetation and crop yields and (2) Are crop yield and weed vegetation in the new crop edge influenced by the type of boundary strip?

Methods

In April 1993, the field boundaries of three arable fields were expanded by taking the outer four metres of the field out of production. All fields were located in the vicinity of Wageningen, had sandy soils and a crop rotation including cereals, sugar beets, potatoes and silage maize. In the expanded boundary strips a perennial vegetation was created in 8 x 4 m plots in three different ways: (1) by sowing a mixture of 30 grassland forbs, (2) by sowing *Lolium perenne* and (3) by allowing natural regeneration. The normal crop rotation was maintained in a fourth plot type which served as control plot. The four plot types were randomly arranged within replicated blocks and each field had three such blocks. The new boundary plots were mown annually in autumn and cuttings were removed. In contrast, in the original boundary standard management was maintained: flail mowing once a year after crop harvest without removing the cuttings. Details of crop rotation, herbicide and fertilizer inputs and vegetation composition in the boundary plots are given in Kleijn *et al.* (1997).

In the crop edge, vegetation assessments were made in 0.5 x 2.0 m large quadrats parallel to the boundary at 0.5 m from the old and new perennial boundary vegetation (Fig. 5.1; PQ1 in control plot and PQ2 next to the boundary plots). In the control plots additional assessments were made at 4.5 and 15 m from the original boundary (PQ2 and PQ3 respectively). This last sample position represented the centre of the field. On both sides of each quadrat, biomass samples were taken in two 0.5 x 0.5 quadrats (Fig. 5.1, S). The weeds in the crop plots were sampled at the time of crop harvest, by cutting all above-ground biomass. Crops were harvested at each position in two 0.5 x 0.5 m quadrats for wheat and phacelia, two times 0.5 m within a row for sugar beet and maize and two times 0.7 m within a row for potatoes. Sugar beets and potatoes were rinsed and wheat was threshed before determining air-dry fresh weight of the harvestable product. Of phacelia and maize as well as the weed samples dry weight was determined after 48 hours at 80° C. Additionally, biomass data of boundary plot productivity 0.5 m from the field (Fig. 5.1, S*) were taken from Kleijn *et al.* (1997)
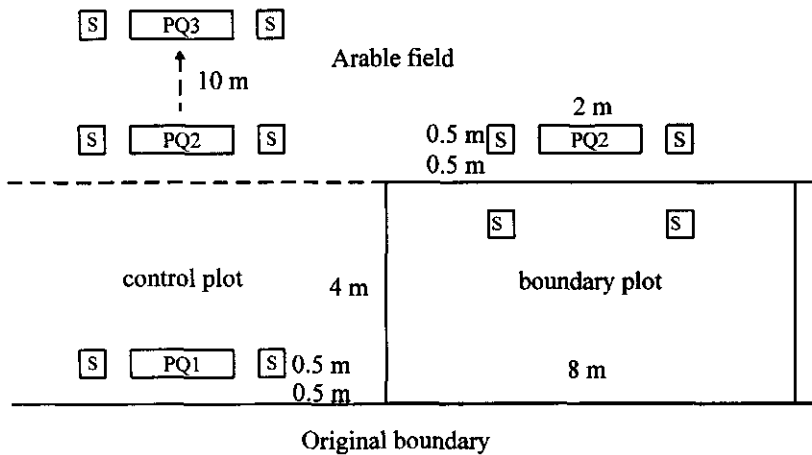
Figure 5.1 *Lay-out of the extended boundary plots. PQ1: position of vegetation assesment 0.5 m from the original boundary, PQ2 at 4.5 m and PQ3 at 15 m. S: biomass sample quadrat; S*: biomass sample quadrat data from Kleijn et al. (1997).*

Analysis

Treatment effects for all variables were analysed by means of a nested analysis of variance with fields as the top stratum. Replicated blocks were nested within fields, years within blocks and the treatments plot type or PQ-position (in the control plots) within year. The effect of plot type and position were analysed separately resulting in 3 fields(3 replicated blocks(2 years(4 plot types))) = 72 experimental units for the plot type effects and 3 fields(3 replicated blocks(2 years(3 positions))) = 54 experimental units for position effects.

Differences between means were tested by means of LSD tests (GENSTAT 1993) only after significant treatment effects were found. Furthermore, means were not compared for significant differences between years. If significant field-treatment effects were found, treatment effects were analysed at the level of individual fields.

The relationship between crop performance in the crop edge and number of weed species, weed biomass production as well as boundary vegetation productivity were analysed by means of regression analysis. Both linear and non-linear models (standard non-linear curves available in the GENSTAT (1993) statistical package) were used to select the model that fitted the data best. For this analysis only plots next to the newly established boundary plots were used and to standardize the data of different crops in the three fields, crop yields at these positions were divided by their field means, resulting in a 'crop yield ratio'. Prior to both the ANOVA's and the regression analysis the variance of the errors was tested. If the error variance was not constant for different values of the response variable, ln-transformed data were used in the analyses.

Table 5.1 *Mean crop yields (g.m^{-2}) in relation to distance from the field boundary in the control plots on the experimental fields Amfoort, Bornsesteeg and Keijenberg in 1994 and 1995. Different characters indicate significant differences (ab 1994, e-g 1995, - missing value).*

distance boundary:	0.5 m	4.5 m	15 m
Amfoort			
1994 (Sugar Beet)[1]	5698[a]	3896[a]	5071[a]
1995 (Potato)[1]	2536[e]	3111[ef]	5435[f]
Bornsesteeg			
1994 (Potato)[1]	1172[a]	2011[b]	1961[b]
1995 (Spring Wheat)[1]	-	-	-
Keijenberg			
1994 (Phacelia)[2]	363[a]	570[b]	360[a]
1995 (Silage Maize)[2]	830[e]	2461[f]	1912[f]

[1] fresh weight, [2] dry weight

Results

In the control plots, crop yield distribution from the field boundary to the centre of the field changed with years and was not constant between fields (Table 5.1, field-position interaction F^6_{36} = 8.11, $P<0.001$). Therefore, the effect of position in the field on crop yields were analysed for each field separately. In general, the 0.5 m sample plots yielded lowest and the 4.5 and 15 m sample plots did not differ statistically significant. A noteworthy exception, however, was the 1994 Phacelia field on Keijenberg, which yielded significantly higher at

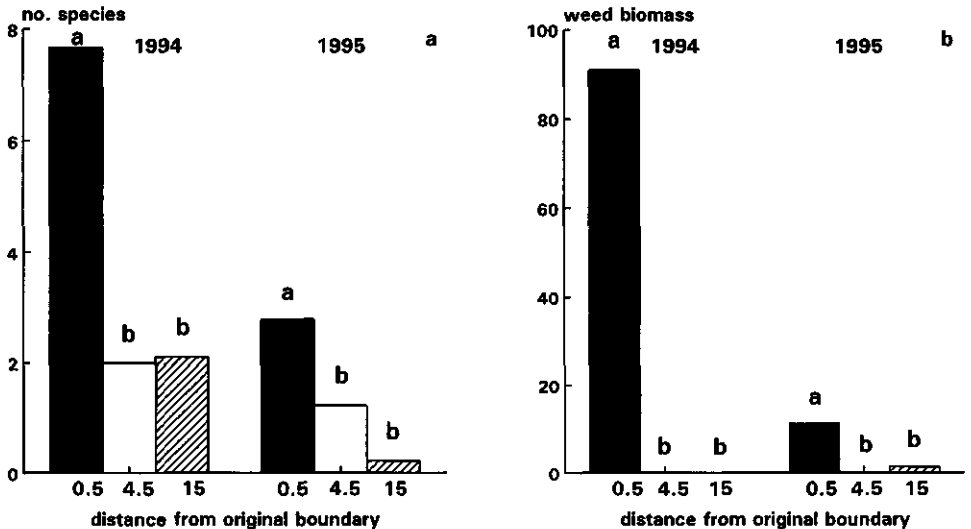**Figure 5.2** *(a) Number of weed species (m^{-2}) and (b) weed biomass production (g dry weight.m^{-2}) in the control plots at 0.5 m (filled bars), 4.5 m (open bars) and 15 m (hatched bars) from the original field boundary in 1994 and 1995. Mean data of the three experimental fields are given. Different characters indicate significant differences (P<0.05).*

Table 5.2 *Mean crop yields (g.m⁻²) in the crop edge 0.5 m (PQ2) next to control, forbs, grass and regeneration plots in 1994 and 1995 on the experimental fields Amfoort, Bornsesteeg and Keijenberg. Different characters indicate significant differences (ab 1994, e-g 1995).*

plot type:	control	forbs	grass	regeneration
Amfoort				
1994 (Sugar Beet)[1]	3896^b	6863^{ab}	6184^{ab}	6797^a
1995 (Potato)[1]	3111^f	3407^{ef}	5969^e	2547^f
Bornsesteeg				
1994 (Potato)[1]	2011^a	1025^b	1548^{ab}	1399^{ab}
1995 (Spring Wheat)[1]	946^e	400^f	718^e	683^{ef}
Keijenberg				
1994 (Phacelia)[2]	570^a	265^b	330^b	329^b
1995 (Silage Maize)[2]	2461^e	313^g	740^f	850^f

[1] fresh weight, [2] dry weight

4.5 m from the boundary compared to the other two positions. The similarity between the 4.5 and 15 m sample plots is relevant to the analysis of the plot type effect since it implies that the yield levels bordering the control plots (PQ2) were representative of yields in the centre of the field. Subsequent differences between PQ2 next to control plots and PQ2 next to boundary plots will then indicate that the establishment of the boundary plots have led to significant deviations from the (pre-establishment) centre-of-field crop yield levels.

The natural vegetation in the control plots was less variable between years and fields (no significant field· position interaction). Species numbers were very low in all but the 0.5

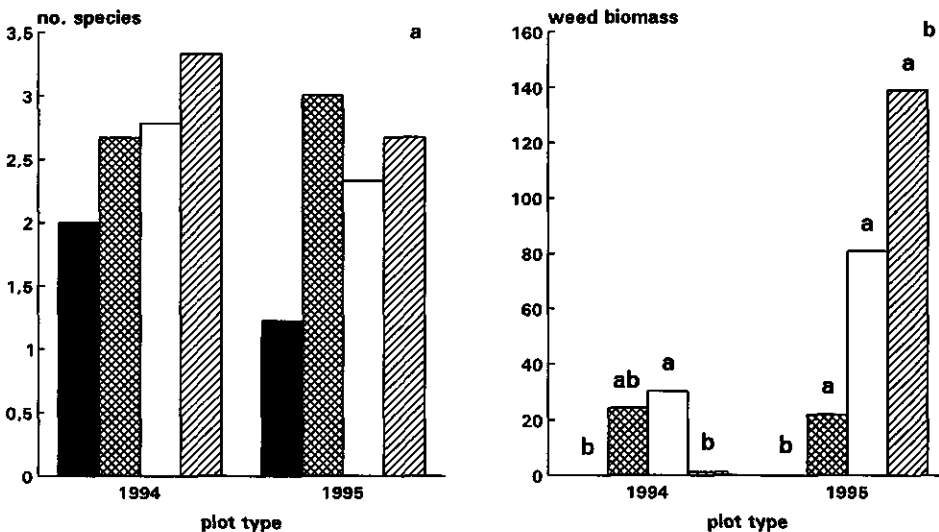**Figure 5.3** *(a) Number of weed species (m⁻²) and (b) weed biomass production (g dry weight.m⁻²) next to control plots (filled bars), forbs plots (cross hatched bars) grass plots (open bars) and regeneration plots (hatched bars) in 1994 and 1995. Mean data of the three experimental fields are given. Different characters indicate significant differences (P<0.05).*
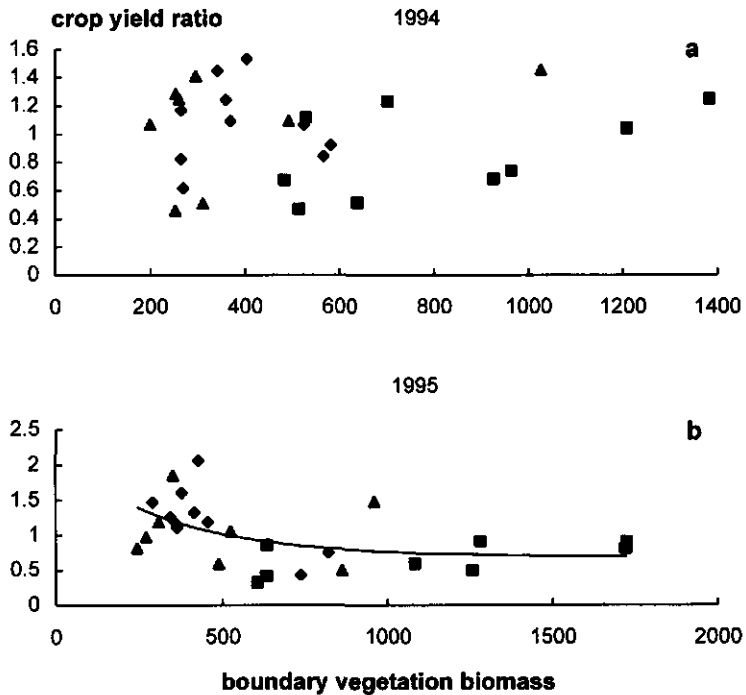
Figure 5.4 The relationship between crop yield ratio (sample plot yield/field mean yield of the quadrats next to the new boundary plots) and boundary productivity (g dry weight.m^{-2}) in (a) 1994 and (b) 1995. Forbs plots: squares, grass plots: diamonds; regeneration plots: triangles. 1994 regression analysis not significant, 1995 regression analysis: $F^2_{24} = 3.85, P = 0.035$.

quadrats in 1994 (Fig. 5.2a). Both weed species numbers and weed biomass production were significantly higher in the 0.5 m sample plots compared to the 4.5 and 15 m sample plots (Fig. 5.2b). Only two species were found which are not very common arable weeds, *Anchusa arvensis* and *Papaver dubium*, however, these were only encountered in the unsprayed Keyenberg field in 1994 (Appendix 5.1).

Analysis of plot type effects revealed a significant field.plot type interaction ($F^4_{20} = 26.93$, *P*<0.001) for crop yield. On the experimental fields of Bornsesteeg and Keijenberg a relatively consistent pattern was found in both years in which the control plots > grass plots ≥ regeneration plots > forbs plots (Table 5.2). In contrast, on Amfoort the control plots yielded lowest. No significant interactions were found for the weed variables. Weed species numbers in the crop edge along different types of plots did not differ significantly in any of the years (Fig. 5.3a). In 1994, differences in weed biomass production next to the four plot types were small but already significant: weed biomass production next to grass plots was significantly higher than that next to regeneration and control plots (Fig. 5.3b). In 1995, differences had increased vastly. Weed biomass production next to all three perennial boundary plots was significantly higher than next to the control plots. Especially noteworthy was the strong weed

biomass increase between 1994 and 1995 next to the regeneration plots.

Regressing crop yields to weed species numbers or biomass production did not reveal any statistically significant relationships in both 1994 and 1995. In 1995, however, the relationship between crop yields and weed biomass production had a significance level of $P =$ 0.097, indicating a trend which may increase with progressing years. The biomass production in the adjacent boundary plots may be a measure of the extent to which the field boundary vegetation competes with the crops in the field edge. In 1994 there was no significant relationship between crop yield and boundary biomass production (Fig. 5.4a), however, in 1995 the yield ratio declined exponentially with increasing productivity of the boundary vegetation ($F^2_{24} = 3.58$, $P = 0.035$). In this year crop yields next to boundary plots with high productivity levels (predominantly the forbs plots) was severely suppressed (Fig. 5.4b).

Discussion

Similar to the findings of Boatman & Sotherton (1988), de Snoo (1995) and Wilson & Aebischer (1995) the original crop edges in these experiments were characterized by lower crop yields and a higher abundance of weeds. However, the lower crop yield levels were limited since at 4.5 m from the boundary crop yields were at least equal to yields in the centre of the field.

Three years after establishment of the boundary plots the sample quadrats next to those plots already showed strong similarities with the original crop edge. A new crop edge had developed characterized by lower crop yields and higher weed biomass production compared to the levels obtained at the same location but without boundary influences. The new crop edge, however, differed by having a similar number of weed species compared to the centre of the field, while the old crop edge contained significantly more species than the centre of the field. A large number of arable weed species decline in abundance with increasing distance from the field boundary (Marshall 1989, Wilson & Aebischer 1995, Kleijn & van der Voort 1997). Therefore, these species may not be present at the location of the new crop edge, or in insufficient numbers to survive weed control measures. The outer metres of arable fields often provide a last refuge for rare arable weeds and the present results suggest that, when such species are present in the crop edge, field boundaries should not be extended.

The three methods of extending a field boundary affected crop production in the field edge differently. While the effects vary somewhat between years and fields, extension through sowing of *Lolium perenne* seems to have the least and the forbs mixture the most negative consequences for crop production. In contrast, weed biomass production in 1995, although not significantly different, was a factor 4 lower in the forbs plots compared to the grass plots. Accordingly, weed biomass production was not significantly related to crop yields. In these experimental fields biomass production of the boundary vegetation proved to be the most important explanatory variable of crop yield. Kleijn (1996) and Kleijn *et al.* (1997) found plants in field boundaries to be able to grow roots into the arable field for a considerable distance and capture nutrients applied to the crop. In these experimental fields the very tall species such as *Cirsium arvense*, *Tanacetum vulgare* and *Urtica dioica* did so most efficiently (Kleijn *et al.* 1997). Thus, tall field boundary vegetation is capable of effectively competing with and reducing yields of crops in the field edge.

These experiments only analysed the effects of an extended field boundary on the first

metre of the arable field. Effects may extend further into the field. However, in the Netherlands fields on sandy soils are generally rather small. The first metre along the boundary of a 1 ha large field comprises at least four per cent of the total field area and usually more due to the irregular shape of many of these fields. A general result of this experiment is that tall productive boundary vegetation such as nettle thickets (*Urtica dioica*) may seriously decrease crop production in the field edge. From a crop production point of view, extended field boundaries may preferentially be created by sowing short grass species since this hardly affects crop yields in the edge. From the perspective of boundary species richness this is undesirable, however, since it significantly decreases species richness compared to natural regeneration or sowing a mixture of forbs species (Kleijn *et al.* 1997, Smith & MacDonald 1992). Thus, when problem weeds or tall dominating ruderal species are present in the original boundary or crop edge, sowing grass species may be the best alternative. However, when such species are absent in (stretches of) the boundary, creating extended boundaries through natural regeneration is the preferred method.

Acknowledgements

Appendix 5.1 *Species occurring in the experimental fields Amfoort, Bornsesteeg and Keijenberg in 1994 and 1995.* [1] *indicates species found only on the Keijenberg in 1994 when no herbicides were applied.*

Achillea millefolium[1]	*Galinsoga parviflora*[1]	*Rumex obtusifolius* ssp
Anchusa arvensis[1]	*Geranium molle*[1]	*obtusifolius*
Artemisia vulgaris[1]	*Holcus mollis*[1]	*Senecio vulgaris*[1]
Capsella bursa-pastoris[1]	*Lamium purpureum*[1]	*Solanum nigrum*
Chenopodium album	*Lapsana communis*[1]	*Solanum tuberosum*
Cirsium arvense	*Lolium perenne*	*Sonchus asper*
Crepis biennis	*Matricaria recutita*	*Spergula arvensis*
Crepis capillaris	*Oxalis fontana*	*Stellaria media*
Echinochloa crus-galli	*Papaver dubium*[1]	*Taraxacum officinalis*
Elymus repens	*Phacelia tanacetifolia*	*Trifolium repens*
Equisetum arvense	*Picris hieracioides*	*Triticum aestivum*
Erigeron canadensis	*Poa annua*	*Veronica arvensis*[1]
Erodium cicutarium ssp	*Polygonum amphibium*	*Vicia hirsuta*[1]
cicutarium	*Polygonum aviculare*	*Vicia sativa* ssp *nigra*[1]
Festuca rubra ssp	*Polygonum convolvulus*	*Viola arvensis*
commutata	*Polygonum persicaria*	

6

The use of nutrient resources from arable fields by plants in field boundaries

Summary

The effect of a nutrient-rich arable field on the biomass production of the bordering field boundary vegetation was examined. Biomass transects were made in experimental boundary plots and normal field boundaries. Experimental boundary plots shielded from the arable field by a physical barrier and field boundaries next to an unfertilized crop edge were used as respective controls. Three clonal and three non-clonal species were transplanted to the edge of the experimental boundary vegetation plots to determine whether growth strategy affected nutrient capture efficiency. The response in biomass production was analyzed after three months of growth. The increase in yield when plants were able to profit from arable field resources was similar, and in some cases greater, in non-clonal species than in clonal species. Biomass production increased significantly only in the first 10 to 20 cm of boundary vegetation. The boundary vegetation further from the field was shielded from direct effects. The effects of the capture of arable field nutrients by the boundary vegetation have consequences for field boundary management. In field boundary vegetation that is annually cut and removed effects will be limited but boundary management that does not include removal of the cuttings may result in an accumulation of arable field nutrients in the boundary vegetation and subsequently in the loss of species diversity of this habitat.

Keywords: clonal species, diversity, eutrophication, field boundary vegetation.

Introduction

Field boundaries in the agricultural landscape are important for preservation of biological diversity. Unlike the adjacent cultivated fields with arable crops the ditches, hedgerows, roadsides and fences, that form these landscape structures are made up of permanent vegetation. Thus in agricultural areas the distribution of many plant species is limited to the boundary vegetation. Kaule & Krebs (1989) reported that almost 45% of the species in the flora of different parts of Southern Germany grow in edge-habitats which cover no more than 8 to 10 per cent of the landscape. These plant species are however essential for the survival of a multitude of animal species that depend on them for food, shelter, reproduction, overwintering or dispersal (eg Bennet *et al.* 1994, Dennis *et al.* 1994, Hooper 1987).

In the last few decades the diversity of field boundaries in Western Europe has decreased substantially (Boatman 1992, Hooper 1987, van Strien 1991). Nowadays the vegetation of most field boundaries is monotonous and, over wide areas and even countries, is characterized by a few dominant species (Boatman & Wilson, 1988, Joenje & Kleijn 1994). The main causes for the decreased species richness are supposed to be drift of pesticides and misplacement of fertilizer (Melman & van der Linden 1988, Rew *et al.* 1992), close cultivation (Marshall 1987) and direct application of herbicides in boundary vegetation to control weeds (Boatman 1992, Davies & Carnegie 1994, de Snoo & Wegener Sleeswijk 1993). The composition of vegetation bordering an arable field is likely to be further affected by the presence of an adjacent nutrient-rich habitat since plants in the field boundary may actively capture nutrients by extensive root growth into the field. Another aspect of modern field boundaries, the presence of a number of serious arable weeds in both the boundary vegetation and the crop (Theaker *et al.* 1995), may be linked to this phenomenon. In the Netherlands most of these weeds are rhizome- or stolon-producing species (de Snoo & Wegener Sleeswijk 1993) whose clonal growth strategy enables them to send out ramets into the arable field. Both Alpert & Mooney (1986) and Stuefer *et al.* (1994) observed biomass increases of both daughter ánd mother ramets of clones growing in heterogeneous habitats, as compared with clones growing in homogeneous habitats. These benefits, attributed to the exchange of limiting resources between mother and daughter ramet, may also occur in field boundaries and give mother ramets a competitive advantage over neighbouring non-clonal species in the boundary.

The active capture of resources from arable fields may have considerable consequences for the diversity of field boundary habitats. Increases in biomass production in perennial herbaceous vegetation types generally result in a loss of species richness (Berendse *et al.* 1992, Grime 1979, Mountford *et al.* 1993, Tilman 1993). Furthermore, if clonal weeds have a competitive advantage in field boundaries, it may be such species that become dominant. Subsequent control by farmers, usually by the application of broad spectrum herbicides (de Snoo & Wegener Sleeswijk 1993), will cause further deterioration in field boundary diversity. Demonstration and quantification of the effects of the capture of arable nutrient resources may therefore make an important contribution to the knowledge of how to manage field boundaries properly for wildlife and crop protection.

The experiments described below address two questions. Firstly, does field boundary vegetation increase its biomass production significantly in response to the high nutrient level in the arable field? Secondly, if so, do clonal plant species profit more efficiently from the presence of the arable field than non-clonal plant species?

Methods

Effects of arable nutrient resources on biomass production of the boundary

Two experiments were carried out. Experiment 1 was aimed at determining accurately the impact of the arable field on the field boundary vegetation; homogeneous boundary vegetation was established experimentally and was then either allowed to grow roots into a fertilized arable field or access to the field was denied by means of a barrier. Experiment 2 was aimed at determining the effect of arable field nutrients in a normal field boundary;

existing boundary vegetation was allowed to grow roots into either a fertilized or a non-fertilized part of an arable field.

Experiment 1

In March 1994 an artificial margin was created next to a recently created arable field. The soil type of the field was loamy sand and the annually-mown meadow from which the field was created had not been fertilized for at least the last five years. As the original vegetation was quite heterogeneous, homogeneous boundary strips were created by removing the original sods and replacing them with a commercially grown turf consisting of *Festuca rubra*, *Lolium perenne* and *Poa pratense*. The arable field was ploughed and sown to spring wheat on 29 April and fertilized according to standard agricultural practice at a rate of 110 kg N/ha (15N:12P:24K).

The experiment was laid out in three replicates of 12 plots of 80 x 90 cm each (see Fig. 6.1). In each replicate, six randomly chosen plots were separated from the arable field by a barrier made of a plastic sheet which was inserted into the soil to a depth of 45 cm. Early in August, at the time of crop harvest, transects were set out in each plot perpendicular to the field edge. Two strips 15 cm wide, were divided into seven 15 x 10 cm subplots, 15 cm from the sides of the plot before harvesting (Fig. 6.1). Above-ground biomass of each subplot was determined on samples cut at ground level. Two 50 x 50 cm quadrats were sampled in the adjacent wheat crop (Fig. 6.1). The samples were dried for 48 hours at 80°C and weighed.

Experiment 2

In 1993, crop edge plots (4 x 8 m) had been established in the outer four metres of two arable fields near Wageningen as part of an experiment described by Marshall *et al.* (1994). The soil type of these fields was loamy sand and the boundaries were ditch banks dominated by grasses, *Festuca rubra* on one field and *Arrhenatherum elatius*, *Dactylis glomerata*, *Festuca rubra*, *Holcus lanatus* and *H. mollis* on the other.

The experiment was laid out in three replicates of two plots within each field. Within each replicate the crop in one plot was treated similarly to the centre of the field whereas the other plot received no fertilizer or herbicides. These plots therefore contrasted only in the amount of fertilizer applied to the crop and the adjacent boundary vegetation was analysed in a similar way to experiment 1. Transects 50 cm wide and 70 cm long, divided in seven 10 x 50 cm subplots were established in the boundary vegetation on 15 and 16 August 1994. The vegetation was cut at ground level, dried for 48 hours at 80°C and weighed to determine dry matter production.

Competitive ability of clonal and non-clonal field boundary species

Experiment 3

An experiment was started in early spring 1994 to test whether clonal species capture arable field resources more efficiently than non-clonal species,. Plant material of three clonal and three non-clonal species typical of field boundaries was collected from boundaries of fields nearby the experimental station. Species were selected to produce a comparable range in
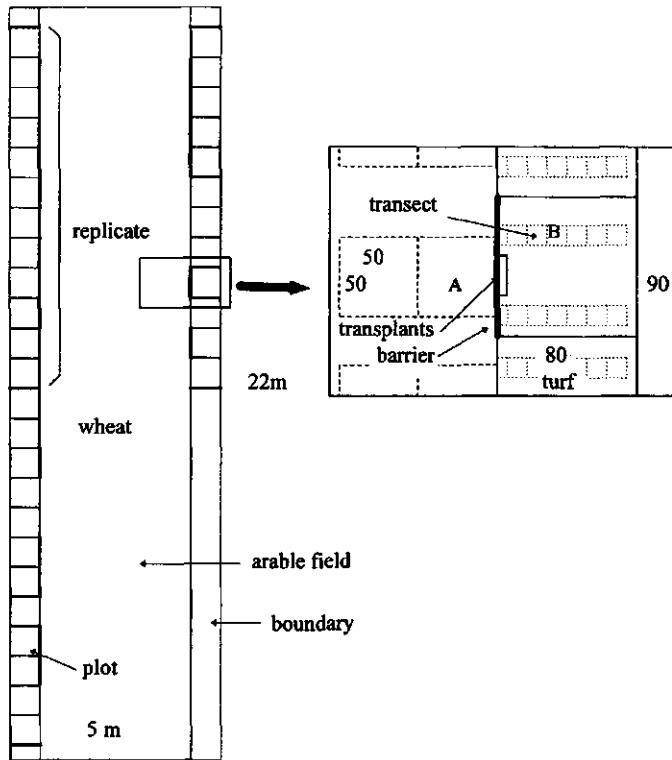
Figure 6.1 *Lay-out of experiment 1. A: 50x50 cm crop sample quadrat, subplot 50-100 cm; B: 10x15 cm sample quadrat of the boundary transects, subplot 20-30 cm. Transplants refer to the transplants of experiment 3.*

plant sizes in the clonal and the non-clonal species. Species, type of plant material used and initial weight of the transplants are given in Table 6.1. Three individuals of a species were planted in a section of soil 20 cm long, 5 cm wide and 5 cm deep. For each species six of these triplets were grown in a glasshouse for one and a half months to develop a root system before transplantation to the field. On 26 April a section of soil containing a triplet was transplanted into the central portion of the field boundary of each of the plots established for experiment 1 (Fig. 6.1). The root systems of both transplants and turf had grown to approximately the same depth at that time. The twelve treatments (6 species * 2 barrier treatments) were randomized over the three replicates. On 3 August above- and below-ground plant parts were sampled, dried for 48 hours at 80°C and weighed.

Experiment 4

Plants growing next to a physical barrier have available only half of the soil volume when compared to free growing plants. On the other hand they are not affected by below-ground competition from plants from the other side of the barrier. In experiment 3 conditions on

Table 6.1 Name, plant material and initial dry weights of species used in the transplantation and control experiments.

species	plant-material	initial weight (g/plant)	
Clonal			
Cirsium arvense	root fragment	0.4	± 0.00
Elymus repens	rhizome fragment	0.2	± 0.01
Ranunculus repens	rosette	0.5	± 0.03
Non-Clonal			
Rumex obtusifolius	seedling	0.007	± 0.002
Dactylis glomerata	seedling	0.009	± 0.003
Rumex acetosa	rosette	0.2	± 0.03

either side of the barrier, both above- and below-ground, are different and effects due to this cannot be distinguished from any influence the barrier itself may have on plants growing behind it.

To quantify and, if necessary, to correct for this effect, a separate validation experiment was carried out in which 36 plots of 50 x 90 cm were established in an area of commercial homogeneous turf in a field next to experiment 1. A 45 cm deep slot was dug into the soil in each plot. A plastic sheet was placed into the slots in half the plots, randomized over each of three replicates, and subsequently all slots were closed. On 26 April triplets of the six species were transplanted directly next to the barrier or the closed slot. Species, type of plant material and initial plant weight were similar to experiment 3. In this way species were transplanted to a situation identical above-, as well as below-ground, on both sides of the slot with exception of the barrier. On 5 August above- and below-ground biomasses were harvested, dried for 48 hours at 80°C and weighed.

Statistical analysis

In both vegetation transects only biomass dry weight was measured. To test the null hypothesis, equality of treatments, the data were analysed using a nested ANOVA. The factors 'barrier' in experiment 1 and 'fertilizer' in experiment 2 were completely randomized and the factor 'subplot', e.g. position within the transect, was nested within these factors. As in experiment 2 field effects were not of primary interest, fields were considered replicates and the analysis for treatment effects was performed without the field stratum. Residuals were plotted versus fitted values to test for constancy of variance of the errors. If variance increased with increasing values of dry weight, log-transformed data were used in the analysis. In case of rejection of the null hypothesis differences between similar subplots with different barrier or fertilizer treatment were analysed using LSD's.

The experimental design of experiment 3 and experiment 4 was identical. Both were complete randomized block designs with two factors (species, barrier) and three replicates. The observed variables, above-ground, below-ground and total biomass as well as shoot-root ratio were screened for constancy of error-variance and analysed separately. To compare clonal and non-clonal species an additional analysis was made with the factors 'barrier' and 'growth strategy' (instead of 'species').

Table 6.2 Biomass dry weights for the sub-plots of the transects in experiments 1 and 2. Asterisks indicate dry weights significantly different from the control situation (+ barrier and - fertilizer).

sub-plot	Boundary biomass (g/m^2)							Crop biomass (g/m^2) (kernel yield)			
	70-60	60-50	50-40	40-30	30-20	20-10	10-0	0-50		50-100	
experiment 1											
+ barrier	624	631	660	629	622	600**	782***	872**	(451)	751	(382)
- barrier	650	662	669	661	645	741**	2009***	755**	(409)	738	(376)
experiment 2											
- fertilizer	521	521	479	549	532	618	709	-		-	
+ fertilizer	469	668	667	544	552	916	1446**	-		-	

* $P<0.05$, ** $P<0.01$, *** $P<0.001$

Results

Experiment 1

The subplots closest to the field (0-10 cm and 10-20 cm) yielded significantly more biomass when there was no barrier than when they were separated from the field by a barrier (Table 6.2). The biomass of subplot 0-10 cm in direct contact with the arable field was more than 2.5 times the biomass of that same subplot shielded from the field. The ratio, although still statistically significant, decreased to 1.2 for subplot 10-20 cm. The other subplots further from the field did not show significant differences.

When subdivision into subplots is not considered and yields of transects as a whole are compared, plots without a barrier yielded higher than plots separated underground from the field ($P<0.001$). The 70cm wide boundary vegetation without access to the arable field produced 650 g dry weight/m^2 whereas that same boundary vegetation with access produced 860 g dw/m^2.

The opposite effect could be seen in the crop. In a wheat crop in contact with the boundary vegetation the edge 50 cm yielded more than 13% ($P<0.01$) less than the wheat crop shielded from the boundary vegetation by a barrier. If only kernel yield is considered the difference was less (9.3%) and not significant. At 50-100cm from the boundary these differences became insignificant (Table 6.2).

Experiment 2

The results of experiment 2 were very similar to those of experiment 1 (Table 6.2). Subplots 0-10 and 10-20 yielded higher next to the fertilized arable field than next to an unfertilized field but the difference was statistically significant only for subplot 0-10. In this case, the differences between the total transects next to a fertilized and an unfertilized arable field were not statistically significant (560 g dw/m^2 and 750 g dw/m^2). The greater number of significant effects in experiment 1 may be explained by the lower variation in the artificially established turf and the higher number of replicates (18 vs 6) in this experiment.
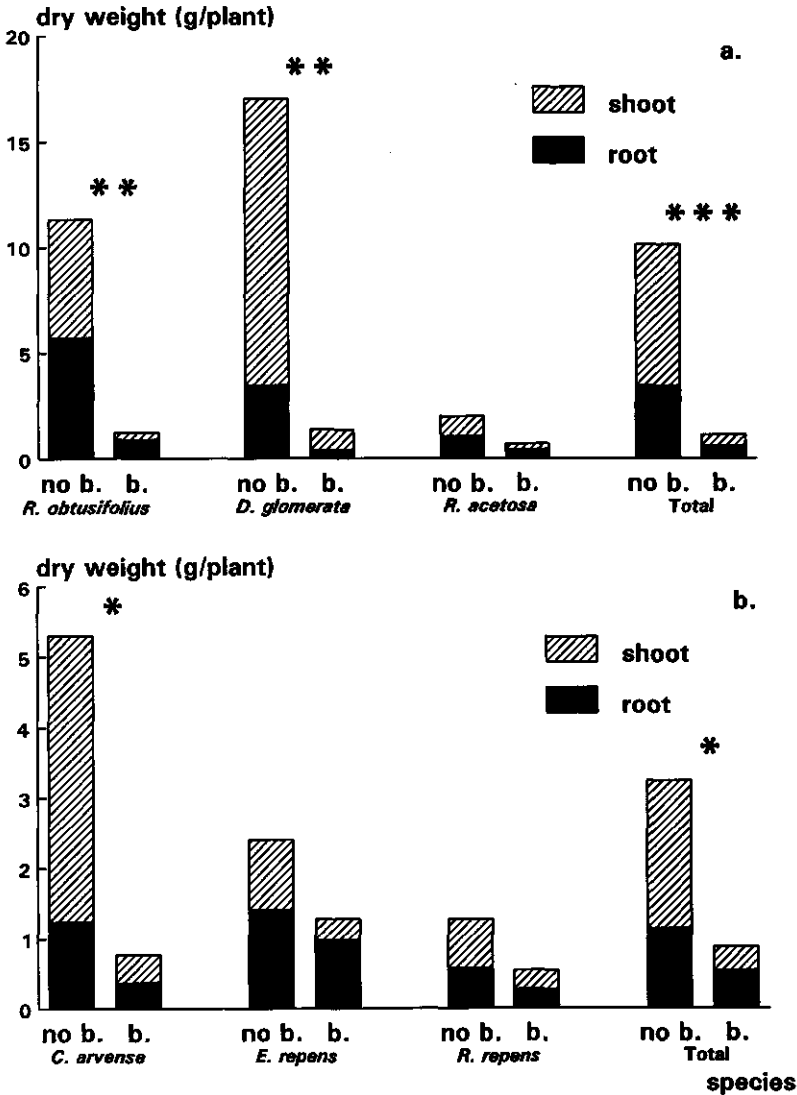
Figure 6.2 Dry weight of (a) non-clonal species and (b) clonal species Total= non-clonal or clonal species analysed together. no b. = no barrier between field and boundary; b. = barrier between field and boundary. Asterisks indicate statistically significant differences of total yield (* P<0.05; ** P<0.01; *** P< 0.001).

Experiment 3

Total biomass of all species increased in the absence of a barrier to the arable field (Fig. 6.2a for non-clonal species, Fig. 6.2b for clonal species). This increase was significant for three species, *C. arvense*, *D. glomerata* and *R. obtusifolius*. The biomass increase of *R. acetosa* was nearly significant but *E. repens* and *R. repens* responded only weakly to the absence of a

Table 6.3 *Shoot/root ratios of the transplanted species in presence and absence of a barrier. Abreviations as in figure 6.2a. Asterisks indicate dry weights significantly different from the control situation (+ barrier).*

	Non-Clonal			Clonal		
	R.o.	D.g.	R.a.	C.a.	E.r.	R.r.
+ barrier	0.38	3.01	0.60	1.30	0.29	1.05
- barrier	0.96	3.83	0.91	4.76*	0.74	1.51
increase (%)	153	27	52	266	155	44

*$P<0.05$

barrier to the field. Both clonal and non-clonal species showed a significant biomass increase when root growth into the field was allowed. However, the non-clonal species increased their biomass by almost three times as much as the clonal species (8.2 fold compared to 2.7).

The response of above- and below-ground plant dry matter production was largely similar to that of the total biomass. Large differences were found in shoot-root ratios (Table 6.3) but these were not related to growth strategy as they occurred both within and between the two species groups. Shoot-root ratio of all species increased with access to the arable field but the increase was significant only for *C. arvense*. Comparisons between clonal species should bear in mind that clonal investments of *C. arvense* and *E. repens* lower shoot-root ratios while similar investments of *R. repens* raise these ratios.

Experiment 4

The dry weights of the species in presence of a barrier in otherwise similar growing conditions were not consistently or significantly higher or lower than in the control (Table 6.4). Half of the species yielded higher total dry weights in presence of a barrier, the other half lower, divided more or less evenly over clonal and non-clonal species. Moreover, in three of the six species the response of the above-ground biomass was different from the response of the below-ground biomass, again evenly distributed over clonal and non-clonal species. Total dry weights of the species in the control experiment corresponded very well with the dry weights of the species of the barrier treatment in experiment 3.

Discussion

These experiments were aimed at answering two questions. Firstly, does the field boundary vegetation increase its biomass production significantly in response to the high nutrient level in the arable field? The results of experiments 1 and 2 showed that the biomass production was raised significantly only in the first 10 to 20 cm of boundary vegetation. This is surprising as lateral root spread of individual plants of all grass species involved can be 37 to 57 cm (Kutschera 1960, Kutschera & Lichtenegger 1982). It may be possible, however, that species provided with a more extensive root system, like full grown individuals of *Urtica dioica* or *Rumex obtusifolius* and also the woody component of a hedgerow, can exploit this

Table 6.4 *Above-ground biomass, below-ground biomass and total biomass (dry weights) of the transplanted species after more than three months of growth in presence or absence of a barrier. No significant differences were found.*

species	above-ground biomass (g/plt)		below-ground biomass (g/plt)		total biomass (g/plt)	
	+ bar	- bar	+ bar	- bar	+ bar	- bar
Clonal						
Cirsium arvense	0.51	0.28	0.38	0.21	0.89	0.48
Elymus repens	0.54	0.40	0.93	1.34	1.47	1.74
Ranunculus repens	0.15	0.18	0.36	0.21	0.51	0.39
Non-Clonal						
Rumex obtusifolius	0.36	0.27	0.94	1.07	1.30	1.33
Dactylis glomerata	0.78	0.90	0.37	0.40	1.16	1.30
Rumex acetosa	0.28	0.18	0.61	0.56	0.89	0.73

nutrient pool from a larger distance. The boundary vegetation showed a similar response in both experiments. Thus the availability of nutrients appears to be the major cause of the observed effect, since there was no increase in biomass in the absence of fertilization although the boundary vegetation was still able to grow into the arable field.

The results of experiment 1 also showed an effect on crop yields. At subplot 0-50 cm these were significantly higher when the crop was separated by a barrier from the field boundary vegetation, indicating competition with the field boundary for nutrients, but they were not reduced when subplots 50-100 cm were compared (Table 6.2). Thus competition between crop and boundary vegetation seems to be not much different from competition between crop and crop. De Snoo (1994) found lower yields for crop edges compared to the centre of the field. The boundaries alongside his crop edges were mainly grassy ditch banks and are therefore comparable with the boundaries in this experiment. The results of experiment 1 suggest that the losses reported by de Snoo (1994) may have other origins such as soil compaction, poor seedbed conditions (Boatman & Sotherton 1988) or lower fertilizer inputs.

The second question stated was: do clonal plant species profit more efficiently from access to the arable field than non-clonal plant species? Experiment 4 showed no significant effects of the barrier itself on biomass production of any of the species. The effects of experiment 3 can therefore be attributed directly to the access or lack of access to the arable field. The results of experiment 3 indicate that clonal species did not profit more from access to the arable field than non-clonal species. The dry summer during the experiment which resulted in poor growth of the plants during the year, may have influenced the results. *Ranunculus repens*, the species which responded least to the treatment, roots very shallowly (< 30 cm) whereas *Cirsium arvense*, the only clonal species with a significant response, can grow roots to a depth of 2 m (Kutschera 1960). Therefore rooting depth may have been a very important factor confounding the effects of growth strategy. The length of the experiment was determined by the length of the growing season of spring wheat and the limited duration may also have played a role. Hardly any stolons or rhizomes grew into the arable field and benefits due to the exchange of limiting resources between mother and daughter ramet could not therefore be expected. If allowed to grow over a longer period the species might have placed more ramets in the arable field. However, at the end of each growing season ramets are

severed from the mother plant due to ploughing or may be killed by herbicides and any benefits to the boundary plants of the ramets placed in the arable field must be achieved within a growing season. The high increase in biomass production of the non-clonal species, within a growing season, is an important result. These species showed some quite opportunistic responses to the availability of the nutrients in the adjacent arable field, as was shown by roots of *Dactylis glomerata* growing horizontally into the arable field over a length of about 30 cm. The results of experiment 3 suggest that the response of the non-clonal species may easily equal that of clonal species even if poor establishment of ramets in the arable field may underestimate the biomass increase of the clonal species in the latter. It is not therefore likely that the clonal growth strategy results in a competitive advantage in field boundaries due to a more efficient capture of arable field resources.

The vegetation in field boundaries captures arable nutrient resources. Decisions related to field boundary management have to be made bearing this in mind. In field boundaries with management regimes that include cutting and removing the vegetation, the effects will be minor as increases in biomass production are apparently limited to the first 20 cm. If cuttings are not removed, and these methods have become increasingly popular as they are cost efficient, the effects may have a much larger impact, as over the years nutrients taken from the arable field may accumulate in the field boundary. Nutrient accumulation and the subsequent increase in biomass production of the vegetation generally results in a reduced species-richness of a habitat (Berendse *et al.* 1993) . The persistence of clonal arable weeds in field boundary vegetation could not be explained by a higher efficiency in capturing arable field resources. Since the presence of weeds mainly determines the use of herbicides in field boundaries (Boatman 1992, Marshall & Smith 1987, de Snoo & Wegener Sleeswijk 1993), understanding how these species maintain viable populations in both an annually cultivated field and a perennial boundary vegetation is crucial to field boundary diversity.

Acknowledgements

7

The effect of time of arrival upon the establishment of six contrasting herbaceous species in a secondary grassland succession

Summary

The establishment success of a species in a secondary succession may vary considerably with (1) the stage of the succession and (2) the life history traits of the species. This study examined seedling emergence, mortality, plant growth and reproduction of six contrasting herbaceous, perennial species which were introduced to the first three years of a secondary grassland succession. Plots with bare soil, one year old vegetation and two year old vegetation were established in a randomized block design to disentangle the effects of the successional stage and the effects of different years. The experiment was executed to determine whether ecologically similar species responded similarly to vegetation change. The results demonstrated that the species could be grouped according to their successional status into an 'early successional' group consisting of *Daucus carota*, *Silene latifolia* ssp *alba* and *Tanacetum vulgare* and a 'late successional' group: *Campanula rotundifolia*, *Galium mollugo* and *Leucanthemum vulgare*. Establishment of the early successional species was good in the initial succession stage (bare soil) but severely reduced in the two older stages. Reduced seedling emergence and very poor plant growth in these stages were mainly responsible for the insignificant establishment. Establishment of the late successional species was generally below that of the early successional species in the first year of the succession. In contrast, in the two older succession stages the late successional species successfully established due to the fact that seedling emergence and plant growth were not reduced (*C. rotundifolia* and *G. mollugo*) or not reduced to insignificant levels (*L. vulgare*). For early successional species the time of arrival in a secondary succession is a crucial factor determining the chances of successful establishment. These species may be part of the vegetation for their entire vegetative life span if they arrive in time to establish from seed. Late successional species may benefit from early arrival mainly by growing faster, flowering earlier and producing more seeds, thus gaining a higher abundance later in the succession.

Keywords: mortality, plant growth, reproduction, seedling emergence, *Campanula rotundifolia*, *Daucus carota*, *Galium mollugo*, *Leucanthemum vulgare*, *Silene latifolia* ssp *alba*, *Tanacetum vulgare*.

Introduction

Three important factors influence vegetation composition at any one point during secondary succession; first, the presence of species at the start of the succession (e.g. as seeds in the soil), second, the immigration of species and third, the differential performance of species once they have arrived (Picket *et al.* 1987). Most species arrive at a site by means of seed dispersal (carried by wind, water or animals). Subsequent establishment depends on four different life cycle characteristics.

First, emergence processes determine how many seeds make it to the seedling stage. Emergence is primarily governed by the germination characteristics of the seeds and these may vary considerably among species (Grime *et al.* 1981, Olff *et al.* 1994, Silvertown 1980). Germination characteristics depend upon the presence or absence of dormancy in the seeds and upon the type of environmental conditions that trigger the germination of dormant seeds, e.g. (fluctuations in) temperature, moisture, (Red/FarRed ratio of) light, soil nitrate content or combinations of these factors (Roberts & Benjamin 1979, Vázquez-Yanes & Orozco-Segovia 1994, Vleeshouwers *et al.* 1995). Furthermore if seeds are buried, pre-emergence growth adds to the complexity since maximum depth from which a seed may successfully emerge varies with seed size and shape of the cotyledons (Vleeshouwers 1997).

Second, relative plant mortality determines how many seedlings or mature plants survive from year to year. Seed size may be an important aspect governing seedling survival (Reader 1993, Ryser 1993); large seeded species suffer less from seedling mortality in a vegetation than small seeded species because the seedling can grow longer on its own reserves. Furthermore, plant mortality in a habitat may differ between vegetated areas and gaps. Both positive and negative effects of gaps on plant mortality have been reported (Hutchings & Booth 1996, Ryser 1993).

Third, the growth rate of plants in a habitat is the main determinant of the vegetative success of a species. Fenner (1978) found large differences between ruderal and closed turf species in their ability to maintain growth in different vegetation types. In contrast to the closed turf species, ruderal species were not able to increase much in weight beyond their initial seed weight when growing in a turf. In bare soil they equalled or surpassed the closed turf species in biomass production, however.

Fourth, species differ considerably in the time they need from germination to reproduction (annuals or biennials *vs.* perennials but also between perennial species) as well as the amount of seeds they produce per plant (Boutin & Harper 1991, Harper 1977).

During the initial stages of a secondary succession, conditions change rapidly (Brown & Southwood 1987). As the habitat is colonized by more and more species the area of bare soil decreases and vegetation cover increases. The time at which a species arrives in a secondary succession may greatly affect its chances of successful establishment. However, considering the large differences in life cycle characteristics between species not all species will be affected alike. Especially the response of perennial species is relevant with respect to the vegetation composition since, once established, these species may dominate or at least persist in the vegetation for many years.

The present study examines the effects of time of arrival upon the establishment of six perennial species of contrasting ecology. The study was aimed at finding out (1) how the subsequent successional stages in the first three years of a secondary succession affect seedling emergence, survival, plant growth as well as reproduction of these species, and (2)

whether ecologically comparable species respond similarly to the increasing age of a secondary succession.

Methods

Six perennial species were selected which have their optimum distribution in different successional stages. *Tanacetum vulgare* and *Silene latifolia* ssp *alba* are tall forbs which often establish after large soil disturbances, for instance along field boundaries and in annual, pioneer communities on fallow land (Weeda *et al.* 1991; nomenclature following van der Meijden 1990). *Daucus carota* is a monocarpic species of medium height with a broad ecological range. On fallow land and in ruderal habitats plants may become very tall but small plants are also found commonly as an element of low productive chalk grasslands (Weeda *et al.* 1987). *Leucanthemum vulgare* and *Galium mollugo* are species of medium height which have their optimum distribution in moderately productive hay meadows (Schaminée *et al.* 1996). *Campanula rotundifolia* is a low to moderately high species of low productive, undisturbed grasslands (Weeda *et al.* 1991). In the remainder of the paper generic names will be used only.

The study site was located in Wageningen, the Netherlands (51°59'N, 5°30'E) on a strip of fallow arable land which was cultivated for the last time in spring 1993. Soil type was loamy sand with pH 4.8 (in 0.01 M $CaCl_2$, Houba *et al.* 1990) and the vegetation, which was mown and removed annually in autumn, gradually developed from a *Chenopodium album, Erigeron canadensis* and *Matricaria recutita* dominated pioneer community in 1993 into a perennial vegetation dominated by *Cirsium arvense, Elymus repens* and *Holcus lanatus* in 1996. In the regenerating vegetation three types of 1 x 1 m plots were established. The first type consisted of the vegetation that regenerated after the soil had last been cultivated by plough in spring 1993. The second type was cultivated by spade in October 1993, while the third type was cultivated similarly in the beginning of September 1994. Thus, in autumn 1994 the three plot types consisted of two year old vegetation, one year old vegetation and bare soil.

On 15 September 1994 the central 0.5 x 0.5 m of each plot was sown with seeds of one of the six species. Each plot type-species combination was replicated three times in a randomized complete block design, resulting in a total of 3 plot types x 6 species x 3 replicated blocks = 54 experimental units. Plots within a block were arranged in two rows of 9 plots with no space in between plots, while blocks were arranged parallel and spaced one metre apart to allow access to all plots.

Of five of the six species 750 seeds were sown to each plot, however, a trial experiment (data not shown) revealed that the low germination rate of *Campanula* necessitated the sowing of 4000 seeds of this species to get comparable numbers of germinated seeds (Table 7.1). The seeds were collected in 1993 and 1994 in the vicinity of Wageningen for all but *Campanula* which was obtained from a 'heemtuin' (a botanical garden specialized in growing local species) in Amstelveen, the Netherlands. Prior to sowing, seed weight was determined of each of the batches of seeds. Furthermore, at this time the germination ratio under laboratory conditions was determined of random samples of the seeds (Table 7.1). Two times 200 seeds of each species were put on moist filter paper in petridishes and were placed in climate chambers. The climate chambers were illuminated and kept at 25°C for twelve hours followed by darkness at 15°C for another twelve hours. Since seeds of umbelliferous species

Table 7.1 *Number of sown seeds, mean seed weight (mg) and the germination ratio (%) of six ecologically contrasting species.*

species	no.seeds sown	seed weight (±se)	germination ratio
Campanula rotundifolia	4000	0.078 (±0.001)	16
Galium mollugo	750	0.777 (±0.029)	93
Leucanthemum vulgare	750	0.520 (±0.010)	95
Daucus carota	750	1.154 (±0.036)	81
Silene latifolia ssp *alba*	750	1.108 (±0.038)	93
Tanacetum vulgare	750	0.151 (±0.012)	81

generally need stratification to be able to germinate, *Daucus* seeds were put (on moist filter paper) at 5°C for a fortnight prior to the germination test.

After sowing, plots were checked regularly for emerging seedlings which were then counted and flagged with pins with coloured heads. When on successive occasions pins were found without plants, these were counted as dead and the pins were removed. Seedlings which emerged outside the central 0.5 x 0.5 m were counted and then removed since their growing conditions were likely to be affected by neighbouring plots. To determine the reproduction rate of the species, the plots were checked on daily or two-daily basis during the flowering season of 1995 and 1996. Seeds were collected when they were nearly ripe to avoid seed loss through shedding. From 3-12 October 1995 and from 16-25 September 1996 plots were cut as part of the mowing regime. Individual plants of all six species were cut close to ground level and dry weight of each individual plant was determined after drying for 48 hours at 80°C. Above-ground biomass production of the vegetation in the central 0.5 x 0.5 m was determined similarly.

Light penetration at ground level was estimated on 29 June 1995 and 26 July 1996 with a 1 cm^2 light sensitive cell (400-700 nm; T.F.D.L. Wageningen, no. 31940.4). Light penetration at ground level on three points in each central quadrat was related to the level measured directly above the vegetation and levels of the three measurements were averaged to result in a mean light penetration estimate.

Analysis

Both mortality and all growth variables were analysed by means of two-way analysis of variance, the two factors being species and succession stage. Percentages (mortality) were angular transformed and all biomass data were ln-transformed prior to analysis with the GENSTAT statistical package (GENSTAT 1993). In case of significant effects, means were tested for significant differences by means of LSD's. Since a seedling either does or does not emerge, the emergence data did not meet the assumption of a normal variance distribution which is necessary for ANOVA. Hence, the emergence data were analysed by means of a Generalized Linear Model with a binomial variance distribution (GENSTAT 1993). Means were tested for significant differences by means of t-tests when significant effects were found.

The effects of the environmental variables (vegetation productivity and light penetration at ground level) on the different life cycle aspects of the species were analysed by means of multiple linear regression. Effects were analysed by means of stepwise selection with a

Table 7.2 *Mean biomass production (g.m^{-2}) and light penetration (%) in 1995 and 1996 in a secondary succession started in spring 1993 (succession stage 2), autumn 1993 (1) and autumn 1994 (0). Standard errors in brackets. Different characters indicate significant differences (P<0.05).*

succession stage		vegetation biomass	(se)	light penetration	(se)
	0	473^a	(±143)	7.34^a	(±6.85)
1995	1	628^b	(±72)	1.41^b	(±1.04)
	2	588^{ab}	(±226)	1.68^b	(±1.53)
	0	303	(±66)	19.22	(±10.20)
1996	1	353	(±67)	15.20	(±7.67)
	2	323	(±88)	14.94	(±11.22)

backward removal of those variables that did not significantly contribute to the fit of the model (Sokal & Rohlf 1995). The full model included the effects of the replicated blocks, species, years, light penetration and vegetation productivity as well as all two factorial interactions.

Results

In 1995, plots representing the initial stage of a secondary succession (succession stage 0) had significantly lower biomass production and significantly higher light penetration levels compared to the one year old successional stage (Table 7.2). The two year old successional stage had intermediate levels and the two older stages did not differ significantly. In the second year of the experiment, the differences of 1995 persisted but had become statistically insignificant. In 1996, vegetation productivity in all successional stages was reduced to almost half the level of 1995, which may have been due to a reduced fertility of the site as a result of the annual mowing and removing of the vegetation. Furthermore, the summer of 1996 was drier: water deficit (precipitation minus potential evapotranspiration) over the months April-September was 200 mm in 1995 and 241 mm in 1996. Although productivity

Table 7.3 *Mean number of emerging seedlings of six contrasting species within the central 0.5 x 0.5 m quadrat (i). In brackets (t) the mean emerging seedlings in the total 1 m^{-2} metre plots. Plots represented three stages in a secondary succession: 2, started in spring 1993; 1, autumn 1993 and (0) autumn 1994. Different characters in superscript indicate significant differences (P<0.05) per year and within species.*

| year:	1995						1996					
succession stage:	0		1		2		0		1		2	
species	i	(t)	i	(t)	i	(t)	i	(t)	i	(t)	i	(t)
C. rotundifolia	1.3^a	(5.0)	5.7^a	(5.7)	12.3^a	(12.3)	0.0^a	(0.0)	1.3^a	(1.3)	1.3^a	(1.3)
G. mollugo	21.6^a	(40.3)	155.3^a	(164.7)	126.3^a	(129.3)	0.0^a	(0.0)	0.0^a	(0.0)	0.0^a	(0.0)
L. vulgare	258.3^a	(384.0)	190.7^a	(201.3)	152.7^b	(157.7)	0.0^a	(0.0)	0.0^a	(0.0)	0.0^a	(0.0)
D. carota	87.0^a	(107.3)	50.3^a	(50.3)	15.7^b	(16.0)	0.0^a	(0.0)	30.7^a	(30.7)	29.3^a	(29.3)
S. lat. ssp *alba*	6.7^a	(18.7)	12.7^a	(12.7)	0.0^a	(0.0)	0.3^a	(0.3)	3.3^a	(3.3)	9.7^a	(9.7)
T. vulgare	21.0^a	(60.0)	5.3^{ab}	(5.3)	1.7^b	(2.7)	1.0^a	(1.0)	0.0^a	(0.0)	0.3^a	(0.3)
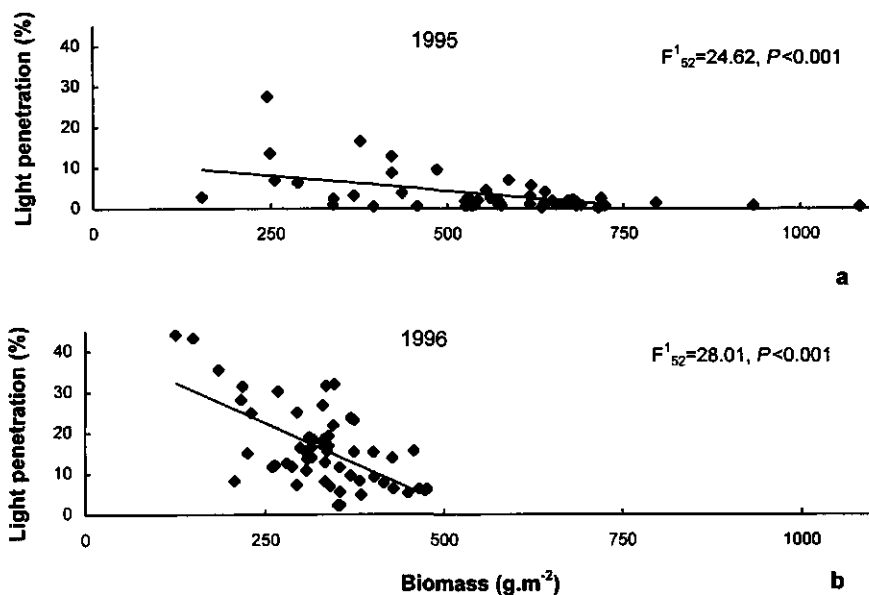
Figure 7.1 *Relationship between biomass production (g.m⁻²) and light penetration (% of ambient) at ground level in (a) 1995 and (b) 1996.*

contrasted sharply in the two years, in both years a strong negative relationship was found between vegetation biomass production and light penetration at ground level (Fig. 7.1a and b).

Emergence

Although, based upon the number of sown seeds and their germination ratios under laboratory conditions, the six species should be able to produce similar amounts of seedlings, the number of emerged seedlings in the experimental plots contrasted sharply between the species. *Galium* and *Leucanthemum* had by far the highest number of emerged seedlings (Table 7.3). *Daucus* had intermediate numbers and *Campanula*, *Silene* and *Tanacetum* had very low numbers of emerged seedlings. All species predominantly emerged in 1995; only *Daucus* and *Silene* had considerable numbers of emerged seedlings in the next season.

In 1995 the number of emerged seedlings of *Leucanthemum*, *Daucus* and *Tanacetum* decreased significantly with increasing age of the succession (Table 7.3). Contrastingly, the number of emerged seedlings of *Campanula* and *Galium* increased with increasing age of the succession, although the former not significantly. *Silene* did not show any obvious trend. In 1996, probably due to the low number of emerged seedlings, no significant differences were found.

Table 7.4 *Plant mortality (in percentage of living plants) in 1995 and 1996. Plots represented three stages in a secondary succession: 2, started in spring 1993; 1, autumn 1993 and (0) autumn 1994. Different characters in superscript indicate significant differences (P<0.05) per year and within species.*

year:	1995			1996		
succession stage:	0	1	2	0	1	2
species						
C. rotundifolia	0.0[b]	56.1[a]	70.8[a]	36.4[a]	8.9[a]	11.1[a]
G. mollugo	40.0[a]	70.5[a]	64.8[a]	45.2[a]	60.4[a]	59.7[a]
L. vulgare	5.5[a]	28.2[a]	37.0[a]	21.1[a]	55.9[a]	66.9[a]
D. carota	58.1[a]	90.9[a]	93.6[a]	35.9[a]	0.0[a]	0.0[a]
S. latifolia ssp *alba*	13.1[b]	67.3[a]	-	11.1[a]	11.1[a]	0.0[a]
T. vulgare[1]	47.1	100.0	-	10.3	-	-

[1] species not part of the analysis due to insufficient plants.

Mortality

Due to the high number of plots with no emerging seedlings (in 1995) or with no surviving plants from the previous year (in 1996) the mortality rate could not be calculated for each species·succession stage combination (Table 7.4). For *Tanacetum*, the number of plots without any plants was too high to analyse the succession stage effect reliably and this species was excluded from the analysis. Average mortality rates differed considerably between the six species, with *Leucanthemum* having the lowest rates and *Daucus* and *Tanacetum* having the highest rates. Interestingly, no significant species·succession stage interaction was found ($F^8_{49}= 0.69$, $P = 0.70$), indicating that all species responded similarly: an increasing age of the succession was accompanied by an increasing mortality rate (Table 7.4).

Plant growth

Similar to the analysis of plant mortality, median plant weight could not be determined for each plot. Due to the large number of plots with no emerged *Tanacetum* seedlings (see Table

Table 7.5 *The median of individual plant dry weight (mg.plant⁻¹) of six contrasting species in 1995 and 1996. Plots represented three stages in a secondary succession: 2, started in spring 1993; 1, autumn 1993 and (0) autumn 1994. Different characters in superscript indicate significant differences (P<0.05) per year and within species.*

year:	1995			1996		
succession stage:	0	1	2	0	1	2
species						
C. rotundifolia	3.8[a]	0.1[b]	0.6[ab]	36.4[a]	8.9[a]	11.1[a]
G. mollugo	14.3[a]	4.4[a]	12.7[a]	91.6[a]	12.9[a]	26.8[a]
L. vulgare	45.3[a]	7.8[a]	6.2[a]	119.0[a]	36.4[a]	49.3[a]
D. carota	31.5[a]	1.1[b]	0.3[b]	590.4[a]	2.3[b]	1.3[b]
S. latifolia ssp *alba*	180.4[a]	3.7[b]	-	1062.1[a]	20.9[b]	4.3[b]
T. vulgare[1]	156.8	-	-	817.5	-	-

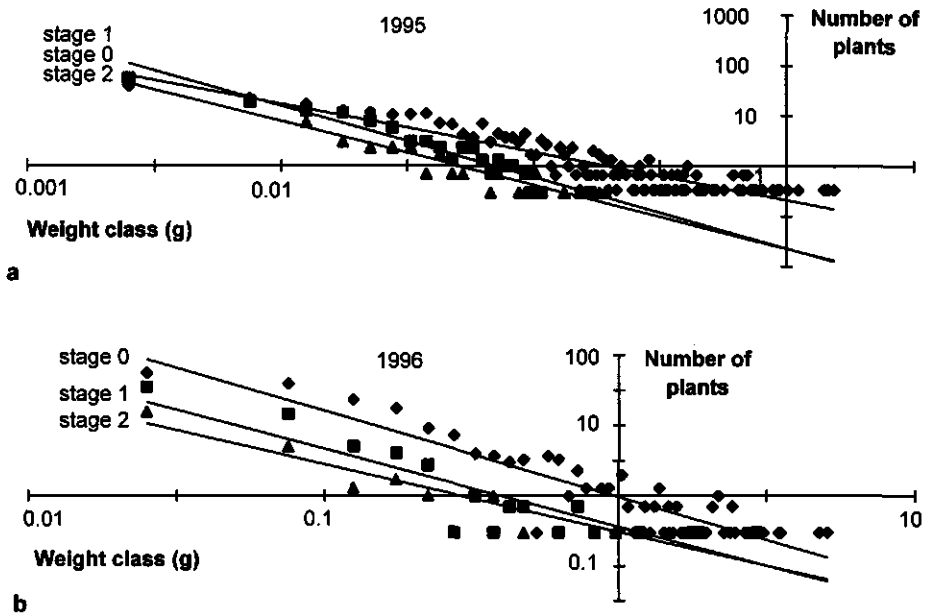[1] species not part of the analysis due to insufficient plants.

Figure 7.2 The mean weight distribution of Leucanthemum vulgare plants originating from 750 seeds sown in autumn 1994 in three consecutive stages of a secondary succession (a) in 1995 and (b) in 1996. Succession stage 2 started in spring 1993, stage 1 in autumn 1993 and stage 0 in autumn 1994. Weight classes in 1995 were 0.005 g, those in 1996 were 0.05. Succession stage 0: diamonds, stage 1: squares, stage 2: triangles.

7.3), this species was omitted from the analysis (Table 7.5). All species had their highest median plant weight in the first successional stage, though not all significantly so. A statistically significant species·succession stage interaction was found (F^8_{44}=3.48, $P = 0.003$) indicating that the response of some species was stronger than that of others. Indeed, median plant weight of *Daucus* and *Silene* was reduced more than 25-fold in the later successional stages compared to the first successional stage, while that reduction was generally less than 10-fold for *Campanula*, *Galium* and *Leucanthemum*. In succession stage 2, median plant weight of the latter three species was considerably higher than that of *Daucus* and *Silene*. In contrast, in succession stage 0 median plant size of *Campanula*, *Galium* and *Leucanthemum* was considerably lower than that of *Daucus*, *Silene* and *Tanacetum*; especially in 1996.

Only for *Leucanthemum* sufficient plants had established to compare their dry weight distribution in all three successional stages reliably. In Fig. 7.2a and b, for each weight class of 0.005 g (1995) or 0.05 g (1996) the number of plants are given on a log-log scale. In both years and all successional stages the number of plants in a weight class decreased exponentially with increasing weight of the class. Thus, in each plot many small and a few large plants were found. On a log-log scale such a distribution produces a linear relationship with a slope of approximately -1 (Fig. 7.2a-b). The slopes as well as the y-axis intercept of the lines in the different successional stages did not reveal any statistically significant differences in any of the two years, although in 1996 there was a statistically non significant

Table 7.6 *Mean total biomass production (g.plot⁻¹) of six contrasting species in 1995 and 1996. Plots represented three stages in a secondary succession: 2, started in spring 1993; 1, autumn 1993 and (0) autumn 1994. Different characters in superscript indicate significant differences (P<0.05) per year within species.*

year:		1995			1996	
succession stage:	0	1	2	0	1	2
species						
C. rotundifolia	0.004^a	0.001^a	0.010^a	0.031^a	0.045^a	0.112^a
G. mollugo	0.412^a	0.468^a	3.367^a	1.367^a	1.117^a	3.926^a
L. vulgare	22.854^a	2.130^a	1.209^a	62.164^a	8.231^a	3.900^a
D. carota	5.700^a	0.078^b	0.002^b	37.754^a	0.341^b	0.064^b
S. latifolia ssp *alba*	2.256^a	0.018^b	0^b	11.155^a	0.111^b	0.095^b
T. vulgare	1.650^a	0^b	0.020^b	8.742^a	0^b	0.101^b

trend for a decrease in y-axis intercept with increasing age of the succession (F^2_6= 3.05, P=0.12).

The total, per plot biomass production of the six species revealed clear and statistically significant contrasts between *Campanula*, *Galium* and *Leucanthemum* on one hand and *Daucus*, *Silene* and *Tanacetum* on the other (species·succession stage interaction: F^{10}_{70}=4.70, P<0.001). Total plant biomass did not significantly differ between the three successional stages for the first three species (Table 7.6) while *Campanula* and *Galium* actually had a higher total biomass production in the later successional stages due to their higher emergence rates in those stages. *Daucus*, *Silene* and *Tanacetum* had severely reduced total biomass production in successional stage 1 and 2 compared to 0.

Reproduction

In 1995, only *Leucanthemum*, *Daucus* and *Silene* managed to produce seeds, and all seed production was restricted to the first successional stage (Table 7.7). In 1996, mean seed production in the first successional stage of *Daucus*, *Leucanthemum*, *Silene* and *Tanacetum* was high enough to replace the 750 initially sown seeds. In the two later successional stages only *Leucanthemum* produced a moderate number of seeds. *Campanula* did not flower at all in the two years; *Galium* flowered sparingly in 1996 but seeds did not mature.

Table 7.7 *Mean number of seeds produced by six contrasting species in 1995 and 1996. Plots represented three stages in a secondary succession: 2, started in spring 1993; 1, autumn 1993 and (0) autumn 1994.*

year:		1995			1996	
succession stage:	0	1	2	0	1	2
species						
C. rotundifolia	0	0	0	0	0	0
G. mollugo	0	0	0	0	0	0
L. vulgare	409	0	0	12126	429	367
D. carota	90	0	0	10723	61	0
S. latifolia ssp *alba*	132	0	0	2576	0	0
T. vulgare	0	0	0	1904	0	0

Table 7.8 Results of the multiple linear regression analysis. Relationships of the environmental variables vegetation productivity (g.plot^{-1}.y^{-1}) and light penetration at ground level (% of ambient photosynthetically active radiation) with the population dynamical parameters of the sown species. The effects of replicated blocks, species and years were included in the regression model. '–': negative relationship, '+': positive relationship.

	vegetation biomass	light pene-tration (%)
emergence	ns	ns
mortality (%)	+***	ns
median plant weight (g)	–**	ns
total biomass (g.plot^{-1})	–**	ns

**P<0.01, ***P<0.001

Relationship between environmental conditions and life cycle characteristics

Emergence was not significantly affected by either vegetation biomass or light penetration (Table 7.8). On the other hand, mortality was positively affected and both median plant weight and total biomass production per species were significantly negatively affected by vegetation biomass production. Light penetration did not show any significant relationships with any of the life cycle characteristics. Furthermore, no significant interactions were found, indicating that the species did not differ significantly in their response to vegetation biomass production.

Discussion

The successful establishment of a plant species in a habitat depends on a complex interplay between the species life history traits and a combination of environmental conditions. Environmental conditions include climate (Tilman & El Haddi 1992), hydrology, soil type, pH and purely biotic conditions like the severity of seed predation (Mittelbach & Gross 1984, Reader 1993, van Tooren 1988), herbivory (Bonser & Reader 1995), presence of pathogens and competition from the surrounding vegetation (Fenner 1978). This study tried to determine the relationship between life cycle characteristics of species with contrasting ecologies and the success they have in the first years of a secondary succession. In the initial stages of such a succession the rapid change from bare soil to a closed vegetation, which is generally accompanied by decreases in available nutrient resources, reduced light penetration at ground level and reduced fluctuations in temperature and humidity, may have important effects.

Indeed, vegetation biomass production increased and light penetration decreased significantly from the first year of the succession to the second and third year. Furthermore, vegetation biomass production was positively related to mortality and negatively related to median plant weight and total species biomass production per plot (Table 7.8). The fact that these life cycle characteristics were significantly related to vegetation biomass and not to light penetration at ground level, probably reflects the fact that light penetration was measured only once during the growing season while the differences in light penetration accumulate during the entire season. Thus, competition from the surrounding vegetation was

probably the most important factor determining the establishment success of the six species (but see Reader 1993, for the possibility of seed predation interacting with vegetation cover).

Of all life cycle characteristics, seedling emergence was most variable amongst the six species. Four species had the highest number of emerged seedlings in the first successional stage, *Campanula* responded indifferent to succession stage and the number of emerged seedlings of *Galium* was actually significantly lower in stage 0. Grime *et al.* (1981) found the germination of five of the six species to be significantly reduced in the dark; only *Galium* was not affected by differences in light availability. On bare soil the microclimate is generally harsher and the impact of environmental stresses such as drought or frost is more severe (Ryser 1993) which may explain the lower emergence of this species in the first succession stage. In contrast to the results of Gross (1984), Reader (1993) and Ryser (1993) I found no indication that large seeded species perform relatively better under a cover of litter or vegetation. The emergence of *Daucus*, the largest seeded species in this study, was significantly reduced while emergence and establishment of *Campanula*, the smallest seeded species, was not affected by the increased ground cover in the older succession stages. The considerable number of emerged *Daucus* and *Silene* seedlings in the second growing season is consistent with the findings of Roberts (1986) and Roberts & Boddrell (1984) who observed a peak in emergence in the first year, but found considerable numbers of emerging seedlings for at least the next four years. They found *Galium* hardly emerging after the first season but, in contrast to the present results, in their experiments *Leucanthemum* displayed a germination pattern similar to *Daucus* and *Silene*. The habit of dormancy in seeds is generally better developed in ruderal, pioneer species (Fenner 1987). The successional position of a species proved to be a good indicator for the response in emergence in relation to the succession stage: the numbers of emerged seedlings of early successional species like *Tanacetum* and *Silene* were negatively affected by the older successional stages while the numbers of emerged seedlings of later successional species like *Campanula* and *Galium* proved to be indifferent or even positively affected by it.

The mortality patterns were similar in all species: a higher mortality in the two older succession stages compared to the initial stage. Mortality of *Leucanthemum* was low in 1995 but the mortality rates of the other species were consistent with the range generally found in old fields and grasslands. In the first and third year of an old field succession, Holt (1972) found mortality rates of *Daucus carota* to be some 70% and 90%, respectively. Silvertown & Dickie (1980) observed 67% mortality in the first year after emergence in a natural population of *Galium mollugo* in a chalk grassland. In 1996 mortality was generally lower except for *Galium* and *Leucanthemum*. This may have been caused by the individual plant harvests. In contrast to the other species, many, very small plants of *Galium* and *Leucanthemum* survived at the end of the first growing season (Fig. 7.2a). Cutting most above-ground biomass of these plants may have resulted in an increased mortality compared to normal cutting practices (with normal cutting equipment these small plants would probably not have been damaged at all).

As with seedling emergence, the plant growth response of the different species, corresponded well with their successional status. Similar to the findings of Fenner (1978), plant growth (as represented by their median weight attained at the end of both growing seasons) of early successional species was significantly reduced in the better developed perennial vegetation of the older succession stages. Naturally, individual plants of the later successional stages (*Campanula*, *Galium* and *Leucanthemum*) were also reduced in growth in

the older stages but to a much lesser, non-significant, extent. Early successional species have been found to demonstrate a greater reduction in photosynthesis under competition compared to full light conditions and may therefore be more shade-intolerant (Bazzaz & Carlson 1982, Burton & Bazzaz 1995). In the initial succession stage, the growth rate of the species *Daucus* and especially *Silene* and *Tanacetum* was much higher compared to the other three species. Interestingly, the size distribution data of *Leucanthemum* (Fig. 7.2ab) suggests that the relative plant weight distribution is similar in al three stages of succession (differences in the slope of the lines in Fig. 7.2ab were not significantly different between successional stages). So, whether the neighbouring plant is from the same or from a different species, there will be a hierarchy of plant sizes: a high number of small plants declining exponentially to a low number of large plants.

In biennial and perennial species reproduction is often restricted to plants that have reached a critical size (Harper 1977). It is therefore not surprising that, both in 1995 and 1996, most of the seeds were produced in the initial succession stage where median plant weight of all species was highest. Only *Campanula* and *Galium* were not able to reproduce at all, indicating that these species have a comparatively long juvenile period.

The total biomass production per plot is the cumulative result of emergence, mortality and plant growth, and may therefore be used as an ultimate measure of success. If conditions are not extremely stressful and genetic differences between populations in different successional stages (see Taylor & Aarsen 1988, Werner & Platt 1976) are neutralized, as has been done in these experiments, reproduction is generally proportional to biomass production (once a critical size has been reached). Total biomass production may therefore also be considered representative of the reproductive success of the species. Considering Table 7.6 we may conclude that the six species generally fall apart in two groups of three species:
- *Daucus*, *Silene* and *Tanacetum* demonstrate a very high growth rate in the initial stage but success in older successional stages was insignificant.
- *Campanula*, *Galium* and *Leucanthemum* are not reduced or not reduced to insignificant levels in older successional stages compared to the first successional stage and they seem to be able to build up a viable population in these stages.

As pointed out before, these groups broadly correspond with the stages in the succession where they have their optimum distribution. The early successional species like *Silene* and *Tanacetum* are most successful on fallow fields, spoil heaps and disturbed field boundaries. In these poorly vegetated and usually productive habitats it is advantageous to have a high initial growth rate to attain dominance during the first period. Mechanisms that prevent germination under conditions where this rapid initial growth rate will be less successful (in a closed vegetation), or that increase the chance of timely arrival when favourable conditions emerge (seed dormancy), are most probably beneficial to these species (Fenner 1978). Species like *Campanula* and *Galium* that have their optimum distribution in later successional stages are able to establish in such a vegetation from seed (although they often perform better when, as in gaps, the competing vegetation has temporarily been removed). In these species such mechanisms most likely did not yield enough benefits to have evolved.

One may furthermore conclude that differences in the germination characteristics and differences in seedling growth have the most pronounced effect on the establishment success of a species in contrasting successional stages.

Finally, the time of arrival of especially the early successional perennial species is a crucial factor determining their chances of successful establishment. Table 7.6 shows that,

once established, early successional perennials are capable of persisting and growing in older successional stages (succession stage 0, second growing season). In that stage they are hardly capable of regenerating from seed however (succession stage 1, first growing season). Thus, early successional species may be able to be part of the vegetation for their entire vegetative life span *if* they arrive in time to establish from seed. For later successional species the main benefit in arriving early during a secondary succession is that after early arrival they grow faster, flower earlier and produce more seeds and may thus be able to gain a higher abundance later in the succession.

Acknowledgements

8

Field boundary vegetation and the effects of drift of agrochemicals: botanical change caused by low levels of herbicide and fertilizer

Summary

To assess the effects of herbicide drift and fertilizer misplacement on the botanical diversity of arable field boundary vegetation, plots in 1) a low productive meadow and 2) a high productive fallow arable field sown with a mixture of grassland forbs were treated annually with all combinations of three levels of fertilizer (NPK; 0, 25 and 50% of the standard agricultural dose) and four levels of herbicide (fluroxypyr; 0, 5, 10 and 50%). Botanical change and biomass production of grasses and forbs were monitored for three years in both experiments. Additionally, phytotoxicity of the four levels of herbicide was screened at the seedling stage for 18 species grown in pots in a glasshouse. In both vegetation types fertilizer application resulted in a decline in species richness through a loss of species of low stature. Fertilizer application affected species-richness gradually, as demonstrated by the rare occurrence of significant effects on colonization and extinction rates. Herbicide application resulted in a decline of species richness and affected biomass production of both grasses (positively) and forbs (negatively) in the high productive fallow only. A small number of species decreased in abundance in the herbicide treated plots in both experiments, however. Significant herbicide effects were mainly limited to the 50% herbicide plots but the 5 and 10% herbicide levels decreased the biomass production of spontaneously colonizing forbs and increased the species extinction rates in individual years. The effects of the fertilizer applications on species-richness, biomass production and the abundance of individual species were far more severe and constant compared to the herbicide applications. The results of the pot experiment did not correspond well with the results of the field experiments. Extrapolation of the results of pot experiments to normal field conditions is therefore difficult and inappropriate. Implications of these results for field boundary management are discussed.

Keywords: fertilizer misplacement, field boundary, herbicide drift, species richness, wildlife conservation.

Introduction

Contemporary agriculture is highly dependent on external inputs. High yielding crops need high fertilizer rates and the use of pesticides for weed and pest control. Most fertilizer or herbicide application devices fail, however, to apply the agrochemicals homogeneously to the crop under standard farming conditions and are incapable of accurately restricting the application to the crop near the field boundary (Melman & van der Linden 1988, Rew *et al.* 1992). Pneumatic and liquid fertilizer spreaders have been developed to deliver a more constant application and have the facility to reduce fertilizer misplacement such as is required at the edges of fields. However, this type of machinery is expensive and its use is not widespread (Rew *et al.* 1992, Kleijn & Verbeek in prep.). Pesticide sprayers that completely prevent spray drift have not yet been developed. Drift of these agrochemicals outside the arable field is economically wasteful and potentially hazardous for the organisms living in the habitats near arable fields.

Most of the agrochemical drift will be deposited in the field boundary and its effect is likely to be greatest in this habitat. Botanical diversity in field boundaries has indeed declined considerably in recent decades (Bunce *et al.* 1994). Arable field boundaries play an important role in the agricultural landscape since they provide a habitat for a range of perennial plant species as well as food, shelter and movement corridors between habitats for a multitude of animal species. Reduction of field boundary diversity is likely to result in a reduction in diversity of the entire agricultural landscape and can thus ultimately be linked to the decline of farmland animals such as the grey partridge (*Perdix perdix*; Maris 1996, Rands 1985) and the brown hare (*Lepus europaeus*; Tapper & Barnes 1986).

Drift of pesticides applied by a common tractor-mounted spray boom is strongly influenced by boom height, nozzle type, wind speed and direction, and tractor speed at the time of spraying (Byass & Lake 1977, Miller 1988, Nordbo *et al.* 1993). Reported drift measurements under normal conditions vary and range from 1 to 15 % of the amount applied to the crop at 1 metre from the last nozzle (Marrs *et al.* 1989b) to 16% at 1.5-2 m from the last nozzle (Van de Zande *et al.* 1995). Misplacement (or for convenience, drift) of fertilizer is even less predictable. Rew *et al.* (1992) found huge differences between different spreader types with a minimum amount of misplacement of 0% of the mean field rate and a maximum of 195%.

The phenomenon of pesticide spray drift is documented rather well. However, the effect such drift has on the adjoining non-crop habitats has been poorly investigated (Freemark & Boutin 1995). In contrast, while the phenomenon of fertilizer misplacement is poorly documented, the effects of fertilizer application on a range of vegetation types has been documented meticulously (e.g. Berendse 1983, Bobbink 1991, Tilman 1993). Limiting our attention to the effects of fertilizer and herbicides we find that in perennial vegetation fertilizer addition usually leads to a reduction of species-richness by eliminating species of low stature. Depending on the herbicides, we may hypothesize that four response types can be found in field boundaries in the event of drift: (1) all species are killed, (2) certain species are killed but not others, (3) certain species are hampered in growth but not others, thus shifting the competitive balance in favour of the unaffected species, (4) none of the species are affected. Marrs *et al.* (1989b) and Marrs *et al.* (1991a) found less than 30% of all full-grown plants tested to be affected by full rate applications of the herbicides glyphosate, MCPA, mecoprop and asulam. Therefore, herbicide drift is not likely to result in the immediate death

of all or some species. Fertilizer and herbicides in combination may neutralize each other when the species that are favoured by fertilizer drift are hampered by herbicide drift. Conversely, when the species that have a disadvantage at higher fertilizer rates are also affected by herbicide drift, the two factors may have additive or synergistic effects. In any event the effects of one or both factors will take time to establish and require delicate, long term monitoring.

In existing field boundaries the effects of agrochemical drift are difficult to examine since these vegetation structures have probably been exposed to drift of such compounds in the past. Demonstration of any botanical change within these habitats due to these factors may therefore fail (Marshall 1992). A comparable vegetation not bordering an arable field does not have this disadvantage. Changes demonstrated in such a vegetation are likely to occur in field boundaries as well.

The experiments described below were established to explore the effects of drift of herbicides and fertilizer on the botanical composition of a perennial non-crop vegetation.

Methods

Experiment 1

In April 1993, 48 quadrats of 2 x 2 m and 0.5 m apart were established on a productively low, *Festuca rubra* ssp *commutata* and *Holcus lanatus* dominated grassland on sandy soil ($\pm$ 3.4 t dry weight.ha^{-1}.year^{-1}; species composition in Appendix 8.1). During the three years of the experiment, the normal management regime of cutting and removing the vegetation once a year in autumn was maintained. Nomenclature follows Van der Meijden (1990).

To each plot one of three levels of fertilizer was applied evenly by hand: 0, 25 and 50 per cent of the mean artificial fertilizer application rate of a rotation of crops on a neighbouring arable field (110 kg N.ha^{-1}.year^{-1}, resulting in 0, 27.5 and 55 kg N.ha^{-1}.year^{-1} for the respective treatment plots). Although nitrogen was expected to be the limiting resource, NPK fertilizer (15-12-24) was applied to ensure that none of the macro elements were limiting. Four levels of herbicides were applied. Following the drift measurement results of Marrs *et al.* (1989b) and Van de Zande *et al.* (1995), 0, 5, 10 and 50 per cent of the standard agricultural dose was applied. The herbicide was fluroxypyr (Starane 200, standard rate 200 g fluroxypyr per ha resulting in the equivalent of 0, 10, 20 and 100 g fluroxypyr. ha^{-1}.y^{-1} for the respective herbicide levels) which controls annual and perennial dicotyledonous species (Schlotter & Schuster 1992), and is recommended for use in crop edges (Boatman 1989). As it was crucial to apply the exact amount of active ingredient to the rather small plots, herbicide was applied by pressurized houseplant sprayer (Hozelock, Model 4078). Before spraying each plot, 250 ml thoroughly mixed herbicide solution (18.5, 37 and 185 mg fluroxypyr per litre for the 5, 10 and 50% plots respectively) was entered into the sprayer. The sprayer was then pressurized to a standard level by hand-pumping 100 times and the herbicide solution sprayed evenly over the plots by hand in a pre-determined period of time and without emptying the sprayer completely to secure a continuous spray quality. After measuring the remaining solution, the exact amount of active ingredient applied to each plot could be determined (Table 8.1).

Fertilizer and herbicide were applied simultaneously once a year in spring for three

Table 8.1 *Mean amount of active ingredient (mg.plot^{-1}) applied per treatment in experiment 1 and 2 for 1993, 1994 and 1995. 0, 5, 10 and 50% of the standard herbicide dose refer to 0, 10, 20 and 100 g fluroxypyr.ha^{-1}.y^{-1} respectively. Standard errors in brackets.*

date of application	herbicide rate in experiment 1			herbicide rate in experiment 2		
	5%	10%	50%	5%	10%	50%
7-10/6/93	3.96 (0.02)	7.98 (0.06)	39.98 (0.27)	3.94 (0.03)	8.00 (0.04)	39.52 (0.27)
20-21/5/94	3.97 (0.07)	7.73 (0.10)	38.49 (0.50)	3.89 (0.11)	8.20 (0.08)	40.83 (0.73)
26/4/95	3.79 (0.05)	7.63 (0.11)	38.80 (0.52)	3.90 (0.07)	7.73 (0.06)	38.90 (0.76)
target rate:	4.00	8.00	40.00	4.00	8.00	40.00

consecutive years. Treatments were applied when vegetation height was approximately 20 cm: on 7-10 June 1993, 20-21 May 1994, 26 April 1995. Each combination of treatments was replicated four times in a randomized complete block design (3 fertilizer levels x 4 herbicide levels x 4 replicated blocks = 48 experimental units).

Assessments of the vegetation composition were made in the central square metre leaving a buffer of 0.5 m on all sides between the permanent quadrat and the edge of the plot. Assessments were made from 12 to 17 May 1993, 10-14 May 1994, 24-25 April 1995 and 20-21 May 1996. Only presence data are presented here. Biomass samples were taken at the end of August in 1993, 1994 and 1995 by cutting above-ground biomass on two 0.3 x 0.3 m quadrats on opposite and annually alternating sides of the central square metre. The samples were separated into grasses and forbs and dry weight was determined after drying for 48 hours at 80 ºC.

Experiment 2

Since the expression of the effects was expected to be more pronounced in a more dynamic vegetation, a second experiment was established on an adjacent fallow arable field which had been cultivated for the last decade. In March 1993 plots were established after the field had been ploughed and seedbed preparation had taken place. A mixture of 30 grassland forbs was sown onto each plot on 7 April 1993 (Appendix 8.1). Individual plots were separated by 1 m wide strips sown with *Lolium perenne*, which was mown twice each year. The sown species were selected from a range of vegetation types representing possible stages in succession on fallow arable land on sandy soil and under a mowing regime (for further details see Kleijn *et al.* 1997). Plot size, soil type, treatment levels and date of application, mowing regime and duration of the experiment were the same as in experiment 1.

Assessments were made twice each year: 18-26 May and 20-30 September 1993; 2-9 May and 19-27 September 1994; 20-22 April and 11-14 September 1995; 6-8 May 1996. Biomass samples and dry weight determination were performed as in experiment 1, but the samples were separated into sown forbs, spontaneously established forbs and grasses.

Experiment 3

In 1995, the sensitivity of seedlings to different levels of fluroxypyr was investigated for an arbitrary selection of species from experiments 1 and 2. Seedlings were raised from seed and individual plants were transplanted 8 days after emergence to 0.5 l pots containing arable soil

from the experiment 2 field. Subsequently, the plants were grown in a glasshouse under additional lighting (8 hours dark, 16 hours lighted by 8 400W lamps). Day temperature was 20 °C, night temperature 17 °C and relative humidity was kept constant at approximately 60%. Within replicated blocks, pots were rotated on a weekly basis to avoid differences in growth conditions.

Before treatment four pots of each species were harvested to determine initial dry weight and treatments were applied when plants of a species had developed four real leaves. The treatments consisted of the three concentrations of fluroxypyr representing 5, 10 and 50% of the standard agricultural rate (resp. 25, 50 and 250 mg fluroxypyr per litre at a spraying volume of 400 l.ha^{-1}) plus the control plants which were sprayed with water only. Each treatment.species combination was replicated four times and arranged in a randomized complete block design. Spraying was executed in a spraying cabin at AB-DLO, Wageningen, simulating normal arable spraying under controlled conditions (boom speed 3.1 km.h^{-1}, 400 l.ha^{-1}, 3 bar pressure, Birckmayer 1.2 mm nozzles). When plants had dried they were put back in the glasshouse. Above and below-ground biomass of the species was harvested six weeks after application of the treatments and dry weight was determined after drying for 48 hours at 80 °C. Subsequently, for each treatment.species combination, biomass increase was determined. Plants that had died were given zero biomass increase.

Analysis

Data related to species numbers and biomass production in experiment 1 and 2 were analysed by means of a two-way analysis of variance (Sokal & Rohlf 1995) with the GENSTAT statistical package (GENSTAT 1993). The data of each sampling date were analysed separately. Data of experiment 3 were analysed by a one-way analysis of variance. If treatment effects were statistically significant, differences between treatment means were tested with a LSD test. Furthermore, if the variance of the response variate was not constant, the data were ln-transformed prior to analysis.

To analyse treatment effects on individual species, the number of times an individual species was present in a plot in consecutive years was determined, giving scores from zero to four (experiment 1) or from zero to seven (experiment 2). Thus a score of seven in experiment 2 indicated that a species was found each time a plot was sampled. These scores were analysed by means of a two-way analysis of variance and significant effects indicated differences in the mean presence of a species during the entire span of the experiment due to one of the factors. Subsequently, for species with significant treatment effects, trends in time were visualized in graphs by depicting mean presence of the species (the percentage of plots in which the species was found) over time.

Results

Experiment 1

In the first year after application, the 50% fertilizer treatment already had significantly lower numbers of species than the two other levels. In 1995 and 1996 a significant difference in species numbers developed between the 0% and the 25 and 50% plots (Fig. 8.1a). No
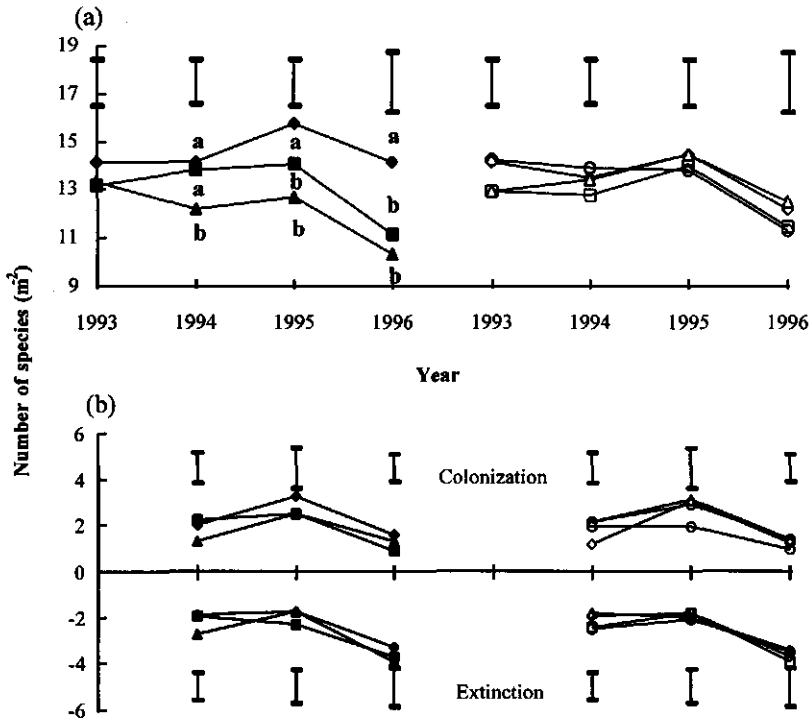
Figure 8.1 Effects of different fertilizer levels (averaged over herbicide levels) and herbicide levels (averaged over fertilizer levels) over time in experiment 1. (a) number of species (b) colonization and extinction rates. Colonization and extinction rates are determined as the number of species appearing and disappearing between two successive assessments. Fertilizer: closed diamonds = 0%, closed squares = 25%, closed triangles = 50% (the equivalent of 0, 27.5 and 55 kg N ha^{-1}.y^{-1} respectively); Herbicide: open diamonds = 0%, open squares = 5%, open triangles = 10%, open circles = 50% (0, 10, 20 and 100 mg fluroxypyr.ha^{-1}.y^{-1} respectively). Error bars (two times standard error) are given for each sample date. Different characters indicate significant differences (P<0.05), no characters: differences not significant.

significant herbicide effects or herbicide.fertilizer interactions were found. The differences between the trajectories of species numbers of the three fertilizer levels were caused by the cumulative effect of an overall higher colonization and a lower extinction rate in the 0% plots (Fig. 8.1b), although colonization and extinction rates in individual years as well as their mean rates over three years did not differ significantly. In 1996 the 0% herbicide-0%fertilizer (14.8 species.m^{-2}) and the 10% herbicide- 0% fertilizer plots (15.0 species.m^{-2}) were most species-rich, while the 10%-50% and the 50% herbicide-50% fertilizer plots had the least species per square metre (both 9.5; difference statistically significant at $P<0.01$). The other plots had intermediate levels of species richness.

During the experiment there was a natural tendency for the forbs to decline in biomass (Table 8.2). The biomass data corroborate the results of number of species (Fig. 8.1a); again the herbicide treatments had no effect on forbs, grasses or the total vegetation. Fertilizer

Table 8.2 *Mean effects of low doses of fertilizer and herbicide on the biomass production (g dry weight.m^{-2}) and composition of the vegetation in experiment 1 and 2 in 1993, 1994 and 1995. Responses to different fertilizer levels are averaged over herbicide levels, while responses to herbicide levels are averaged over fertilizer levels. 0, 25 and 50% of the standard fertilizer dose refer to 0, 27.5 and 55 kg N ha^{-1}.y^{-1} respectively; 0, 5, 10 and 50% of the standard herbicide dose refer to 0, 10, 20 and 100 g fluroxypyr.ha^{-1}.y^{-1} respectively. Different characters in superscript indicate significant differences (P< 0.05); a-c due to fertilizer effects, e-f due to herbicide effects.*

	fertilizer rate			herbicide rate			
	0%	25%	50%	0%	5%	10%	50%
Experiment 1							
1993							
Total vegetation	335[a]	379[ab]	419[b]	386	373	368	385
Forbs	118	111	116	129	102	95	135
Grasses	217[a]	268[ab]	303[b]	257	271	273	250
1994							
Total vegetation	297[a]	430[b]	553[c]	395	458	414	437
Forbs	94	109	146	106	172	91	96
Grasses	203[a]	321[b]	406[c]	289	286	323	341
1995							
Total vegetation	392[a]	554[b]	612[b]	503	514	527	532
Forbs	35	65	66	34	88	59	40
Grasses	357[a]	489[b]	546[b]	469	426	469	492
Experiment 2							
1993							
Total vegetation	558[ab]	536[a]	687[b]	645	668	504	557
Sown forbs	279	276	349	341	299	249	316
Unsown forbs	238	226	303	268	338	227	189
Grasses	41	34	35	36	31	28	52
1994							
Total vegetation	766[a]	955[ab]	1119[b]	948	1065	897	876
Sown forbs	745[a]	945[ab]	1116[b]	936	1060	888	869
Unsown forbs	9.4	5.3	1.7	10.0[f]	4.4[e]	6.9[e]	0.6[e]
Grasses	2.4	4.2	1.7	2.3	0.8	1.9	6.0
1995							
Total vegetation	1179	1429	1478	1655[f]	1423[f]	1471[f]	900[e]
Sown forbs	1151	1409	1440	1632[f]	1409[f]	1454[f]	838[e]
Unsown forbs	10.6	1.8	0.9	13	1	2	2
Grasses	17.8	18.4	37.4	9[e]	13[e]	16[e]	61[f]

application resulted in a significant increase in total biomass production in all years. This was, however, entirely caused by an increase in grass biomass. Forb biomass production was unaffected by fertilizer application (Table 8.2).

Four species showed significant differences in mean presence over the years 1993-1996 which proved to be related to treatment effects. *Hypochaeris radicata* and *Picris hieracioidis* declined in occurrence more rapidly on the fertilized plots than on the unfertilized plots (Fig. 8.2b,c). Furthermore, *H. radicata* showed a significant herbicide.fertilizer interaction (P<0.05). The response to fertilization in the different herbicide plots however showed similar trends to the main fertilizer effects, declining from low to high fertilizer application rates. In
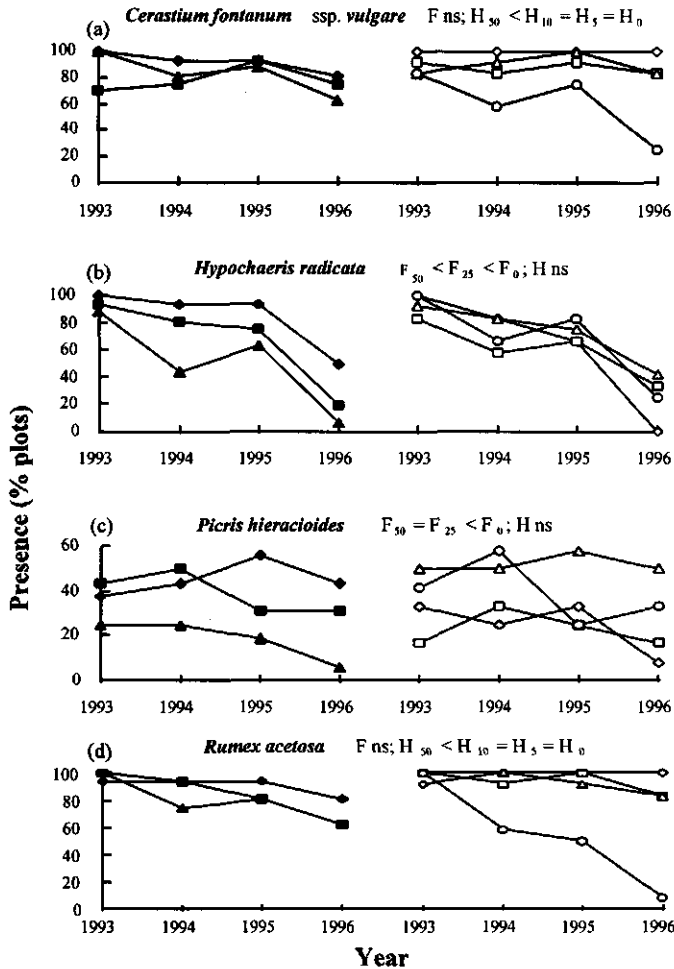
Figure 8.2a-d *Trends in time (experiment 1) in mean presence (percentage of plots in which a species was present) of four species with significant fertilizer (F) or herbicide effects (H; P<0.05). Fertilizer: closed diamonds = 0%, closed squares = 25%, closed triangles = 50% (the equivalent of 0, 27.5 and 55 kg N ha^{-1}.y^{-1} respectively); Herbicide: open diamonds = 0%, open squares = 5%, open triangles = 10%, open circles = 50% (0, 10, 20 and 100 mg fluroxypyr.ha^{-1} .y^{-1} respectively).*

contrast, *Cerastium fontanum* ssp *vulgare* and *Rumex acetosa* showed a sharp decline in time in the 50% herbicide plots (Fig. 8.2a,d).

Experiment 2

The establishment of the sown forbs was above expectation. At the end of the experiment 25 of the 30 species still persisted in considerable numbers. Another 19 species were found regularly that had colonized the plots spontaneously (Appendix 8.1). Already in the first year
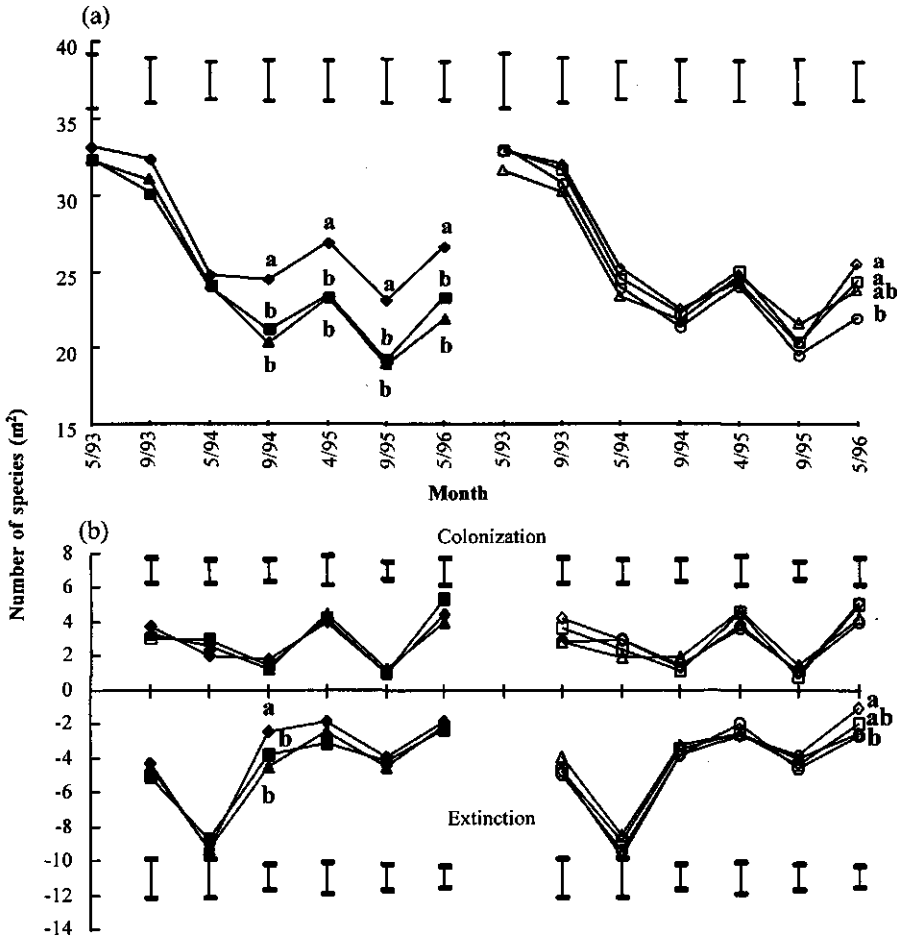
Figure 8.3. Effects of different fertilizer levels (averaged over herbicide levels) and herbicide levels (averaged over fertilizer levels) over time in experiment 2. (a) number of species (b) colonization and extinction rates. Colonization and extinction rates are determined as the number of species appearing and disappearing between two successive assessments. Fertilizer: closed diamonds = 0%, closed squares = 25%, closed triangles = 50% (the equivalent of 0, 27.5 and 55 kg N ha^{-1}.y^{-1} respectively); Herbicide: open diamonds = 0%, open squares = 5%, open triangles = 10%, open circles = 50% (0, 10, 20 and 100 mg fluroxypyr.ha^{-1} .y^{-1} respectively). Error bars (two times standard error) are given for each sample date. Different characters indicate significant differences (P<0.05), no characters: differences not significant.

the sown species contributed for some 50% to the total biomass production, with a limited number of species dominating the vegetation throughout the experiment: *Centaurea jacea*, *Leucanthemum vulgare*, *Saponaria officinalis*, *Silene latifolia* ssp *alba* and *Tanacetum vulgare*.

Species numbers declined sharply after the first year as annual weeds failed to establish in the second season (Fig. 8.3a). In the autumn of 1994 a significant difference appeared
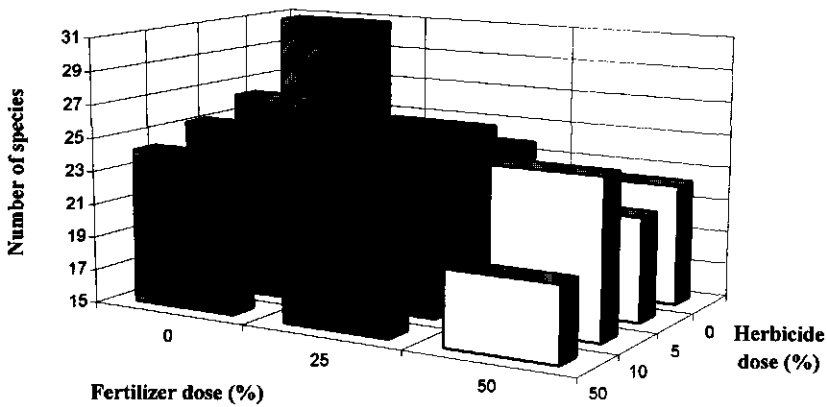
Figure 8.4 *The effects of three years of fertilizer and herbicide application (both in % of standard dose) on the species richness (no species.m⁻²) of a mixture of grassland species sown to a fallow arable field. 0, 25 and 50% fertilizer refer to 0, 27.5 and 55 kg N ha⁻¹.y⁻¹ respectively and 0, 5, 10 and 50% herbicide refer to 0, 10, 20 and 100 mg fluroxypyr.ha⁻¹ .y⁻¹ respectively. Experiment 2; May 1996.*

between the 0% fertilizer plots on one hand and 25 and 50% plots on the other. This difference persisted and remained constant for the rest of the experiment. Significant herbicide effects were absent but for the last assessment when the 0 and 5% plots yielded significantly higher species numbers than the 50% plots (Fig. 8.3a). The colonization rates for different treatments did not show distinct differences and fluctuated simultaneously between high spring levels and low autumn levels (Fig. 8.3b). Extinction rates were characterized by a sharp peak in May 1994 signifying the disappearance of most annual weeds. In September 1994 extinction rates in the fertilized plots were significantly higher than in the unfertilized plots, coinciding with the time the first fertilizer effects became apparent in species numbers. In May 1996 extinction rates were significantly influenced by the herbicide treatments, 0% plots having lower values than 10 and 50% plots. As for the fertilizer treatments, the time of the significant effects on extinction rates coincided with the first significant herbicide effect on total species numbers. In 1996, a significant ($P<0.05$) herbicide.fertilizer interaction was found, possibly due to peculiarly high species numbers in the 10%-50% and the 5% herbicide-25% fertilizer plots (Fig. 8.4). However, in general the effects of the herbicide and fertilizer treatments appeared to be additive: the species numbers decline increasing with levels of both herbicide and fertilizer. The control plots were significantly more species-rich (30.8 species.m⁻², $P<0.05$) than any other plot type; the 50%-50% plots were with 19.5 species.m⁻² the least species rich.

Biomass production of the total vegetation was significantly raised after application of fertilizer in 1993 and 1994 but not in 1995 (Table 8.2). In 1994, biomass production of spontaneously established forbs was significantly reduced, even by the lowest herbicide level. In 1995 the 50% herbicide treatment had a severe negative impact on total biomass production, while in the same plots the uncontrolled and spontaneously established grasses increased in biomass.
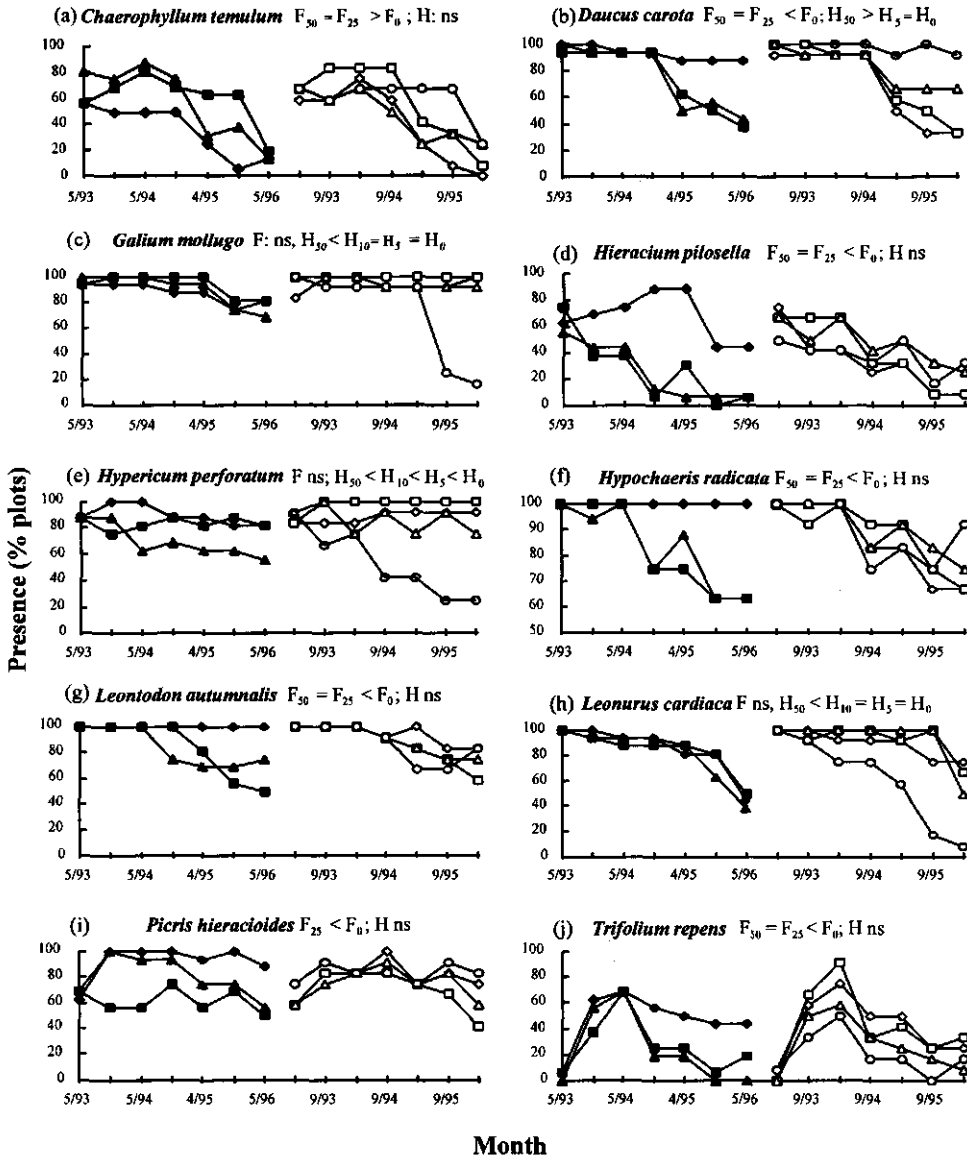
Month

Figure 8.5a-j Trends in time (experiment 2) in mean presence (percentage of plots in which a species was present) of ten species with significant fertilizer (F) or herbicide effects (H; P<0.05). Fertilizer: closed diamonds = 0%, closed squares = 25%, closed triangles = 50% (the equivalent of 0, 27.5 and 55 kg N ha^{-1}.y^{-1} respectively); Herbicide: open diamonds = 0%, open squares = 5%, open triangles = 10%, open circles = 50% (0, 10, 20 and 100 mg fluroxypyr.ha^{-1}.y^{-1} respectively).

Four types (1-4) of responses to the treatments could be recognized for individual species (Fig. 8.5a-j). (1) *Hieracium pilosella, Hypochaeris radicata, Leontodon autumnalis, Picris hieracioides* and *Trifolium repens* all occurred less frequently in fertilized plots compared to

Table 8.3 *Mean dry weight increase (g.plant^{-1}) of a selection of forb species six weeks after application of different doses of fluroxypyr. 0, 5, 10 and 50% of the standard herbicide dose refer to 0, 10, 20 and 100 g fluroxypyr.ha^{-1}. y^{-1} respectively. Individual species standard error: 0.139; species mean se: 0.033. Different characters in superscript indicate significant differences.*

species	herbicide (% standard dose)				P
	0	5	10	50	
Campanula rotundifolia	0.53	0.43	0.83	0.25	ns
Centaurea jacea	0.74	0.68	0.97	0.67	ns
Cichorium intibus	0.58	0.53	0.87	0.32	ns
Crepis biennis	0.54	0.44	0.54	0.49	ns
Daucus carota	0.56	0.59	0.90	0.34	ns
Galium mollugo	0.40^b	0.50^b	0.53^b	0.03^a	<0.01
Galium verum ssp *verum*	0.24^b	0.18^b	0.28^b	0^a	<0.01
Hieracium pilosella	0.44	0.33	0.41	0.12	ns
Hypericum perforatum	0.31^b	0.27^b	0.20^b	0.05^a	<0.01
Leontodon autumnalis	0.48	0.76	0.44	0.52	ns
Leonurus cardiaca	0.50	0.52	0.63	0.16	ns
Leucanthemum vulgare	0.34	0.42	0.56	0.34	ns
Lotus corniculatus spp *corniculatus*	0.53	0.61	0.57	0.31	ns
Malva moschata	0.36	0.59	0.71	0.23	ns
Medicago lupulina	0.32	0.34	0.21	0.32	ns
Picris hieracioides	0.59	0.78	0.62	0.57	ns
Trifolium dubium	2.02	1.49	1.91	0.41	ns
Silene latifolia ssp *alba*	0.69	0.72	0.74	0.43	ns
Species mean	0.57^b	0.57^b	0.66^b	0.31^a	<0.001

unfertilized plots and showed little response to the herbicide treatments. *H. pilosella* showed the most extreme response as in September 1994 its presence in fertilized plots had already declined to negligible levels while at the same time it still occurred in 90% of the unfertilized plots. (2) *Chaerophyllum temulum* showed an increased presence ratio in fertilized plots and no response to the herbicide treatments. (3) *Daucus carota* was encountered less frequently in the fertilized plots but was present in a larger proportion of the 50% herbicide plots compared to the 0% plots. (4) *Galium mollugo, Hypericum perforatum* and *Leonurus cardiaca* had a significantly lower mean presence ratio in the 50% herbicide plots compared to the other herbicide levels, while fertilizer application had no effects. No significant herbicide.fertilizer interactions were found.

Experiment 3

Immediately after application of the herbicide treatments all treated species showed symptoms, ranging from slight curling of the leaves to death of entire plants. Except for the few plants that had died, recovery was fast, and differences between treated and control plants of most species could hardly be detected by eye after six weeks. Analysis of the dry weight increments confirmed these observations (Table 8.3; above-, below-ground and total dry weights gave similar results, thus only total dry weight data are presented). The treatments produced significant effects for only three species, *Galium mollugo, Galium verum* ssp *verum* and *Hypericum perforatum*. For these species the 50% treatments resulted in death of all or three out of four plants, and subsequently in significantly lower dry weight increments over

the six weeks of the experiment. A significant reduction of some 50% in mean dry weight increment was found however for all species combined.

Discussion

Effects of low levels of herbicide and fertilizer

A plant community may be stable but the species composition is dynamic. On a small scale (0.01-0.025 m^2) grasslands of low productivity have a high turn-over of species. Species become extinct in one patch but may colonize other nearby patches (Van der Maarel & Sykes 1993). Similarly, on a large scale (160-500 m^2) apparently stable plant communities are characterized by outbreaks of species; in any number of years species may show a sudden increase and subsequent decrease in abundance for no obvious reason (Dodd *et al.* 1995). In these experiments, similar trends occurred such as the overall decrease in biomass of forbs and the overall decline of *Hypochaeris radicata* (Fig. 8.2b) in experiment 1. However, the orthogonal design of the experiments allows us to separate between changes due to natural trends and changes due to the treatments.

Fertilizer application resulted in an increase in total biomass production and a decrease in species numbers. Species that responded negatively to fertilizer application in both experiment 1 and 2 were small and prostrate growing (e.g. *Hieracium pilosella, Leontodon autumnalis, Trifolium repens*), or at least during part of their life-cycle (*Picris hieracioides*). These results support the well documented theory that an increase in nutrient resources in a vegetation will lead to an increase in competition for light (Bobbink 1991, Tilman 1993). Prostrate species, unadapted to the new habitat conditions are at a competitive disadvantage and will eventually become extinct. In experiment 2, the significantly higher autumn 1994 extinction rates in the fertilized plots demonstrated this clearly. In experiment 1, however, significant differences in species numbers were found without any observed significant differences in colonization or extinction rates. This indicates that in the more stable vegetation of the well established grassland, treatment effects built up more gradually but nevertheless led to significant differences in species-richness.

In contrast, the herbicide applications did not have similar effects in experiments 1 and 2. In experiment 1 no herbicide effects were observed while in experiment 2 a number of effects were observed. In 1994 the major vegetation components were unaffected by the herbicide treatments but the spontaneously established forbs, species like *Cerastium fontanum* ssp *vulgare, Ranunculus repens* and *Trifolium repens*, were significantly reduced in abundance even by the lowest level of herbicide. In 1995 in experiment 2, the 50% herbicide treatments led to a 46% decrease in total biomass production compared to the 0% plots. At the same time, probably as a result of the suppression of the dominant species, the unaffected grasses showed a more than 6-fold increase in the same plots (Table 8.2). Finally, the trends in species richness between the different herbicide treatments diverged significantly in the spring of 1996, a year after the last application. The differences between the two experiments may be explained by the higher number of species in experiment 2, all potentially sensitive forbs, and the more dynamic nature of this early successional vegetation type. Another important factor may be the productivity of the vegetation. De Ruiter & Meinen (1995) found a reduced efficacy of glyphosate when plants experienced water stress. Plants experiencing

stress in general will have a reduced growth rate and subsequently processes determining herbicide efficacy such as translocation and protein synthesis (the main mode of action of fluroxypyr; Schlotter & Schuster 1992) will be lower. Since, in 1995, annual productivity in experiment 2 was much higher than that in experiment 1 (1362 vs. 519 $g.m^{-2}$), growth rate after application will also have been much larger which may explain the observed differences in efficacy of the herbicide. Individual species were responding significantly to the herbicide treatments in both experiments, however, and most were negatively affected by them. The exception was *Daucus carota* (Fig. 8.5b) which was present in a significantly larger proportion of the 50% herbicide plots compared to the 0% plots. *D. carota* was also strongly negatively affected by fertilizer application and the reduced biomass production in the 50% plots, resulting in a reduced competition for light, possibly explains the success of this species in the 50% herbicide plots.

The results from experiment 3 only partly correspond with those from experiment 2. While *Galium mollugo* and *Hypericum perforatum* proved to be sensitive to fluroxypyr in both experiments, *Leonurus cardiaca* was significantly affected in experiment 2 but not in 3 and *Galium verum* ssp *verum* was affected in experiment 3 but not in 2. *Daucus carota* was not affected in experiment 3 and positively influenced in experiment 2 as discussed in the previous paragraph. The difference in effect for *G. verum* ssp *verum* may be explained by differences in the leaf morphology between seedlings which have lanceolate leaves and adult plants which have needle-like leaves. Thus interception and efficiency of the herbicide may be much larger for seedlings of this species than for adult plants. This supports the results of Marrs *et al.* (1993) who found an increased sensitivity to glyphosate drift in *Lychnis flos-cuculi* seedlings compared to adult plants. The combined results of these experiments point out the limited predictive value of short term, monoculture pot experiments which are most frequently used to evaluate effects of herbicides on non-target plants (Marrs *et al.* 1989a,b, 1991, 1993, Marshall & Birnie 1985). The outcome of interactions between species in a community differs from the performance of species in pots and is likely to differ with the type of vegetation as well. Furthermore, the fact that significant herbicide effects on species numbers became apparent one full year after the last application in experiment 2 emphasizes the importance of longer term experiments. Plants may survive the year in which the application took place but may not have build up enough reserves to survive the following winter.

The previous paragraphs make clear that generalization of especially the herbicide effects is rather difficult. Furthermore, the experiments are a simplification of real field boundaries. The results may underestimate the effects herbicides have in field boundaries (1) Fluroxypyr is a rather selective herbicide and herbicides such as MCPA, with a wider control spectrum, may have more severe effects. (2) Fluroxypyr was applied once a year; herbicides are commonly applied more than once a year. (3) Seed sources of species that had gone extinct in herbicide treated plots were never far away in these experiments since they persisted in other plots. In a normal field boundary, drift is likely to affect a large part, if not all, of the boundary. Re-colonization may therefore be much more limited in field boundaries compared to these experiments. (4) While individual species may decline more rapidly by the use of only one herbicide, a larger proportion of the species may be affected when more than one herbicide is used. Probably a small number of species in any vegetation will not or hardly be affected by most herbicides and these may gain competitive advantages each time any

herbicide drift occurs. Given sufficient time only these species may remain in a field boundary.

On the other hand the results may overestimate the effects of herbicides in normal boundaries (1) because in experiment 1 and 2 in three consecutive years the same herbicide was used. Sensitive species will consequently decline more rapidly than when different herbicides were used which were not all phytotoxic to these species. (2) The effects of other important factors, such as mowing regime or soil type, have not been included in the present experiments. These factors may have overriding effects compared to herbicide drift.

Some generalizations can be made however. In both experiments herbicide application affected only a small number of species and none were directly eliminated. Although, the two agrochemicals proved to counteract each other for *D. carota*, most affected species were reduced in presence by one or the other factor. Thus, drift of both agrochemicals is harmful to the botanical richness of field boundaries. An important aspect illustrated by the present experiments is that species that were affected significantly were minor components of the vegetation like *Cerastium fontanum* ssp *vulgare* and *Rumex acetosa*, the so-called subordinate species of Grime (1987). Thus in the long run, the deterioration of field boundary vegetation due to drift of the two agrochemicals will take place by elimination of (part of) the subordinate species from the field boundary. The effects of low doses of fluroxypyr and NPK fertilizer appeared to be additive and while so far research efforts have focused on herbicide drift as a major threat to botanical diversity of arable field boundaries, these experiments suggest that the effects of fertilizer drift are considerably more severe and predictable than the effects of herbicide drift.

Implications for field boundary management

Some 60% of the farmers in the United Kingdom and The Netherlands spray their field boundaries with broad spectrum herbicides in attempts to control weed infestations (Marshall & Smith, 1987, Boatman 1992, De Snoo & Wegener Sleeswijk 1993). Besides worsening weed problems instead of solving them (Boatman 1992) these activities are detrimental for field boundary diversity and any discussion about the effects of drift of agrochemicals on field boundary diversity should be made under the assumption that this type of herbicide use will be abandoned shortly.

So far, decisions to take precautions against herbicide drift or fertilizer misplacement have been mostly based on economic and agronomic grounds (Marshall & Birnie 1985, Rew *et al.* 1992). Lack of information on the effects of drift on non-target flora and fauna make it difficult for farmers to take appropriate steps to protect wildlife. These experiments shed some light on the botanical consequences of fertilizer and herbicide drift and may contribute to the construction of a decision framework for preventative measures against drift of agrochemicals based on economic and wildlife criteria. Van de Zande *et al.* (1995) found drift deposition to be 4% of the applied dose at 3-4 m from the last nozzle for a conventional spray boom. This suggests that no negative effects on the boundary vegetation are likely to occur when herbicides are applied with a distance of 3 m between the last nozzle and the field boundary. Sufficient data to translate effects of fertilizer misplacement to safe application distances are lacking, however.

Thus, to be able to use wildlife criteria for the implementation of drift precautions, we need to quantify the distribution patterns of the most common fertilizer spreaders under field

conditions more accurately. Furthermore, the effects of low doses of the herbicide fluroxypyr need to be compared with the effects of a number of other herbicides to be able to generalize herbicide drift effects more exactly. Inclusion of fertilizer treatments in such experiments will facilitate comparisons between experiments with different herbicides or in different vegetation types. Finally, the effects of low doses of pesticides on insect diversity in a vegetation need to be assessed. Bioassay experiments (Davis *et al.* 1993) indicate that insects may be even more sensitive to pesticide drift than plants.

Acknowledgements

Appendix 8.1 *Species occurring naturally in experiment 1 and 2 (found in at least three years). Of the sown species in experiment 2, the percentage weight they contributed in the mixture and their germination rate is given. Germination rate was determined from 200 seeds on wetted filter paper in petridishes at alternating temperatures of 12 hours 15 °C/12 hours 25 °C. Germinating seeds were counted until seeds ceased to germinate. Seeding rate of the mixture was 1g.m⁻².*

experiment 1	experiment 2	experiment 2	weight (%)	germination (%)
	spontaneously established	sown species		
Achillea millefolium	*Agrostis stolonifera*	*Campanula rotundifolia*	2.6	63
Agrostis capillaris	*Anthoxanthum odoratum*	*Centaurea jacea*	8.1	44
Ajuga reptans	*Berteroa incana*	*Chaerophyllum temulum*	5.2	1
Anthoxanthum odoratum	*Carex ovalis*	*Cichorium intybus*	1.6	47
Arrhenatherum elatius	*Cirsium arvense*	*Crepis capillaris*	0.1	45
Bromus hordeaceus	*Elymus repens*	*Crepis biennis*	1.9	80
Campanula rapunculus	*Holcus lanatus*	*Daucus carota*	3.4	84
Cardamine pratensis	*Juncus effusus*	*Euphrasia stricta†*	0.8	55
Carex ovalis	*Lolium perenne*	*Galium mollugo*	0.7	98
Cerastium fontanum	*Poa annua*	*Galium verum* ssp *verum*	0.6	77
ssp *vulgare*	*Poa trivialis*	*Hieracium pilosella*	1.8	86
Cirsium arvense	*Ranunculus repens*	*Hypericum perforatum*	3.2	68
Crepis biennis	*Rumex acetosa*	*Hypochaeris radicata*	2.1	65
Crepis capillaris	*Rumex acetosella*	*Jasione montana†*	0.3	30
Dactylis glomerata	*Senecio vulgaris*	*Lathyrus pratensis*	2.1	4
Daucus carota	*Stellaria media*	*Leontodon autumnalis*	4.0	84
Elymus repens	*Trifolium pratense*	*Leonurus cardiaca*	1.6	47
Festuca rubra ssp	*Trifolium repens*	*Leucanthemum vulgare*	2.0	92
commutata	*Urtica dioica*	*Linaria vulgaris*	0.9	35
Geranium pratense		*Lotus corn.* ssp *corniculatus*	0.7	26
Holcus lanatus		*Lysimachia vulgare‡*	1.3	76
Hypericum perforatum		*Malva moschata*	18.1	18
Juncus conglomeratus		*Medicago lupulina†*	1.9	77
Lathyrus tuberosus		*Picris hieracioides*	0.4	75
Leontodon autumnalis		*Pimpinella saxifraga*	5.2	8
Lotus uliginosus		*Saponaria officinalis*	16.1	68
Luzula campestris		*Silene latifolia* ssp *alba*	5.4	41
Lychnis flos-cuculi		*Tanacetum vulgare*	5.2	30
Myosotis discolor		*Trifolium arvense*	0.5	31
Picris hieracioides		*Trifolium dubium*	2.2	22
Pimpinella major				
Pimpinella saxifraga				
Plantago lanceolata				
Poa trivialis				
Ranunculus acris				
Ranunculus ficaria ssp				
bulbilifer				
Ranunculus repens				
Rumex acetosa				
Rumex acetosella				
Senecio jacobaea ssp				
jacobaea				
Taraxacum officinale				
Trifolium pratense				
Trifolium repens				
Veronica serpyllifolia				
Vicia hirsuta				
Vicia sativa ssp *nigra*				

‡ Sown species that did not establish at all; † Sown species found in the first year only.

9

The exploitation of heterogeneity by a clonal plant in habitats with contrasting productivity levels

Summary

We investigated whether the clonal grass *Elymus repens* exploits a heterogeneous environment by means of (1) simple growth responses, (2) foraging responses or (3) clonal integration. Furthermore, the hypothesis was tested that the exploitation of heterogeneity by this clonal plant was more beneficial in high compared to low productive environments. In trays, partitioned into four quadrants connected in the center, a homogeneous environment was created by vegetating all quadrants and the center; a heterogeneous environment by keeping two opposite quadrants bare. Contrasting productivity levels were established by fertilizing half the number of trays of each environment type and a single rhizome fragment was planted in the center of the trays. After two growing seasons the primary rhizomes of *Elymus repens* in the low productive heterogeneous trays had grown selectively into the bare quadrants (response type 2), resulting in a marked concentration of biomass in the favourable bare quadrants and a total plant biomass 3.0 times that of the low productive homogeneous trays. We hypothesize that sectorial transport of nutrients through the rhizomes, resulting in the selective outgrowth of buds into the bare quadrants, was responsible for this foraging response. In the high productivity heterogeneous trays no selectivity in primary rhizome placement was found (response type 1), which may have been caused by the repeated neutralization of a contrast in nutrient supply between the bare and the vegetated quadrants due to the fertilizer applications. However, those that grew into a bare quadrant produced disproportionately more biomass which resulted in an increase of total plant biomass by a factor 2.7 relative to the high productivity homogeneous trays. Thus, due to the high returns per daughter ramet in the bare quadrants at the high productivity level and the selective placement of ramets in these favourable quadrants at the low productivity level, benefits of exploiting heterogeneity were not significantly different at the two productivity levels.

Key words: clonal plant, *Elymus repens*, *Agropyron repens*, foraging, physiological integration, environmental heterogeneity, directional meristem outgrowth, selective ramet placement.

Introduction

In most habitats resources are distributed patchily (Gross *et al.* 1995, Robertson *et al.* 1988, Smith *et al.* 1992). Many plant species have demonstrated the ability to cope with this patchy distribution by concentrating root or shoot growth in resource rich areas (Campbell *et al.* 1991, Birch & Hutchings 1994, Jackson & Caldwell 1989). Such a concentration is generally achieved by the production of new shoots and roots made possible by the acquisition of resources in the resource rich patch (Gross *et al.* 1993, St John *et al.* 1983).

Clonal species may respond to the heterogeneous distribution of resources in their environment in a number of ways. (1) Mother-plants place their ramets randomly in the surrounding vegetation. Daughter-ramets placed in favourable patches will produce more biomass than those in less favourable patches and will produce more daughter-ramets of their own which, in turn, are send out randomly. Thus, the clonal growth mode facilitates a continuous search and simple growth responses result in a concentration of shoot and root biomass in favourable patches (de Kroon & Hutchings 1995). (2) Mother-plants place their ramets selectively in the surrounding vegetation. If a mother-plant experiences favourable growing conditions, daughter-ramets are placed nearby usually by reducing spacer internode length and/or increased branching intensities (Cain 1994, Slade & Hutchings 1987ab). The result of these responses is a concentration of ramets and an increased residence time of the clone in the favourable microsite. However, the subsequent exploitation of the extra resources will again result in growth responses and while foraging responses have been documented extensively (Dong 1993, Dong & de Kroon 1994, Evans & Cain 1995, Slade & Hutchings 1987ab, Waite 1994) it has not yet been established that a higher concentration of ramets in a good patch results in a more efficient capture of resources and subsequently in increased plant growth or production of offspring. (3) The spacers by which individual ramets are connected may allow transport of water, nutrients and assimilates between ramets (Marshall 1990, 1996). Ramets growing under less favourable conditions may be supported by those growing in a favourable environment. The benefits received by ramets in a stressful environment may outweigh the costs incurred by their connected neighbours in a favourable environment (Salzman & Parker 1985). When patches are rich in complementary resources, interconnected ramets may show a division of labour (Stuefer *et al.* 1996). Under such conditions exchange of mutually limiting resources between ramets through physiological integration may benefit ramets in both patches (Stuefer *et al.* 1994). Thus, the second type of response results in individual plants that differ significantly in morphology (internode length, branching intensity) from plants that demonstrate the first type of response, while the third type of response will lead to individual plants with significantly reduced differences between their ramets in the favourable and less favourable site.

However, all potential responses have in common that a plant first has to place ramets into an area with a degree of difference, or contrast (Kotliar & Wiens 1990) before it experiences the environment as heterogeneous. The net 'investment' costs for the entire clone depend upon the benefits it gains from the new ramet. It has been hypothesized that investments in new plant parts are only rewarding in high productive habitats as the returns upon the encounter of a favourable microsite in low productive habitats may not be sufficient to compensate for those investments (Balaré 1994, Crick & Grime 1987, Grime 1979). So far, this has been confirmed by comparing biomass investment patterns of species from high and low productive habitats (e.g. Campbell *et al.* 1991, Dong *et al.* 1996, Grime *et al.* 1986). The

same principle should apply to individual plants, however, as returns of new ramets should likewise be higher in habitats with a high productivity compared to those in low productive ones.

In this study we compare the responses of the rhizomatous grass *Elymus repens* in heterogeneous relative to homogeneous environments at two productivity levels. A favourable patch is a bare gap in an otherwise vegetated environment (as in Evans & Cain 1995, MacDonald & Lieffers 1993, Oborny 1994, Price & Hutchings 1996, Waite 1994). Benefits are expressed as increased biomass production of the total clone at the end of the experiment. The experiment lasted for 16 months. Natural, usually animal created gaps rarely exist longer (Goldberg & Gross 1988) and potential benefits should become evident within this period of time or have no ecological relevance. The aims of the experiment were (1) to determine whether the heterogeneous environment is exploited by mere growth responses, by foraging responses or by clonal integration. (2) to determine whether the exploitation of a heterogeneous environment by a clonal plant is more beneficial in high compared to low productive environments

Methods

Elymus repens (L.) Gould (syn. *Agropyron repens* (L.) Beauv.) is a perennial, rhizomatous hemicryptophytic grass which is most abundant in a range of fertile, disturbed habitats. It is particularly abundant in arable fields, road verges, hedgerows and spoil heaps and frequently found in meadows and pastures. It is less frequent in very unproductive situations, heavily grazed or waterlogged habitats (Grime *et al.* 1988). Within habitats, it is known to increase in abundance with the productivity of a site (Tilman 1987). Main mode of reproduction is by rhizomes as seed production is often poor. Because of its widespread occurrence and agronomic importance as an arable weed, a considerable amount of information is available regarding plant physiology and development (e.g. McIntyre 1967, Qureshi & McIntyre 1979, Rogan & Smith 1974, Taylor & Aarssen 1988).

To create heterogeneous habitats under controlled conditions, trays (0.7 x 0.9 x 0.4 m) were subdivided with wooden partitions in four quadrants which were connected in the central 0.15 x 0.15 m^{-2}. The bottom 0.1 m was filled with gravel, the remaining 0.3 m with topsoil from an unfertilized lawn from which the sod was removed. Gravel and soil were separated with rooting-cloth. Soil type was loamy-sand with a pH of 5.1 ± 0.1. Further details of the trays are given in Fig. 9.1a.

On 7 April 1995 the quadrants within trays were planted with seedlings of two non-clonal grassland species with a broad ecological range: *Holcus lanatus* and *Rumex acetosa* (Fig. 9.1b; hereafter species will only be referred to by generic name). Trays were either 'homogeneous', with all quadrants vegetated or 'heterogeneous' with only two opposite quadrants vegetated. The center was vegetated in all trays (Fig. 9.1b). Since the trays were not square, half of the replicated treatments described below had the East-West quadrants, the other half the North-South quadrants vegetated to avoid systematic differences due to quadrant shape. Throughout the experiment the bare quadrants were kept free of all plants except *Elymus* but below-ground root growth into these quadrants from the center was not hindered for any of the three species.

Just prior to planting the trays, rhizomes of *Elymus* were collected from a 0.5 x 0.5 m large
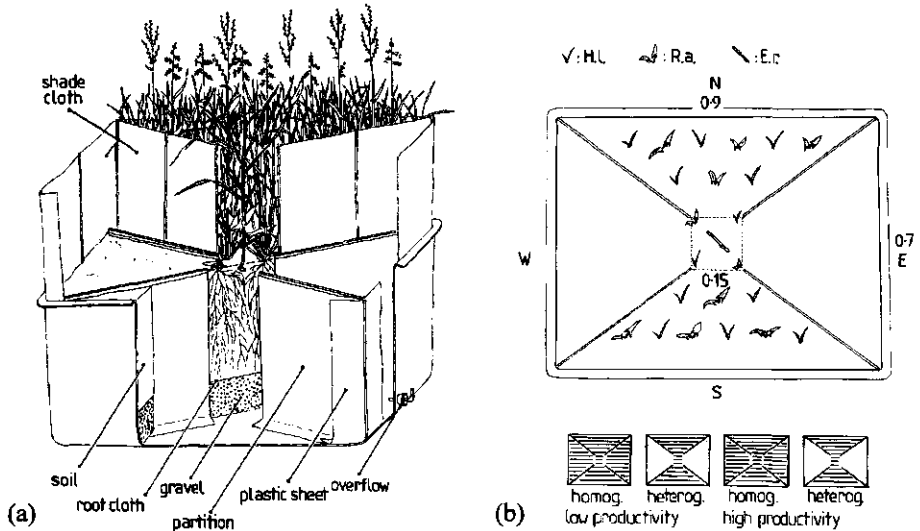
Figure 9.1 The design of a tray partitioned into four quadrants interconnected by the center (a) cross-section of a heterogeneous tray in the middle of the growing season (b) top-view of the four tray-types. The enlarged tray is showing the orientation of the rhizome fragments and the North-South orientation of the vegetated quadrants in the heterogeneous trays; dashed lines indicate where different sections were severed at harvest.

patch in a three year old fallow arable field. Two-node rhizome sections were cut and 44 sections of homogeneous size were selected; 24 were used for planting, the remaining 20 were used to determine initial dry weight (0.151 ± 0.046 g). The two-node rhizome sections were planted diagonally in the center of the trays (Fig. 9.1b) at the time the *Holcus* and *Rumex* seedlings were planted. During the growing season 90% shade-cloth was used to separate quadrants above-ground and to avoid edge effects (Fig. 9.1a).

To produce contrasting productivity levels, half of both the homogeneous and heterogeneous trays were subsequently fertilized by distributing an artificial NPK-fertilizer evenly over the entire tray every three months (8 g $N.m^{-2}.y^{-1}$ as NO_3 and NH_4, 6.4 g $P.m^{-2}.y^{-1}$ as P_2O_5 and 12.8 g $K.m^{-2}.y^{-1}$ as K_2O). The other half of the trays were not fertilized.

The trays were placed in four replicated blocks, each with one pair of homogeneous trays and two pairs of heterogeneous trays, giving a total of (1 homogeneous + 2 heterogeneous) x 2 productivity levels x 4 replicated blocks = 24 trays. The experiment was conducted in a greenhouse with partially open sides. Temperature in the greenhouse was somewhat higher than ambient temperature but followed the normal fluctuations well. Photosynthetic active radiation was 73% of incoming radiation. The trays were watered as necessary and were cut in September 1995, at the end of the first growing season.

From 12 to 22 August 1996 the trays were harvested block-wise. To estimate total productivity of the trays the above-ground vegetation of the *Holcus-Rumex* mixture was harvested in each quadrant as well as in the center. For each quadrant and center in all trays, the number of *Elymus* shoots was determined. Soil sections from the four quadrants and the center were separated by cutting the soil including roots and rhizomes between the center-end

of the partitions. Number of rhizomes entering the quadrants was determined. As these predominantly originated directly from the shoot-complex in the center they will be called primary rhizomes. Soil was carefully washed from the rhizomes, and roots and rhizomes were separated. Number of rhizome nodes was counted for the quadrants and center of each tray. Dry weight was determined for the *Holcus-Rumex* above-ground vegetation and the total of shoots, roots and rhizomes of *Elymus* after 48 hours at 80 °C.

Analysis

Testing whether ramets are placed randomly (response type 1) or selectively (2) in bare quadrants requires a comparison between the number of ramets produced in bare and vegetated quadrants. However, as the parent *Elymus* plants in the center of the heterogeneous trays could reproduce in either the vegetated or the bare quadrants, within-tray ramet distribution data are distributed binomial. Therefore, the data were transformed to a linear scale with a logit function ($y' = \ln(y/(n-y))$) with y being the number of observations in the bare quadrants and n being the total number of observations in a tray; General Linear Regression procedure, GENSTAT 1993). On the linear scale, means in the bare quadrants were tested for significant deviance from a random distribution (e.g. 50% of the ramets in bare and 50% in vegetated quadrants) by means of a t-test. Absence of any significant defiance would support the response type 1 while its presence would support response type 2. To test whether the observed distribution of *Elymus* ramets was not due to non-treatment effects the homogeneous trays were analyzed in a similar fashion. For this purpose vegetated quadrants that had the same orientation as the bare quadrants in the heterogeneous trays in their replicated block were labeled 'pseudo-bare quadrants'.

Testing whether clonal integration resulted in benefits (response type 3) may be done by comparing the average biomass production per primary rhizome in three types of quadrants. First, in bare quadrants next to vegetated quadrants. Second, in vegetated quadrants next to bare quadrants and third, in vegetated quadrants next to vegetated quadrants. Half of the heterogeneous trays were randomly assigned to represent the first type of quadrant and half to the second type of quadrant. A comparison of the second and the third type of quadrants gives an estimate of the benefits. The lay-out of the experiment did not allow for an estimate of the costs since no trays with four bare quadrants were included in the experiment.

Between tray biomass production of both the *Holcus/Rumex* vegetation and *Elymus* was tested by Analysis of Variance. Data were ln-transformed prior to analysis if variance of the response variate changed with the dimension of the response variate.

Results

In the high productivity treatments, the *Holcus/Rumex* vegetation was significantly more productive than in the low productivity treatments (Table 9.1). In the homogeneous trays, productivity of the pseudo-bare and the vegetated quadrants was similar, thus providing a homogeneous environment to the *Elymus* plants in the center. In the heterogeneous trays, above-ground productivity showed the obvious sharp contrast between bare and vegetated quadrants, however, this contrast was much more pronounced in the high productivity trays (0 - 834 versus 0 - 639 g/m^2). Productivity in the center was much higher than average. In the

Table 9.1 *Mean above-ground biomass production (± se) of the* Holcus lanatus/Rumex acetosa *vegetation in four tray types (in g/m². The homogeneous trays were replicated 4 times, the heterogeneous trays 8 times. Only total tray data were statistically analysed; different characters indicate significant differences (P<0.05).*

tray type:	low productivity		high productivity	
	homogeneous	heterogeneous	homogeneous	heterogeneous
(pseudo-) bare quadrants	389 ± 30	0 ± 0	672 ± 87	0 ± 0
center	974 ±113	3897 ± 1069	1392 ± 108	5300 ± 1004
vegetated quadrants	435 ± 30	630 ± 114	638 ± 67	834 ± 113
total tray	432^a ± 14	443^a ± 36	681^c ± 20	591^b ± 65

homogeneous trays this may have been caused by the fact that these plants were not limited by partitions or the tray-edge in any direction. In the heterogeneous trays these plants additionally were able to grow roots into bare quadrants.

The primary rhizomes and subsequently the shoots of *Elymus* were primarily found in the North and West quadrants, in correspondence with the orientation of the buds (Table 9.2, Fig. 9.1). Since half of the heterogeneous trays had vegetated North/South quadrants and half had vegetated East/West quadrants this preference did not invalidate any further analysis of treatment effects.

The placement of primary rhizomes by *Elymus* in the bare and vegetated quadrants deviated significantly from the expected 50%-50% distribution in the low productivity heterogeneous trays only (Fig. 9.2a). In these trays a significantly higher proportion of primary rhizomes had grown into the bare quadrants. The homogeneous trays at the same productivity level showed an even distribution of primary rhizomes. Placement in both high productivity treatments was biased towards the vegetated quadrants, but not significantly so. The distribution of the number of nodes and shoots and the total biomass production of *Elymus* reflected the pattern of the primary rhizomes closely in all but the high productivity heterogeneous trays (Fig. 9.2b-d). In these trays, although more primary rhizomes had grown into the vegetated quadrants, most nodes, shoots and biomass were produced in the bare quadrants.

The average productivity per primary rhizome of nodes, shoots and biomass did not deviate significantly in the low productivity heterogeneous trays but did so in the high productivity heterogeneous trays (Fig. 9.3a-c). Thus, in contrast to the heterogeneous, low productivity trays, where a higher biomass allocation to the favorable bare quadrants was primarily due to a selective placement of primary rhizomes, in the heterogeneous, high productivity trays primary rhizomes, once grown into a bare quadrant, produced on average significantly more nodes, shoots and biomass.

No evidence was found for benefits of clonal integration in the heterogeneous trays. At both productivity levels mean biomass production of primary rhizomes in the vegetated quadrants connected to rhizomes in bare quadrants was similar to those connected to

Table 9.2 *Distribution of primary rhizomes and shoots over the four quadrants within the trays, at the end of the experiment in August 1996.*

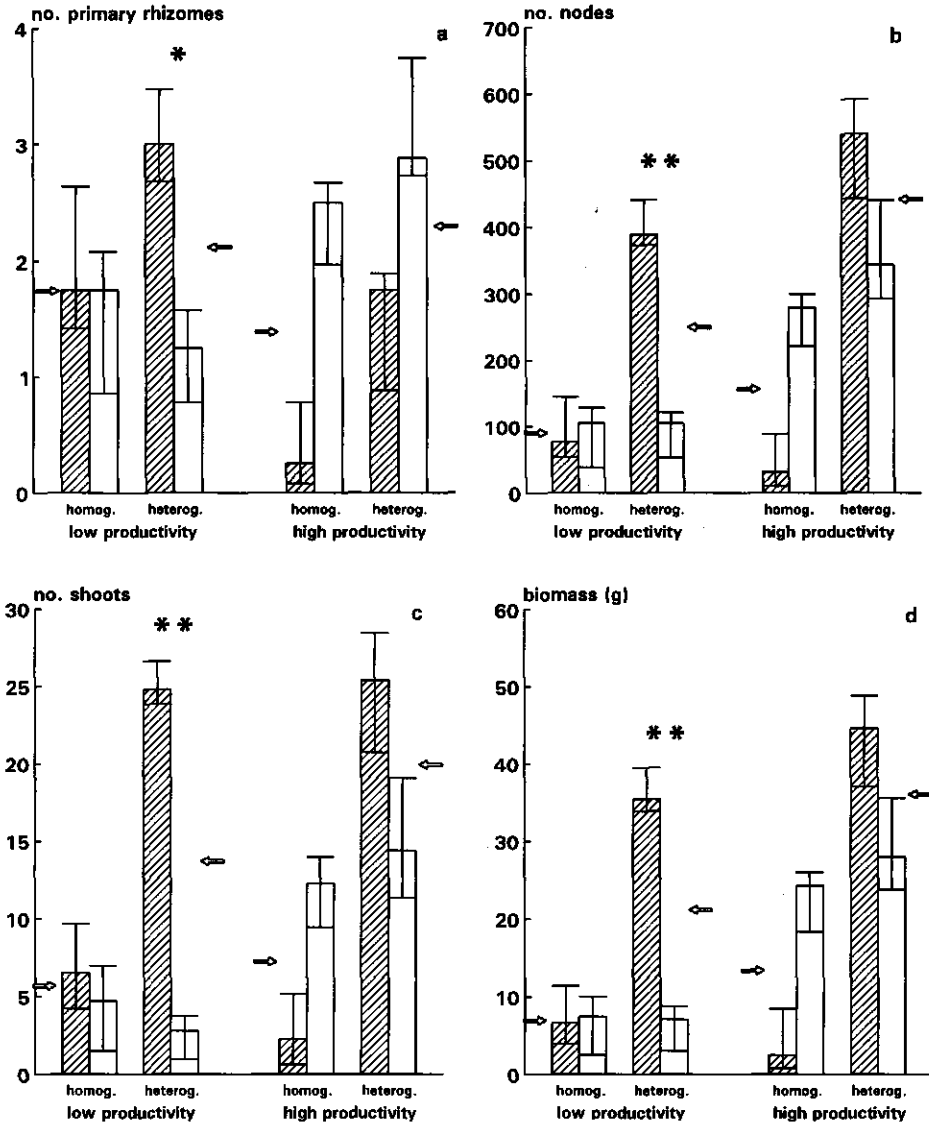| quadrat orientation	North	West	South	East	Center
no. primairy rhizomes	58	30	4	4	-
no. shoots	398	202	8	34	108

Figure 9.2 The mean distribution of Elymus repens clones over bare (shaded bars) and vegetated quadrants (open bars) at the end of the second growing season in the homogeneous (n=4) and heterogeneous trays (n=8) at high and low productivity levels. (a) number of primary rhizomes (b) number of nodes (c) number of shoots and (d) total biomass (g). Error bars: 2 x standard error. Arrows indicate a completely random (50-50%) distribution, asterisks indicate a significant deviance from random distribution (P≤0.05).

rhizomes in vegetated quadrants (Fig. 9.4). Mean primary rhizome production in bare quadrants was significantly higher in the low productive trays only. However, in the high productive trays the biomass increase was similar but the variance was considerably higher.
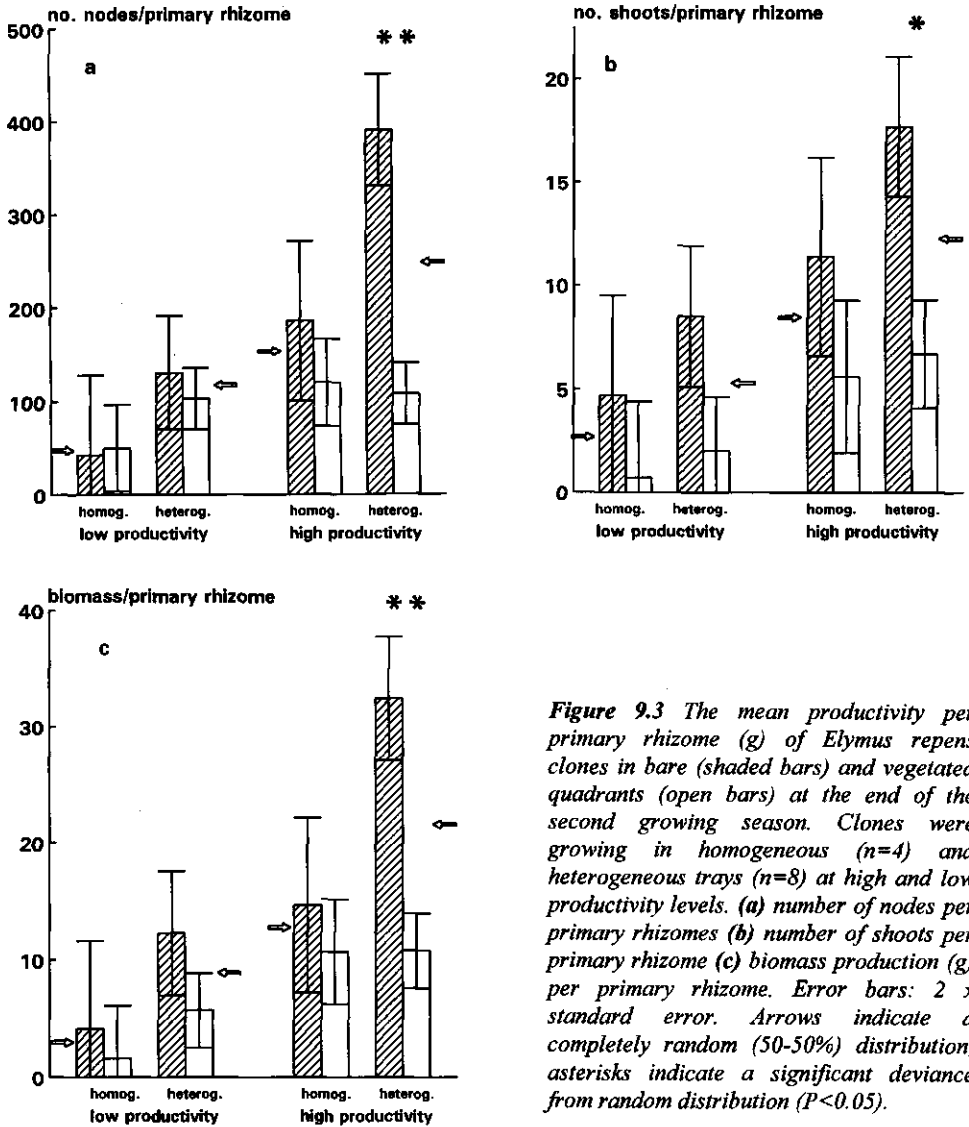
Figure 9.3 The mean productivity per primary rhizome (g) of Elymus repens clones in bare (shaded bars) and vegetated quadrants (open bars) at the end of the second growing season. Clones were growing in homogeneous (n=4) and heterogeneous trays (n=8) at high and low productivity levels. (a) number of nodes per primary rhizomes (b) number of shoots per primary rhizome (c) biomass production (g) per primary rhizome. Error bars: 2 x standard error. Arrows indicate a completely random (50-50%) distribution, asterisks indicate a significant deviance from random distribution (P<0.05).

The net result of these responses in the presence of bare quadrants is that compared to the homogeneous trays, in the heterogeneous trays *Elymus* total tray dry weight increased with a factor 3.01 at the low and by 2.67 at the high productivity level (Fig. 9.5). The relative increases do not differ significantly between the two productivity levels.

Discussion

Gaps in a vegetation are generally created by animal activities. In a midsuccessional old field Goldberg & Gross (1988) found that 95% of the gaps was created by animals such as moles
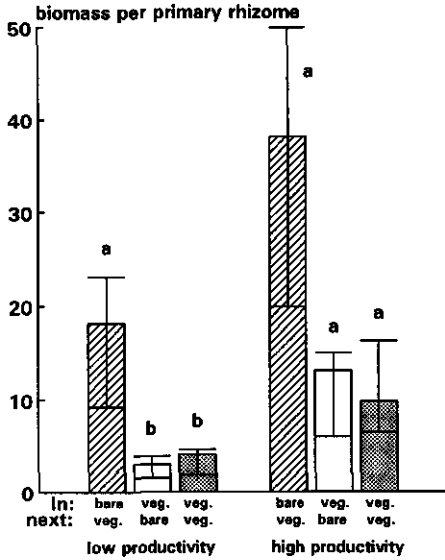
biomass per primary rhizome

Figure 9.4 Mean productivity (g) per primary rhizome of (hatched bars) primary rhizomes in bare quadrants connected to rhizomes in vegetated quadrants; (open bars) primary rhizomes in vegetated quadrants connected to rhizomes in bare quadrants and (shaded bars) primary rhizomes in vegetated quadrants connected to rhizomes in vegetated quadrants. Error bars: 2 x standard error. Different characters indicate significant differences (P< 0.05).

(*Scalopus aquaticus*), mice (*Peromyscus* spp.) and woodchucks (*Marmota monax*) and may be as large as 0.35 m^2 but on average are rather small ($\leq$ 0.03 m^2). Individual gaps in these fields could remain bare for up to two years but the majority had been overgrown within a year. Parish & Turkington (1989) found, upon examining the colonization of molehills and dungpats with an average size of ± 0.07 m^2, that most colonization took place by clonal species, most notably *Elymus repens, Poa compressa* and *Trifolium repens*. Thus, although in the present experiment treatments may have been somewhat larger (a single bare quadrant: 0.15 m^2) and more persistent than observed in the field, they do not represent unrealistic environmental conditions with respect to the temporal and spatial scale of the heterogeneity perceived by the *Elymus* plants.

Dry weight production of the *Holcus/Rumex* vegetation differed significantly between the two productivity treatments. Therefore the application of fertilizer was successful in producing vegetation that contrasted with respect to productivity. As a consequence, contrasts between bare and vegetated quadrants were larger in the high productivity than in the low productivity heterogeneous trays. A larger contrast between patches may result in higher benefits for clonal plants growing in the two patches (Wijesinghe & Handel 1994). Therefore, it is remarkable that in the low, and not in the high productivity heterogeneous trays primary rhizomes were selectively located in the bare quadrants (Fig. 9.2a). MacDonald & Lieffers (1993) observed a similar phenomenon when the rhizomatous grass *Calamagrostis canadensis* planted on the edge of a vegetated and a bare compartment grew significantly more rhizomes into the bare section compared to the vegetated section. Furthermore, Evans & Cain (1995) found that the rhizomatous forb *Hydrocotyle bonariensis* was able to veer away from patches of grass in heterogeneous environments. The inability of *Elymus* to grow its primary rhizomes selectively into high productivity bare quadrants despite the larger contrast in above-ground vegetation points out that contrasts below- rather than above-ground must have played a crucial role. Since rooting density in the bare quadrants was much lower than in the vegetated quadrants nutrient resources must have been depleted more extensively in the vegetated quadrants (Nye 1966, Bath & Nye 1973, Yanai *et al.* 1995) creating a perceptible contrast. However, in the high productivity trays both the bare and the vegetated quadrants were fertilized every three months. This may repeatedly have led to a temporal neutralization

dry weight (g)

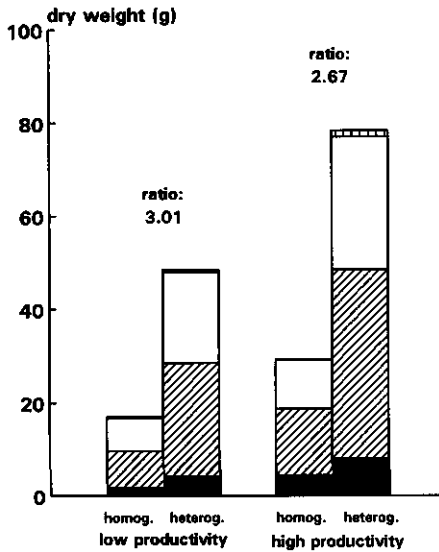*Figure 9.5 Mean total biomass production (g) per tray of Elymus repens in homogeneous (n=4) and heterogeneous trays (n=8) at high and low productivity levels. The dw heterogeneous/dw homogeneous ratio did not differ significantly between the two productivity levels. Bars: black, roots; diagonally hatched, rhizomes; open, shoots; vertically hatched, ears.*

of this contrast.

The mechanism which triggered the selective placement of primary rhizomes in bare quadrants may have been sectorial transport of nutrients. Sectoriality implies that buds arrayed in a common orthostichy, or rank, are connected to each other by common vascular bundles (Watson & Casper 1984). Sectoriality in clonal plants has been well documented for members of the *Lamiaceae* (Price *et al.* 1996, Murphy & Watson 1996) but grasses are generally not considered to be sectorial (Watson & Casper 1984, Pitelka & Ashmun 1985, Marshall 1996). However, preliminary results of a study regarding the sectoriality of xylem transport in an *Elymus* rhizome using fuchsin dye, revealed a predominantly sectorial transport (Fig. 9.6). *Elymus* rhizomes have a 1/2 phyllotaxy. The extra nutrients obtained by rhizome-connected roots growing into the bare quadrant may have been restricted to vascular bundles on the bare quadrant-facing side of the rhizome. Since nitrogen releases bud dormancy (McIntyre 1965, Leakey *et al.* 1977, Qureshi & McIntyre 1979) only buds on this side of the rhizome may have grown out. Therefore, we hypothesize that directional meristem outgrowth, caused by sectorial transport of nutrient, was responsible for the observed selective placement of primary rhizomes in the bare quadrants. Such a mechanism may in general provide those clonal plants that have a limited number of meristems per ramet (e.g. *Trifolium*, *Glechoma*, *Hydrocotyle*, *Poacae*) with the means to direct spacers towards favourable patches once they have been detected.

The present results indicate that the rhizomatous grass *Elymus repens* can exploit a heterogeneous habitat by foraging responses (response type 2). Foraging responses depend upon the existence of a perceptible contrast between two patches (Stuefer 1996). In the high productivity heterogeneous trays, contrasts in nutrient availability between patches were neutralized repeatedly during the experiment as a side-effect of the fertilizer treatments, and in these trays only significant growth responses (type 1) were found. Individual primary rhizomes were disproportionally successful in producing shoots, nodes and biomass once they had grown into a bare quadrant (Fig. 9.3a-c). Thus the net returns in terms of biomass production for each primary rhizome the mother-plant invested in were indeed higher in the high productivity heterogeneous trays compared to the low productivity heterogeneous trays as has been suggested by Grime (1979, 1994) and co-workers. The lack of support for the hypothesis that exploitation of heterogeneity is more beneficial in high compared to low productive environments (Fig. 9.5) may be explained by the absence of any foraging
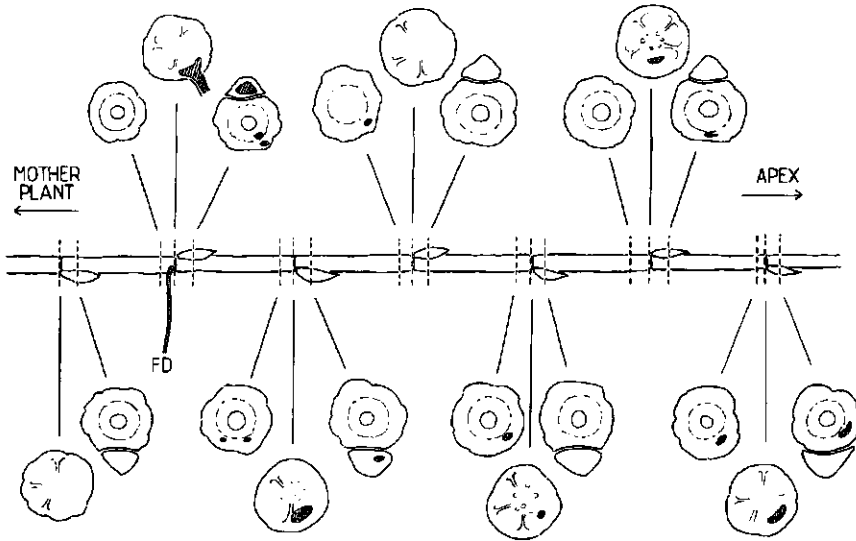
Figure 9.6 *Translocation through the rhizome of Elymus repens of Fuchsin Dye (FD; adapted from Roach 1939) taken up by a single root. The root was cut and placed into a 0.5% aqueous solution of FD for 24 hours while the rhizome was suspended in air while connected to the motherplant. The motherplant was growing on a Steiner solution. Cross-sections of the rhizome apically of, at and basipetally of each node were examined under binoculars. One of four examined rhizomes is depicted; transport in other rhizomes was comparable. Hatched areas indicate observed coloration by fuchsin dye.*

responses in the high productivity trays. Selective placement of primary rhizomes in the high productivity heterogeneous trays in combination with the higher returns per primary rhizome in these trays may have increased the relative performance of the total clone substantially.

No evidence was found for support of ramets in vegetated quadrants by connected ramets in bare quadrants. This agrees with the results of Forde (1966) and Rogan & Smith (1974) who found that for transport of assimilates mature *Elymus* plants can be regarded as an association of largely independent units or modules each consisting of an established tiller. Only after repeated defoliation any $^{14}CO_2$ was found to be transported from undamaged to damaged tillers. This pattern of largely independent units under normal conditions, while clones may become re-integrated under extreme conditions, has been observed for more species (Price *et al.* 1992, Marshall 1996). Such independent growth of different connected plant parts facilitates a rapid concentration of plant biomass in the favourable patches as was observed in the heterogeneous trays (de Kroon & Schieving 1990).

In conclusion, we demonstrated that the clonal grass *Elymus repens* is capable of exploiting heterogeneity in its environment through morphological adaptations: the selective placement of primary rhizomes in favourable patches (response type 2). However, when contrasts between favourable and unfavourable patches were not constant in time, primary rhizomes were placed randomly (response type 1). No evidence was found for benefits of physiological integration (type 3).

Acknowledgments

10

Conservation headlands for rare arable weeds: the effects of fertilizer application and light penetration on plant growth

Summary

In addition to promoting agricultural wildlife in general, conservation headlands may be a method to provide a refuge to endangered arable weeds. The conservation headland technique excludes herbicide and insecticide use in the outer 2-3 m of the arable field but does not restrict fertilizer inputs. We studied the effects of fertilizer application on the weed vegetation in relation to light penetration, in three crop edges in the vicinity of Wageningen, the Netherlands. Furthermore, the growth response of five endangered arable weeds to different fertilizer treatments and light penetration levels was examined. Species richness and weed growth were significantly reduced in the fertilized crop edges but individual species showed both significant increases and decreases. In the fertilized crop edges, light penetration was directly related to weed performance, limiting species richness and plant growth of both the total weed vegetation and individual species, while in the unfertilized crop edges no such relation existed. Likewise, light penetration proved to be the most important correlate of plant growth of all five endangered arable weeds. Assuming that biomass production is closely related to seed production, fertilizing conservation headlands will result in reduced viability of populations of rare weeds. If preservation of rare arable weeds is one of the main goals of conservation headlands, cessation of fertilizer inputs may be required.

Keywords: cereal crop edge, conservation headlands, rare arable weeds, light penetration, fertilization.

Introduction

Almost 60 years ago, after finishing the first classification of the arable plant communities of the Netherlands, Kruseman & Vlieger (1939) commented that 'these communities continuously become more species-rich, mainly due to human activities leading to the introduction of new species'. Since then, six decades of increasing intensification of agriculture have resulted in a dramatic loss of arable weed species. Of the approximately 190 arable weeds in the Netherlands, 53 are on the Red Data List. In other West-European countries the current situation is similar. In Germany, about one-third of the 250-300 arable

weeds are listed in the Red Data Book of Endangered Plant Species (Eggers 1987). In the United Kingdom once very common species, like *Centaurea cyanus, Ranunculus arvensis* and *Scandix pecten-veneris*, have become extremely rare Wilson (1994*a*).

In the 1990s most arable weeds are confined to the extreme edge of the field where competition from the crop is less intense due to soil compaction from farm machinery, poor seed-bed preparation, and damage to the growing crop (Marshall 1989, Wilson & Aebischer 1995) and the less efficient application of fertilizer (Melman & van der Linden 1988). Several initiatives to provide a safe haven for endangered arable weeds have therefore concentrated on the crop edge. Possibilities and limitations of conservation headlands, i.e. crop edges 2 or 3 m wide without herbicide or insecticide inputs and usually in cereals, have been evaluated in the Netherlands (de Snoo 1995, Pancras 1995), the United Kingdom (Boatman & Sotherton 1988, Boatman & Wilson 1988), Sweden (Chiverton 1994) and Germany (Schumacher 1980, 1987). In the United Kingdom and Sweden the primary goal of such headlands has been game conservation.

The conservation headland technique excludes pesticide use but does not impose any restrictions on fertilization (although presently in Germany most conservation headland programmes that were introduced, following the findings of Schumacher (1980), limit or prohibit fertilizer use (Klein 1994)). This is notwithstanding the fact that other authors found adverse effects of fertilization on the diversity of weed communities (Pysek & Pysek 1987, Mahn 1988, Goldberg & Miller 1990, Pysek & Leps 1991), especially on species of conservation interest (Wilson 1990, 1994*b*). Fertilization can have direct and indirect effects. Direct effects may originate from differences between weeds and crops in adaptation to nutrient uptake. Crops are bred to use mineral fertilizers with a high solubility which can be taken up quickly. Arable weeds are thought to be more adapted to the uptake of organic nutrients (Schneider *et al.* 1994). Pysek & Leps (1991) in fact found marked differences between the weed vegetation of fields fertilized with liquid urea on the one hand and nitrate or sulphate on the other.

An indirect effect of fertilization can be an increase in competition with the crop. In most terrestrial vegetation types, high nutrient inputs reduce plant diversity. An increased supply of the most limiting resources will lead to an increased biomass production and subsequently to an increased competition for light (Stern & Donald 1961, Glauninger & Holzner 1982, Bobbink 1991, Wilson & Tilman 1993). Species which are poor competitors for light disappear from these habitats. Arable fields harbour annual plant communities with a high dominance of one species, the crop. Arable plant communities, especially of poor sandy soils, include many species which are adapted to annual disturbance but which are poor light competitors. Over recent decades vigorous crops have been grown even on very nutrient-poor soils as a result of heavy fertilization. At the same time, arable weed species associated with cereal cultivation on these poor soils have dramatically decreased in numbers.

If one of the main goals of conservation headlands is to provide a refuge for endangered arable weeds, we need to evaluate whether cessation of pesticide inputs alone is sufficient to provide a suitable habitat. The experiments described below address this problem by determining (1) the effect of fertilization and light penetration on the growth of weed species in cereal crop edges, and (2) the growth-responses of five endangered arable weeds to fertilization and light penetration.

C

Methods

The ultimate success of annual species depends on seed production rather than on biomass production. However, the determination of seed production of a large number of species is difficult and prone to inaccuracies. Therefore, under the explicit assumption that seed production is proportional to biomass production (Harper & Ogden 1970, Harper 1977, Wright 1993, Grundy *et al.* 1995), this study focusses on the biomass production of the different species.

Experiment I

To determine the effects of fertilizer application on light penetration, diversity, plant growth and plant distribution in the crop edge, the crop edges of three fields in the vicinity of Wageningen were left partially unfertilized in early spring 1991. In both the unfertilized and the fertilized parts no herbicides were applied. All fields were sown to winter rye and had sandy soils in a small-scale landscape dominated by woodlots.

In each crop edge, 0.5 x 2 m quadrats parallel to the boundary were established at distances of 0.25, 1.25 and 2.25 m from the boundary. The plots were established in a split-plot design in which the three fields were considered replicates, each field having two levels of fertilizer and within the fertilizer treatment three levels of distance in two replicates (3 fields * 2 fertilizer levels * (2 replicates*3 distances) = 36 plots).

Above-ground weed biomass in the plots was harvested during 2-13 August 1991 and the number of individuals of each species as well as the proportion of individuals taller than 20 cm was determined. Subsequently dry weight was determined for each species after drying for 24 h at 80°C.

On 10 May, light measurements were made in the quadrats using a 1 m long sensor (measuring radiation between 400 and 700 nm; TFDL Wageningen, no. 01959.4) above the crop and *c.*4 cm above the soil surface (the height of the sensor). Light penetration at ground level was determined proportional to light levels above the vegetation.

Experiment II

Experiment I did not contain any rare weed species. Thus, to be able to determine the response of endangered arable weeds to light penetration and fertilizer application, five such species were selected: *Centaurea cyanus*, *Chrysanthemum segetum* and *Misopates orontium* are currently in serious decline in the Netherlands, *Hypochaeris glabra* is threatened with extinction and *Papaver argemone* is nearly extinct on arable fields. Nomenclature follows van der Meijden (1990).

On 25 April 1994 (day 0) seeds of these species were sown in trays in a glasshouse at the same time as spring barley was sown in the field. The seedlings were transplanted into 2 x 4 m plots in the field when the barley rows were clearly visible. In each plot 36 seedlings were planted in between the rows (spaced at 12.5 cm) at 25 cm intervals. Two factors were varied over the plots. First, the equivalent of 0, 45 or 90 kg N/ha (NPK-fertilizer) was applied to each plot, of which 90 kg/ha would have been the normal dose for spring barley on this field. Second, immediately after transplantation of the seedlings the crop was thinned in various degrees. The aim was to establish a range of light regimes relatively independent of

fertilization. Thinning varied from unthinned to removal of 20, 40, 50, 60 and 90% of the rows. The species and the fertilizer levels were replicated in six blocks (5 species * 3 N-levels * 6 replicates = 90 plots). However, the thinning levels were established once for each species*fertilizer combination, so in this respect the experiment does not have a replicated design. During the season spontaneously emerging weeds were removed.

On seven dates during the season, plants were harvested from each plot. A single harvest of a single plot consisted of cutting the above-ground biomass of four, non-neighbouring plants. Before each plant was cut, light was measured at ground-level within the crop row on both sides of each plant using a 1 cm^2 light-sensitive cell (400-700 nm; T.F.D.L. Wageningen, no. 31940.4). Light penetration was determined as in experiment I. Height of each plant was measured and dry weight was determined after drying for 48 h at 80°C. On the last harvest (22 August, day 119) the numbers of remaining plants of three species, *H. glabra*, *M. orontium* and *P. argemone*, were insufficient to obtain reliable data so this harvest date has been omitted for these species.

Analysis

The weed vegetation data of experiment I were analysed by means of ANOVA for effects of fertilization and distance from the boundary. The relation between light penetration and the weed vegetation data was analysed using regression analysis. To reduce the number of missing values in the analysis of individual species, data of only two fields were used and species absent from more than nine of the 24 plots were discarded. The response of the remaining 12 species was analysed for fertilizer and distance effects using ANOVA. As regression analysis is more sensitive to outliers, the relation between light and individual species was analysed for only four species which were present in at least 19 plots.

The data of experiment II were analysed in three steps. First, for each plot, biomass was plotted against time and a logistic curve was fitted to the data using GENSTAT statistical package (GENSTAT 1993):

$$B = \frac{B_{max}}{1 + e^{-b_B*(x - m_B)}}$$

where B is biomass production (in g) at time x (days), B_{max} represents potential biomass production (g), m_B is the day at which unrestricted growth changes to restricted growth and b_B is the maximum relative growth rate (days^{-1}). Likewise plant height H (cm) at day x is described by H_{max} (cm), m_H (days) and b_H (days^{-1}). Other curves were compared but the logistic curve gave the the the best fit. Secondly, the derived parameters B_{max}, m_B, b_B and H_{max}, m_H, and b_H of each plot were entered into a new database and the parameters were analysed for effects of fertilization, light, species and thinning using Multiple Linear Regression. Thirdly, the best regression models were selected by comparing all submodels (with a limit at two-way factor interactions) and selecting those with the highest r^2, the lowest MS$_{residuals}$ and the lowest Mallows' Cp (Montgomery & Peck 1982, Sen & Srivastava 1990). In this study, r^2 is the adjusted r^2 statistic (GENSTAT 1993) calculated as (1 - (residual MS/total MS)). Additionally the effect of light alone was analysed for each species by means of regression analysis.

Table 10.1 *Mean values of weed vegetation variables in fertilized (+) and unfertilized (-) crop edges. Samples were taken from 0.5x2m quadrats at 0.5, 1.5 and 2.5 m from the field boundary. F indicates a significant fertilizer effect and D indicates a significant distance effect (p<0.05).*

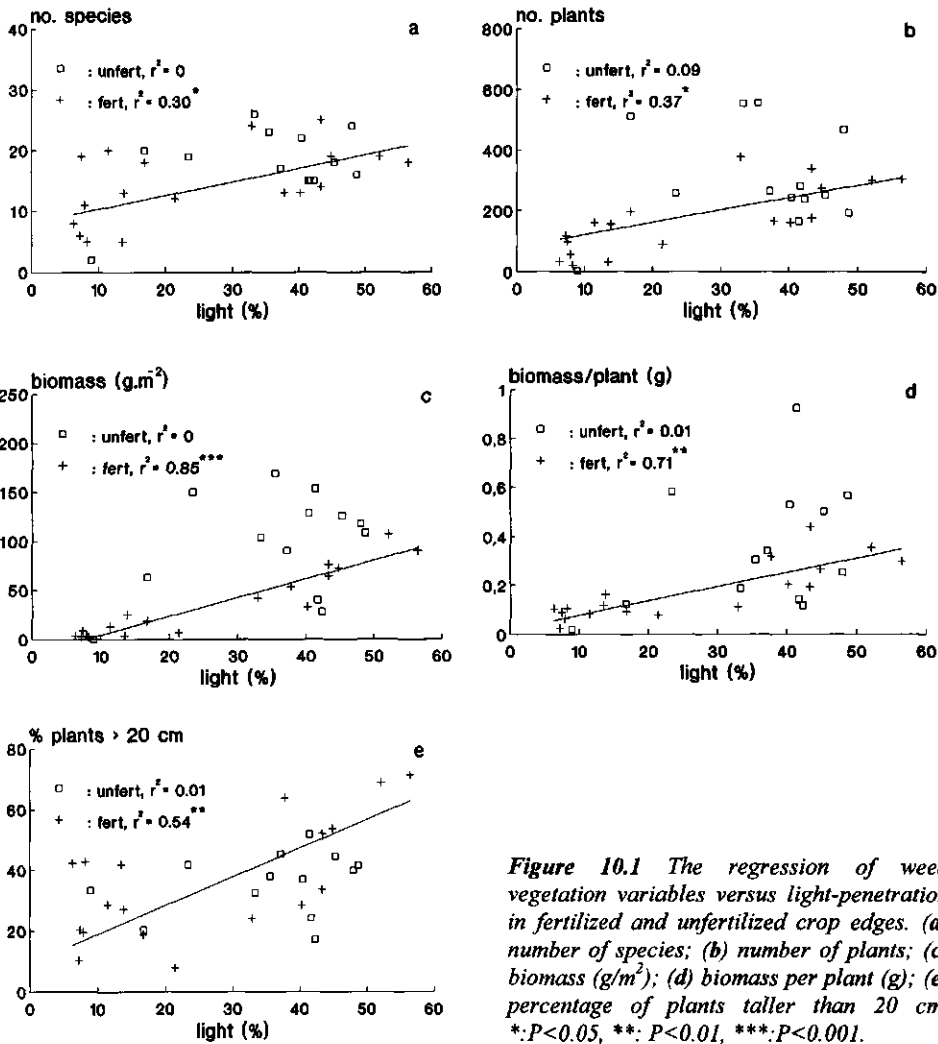|	No. of species (spec/m²)		No. of plants (plants/m²)		Total biomass (g/m²)		Mean plant weight (g)		Height ratio (%)		Light penetration (%)	
fertilizer:	-	+	-	+	-	+	-	+	-	+	-	+
distance (m)												
0.5	19.6	19.8	317	257	106.0	51.2	0.307	0.181	31.1	36.1	30.4	34.3
1.5	19.8	15.3	335	162	88.5	29.9	0.307	0.152	29.3	30.9	27.0	23.8
2.5	12.5	8.0$_D$	175	91$_D$	70.0	23.7$_D$	0.341	0.185	33.8	42.2	27.6	19.4$_D$
mean	17.3	14.4$_F$	276	170$_F$	88.2	34.9$_F$	0.318	0.173$_F$	31.4	36.4	28.3	25.8

Figure 10.1 *The regression of weed vegetation variables versus light-penetration in fertilized and unfertilized crop edges. (a) number of species; (b) number of plants; (c) biomass (g/m²); (d) biomass per plant (g); (e) percentage of plants taller than 20 cm.* *:P<0.05, **: P<0.01, ***:P<0.001.

Results

Experiment I

Weed vegetation
The application of fertilizer in the crop edges resulted in a less species-rich weed vegetation (Table 10.1). Total weed biomass production decreased significantly. Furthermore, fewer individual plants survived until crop harvest and the surviving plants produced less biomass. Remarkably, light penetration was hardly lower in the fertilized crop edge than in the unfertilized crop edge. However, the difference between 0.5 and 2.5 m in the fertilized crop edge was much larger (14.9%) than in the unfertilized crop edge (2.8%) although the interaction term was not significant ($P = 0.13$).

Table 10.2 *Mean biomass production, plant numbers and plant weight of twelve of the most common weed species in fertilized (+) and unfertilized (-) crop edges. Samples were taken from 0.5x2 m quadrats at 0.5, 1.5 and 2.5 m from the boundary. F indicates a significant fertilizer effect and D indicates a significant distance effect (P<0.05).*

	J.bufonius		P.convolvulus		G.uliginosum		S. media		A.spica-venti		M.recutita	
fertilizer:	-	+	-	+	-	+	-	+	-	+	-	+
No. plants (no./m²)												
0.5 m	115.5	58.0	25.0	13.5	6.0	7.8	3.8	4.3	4.3	3.0	18.5	39.2
1.5 m	98.8	20.8	13.0	2.5	15.3	7.5	3.5	3.0	3.0	0.5	18.8	23.3
2.5 m	67.7	6.5$_D$	5.0	1.5$_D$	14.8	2.3	1.5	0.0	1.5	0.5$_D$	29.0	18.3
mean	94.0	28.4	14.3	5.8	12.0	5.8	2.9	2.4	2.9	1.3	22.1	26.9
Total biom. (g/m²)												
0.5 m	1.57	0.86	29.54	12.48	0.14	0.30	0.56	0.37	5.37	5.88	7.02	9.38
1.5 m	2.57	0.37	28.74	4.37	0.50	0.48	3.39	0.34	3.86	0.14	17.38	11.56
2.5 m	1.23	0.11$_D$	38.07	5.13	0.54	0.19	0.12	0.0	1.05	0.22	24.40	16.67
mean	1.79	0.45$_F$	32.12	7.32$_F$	0.39	0.33$_F$	1.36	0.24	3.43	2.08	16.27	12.54
Biom./plant (g)												
0.5 m	0.024	0.023	2.003	0.984	0.018	0.022	0.079	0.085	1.117	1.519	0.203	0.114
1.5 m	0.033	0.015	2.376	1.038	0.044	0.032	0.949	0.048	0.621	0.138	0.474	0.266
2.5 m	0.032	0.009	3.807	1.930	0.035	0.045	0.100	0.0	0.535	0.220	0.428	0.500
mean	0.030	0.016$_F$	2.728	1.317$_F$	0.032	0.033	0.376	0.044	0.758	0.625	0.368	0.293

	C.album		C.b.-pastoris		S.arvensis		P.annua		Ve.arvensis		Vi.arvensis	
fertilizer:	-	+	-	+	-	+	-	+	-	+	-	+
No. plants (no./m²)												
0.5 m	1.5	9.3	3.8	8.5	9.0	32.2	3.5	3.5	5.3	1.3	32.2	19.0
1.5 m	4.3	8.8	7.5	8.0	22.5	24.3	3.0	6.0	0.5	1.0	29.0	16.3
2.5 m	3.0	5.0	4.3	12.0	11.3	14.0	3.7	5.2	1.0	1.0	31.5	15.3
mean	2.9	7.7$_F$	5.2	9.5	14.3	23.5	3.4	4.9	2.3	1.1	27.6	16.8$_F$
Total biom. (g/m²)												
0.5 m	0.12	0.51	0.59	2.70	2.24	4.80	0.12	0.20	0.94	0.43	4.30	7.12
1.5 m	0.61	0.81	2.51	2.98	4.42	5.19	0.08	0.16	0.05	0.33	3.55	3.25
2.5 m	0.10	0.33	1.73	4.65	1.20	3.12	0.10	0.11	0.07	0.08	3.47	1.23$_D$
mean	0.28	0.55$_F$	1.61	3.44	2.62	4.37	0.10	0.16	0.36	0.28	3.77	3.87
Biom./plant (g)												
0.5 m	0.032	0.037	0.078	0.148	0.140	0.081	0.017	0.036	0.055	0.218	0.117	0.301
1.5 m	0.080	0.044	0.211	0.169	0.097	0.090	0.016	0.130	0.053	0.120	0.156	0.249
2.5 m	0.019	0.040	0.147	0.183	0.064	0.105	0.033	0.100	0.047	0.032	0.224	0.104
mean	0.044	0.040	0.145	0.167	0.100	0.092	0.022	0.020	0.052	0.123	0.166	0.218

With increasing distance from the field boundary species richness, plant numbers, total weed biomass and light penetration decreased significantly. No significant interactions were found.

The analysis of the effect of light penetration resulted in a clear-cut difference between the fertilized and the unfertilized crop edge plots. The regressions between light and the weed variables were statistically highly significant in the fertilized plots while there was no relation at all in the unfertilized plots (Fig. 10.1a-e).

Individual species

The effects of fertilization and distance from the field boundary on the individual species are more complex. Generalizing we can discern three patterns (Table 10.2). The first group of species (*Apera spica-venti, Gnaphalium uliginosum, Juncus bufonius, Matricaria recutita, Polygonum convolvulus* and *Stellaria media*) was characterized by high total biomass production in the unfertilized crop edge, which was the product of both higher plant numbers and higher biomass production per plant in unfertilized plots. This group showed decreasing plant numbers with increasing distance from the field boundary. Biomass production per plant and total biomass production showed no clear trends with increasing distance from the boundary.

Capsella bursa-pastoris, Chenopodium album, Poa annua and *Spergula arvensis*, the

Table 10.3a *Regression coefficients (± se) of mean dry weight (g) versus light of five annuals during the growing season. ' - ' indicates dates for which regressions were not made due to early senescence of the plants. Day 0 is 25 April 1994.*

Days	C.cyanus		C.segetum		H.glabra		M.orontium		P.argemone	
35	0.039	(0.047)	0.037	(0.041)	0.010	(0.030)	0.041	(0.019)	0.013	(0.010)
42	0.052	(0.128)	-.015	(0.081)	0.061	(0.142)	0.107	(0.044)	0.033	(0.019)
52	0.043	(0.279)	0.023	(0.129)	0.044	(0.259)	0.241	(0.105)	0.062	(0.041)
63	0.172	(0.739)	0.279	(0.516)	-.015	(0.267)	0.389	(0.210)	0.079	(0.060)
77	4.480	(1.52)**	0.531	(0.878)	0.856	(0.545)	0.458	(0.452)	-.097	(0.142)
99	12.70	(2.59)***	3.490	(0.820)	5.000	(1.170)*	1.919	(0.621)*	0.566	(0.365)
119	12.68	(1.73)***	25.72	(9.980)*	-		-		-	

* $P<0.05;$ ** $P<0.01;$ *** $P<0.001$

Table 10.3b *Regression coefficients (± se) of mean plant height (cm) versus light of five annuals during the season. ' - ' indicates dates for which regressions were not made due to early senescence of the plants. Day 0 is 25 April 1994.*

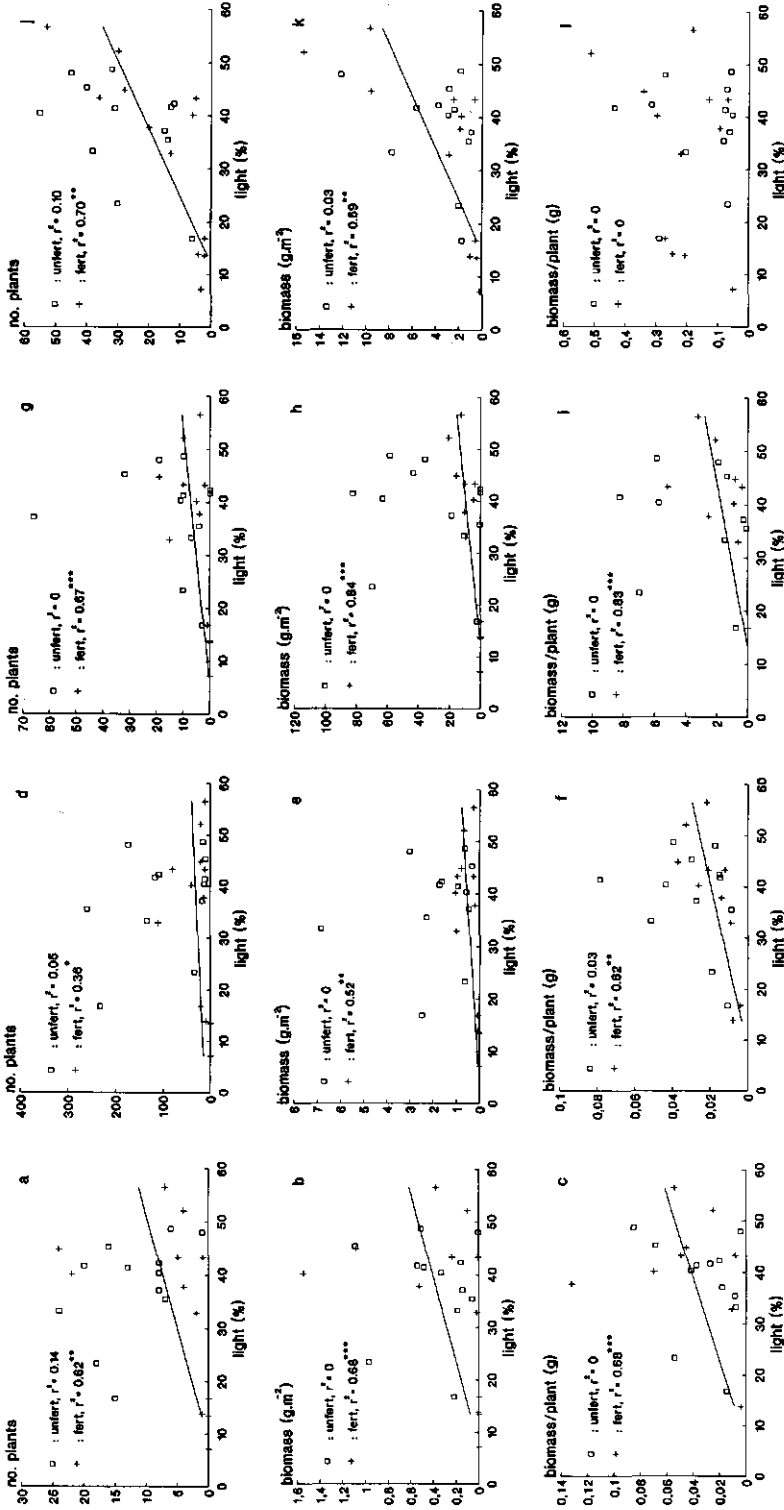| Days	C.cyanus		C.segetum		H.glabra		M.orontium		P.argemone	
35	- 9.93	(2.16)***	- 6.68	(1.68)***	- 8.06	(1.11)***	- 1.04	(1.04)	- 3.28	(0.93)**
42	-14.24	(4.60)**	-18.12	(3.64)***	-12.53	(1.16)***	- 3.64	(2.02)	- 0.97	(0.87)
52	-34.48	(8.55)***	-35.71	(6.76)***	-17.24	(4.13)***	- 1.29	(5.96)	- 3.55	(2.07)
63	-37.20	(13.6)*	-46.71	(13.3)*	-15.70	(12.3)	-14.62	(9.70)	0.46	(9.22)
77	-23.00	(16.6)	-51.90	(16.5)**	- 3.70	(14.6)	-17.72	(7.51)*	-28.10	(11.1)*
99	-10.50	(21.1)	-122.2	(24.8)***	-25.20	(15.5)	13.80	(18.30)	-19.00	(24.2)
119	0.70	(20.3)	2.90	(59.5)	-		-		-	

* $P<0.05;$ ** $P<0.01;$ *** $P<0.001$

Figure 10.2 The regression of number of plants, biomass and biomass per plant respectively versus light-penetration in fertilized and unfertilized crop edges for the species Gnaphalium uliginosum (a-c), Juncus bufonius (d-f), Polygonum convolvulus (g-i) and Viola arvensis (j-l). When necessary, data were log-transformed to meet the assumptions of regression analysis. Only the original data are depicted. *:P<0.05, **: P<0.01, ***:P<0.001.

second group, are characterized by higher total biomass production in the fertilized crop edge. This was mainly the result of higher plant numbers in the fertilized plots as biomass production per plant is not significantly enhanced in these plots. This group does not show a clear pattern with increasing distance from the field boundary.

The third group consisted of the species *Veronica arvensis* and *Viola arvensis* which were rather indifferent to fertilizer application. This seemed to be caused by higher plant numbers in the unfertilized plots combined with a tendency to produce more biomass per plant in thefertilized plots. These two species showed a strong, though not significant, negative trend for all variables with increasing distance from the boundary.

The relation between light penetration and the single species variables were only analysed for the species *G. uliginosum, J. bufonius, P. convolvulus* and *Viola arvensis* (Fig. 10.2a-l). As with weed vegetation variables, significant relationships for individual species variables to light were only found in fertilized plots. All variables gave highly significant regressions with the exception of biomass per plant for *Viola arvensis*. This result confirms the ANOVA results for this species which indicated the ability of *V. arvensis* to produce large plants in the fertilized plots.

Experiment II

The effect of fertilization on light penetration during the season is given in Fig. 10.3. During the season, light penetration was highest in the unfertilized plots and lowest in the 90 kg N/ha plots. Early and late in the growing season differences in light penetration were not very large but between day 40 and 80 (c. the beginning of June to mid-July, a period corresponding with canopy closure of the crop) light penetration in the unfertilized plots was three to four times as high as in the 90 kg N/ha plots.

As in the results of experiment I, all species produced more biomass in unfertilized plots than in plots fertilized with the standard agricultural dose (Fig. 10.4a-e). The intermediate level yielded biomass higher than in unfertilized plots for *H. glabra* and *P. argemone*, lower than in 90 kg N/ha plots for *C. cyanus* and *C. segetum*, and intermediate biomass for
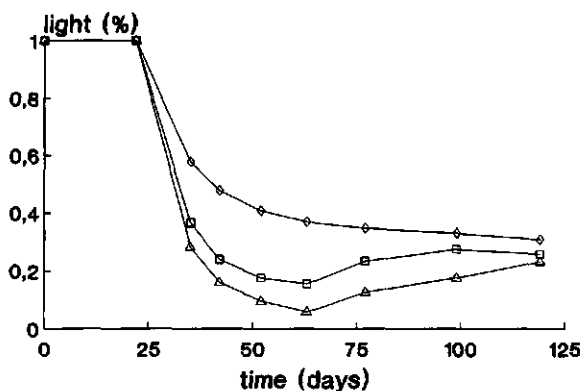

Figure 10.3 The effect of fertilization, averaged over all thinning treatments, on light penetration in spring barley during the growing season. Diamonds: 0 kg N.ha⁻¹, squares: 45 kg N.ha⁻¹, triangles: 90 kg N.ha⁻¹. Day 0 is 25 April 1994.
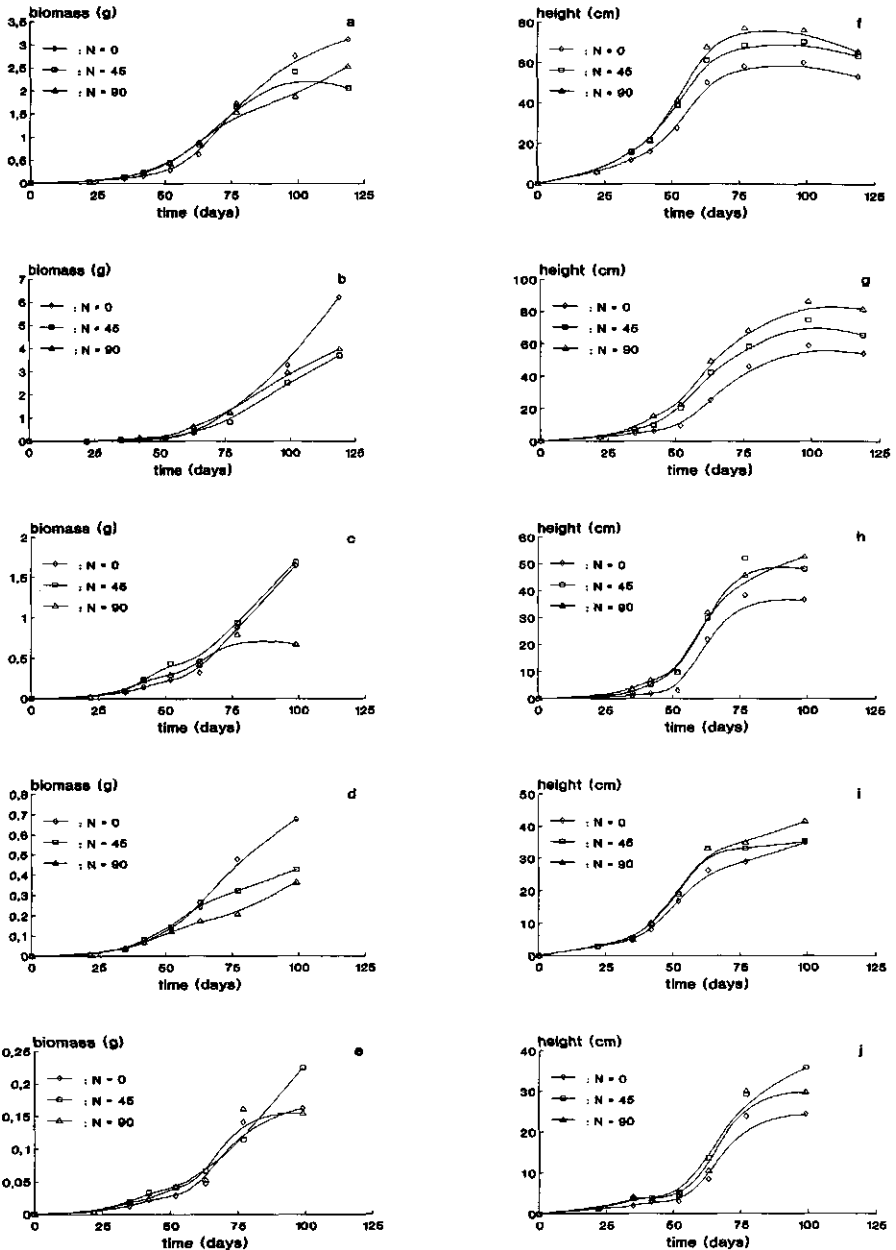
Figure 10.4 *The effect of fertilization averaged over all thinning treatments on biomass production (a-e) and plant height (f-j) during the growing season for the species* Centaurea cyanus, Chrysanthemum segetum, Hypochaeris glabra, Misopates orontium *and* Papaver argemone *respectively.*
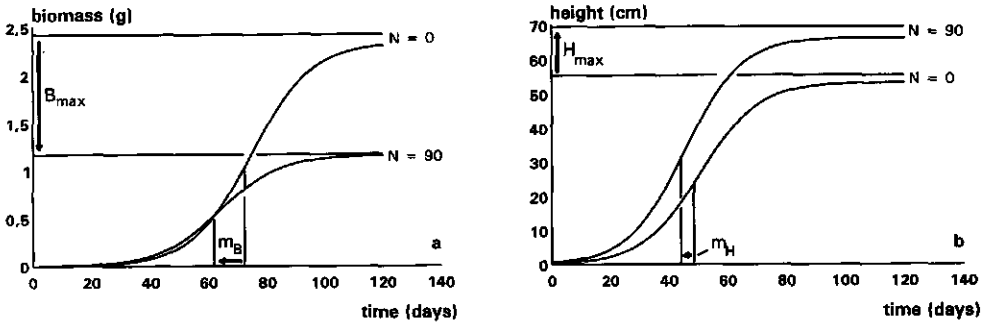
Figure 10.5 *Biomass production (a) and plant height (b) of* Centaurea cyanus *in an unthinned crop as described by the logistic growth equations given in Table 4. Mean light-penetration at 0 kg N/ha is 0.52 (average of all unfertilized, unthinned plots) and 0.33 at 90 kg N/ha (average of all 90 kg N/ha, unthinned plots).*

Table 10.4 *The regression models for the growth parameters B_{max}, m_B and b_B for biomass production and H_{max}, m_H and b_H for plant height. All factors contribute significantly ($P<0.05$) to the fit of the model. For ease of interpretation the parameter values for single species have been omitted and replaced by $x_{(n)species}$. r^2 is calculated as $(1 - (MS_{residuals}/MS_{total}))$.*

Biomass	$B = B_{max}/(1 + e^{-b_B *(x-m_B)})$					r^2
B_{max} = -1.17 +	$x_{(1)species}$ +	0.35 *thinning +	6.07*light			0.89
m_B = 45.02 +	$x_{(2)species}$ +	56.80 *light				0.46
b_B = 0.099						-
Height	$H = H_{max}/(1 + e^{-b_H *(x-m_H)})$					r^2
H_{max} = 50.68 +	$x_{(3)species}$ +	0 (0-fert) 8.86 (50-fert) + 12.92 (100-fert)	2.66*thinning			0.75
m_H = 36.20 +	$x_{(4)species}$ +	27.85 *light				0.42
b_H = 0.111 +	$x_{(5)species}$ +	-0.016 *light +	$x_{(6)species}$*light +	$x_{(7)species}$*thin.		0.37

M.orontium. The effect of fertilization on height growth was more explicit (Fig. 10.4f-j). With the exception of *P. argemone*, all species grew taller with increasing fertilization.

Table 10.3a and 10.3b gives the regression coefficients for biomass production for respectively, plant height versus light penetration for the successive harvest dates. It demonstrates that only late in the season could biomass production be explained significantly by light penetration. Only *C. cyanus* showed a significant positive regression coefficient before the latest harvest. *P. argemone* did not show significant regressions at all. In contrast to biomass production, significant regressions between plant height and light occurred early in the season and were strongly negative. Exceptions were *C. segetum*, which had a significant regression for all but the last harvest and *M. orontium* which had only one regression coefficient differing significantly from zero, on 11 July (day 77).

The results of the combined analysis of the effects of species, fertilizer and light with the inclusion of thinning, using Multiple Linear Regression, are presented in Table 10.4 while Fig. 10.5a and b illustrate these for a single species*thinning combination. Figure 10.5a

shows that fertilization led to a reduced potential biomass (B_{max}) and to a reduced m_B, i.e. growth became restricted earlier in the growth season. Table 10.4 shows that the response of B_{max} could be explained by a combination of light (a positive relationship, a higher light penetration results in a higher potential biomass) and thinning (positive), while m_B was described solely by light penetration (positive). Parameter b_B could not significantly be described by any of the factors. Remarkably, the factor fertilizer is missing in both equations. This does not mean that fertilizer application does not have any effect on B_{max} and m_B. Other models with a significant fit could have been selected which included the factor fertilizer. However, the fit of these models was less than those in Table 10.4, indicating that the factors light and thinning had a higher explanatory value than fertilizer for these parameters. H_{max}, The potential height growth was enhanced by fertilization while m_H (number of days until growth becomes restricted) is reduced (Fig. 10.5b). H_{max} was described by the effects of fertilizer in combination with thinning effects. Both relationships were positive. Parameter m_H was, similar to m_B, described solely by light penetration while b_H was the only parameter in which species differed significantly in their response to light and thinning.

Discussion

The effect of fertilization and light penetration on weed species in cereal crop edges

The distribution of species and plant numbers within the crop edge is in accordance with the findings of Marshall (1989) and Wilson and Aebischer (1995): the weed vegetation was most diverse in the outermost edge of the field. We found significantly more species at 0.5 m than at 2.5 m from the boundary while plant numbers and biomass production were also higher there. The effect on individual species was less explicit, which might be expected because confounding factors, such as seed distribution patterns, will have a more pronounced effect on individual species than on the total weed vegetation. Nevertheless, all significant distance effects pointed to decreasing biomass production or plant numbers with increasing distance from the boundary. Light penetration was significantly higher close to the boundary than further into the field. Although the trends within the fertilized and the unfertilized crop edge were not significantly different, light penetration was much more reduced at 2.5 m in the fertilized crop edge than in the unfertilized crop edge.

Fertilizer application resulted in a reduced species richness in the crop edge. Furthermore, all variables except height ratio were negatively affected. Fig. 10.1a-e in fact shows that in the fertilized crop edge the better development of the crop results in light penetration levels which become the growth limiting factor for the weed vegetation. Whereas at high light penetration levels the performance in fertilized plots is approximately similar to unfertilized plots, at low light penetration levels performance in fertilized plots is much lower.

Individual species showed more varied responses; *C. bursa-pastoris*, *C. album*, *P. annua* and *S. arvensis* actually produced more biomass in the fertilized plots. This was mainly the result of higher plant numbers in these plots. Nitrate released by mineral fertilizers is known to have a stimulating effect in various degrees on seed germination of different species (Bewley & Black 1982). We could trace the response of only four of the species in Table 10.2 in the literature, all belonging to the *C. bursa-pastoris* group, for all of which nitrate had a marked stimulative effect on germination (Popay & Roberts 1970, Vincent & Roberts 1977,

Roberts & Benjamin, 1979). The positive response of this group to fertilization is therefore likely to be caused by a direct fertilizer effect resulting in the higher germination rate of these species in the fertilized plots. *Veronica arvensis* and *Viola arvensis* are exceptional in showing increased biomass production per plant in fertilized plots. Although not significant, the results were confirmed by the regression analysis for biomass production per plant against light for *Viola arvensis* which was the only non-significant response (Fig. 10.2l). Grundy *et al.* (1995) reported increased biomass production with increased nitrogen inputs in a winter wheat crop while Wilson & Aebischer (1995) found *Viola arvensis* to be the only species of some 30 examined whose numbers increased consistently with increasing distance from the boundary. This may indicate that it is physiologically more tolerant to shading than the other species so that it can profit from the increase of nutrients in fertilized crop edges or in the centre of the field. However, Fogelfors (1972) found *Viola arvensis* to be a poorer shade-tolerator than *Chenopodium album*. Matters may be complicated by its self-pollinating habit which may result in the quick development of 'pure lines' adapted to specific cropping systems (Weeda *et al.* 1987). As a result, different authors may have done research on plants with considerably different genetic backgrounds. The regressions of light versus plant performance variables for *C. album*, *G. uliginosum*, *J. bufonius* and *Viola arvensis* show that, as with total weed vegetation, individual species are limited in growth by light penetration in the fertilized plots.

The growth response of five endangered arable weeds to fertilization and light penetration

In general, the five rare species responded similarly to increasing fertilization by reduced biomass production. Wilson (1990) found similar results for *M. orontium* and *P. argemone* while in his experiment *C. segetum* was not negatively affected by fertilizer application. Despite the lower biomass, all species grew taller with increasing fertilizer levels. This is probably the result of the more intense shading by the fertilized crop (Fig. 10.3) leading to a reduced Red-FarRed ratio in the light spectrum and causing an increase in the stem elongation rate (Ballaré 1994).

The thinning of the crop was done in order to create a range of light regimes and thus separate light effects from fertilizer effects. A confounding factor was the formation of side-shoots of the crop which, especially in the fertilizer treatments, may have compensated for the thinning. In this case, the target weed species would have benefited for only a limited period of time from higher light penetration levels.

The effect of light penetration on plant growth of the five species was positive but in general no significant regression was found between biomass and light pentration until the end of the growing season. This indicates that this effect is probably cumulative, with the differences between treatments increasing over the season. The general increase in regression slope over the successive harvest dates in Table 10.3a points in this direction. Light penetration was negatively related to plant height early in the growing season but this relationship disappeared with time.

Particularly interesting is the fact that weed biomass was better described in terms of light penetration than in terms of fertilizer. This indicates that, in this experiment, the most important effect of fertilization was indirect: by stimulating crop growth it decreased light penetration through the crop which reduced weed growth. This reduction occurs at an early stage as indicated by the positive relationship between light penetration and both m_B and m_H.

In fertilized plots light penetration levels decrease more rapidly than in unfertilized plots resulting in an earlier onset of the restricted growth. Only H_{max}, the potential height growth, was described best by direct fertilizer effects and this may be the result of the sensitive height growth response to the Red-FarRed ratio mentioned above.

Summarizing, we can conclude that growth of all five species becomes restricted at a certain critical light penetration level. This critical level is reached sooner in fertilized than in unfertilized plots. The prolonged unrestricted growth in unfertilized plots subsequently results in higher final biomass production.

Implications for conservation headlands

The decline of arable weed species can be ascribed to numerous factors. Some of the most important are improved seed cleaning, changes in crop rotations, abandonment of cultivation of crops such as flax *Linum usitatissimum* and buckwheat *Fagopyrum esculentum*, increased fertilizer inputs (Mahn & Muslemanie 1989) in combination with high yielding crop varieties and the introduction of herbicides (Schneider *et al.* 1994). In addition to benefits to game and butterflies (Rands 1985, Rands & Sotherton 1986) the conservation headland technique promises to be an elegant method for providing a refuge for those endangered arable weeds that are not linked to specific crops or seed cleaning methods. The modern distribution patterns reported by Marshall (1989) and Wilson & Aebischer (1995) indicate that most (endangered) weed species have their optimum in the crop edge coinciding with the location of the conservation headland. The cessation of herbicide applications, by far the most lethal aspect of modern agriculture for arable weeds, in conservation headlands, will facilitate their establishment early in the season. The success of a species, i.e. its reproductive output, also depends on the outcome of the competition with the crop whose performance in edges of arable fields is in general less than in the centre of the field (Boatman & Sotherton 1988, de Snoo 1994).

However, considering the significant negative effect of fertilizer application on light penetration in the crop edge, and the close relationship between light penetration and plant growth, conservation headlands may not be a suitable habitat for the most vulnerable species, if fertilization is maintained at standard levels. If conservation headlands are established with preservation of rare arable weeds as one of the principal objectives, cessation of fertilizer inputs in conservation headlands must be included in the management practices.

Acknowledgements

11

General discussion

Contemporary herbaceous field boundaries on sandy soils in the Netherlands

When asked for their preferred type of herbaceous field boundary, 7% of the farmers mentioned wildlife aspects such as the promotion of bird-life, while 85% of the farmers stated that weeds in general (*Elymus repens, Cirsium arvense* and *Urtica dioica* mentioned specifically) or seed production by weeds should be kept at bay (Chapter 2). Evidently, from a farmers point of view the occurrence of weeds is one of the most important aspects of arable field boundaries. In this respect it is remarkable that only some 10% of the farmers used herbicides in attempts to control weeds in the field boundary. The large difference in herbicide use between the investigated area and previously reported results in the United Kingdom and the Netherlands (± 60% of the farmers use herbicides in their boundaries; Boatman 1992; De Snoo & Wegener Sleeswijk 1993; Marshall & Smith, 1987) may be the result of cultural differences between regions (van der Meulen *et al.* 1996). Farmers in different regions may have different perceptions about aspects of crop cultivation such as the potential threat posed by weeds.

The results of the survey presented in Chapter 2 revealed that herbaceous field boundaries with a width of at least one metre are hard to find in the Central and Eastern Netherlands. Many boundaries in this area consist of woodlots, lanes of trees, or are dominated by shrubs and brambles. Still, quite a substantial number of grass dominated field boundaries were found but most of these boundaries were less than one metre wide, and therefore not suitable to be used in the survey. Apparently, the aim of farmers to maximize crop production results in a maximization of the area that is being cultivated. With modern powerful farming machinery it is easy, especially in herbaceous field boundaries, to marginally expand the arable field by close ploughing. Typically, approximately 50% of the more than one metre wide boundaries that were finally selected were owned by counties or governmental institutions and not by farmers.

Boundary management is generally economized: either boundaries are not managed at all or they are cut once annually without removal of the cuttings. Both types of management generally reduce the species richness in grassland systems (e.g. Berendse *et al.* 1992, Parr & Way 1988, Smith & MacDonald 1992, van Schaik & van den Hengel 1994). Furthermore, these types of management tend to favour the species that are unwanted by farmers: *Elymus repens* and *Cirsium arvense* (Parr & Way 1988, van Schaik & van den Hengel 1994).

The vegetation of contemporary, herbaceous field boundaries on sandy soils in the Central and Eastern Netherlands was generally dominated by species characteristic of *Koelerio-*

Corynephoretea communities, *Molinio-Arrhenatheretea* communities, or *Artemisietea vulgaris* communities. *Koelerio-Corynephoretea* communities are characterized as open to closed, mostly pioneer communities on nutrient poor, dry and warm, sandy soils (Westhof & den Held 1969). *Molinio-Arrhenatheretea* communities predominantly are anthropogenic grasslands and natural/anthropogenic ruderal communities occurring on different types of soil that may or may not have been fertilized. *Artemisietea vulgaris* communities usually are natural and anthropogenic communities consisting of tall, perennial forbs on fertile, irregularly disturbed soils (Westhof & den Held 1969). The vegetation could not be classified into syntaxonomically distinct entities. Too many of the character-species of more specific plant associations were missing, therefore only frame communities were identified (Chapter 2). The development of vegetation into frame communities is generally indicative of habitats too small for development into a more characteristic community and of the adverse effects of activities by men (Schaminée *et al.* 1995). The vegetation characteristics infer that modern arable field boundaries on sandy soils are subject to irregular disturbances, eutrophication and poor and irregular management. These conditions favour the establishment of generalist species, that is, species with a wide ecological amplitude that perform well at a wide range of disturbance levels as well as a wide range of productivity levels. The most frequent species in these boundaries were *Elymus repens*, *Agrostis capillaris*, *Dactylis glomerata*, *Holcus lanatus*, *H. mollis*, *Poa pratensis* and *Lolium perenne* respectively. Especially the fact that *Elymus repens* was the most abundant species is typical to the disturbed and fertile nature of modern field boundaries as this species thrives in fertile and disturbed habitats (Schmidt & Brübach 1993, Tilman 1987). As a result, the vegetation composition in most field boundaries is quite similar and the average species richness is very low: ± 11 species per four square metres.

We may furthermore conclude that the basic assumptions made in the approach to restore botanically diverse boundaries, as suggested in Chapter 1, are confirmed. Species richness is low and at the same time arable weeds are growing abundantly in modern field boundary vegetation: on average some 25% of the total biomass consists of weeds (Chapter 2). Interestingly, a single species (*Elymus repens*) contributes some 20% to the total weed biomass. *E. repens* generally invades arable fields from the boundary by means of rhizome growth (Oesau 1992). It is furthermore a species which is difficult to control chemically since herbicides against broad-leaved species are not effective and the use of graminoid or non-selective herbicides kill most or all of the vegetation thereby creating ideal establishment conditions for annual weed species (Boatman 1992). Thus, if management strategies can be found that reduce the abundance of *E. repens* and other weeds and simultaneously increase the botanical diversity of the boundary vegetation, farmers may be motivated on agronomic grounds to manage their field boundaries in a way that promotes the floral wildlife.

In the following sections first the effects of the three factors affecting the botanical species richness and the abundance of weeds in field boundaries are discussed: herbicides, nutrients and management. Next, it is discussed what (combination of these) factors are responsible for the low level of diversity in modern arable field boundaries. Effects of the field boundary vegetation on crop yields in the crop edge are briefly summarized. Finally, perspectives for the restoration of botanically diverse field boundaries are discussed based upon the approach that integrates floristic diversity with the weed suppressive ability of the boundary vegetation. This chapter concludes with discussing what pieces of information are still missing and what

needs to be done next in the long way towards a productive, yet sustainable and diverse arable landscape.

Factors affecting the species composition of field boundary vegetation: herbicides

Herbicides may affect the species composition of arable field boundaries in two distinct ways. First, herbicides can be applied directly in the boundary vegetation and second, herbicides may reach the boundary as a side effect of crop protection activities; small droplets of spray applied to the crop may drift with the wind into the boundary vegetation.

Direct application of herbicides in field boundary vegetation

Farmers may apply a variety of herbicides directly to their field boundaries in attempts to reduce weed development, usually with dosages high above the recommended rate (De Snoo & Wegener Sleeswijk, 1993). Most commonly used compounds were glyphosate and MCPA. The use of these unselective herbicides at such high dosages generally results in the die-back of all species or all broad leafed species. The death of (part of) the vegetation creates large strips of bare soil. The first species to establish on the bare soil of a regenerating habitat are annual arable weeds (Chapter 3) and ruderal perennials (Chapter 7). Thus, by the end of the growing season, weeds will be more abundant in the boundary vegetation than before the herbicide application. Subsequently, many farmers will respond by applying herbicides once more, thus creating a herbicide 'treadmill' (Boatman 1992). Furthermore, many field boundary species are relatively long-lived grassland species. Once killed, these species may not be able to re-establish themselves since they generally do not have a persistent seed bank (van Andel *et al.* 1993) and the nearest seed source may be too far for successful (re-)colonization (van Dorp 1996). Therefore, the use of broad-spectrum herbicides in field boundaries is likely to result in drastic decreases in species-richness.

We may conclude that in general, application of herbicides in field boundaries is undesirable both from a weed control point of view and from a wildlife point of view. In case of severe weed infestations herbicides might be used to help the perennial non-weedy field boundary vegetation get the upper hand over the weed species. Even in this case, spraying of herbicides should be prevented since this might damage the boundary vegetation as well, but a 'weed wiper', which can be used to apply herbicides manually to individual plants may do the job.

Drift of herbicides in field boundary vegetation

The environmental hazards of herbicide drift have received much attention in the recent past. Research predominantly focused on (1) the determination of drift patterns (e.g. Byass & Lake 1977, Cuthbertson 1988, de Snoo & de Wit 1993, Miller 1988, Nordbo *et al.* 1993, Thomson & Lay 1982) or (2) the determination of the effects of herbicide drift by placing individually potted plants at intervals downwind a sprayboom and monitoring subsequent death or growth reduction (Marrs *et al.* 1989, 1991, 1993). Thus, most research focused on aspects of herbicide drift rather than on its effects on perennial vegetation. This is not surprising since

the effects of herbicide drift on a perennial vegetation may be influenced by a range of factors. Effects observed in the field are therefore difficult to generalize. We can make a distinction between factors that influence the spray drift deposition pattern and factors that influence the effects herbicides may have on a perennial vegetation. With respect to the first category of factors, those that may influence the spray drift deposition pattern, two categories of aspects may be distinguished: (1) Technical aspects. These include nozzle type, spraying angle, size spectrum of the emitted drops, spray boom height and tractor speed (van de Zande *et al.* 1995). (2) Meteorological aspects. The most important are wind speed and profile, relative humidity, temperature and atmospheric stability (van de Zande *et al.* 1995). Meteorological aspects may be influenced additionally by environmental conditions such as crop height, type of field boundary (for instance presence of a hedgerow) or the proximity of buildings. Besides these aspects, wind direction will ultimately determine whether a particular field boundary will be exposed to drift or not. Since the meteorological conditions are extremely variable, it is not possible to estimate the average amount of herbicide that is deposited in field boundaries under standard agricultural activities. Recently a spray drift deposition simulation model has been developed (Holterman & van de Zande 1995). This model has primarily been used to quantify drift reductions achieved by different preventative measures such as no-spray zones or special nozzle types. Simulating herbicide drift based on the climatological data of a range of years with such a spray drift simulation model may, however, also give an indication of the fluctuations in, and the amount of herbicide that drifts into the field boundary.

The second category of factors that makes generalizations about the effects of herbicide drift highly speculative is related to the effects of herbicides on a perennial vegetation. To name the most important aspects, effects of herbicides on a semi-natural vegetation may change with:
- The type of herbicide used and the sequence the different compounds are used in. Different herbicides generally have different effects on a vegetation (Marshall 1988, Parr 1988). No information was found in the literature on the effects of alternating different types of herbicides on a perennial vegetation.
- The frequency with which herbicides are applied. This determines the number of times drift may occur. In theory, effects of herbicides increase with increasing frequency of application.
- The climatic conditions at and shortly after the time of application. Optimal control of annual weeds in the field is generally achieved when herbicides are applied during a spell of weather favourable to crop growth (Schlotter & Schuster 1992). For example, Boatman (1989) and Lutman *et al.* (1987) found considerable differences between the efficacy of the same herbicide when applied at different dates early in the season.
- The amount of stress experienced by plants in a vegetation. De Ruiter & Meinen (1995) found reduced efficacy of the broad spectrum herbicide glyphosate when applied to plants that experienced increasing levels of water stress.
- The species composition of the vegetation. A boundary with many susceptible species will show more pronounced effects when exposed to a herbicide than a vegetation consisting of few or no susceptible species.
- The age distribution of the plants that make up the vegetation. Marrs *et al.* (1991a, 1993) found seedlings and young plants to be more susceptible to exposure of herbicide drift than old plants. A vegetation consisting of many annual and biennial species, which consequently has many seedlings in spring and fall, will probably be more susceptible to herbicide

exposure compared to a vegetation with perennial species only.

Marrs *et al.* (1991b) and Perky *et al.* (1996) studied the effect of drift of herbicides on a highly simplified vegetation. They created microcosms: standardized mixtures of up to six species and exposed these to herbicide drift or herbicide dosages that simulated drift (similar to the approach in Chapter 8). Effects after one or two years indicated that no species went extinct but that the relative contribution of different species to the mixture changed due to the herbicide application.

The study presented in Chapter 8 was the first to investigate the effect of sub-lethal dosages of herbicides upon a naturally developed vegetation. The results demonstrate that the effects caused by low dosages of herbicides are indeed unpredictable. Effects of the herbicide fluroxypyr were different in all three years. In 1993 no significant effects were found while in 1994 biomass production of spontaneously established forb species was significantly reduced by all herbicide application rates. In 1995 biomass production of the sown forb species was reduced and that of the spontaneously established grass species was significantly enhanced by herbicide levels of half the field rate. Furthermore, the effects of fluroxypyr differed markedly between the grassland and the fallow arable field site. The experiments in the two different habitats had in common, however, that a number of individual species was significantly affected. Almost all species were adversely affected while none increased in abundance (with the exception of *Daucus carota*; see Chapter 8).

The vegetation in the boundary plots of Chapter 4, which bordered a conventionally tilled arable field did not show any patterns in botanical composition which might be contributed to herbicide drift. In fact, hardly any symptoms were found in the three strips in any of the years, although weeds were being controlled up to the very edge of the boundary plots and especially the forb plots consisted of a range of potentially sensitive species. However, in 1996, one year after the study described in Chapter 4, the outer 0.5 m of all boundary plots on the Amfoort field were accidentally sprayed with an MCPA/MCPP mixture at field rate (MCPA/MCPP controls broad-leaved species). Damage symptoms were severe and during the season grasses were able to establish in the narrow strip bordering the arable field; an area previously the exclusive domain of tall sown forbs such as *Tanacetum vulgare* and *Centaurea jacea* (Kleijn, personal observations).

Thus one may conclude by stating that drift of herbicides has the potential to decrease the species richness in field boundary vegetation, but it is especially the misapplication of herbicides that pose the largest threat to field boundary diversity. A single event of misapplication may result in a decline in species richness that will take a very long time to restore.

Factors affecting the species composition of field boundary vegetation: nutrients

The use of externally obtained or produced nutrients in the arable landscape has increased drastically in the last century (Pimentel *et al.* 1990). Nutrients may have profound negative effects on the species richness of herbaceous vegetation and the increased nutrient inputs are therefore a prominent factor to investigate when one is interested in the botanical decline of field boundaries in the last few decades. Al-Mufti *et al.* (1977) found a relationship between the productivity of a vegetation and the species richness that was characterized by a low

species richness at very low productivity levels, high species richness at productivity levels between 350 and 750 g standing biomass (and litter) per square metre and a strong decline in species richness at productivity levels above 750 $g.m^{-2}$. Indeed, many authors have found adverse relationships between vegetation productivity (above 400 g dry weight.m^{-2}) and the species richness of a habitat (Bobbink 1991, Carson & Barret 1988, Mountford *et al.* 1993, Tilman 1987) after fertilization of herbaceous vegetation. The reduced species richness at higher nutrient levels is generally contributed to an increased competition for light (Bobbink 1991, Goldberg & Miller 1990, Tilman 1993) which eradicates small-statured species from the vegetation and reduces the (re-)establishment success of species regenerating from seed. The above-mentioned relationship was the rationale behind the determination of the productivity as well as the species richness of the vegetation in Chapters 2, 3, 4, 6, and 8.

An interesting result of these studies is that the boundary vegetation is able to increase its productivity supported by nutrients from the arable field. The results in Chapters 4 and 6 clearly demonstrate that plants are able to grow their roots into the arable field and relocate the nutrients obtained there into their shoots in the boundary. Not all species are equally efficient in doing so, however. An important aspect governing the vegetative success of field boundary plants at the edge of the arable field is the ability to use the extra nutrients for vertical growth so that shorter competitors can be outshaded. Consequently, when grown together, tall forbs such as *Cirsium arvense, Tanacetum vulgare* and *Urtica dioica* are successful while short grasses and forbs like *Lolium perenne* or *Hieracium pilosella* are unsuccessful at the edge. *If* the boundary is wide enough a biomass gradient may be the result: high biomass production near the arable field and low biomass production far from the arable field.

However, as we saw in Chapter 2, herbaceous field boundaries are rarely wider than one metre. If tall forbs are present in these narrow boundaries (for instance nettle thickets, *Urtica dioica*, which can be found in almost every Dutch field boundary) the entire boundary vegetation will become homogeneously productive and small statured species will have no place to retreat. As a consequence species richness in the boundary will decline drastically as was observed in the zone bordering the arable field in Chapter 4 and in the fertilized plots in Chapter 8. On the other hand, the boundaries surveyed in Chapter 2 were not dominated by tall forbs and the productivity in these boundaries was, with an average biomass production of some 500 $g.m^{-2}$, well within the range given by Al-Mufti *et al.* (1977) as potentially species rich. Still, these boundaries were rather species poor with on average 11 species per 4 m^2. Furthermore, although individual boundaries contrasted sharply in productivity, no negative relationship was found between the biomass production of the vegetation and its species richness. Likewise, in the grass and regeneration plots of the experimental field boundaries (Chapter 4) no such relationship was found. However, in the forbs plots, where a large number of species had been introduced, such a relationship was found indeed. These results suggest that contemporary field boundary vegetation is floristically impoverished and unsaturated with species. *A lower productivity will therefore not result in increased species richness since most potential boundary species have disappeared and are unable to return within a short period of time.*

Besides raising the productivity and adversely affecting boundary species richness, the capture of nutrient resources from arable fields by plants in field boundaries has another important consequence. Among the species that are best adapted to benefit by it is an arable weed (*Cirsium arvense*) and an otherwise undesired species (*Urtica dioica*). Farmers spend a

considerable amount of time and energy to control these species (Chapter 2, de Snoo & Wegener Sleeswijk 1993, Marshall & Smith 1987). The most important boundary associated arable weed in the investigated area, *Elymus repens,* is not highly efficient in capturing arable nutrients (Chapter 6) but the nutrient status of the boundary does affect the abundance of this species. The results of Chapter 9 show that an increased nutrient supply may preferentially favour this species. Application of the equivalent of 80 kg N.ha^{-1}.y^{-1} resulted in a 37% increase in vegetation productivity, while *E. repens* rhizome biomass increased by 45%. We may therefore assume that the level of weed infestation, caused by *E. repens* rhizomes colonizing the arable field from the boundary, will likewise increase with increased productivity of the boundary vegetation. An even stronger effect than the supply of nutrients, had the presence of bare soil on the vegetative success of *E. repens*. The amount of bare soil in arable field boundaries is generally related to the type of boundary management.

Factors affecting the species composition of field boundary vegetation: management

The results in Chapter 2 & 4 suggest that there are two important aspects governing the weed abundance and species richness in field boundaries that are related to field boundary management.

First, the mowing regime: 60% of the surveyed boundaries were cut but cuttings were not removed while another 34% of the boundaries were not cut at all (Chapter 2). Not cutting the vegetation generally results in an accumulation of vegetation biomass and litter (Tilman 1987). An increase in above-ground plant biomass and litter layer may result in a decrease in regeneration from seed (Tilman 1993) and subsequently in a decline in species richness (Carson & Peterson 1990). Not removing the vegetation annually increases the productivity of the boundary (Berendse *et al.* 1992). This effect will be more pronounced in field boundaries where the vegetation is able to capture a considerable amount of nutrients from the arable field each year (Chapter 6). Therefore, not removing the cuttings will lead to a very strong accumulation of nutrients in de field boundary, raising the productivity of the habitat. These conditions do not support species richness (Chapter 8). Additionally, each year a thick layer of cuttings is covering the vegetation. Below this mat of decomposing plant material, many plants will suffocate and die, creating gaps in the vegetation (Parr & Way 1988). Especially low statured, rosette shaped species will not be able to penetrate the layer of cuttings while species with erect shoots and a lot of below-ground reserves generally manage to do so. Usually the latter type of species are tall forbs and grasses (*Urtica dioica, Dactylis glomerata*) and perennial weeds (*Cirsium arvense, Elymus repens*). Summarizing: consistency in the cutting regime (with removal of the cuttings) will lead to a suppression of arable weed species in the boundary and will promote the development of a species rich vegetation. Less consistent mowing regimes will reduce botanical species richness and increase the proportion of weeds in the vegetation.

The second important management aspect is the fact that the position of the field boundary-crop edge transition is not fixed over the years. Farmers generally do not plough exactly the same area in consecutive years. Thus, in some years a strip of the perennial field boundary may be turned into bare soil while in other years a narrow strip of bare soil may not be cultivated and left regenerating: the boundary crop-edge transition is shifting. In the

Chapter 4 strips these fluctuations averaged annually 0.23 m ± 0.16 (Kleijn unpublished results). The results in Chapter 2 confirmed these observations by demonstrating that the species composition of the first 0.33 m of the boundary was significantly different compared to 0.67 m further from the arable field. The first 0.33 m of the boundary contained significantly more annual weeds and the clonal weed *Elymus repens* had its peak abundance at this position. The results of Chapter 9 show that *E. repens* concentrates above ground biomass in patches with bare soil. The shifts in the location of the boundary-field edge transition increase the amount of bare soil available to boundary species which favours the establishment of arable weed species in this habitat. It furthermore promotes the establishment of ruderal perennials such as *Tanacetum vulgare* (Chapter 7). After establishment, these species may quickly dominate the field boundary thereby reducing species richness (Chapter 4) and adversely affecting crop production in the field edge (Chapter 5).

Strictly speaking, the use of herbicides in the boundary is a form of boundary management. The effects of herbicide use for boundary species richness and the abundance of weeds have, however, already been discussed in a previous section.

An integrated view on factors affecting the species composition of field boundary vegetation

Not all factors discussed in the previous sections affect the species composition of the field boundary vegetation to the same extent. Furthermore, most factors are closely related. A simplified graphical presentation of the relationships between the most important factors and the species richness and weed abundance in the field boundary is given in Fig. 11.1. Three types of variables are distinguished: first (in striped boxes) those determined by the activities of the farmer. They consist of herbicide use in the boundary, fertilizer misapplication, the mowing regime of the boundary and the extent to which the boundary-crop edge transition fluctuates from year to year. Second (in ellipses) the most important characteristics of the boundary vegetation; the amount of bare soil and the nutrient status of the field boundary. Third (in solid boxes) the 'target variables' species richness and the proportional abundance of weeds. In Fig. 11.1, the abundance of weeds and other tall dominating species (such as *Urtica dioica*) have been put together since they affect, and are affected by, other variables in a similar fashion.

It may be concluded from Fig. 11.1 that herbicide use in the boundary and the mowing regime are clearly the most important factors governing species richness. They affect species richness directly as well as indirectly through the amount of bare soil and/or the nutrient status of the boundary. If herbicides are used in the boundary vegetation or if the proper mowing regime is not adopted, measures taken to reduce the impact of other factors such as herbicide drift or fertilizer misapplication will not be very effective in restoring plant species richness in the field boundary. The fluctuations in the boundary-crop edge transition are by themselves not extremely harmful to plant species richness but they promote the dominance of weeds and other tall species which may result in increased herbicide use in the boundary. Fig. 11.1 (lower left side) furthermore clearly illustrates 'the herbicide treadmill': herbicide use in the boundary creates bare soil which promotes weed growth which will be controlled with herbicides etc, etc. It furthermore illustrates the only alternative to this cycle of
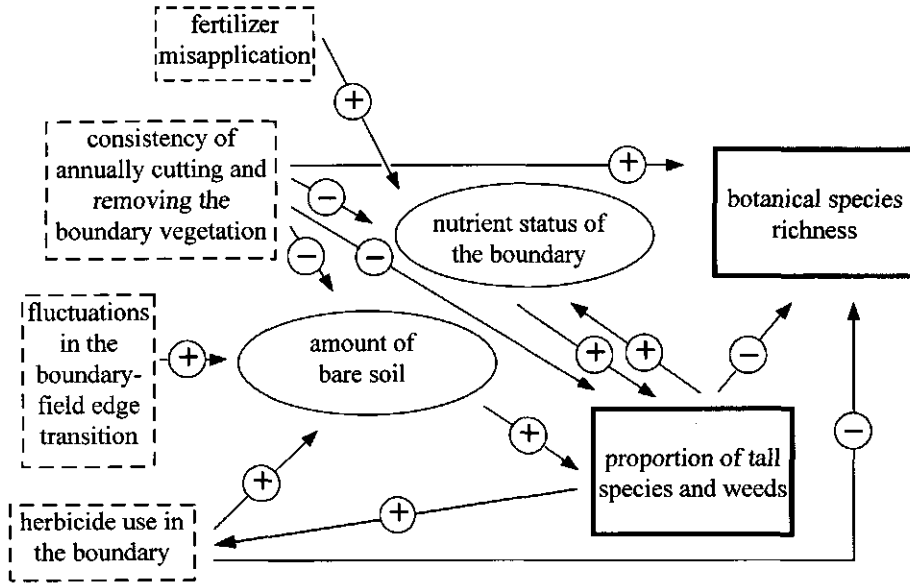
Figure 11.1 *Relational diagram of the key processes governing species richness and the abundance of weedy species in herbaceous arable field boundaries.*

increasing herbicide use; mowing and removing the vegetation will reduce the amount of bare soil, lower the nutrient status of the boundary and affect the weed species directly since most of their above-ground biomass is removed on a regular basis.

Finally, Fig. 11.1 may be used as an illustration of the intimate connection between the species richness and the abundance of weeds/tall forbs in the field boundary. The species richness can be directly affected by weeds as a result of competitive outplacement or indirectly by the use of herbicides provoked by the presence of weeds in the boundary.

The effect of the field boundary on the crop edge

In the crop edge, the outer metres of the arable field, crop yields are usually lower compared to the centre of the field (Boatman & Sotherton 1988, De Snoo 1994). The results of the existing boundaries, presented in Chapter 5, are consistent with this trend. On the other hand in the crop edges next to the newly established field boundaries, crop yields were not consistently lower compared to the centre of the field and depended on the type of vegetation in boundary plots: yields of different crops were significantly reduced next to plots with a highly productive boundary vegetation but were not affected next to plots with a low productive boundary vegetation (Chapter 5). *Obviously, a tall, competitive vegetation in the boundary may depress crop yield in the edge whereas a low, uncompetitive vegetation is unlikely to do so.*

In the new crop edges next to the new boundary plots, weed pressure was very low, although it was increasing through the years. The results from Chapter 10 suggest that the abundance of the weed flora in the crop edge may be the result rather than the cause of the poor crop performance. Poor crop performance may be the result of soil compaction, poor seedbed conditions (Boatman & Sotherton 1988), lower fertilizer inputs (see Melman & van der Linden 1988), or competition from the boundary vegetation (Chapter 5). However, experimental studies (carried out in the centre of experimental fields) reveal that weeds may indeed have very significant negative effects on crop yields (e.g. Glauninger & Holzner 1982, Joenje & Kropff 1987, Kropff & van Laar 1993, Melander 1995, Rooney 1991). To separate these two effects in crop edges, that is, to determine what effect is the cause and what is the consequence, additional experimental work is needed. This may allow us to quantify to what extent field boundaries contribute to the weed pressure in the arable field.

Crop edges may function as refugia for endangered arable weed species (Wilson & Aebischer 1995). There has been increased attention for this subject in the Netherlands since Dutch governmental policies became more strict with respect to emission of pesticides to surface waters (LNV 1990). As a result, agreements have been made between flower bulb producers and water supplying companies to cease herbicide use in the outer 1.5 metre of the arable field (Udo de Haes 1995). The results of Chapter 10, however, clearly demonstrate that cessation of herbicides alone is not sufficient to maintain viable populations of the most vulnerable species: the amount of fertilizer applied to the crop should be reduced as well. Cessation of both herbicides and fertilizer inputs would reduce crop yields to extremely low levels and result in problems with harvesting or sale of the qualitatively inferior product. Furthermore, the results of Chapter 10 and those of a more widespread conservation headland program of the Dutch province of Gelderland (Pancras 1995) revealed that on most arable fields in the Netherlands rare arable species have gone extinct even from the seed bank and do not return spontaneously when more favourable growing conditions are restored.

Therefore, it is doubtful whether crop edges on conventional farms may function as refugia for rare arable weeds. These no-input crop edges offer, however, very promising opportunities for increasing animal wildlife such as partridges or butterflies (Longley & Sotherton 1997, Rands 1985, Rands & Sotherton 1986).

Perspectives for the restoration of botanically diverse field boundaries

In the previous sections, the results of the various chapters were discussed. The most important factors determining the success of arable weeds as well as the species richness in the boundary vegetation were identified and the relationships between these factors were established. These relationships, summarized in Fig. 11.1, are the basic elements needed to construct a guideline for farmers how to manage boundaries in such a way that a weed free ánd species rich boundary vegetation may develop.

Fig. 11.1 shows that the one option that combines optimal and sustainable weed control with botanical diversity in arable field boundaries is a management regime that combines cutting and removing the vegetation at least once a year, with crop cultivation activities that minimize fluctuations in the boundary-crop edge transition. Strictly speaking, this set of simple management rules can be considered to be the 'boundary vegetation restoration approach'. The present studies, together with information from literature have demonstrated

that cutting and removing the vegetation and prevention of disturbances due to cultivation activities will result in weed control in boundaries. Moreover, it sets a development in motion towards a relatively short, less competitive boundary vegetation that has no or less adverse effects on crop yields in the crop edge. A farmer interested in sustainable weed control in his boundaries (bearing in mind the ever tightening restrictions regarding pesticide use) may adopt these management rules, thereby creating conditions favourable to the development of a more species rich vegetation.

However, most farmers don't have the equipment to mow or collect and remove the cuttings. Furthermore, as with the cuttings of many Dutch road verges (see Trommelen 1994), the relatively low quality of the vegetation in both road verges and field boundaries makes it difficult to find use for its cuttings. If no use can be found, it may have to be dumped which may be quite costly.

These objections can be avoided if the cuttings from the boundary are deposited on the outer metres of the arable field: the crop edge. The boundary vegetation is most easily cut when the crops are harvested, since otherwise access to the boundary without incurring damage to the growing crop is difficult. Thus, after crop harvest the boundary vegetation is cut and cuttings are deposited on the stubble in the crop edge. These may then be incorporated into the soil to stimulate decomposition of the material. Kleijn & Verbeek (unpublished results) asked farmers for their opinion of this approach. 46% of the farmers (n=74) did not have any objections, however, 54% argued against this approach on grounds of increased weed pressure in the crop edge.

In modern, weed covered field boundaries, deposition of boundary cuttings onto the crop edge may indeed result in increased weed pressure. However, in a well developed, undisturbed boundary vegetation hardly any weed species will be present (Schmidt 1993, Sykora *et al.* 1993). Seeds of grassland species are not able to establish or compete with the crop. Moreover, especially clonal weeds invade the arable field from the boundary, usually by means of rhizomes. The results presented in Chapter 9 showed that a 37% reduction in vegetation productivity was accompanied by a 45% reduction in rhizome biomass produced by the clonal weed *Elymus repens*. Thus, putting the boundary cuttings on the crop edge will increase the inputs of seeds of clonal species but reduce the ingress of the more competitive rhizomes (rhizomes contain more reserves than seeds). On ecological grounds, increased weed pressure is therefore not a valid argument against this approach.

Depositing the boundary cuttings on the crop edge has some additional benefits. A number of these benefits are related to nutrient flows between the crop edge, the field boundary and the environment and have been depicted in Fig 11.2.

1. Since removal of the cuttings will make the boundary vegetation more nutrient deficient, the nutrient buffering capacity of the vegetation will increase. The rooting density of vegetation growing on nutrient poor substrate is generally higher than that of vegetation growing on nutrient rich substrate (Sprangers 1996). This will result in an increased interception of nutrients leaching laterally from the arable field to drainage ditches. Furthermore, cut material left in the boundary in autumn may be subject to run off and nutrients may leach from the boundary vegetation itself. Thus, removing cuttings will result in a reduced pollution of, for instance, surface waters with nitrate or phosphate.

2. The boundary cuttings may be considered as an additional fertilization of the crop edge. Crop edges are generally fertilized below the target level since the most common type of spreader, the oscillating spout and disc spreaders, rely on overlap of consecutive fertilizer

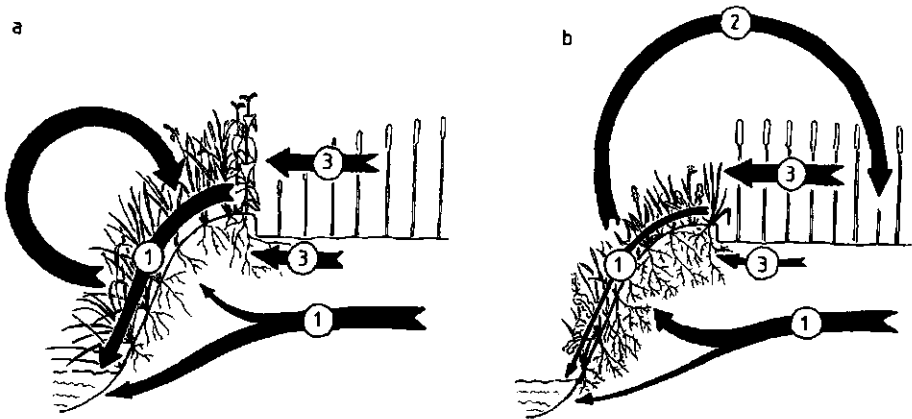a   b

Figure 11.2 Simplified graphical representation of the nutrient flows (arrows) in field boundaries (a) when boundaries are cut but no cuttings are removed and (b) when the boundary vegetation is annually cut and cuttings are deposited on the outer metres of the arable field. Thickness of the arrows indicate the size of the flow. Numbers refer to aspects mentioned in the text.

applications for an even distribution (Melman & van der Linden 1988, Rew *et al.* 1992). Boundary cuttings may supplement the nutrient deficit and therefore contribute to crop production.

3. Nutrients, applied to support crop growth, are lost through misapplication of fertilizers and by capture by the vegetation in field boundaries. Deposition of field boundary cuttings on the crop edge may reduce economic loss since it returns (part of the) misplaced and captured nutrients to the arable field. Furthermore, regular removal of cuttings from the boundary will reduce the dominance of tall species that are most efficient in capturing nutrients from the arable field. Thus, indirectly as well as directly, more nutrients will be kept in the cropping system.

General benefits not related to nutrients are:

- Since the cut material will be deposited on the arable field, activities that promote weed growth in the boundary, such as close ploughing, result in extra weed seed inputs. Thus, field boundary management is directly linked with the cropping system which is very perceptible to farmers and they may be expected to manage their field boundary more carefully.

- This type of management requires no or little extra activities compared to conventional boundary management and is therefore labour efficient.

This last point raises the only disadvantage of the approach. Equipment is currently available that simultaneously or successively cuts and transports the vegetation, however, this type of equipment is not widely available to farmers or contractors. Development of cheap transporters or devices that can be used to adapt currently common mowing equipment for this purpose might greatly improve the chances of successful adaptation of this approach.

The second management rule: minimization of the fluctuations in the boundary-crop edge transition, may easily be achieved by marking the position of the transition permanently with a limited number of durable, clearly visible stalks. This will aid the farmer to adjust his ploughing to just the right extent so that he ends up at the same position each year.

Of course, the proposed approach needs validation in scale experiments. More specifically, experiments are needed that (1) quantify extra weed pressure in the initial years after adoption of the approach, (2) determine the average period needed to control/eliminate weeds in the boundary vegetation and (3) determine what practical problems may arise after implementation, for instance, with respect to timing of activities, machinery needed or labour peaks.

This approach may result in botanically more diverse field boundaries. However, it may have adverse side-effects on other farmland wildlife. The partridge (*Perdix perdix*) prefers tall vegetation for its nesting sites (Potts 1986, Maris 1996). Mowing the vegetation after crop harvest may thus reduce the number of available nesting sites and affect partridge populations adversely. This example simply illustrates that, with respect to natural wildlife, not all boundaries should be managed in a similar fashion. Structural diversity is at least as important as taxonomical diversity for most animal species (Southwood *et al.* 1979)

Finally, although the experiments described in this thesis increase our understanding of the ecology of field boundary vegetation considerably, our knowledge is still far from complete. At three levels of ecological aggregation I would like to point out subjects that need extra attention. At the *ecosystem level*, food web studies need to be done determining the relationships between organisms at different trophic levels. For example, to what extent is the population density of the kestrel (*Falco tinnunculus*), a common bird of prey in the agricultural landscape, related to diversity in or quantity of arable field boundaries habitats. This type of studies will help us understand the impacts of simplification of the agricultural landscape (due to intensification or reallotment schemes) on arable ecosystems. At the *population level*, we need more insight in dispersal processes of plant species in agricultural habitats. Despite recent research efforts on this subject (van Dorp 1996) more information is needed with respect to the time needed for spontaneous (re-)colonization of restored field boundaries or to what extent farmland animals like hares contribute to these processes (see Welch 1985). At the *plant level*, we need to know more about the autoecology of especially the clonal weed species that occur both in the boundary and in the field. Insight in and quantification of the life cycle stages of these remarkable species is needed to construct highly specific control strategies that give farmers a good alternative to chemical control in the arable field and may increase the effectivity of the currently proposed control approach.

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Summary

In most contemporary arable landscapes, field boundaries comprise the largest area of (semi-) natural vegetation. Therefore they are the keystone of the arable ecosystem. Arable field boundaries provide food, shelter, nesting and overwintering sites for most farmland wildlife. They may be used as corridors between habitats or function as the last refuge for non-arable plant and animal species as natural habitats diminish due to human population growth. In the second half of the twentieth century agriculture intensified and field boundaries lost most or all of their agronomic functions. In the same period the botanical diversity of field boundaries declined drastically. This trend resulted in the extinction of many plant species from the arable landscape and has had adverse effects on farmland animals. Identifying methods to reverse this trend was an important motivation to start the research which is summarized in this thesis.

Presently, most farmers perceive the boundary vegetation as a source of weeds. This perception largely determines their boundary management activities. However, life history characteristics of species from weed communities and those of species from perennial grassland communities suggest that vegetation development towards perennial, species rich vegetation will result in a decline or extinction of arable weed species. Therefore, if management strategies can be developed that reduce the abundance of weeds and simultaneously increase the botanical richness of the boundary vegetation, farmers may be motivated on agronomic grounds to manage their field boundaries in a way that promotes floral wildlife. Consequently, this thesis aims at identifying the most important factors determining the species richness and the abundance of weeds in arable field boundary vegetation.

The results presented in chapter 2 demonstrate that the vegetation composition of contemporary herbaceous arable field boundaries on sandy soils in the Central and Eastern Netherlands was generally species poor (11 species per 4 m^2) and uniform. Since too many character-species of more specific plant associations were missing, the boundary vegetation could merely be classified into closely related frame communities characterized predominantly by species indicative of the *Molinio-Arrhenatheretea, Koelerio-Corynephoretea* and *Artemisietea vulgaris*. In general, boundaries were not cut, or they were cut but cuttings were not removed and no significant relationship between boundary management and vegetation composition was found. Nitrogen inputs and the type of crop rotation were important land use characteristics that significantly affected the boundary vegetation composition, however. The boundary vegetation was furthermore characterized by a declining biomass gradient with increasing distance from the arable field. Over this gradient, the proportion of weedy species (annual dicots and the perennial rhizomatous grass *Elymus repens*) declined and the proportion of perennial dicots and monocots increased, indicating an increased level of disturbance near the arable field.

In chapter 3 vegetation development in newly established vegetation strips along contrasting types of field boundaries in France, the Netherlands and the United Kingdom was compared. A number of vegetation characteristics showed a predictable pattern: within three years of establishment, species-richness, biomass production and monocot/dicot ratio in the new strip converged to the levels of the original boundary in all three countries. Species

composition in the new strip was not closely related to the original boundary. The low similarity was mainly due to low establishment rates of annuals and woodland species in the new strip while mobile, perennial grassland species were generally very successful. Hardly any species were found that were not encountered in the original boundary.

A more in-depth study of the Dutch vegetation strips three years after establishment revealed that tall, competitive species concentrated biomass production in a narrow zone bordering the arable field, while small, stress tolerant species were predominantly found in a zone at considerable distance from the field (chapter 4). The tall species were able to increase total vegetation biomass production significantly at the edge near the arable field, probably by means of capturing nutrients from the arable field. The abundance of the two major arable weed species growing in the new boundary strip, the perennials *Cirsium arvense* and *Elymus repens*, was significantly reduced by sowing a competing vegetation (either grass or a mixture of forbs) at the onset of the experiment.

In 1994 and 1995, the effects of the establishment of the vegetation strips, described in chapter 4, on the crop edge of conventionally cultivated fields were examined. The results presented in Chapter 5 demonstrate that in existing field edges crop yields were generally lower and weeds more abundant near the field boundary compared to the centre of the field. Three years after establishment of the vegetation strips, crop yields next to those strips were significantly lower compared to those obtained under pre-establishment conditions. However, boundary vegetation productivity, rather than weed pressure, proved to be the most important correlate of crop yields in the field edge. This indicates that in these strips, competition from the boundary had more adverse effects than competition from weeds.

Chapter 6 elaborates upon the observation made in chapter 4 that plants in field boundaries may capture nutrient resources from arable fields. A number of experiments demonstrated that the boundary vegetation may increase biomass production supported by nutrients obtained from the arable field. In the examined, grass dominated boundaries this effect was limited to the first 0.2 m bordering the arable field, however. A comparison between individual species revealed that clonal (e.g. *Cirsium arvense*, *Elymus repens*) and non-clonal perennial species were equally effective in capturing arable nutrient resources and that especially tall species significantly profited from access to the arable field.

An important aspect in the restoration of arable field boundaries is the establishment of (new) species in a boundary, once conditions have improved. In chapter 7 the establishment success of six ecologically contrasting grassland forbs in the first three years of a secondary succession (similar to those in the strips of chapter 4) was examined. In general, tall, early successional species were very successful on the bare soil of the initial succession stage but failed almost completely to establish in the older succession stages. This was mainly due to significantly reduced seedling emergence and plant growth in the later stages. In terms of final total biomass production, late successional species were less successful on the bare soil. However, they were able to establish successfully in later successional stages, due to seedling emergence that was either not significantly affected or not reduced to insignificant levels by the succession stage of the vegetation. Furthermore, plant growth of these species was less affected by the increasing age of the succession compared to the early successional species. The results demonstrate that establishment of (often undesired) tall early successional perennials can be seriously hampered by the presence of a well developed perennial vegetation.

Contemporary agriculture relies heavily upon the use of agrochemicals. Drift of herbicides

and misplacement of fertilizer may seriously affect the vegetation composition of arable field boundaries. The experiments described in chapter 8 were performed in two different types of vegetation and in the glasshouse and demonstrated that both agrochemicals can have significant effects upon the species composition of arable field boundaries. Both the herbicides and the fertilizer applications adversely affected predominantly the sub-ordinate species in the vegetation. The effects of the fertilizer applications on species-richness, biomass production and the abundance of individual species were far more severe and consistent compared to the herbicide applications. The experiments furthermore illustrate the inappropriateness of extrapolating the results of glasshouse experiments to normal field conditions.

In chapter 9, the ecological responses of the clonal species *Elymus repens*, the most important boundary associated weed in the study area, was examined with respect to two environmental conditions: the presence of unvegetated gaps in its habitat and the productivity of that habitat. The results showed that *Elymus repens* responded to the contrast in nutrient supply that was present between the bare and vegetated parts of a habitat, by selectively growing its rhizomes into the areas with bare soil. It thus concentrated its biomass in patches with favourable growing conditions. Fertilization merely resulted in a more elaborate growth of the rhizomes, resulting in more nodes and shoots being produced.

Crop performance in field edges is relatively poor compared to the centre of the field and conditions are generally more favourable for weed growth. If pesticide use is restricted, rare arable weeds may find a last refuge in these 'conservation headlands'. The experiments presented in chapter 10 show that, next to herbicide use, fertilizer use should be restricted as well for those conservation headlands aimed primarily at sustaining viable populations of rare arable weeds. Fertilizer application results in a better development and an increased light interception of the crop. Reduced light penetration levels at ground surface resulted in a significantly reduced growth of both rare and common weed species.

This thesis concludes with a chapter that integrates and discusses the results of the preceding chapters. Three key-factors are suggested causing the low levels of species richness and the high abundance of weeds in contemporary arable field boundaries: (1) the use of herbicides in the boundary, (2) boundary management strategies in which the vegetation is not cut and removed and (3) crop cultivation activities that result in the creation of bare soil in the boundary. Sustainable weed control in field boundaries may be achieved by consistently cutting and removing the vegetation on at least an annual basis and by avoiding large scale soil disturbances caused by cultivation activities. This will simultaneously result in the development towards a more species rich boundary vegetation. An approach is suggested which deposits the boundary cuttings on the crop edge. Advantages and disadvantages of this method are discussed and areas where more detailed information is needed are identified.

Samenvatting

In hedendaagse akkerbouwgebieden is de grootste oppervlakte aan (half-)natuurlijke vegetaties te vinden als lintvormige elementen langs akkers: de akkerzomen. Hierdoor vormen zij het voornaamste dragende element van het agrarisch ecosysteem. Akkerzomen dienen voor vele diersoorten als voedselbron, schuilplaats, nestplaats en als locatie om te overwinteren. Ze worden bovendien gebruikt als verbindingszone tussen habitats of als laatste uitwijkplaats voor wilde planten- en diersoorten naarmate natuurlijke habitats verdwijnen door de toenemende bevolkingsdruk. In de tweede helft van de twintigste eeuw intensiveerde de landbouw. Akkerzomen verloren in deze periode een deel of alle landbouwkundige functies die zij voordien hadden (omheining, levering van geriefhout e.d.). In diezelfde periode nam ook de botanische diversiteit van akkerzomen drastistisch af. Deze tendens resulteerde in het uitsterven van vele plantensoorten in akkerbouwgebieden en had sterke nadelige gevolgen voor vele diersoorten die karakteristiek zijn voor deze gebieden. Het vinden van methoden die de neerwaartse trend terug kunnen draaien was een belangrijke motivatie bij het doen van het onderzoek dat is samengevat in dit proefschrift.

Momenteel beschouwen de meeste boeren akkerzoomvegetaties als een bron van onkruiden en deze visie bepaalt grotendeels de aard van het zoombeheer dat zij voeren. Een vergelijking van de groeikenmerken van onkruidsoorten en graslandsoorten leert ons dat de ontwikkeling van een vegetatie richting meerjarige, soortenrijke(re) plantengemeenschappen gepaard zal gaan met een afname of verdwijning van onkruidsoorten. Het ontwikkelen van beheersstrategieën die het voorkomen van onkruiden tegengaan en gelijktijdig de soortenrijkdom van de zoomvegetatie doen toenemen, kan er toe leiden dat boeren, op grond van landbouwkundige argumenten, hun akkerzomen gaan beheren op een manier die de soortenrijkdom doet toenemen.

De resultaten van hoofdstuk 2 tonen aan dat de vegetatie van hedendaagse, door gras gedomineerde akkerzomen op de zandgronden van midden en oost Nederland uniform en soortenarm zijn (11 soorten per 4 m^2). De zoomvegetaties konden worden geclassificeerd in nauw verwante rompgemeenschappen die voornamelijk gekenmerkt werden door soorten van de *Molinio-Arrhenatheretea*, *Koelerio-Corynephoretea* en *Artemisietea vulgaris*. Karakteristieke (ken)soorten om de rompgemeenschappen in te delen in meer specifieke plantengemeenschappen ontbraken over het algemeen. De akkerzomen werden gewoonlijk niet gemaaid of werden wel gemaaid maar het maaisel werd niet afgevoerd en er kon geen enkele verband gevonden worden tussen het maaibeheer en de vegetatiesamenstelling. De hoogte van de stikstofgift en de gewasrotatie op de akker waren belangrijke landgebruikskarakteristieken die wel een statistisch significant effect op de samenstelling van de akkerzoomvegetatie hadden. Daarnaast werd de akkerzoom gekenmerkt door een biomassa gradiënt: de totale biomassaproduktie van de vegetatie nam af met toenemende afstand van de akker. Met afnemende biomassa produktie nam het aandeel onkruidsoorten (eenjarige dicotyle soorten en het meerjarige, rhizoomvormende gras *Elymus repens*) in de vegetatie af en het aandeel meerjarige mono- en dicotyle soorten nam toe. Dit duidt op een hoger verstoringsniveau van de vegetatie nabij de akker.

In hoofdstuk 3 werd de vegetatieontwikkeling gevolgd in, in 1993 nieuw aangelegde, vegetatiestroken langs verschillende typen akkerzomen (slootkant, haag, houtwal) in

Frankrijk, Nederland en Engeland. Een aantal vegetatiekenmerken vertoonden een voorspelbaar patroon in alle drie de landen: drie jaar na aanleg hadden de soortenrijkdom, biomassaproduktie en de monocotylen/dicotylen ratio waarden aangenomen die vergelijkbaar waren met die in de oorspronkelijk akkerzoom. De vegetatiesamenstelling was echter niet vergelijkbaar met die in de oorspronkelijke zoomvegetatie. Het verschil in vegetatiesamenstelling tussen de nieuwe vegetatiestrook en de oorspronkelijke akkerzoom werd voornamelijk veroorzaakt door de slechte vestiging in de nieuwe strook van eenjarige soorten en bos-soorten terwijl zich gemakkelijk verspreidende meerjarige graslandsoorten juist zeer succesvol waren. In de stroken in alle drie de landen werden overigens nauwlijks soorten aangetroffen die voordien niet al aanwezig waren in de oorspronkelijke akkerzomen.

Een detail-studie van de Nederlandse vegetatiestroken in het derde jaar na aanleg liet zien dat hoog opgroeiende concurrentiekrachtige plantensoorten hun biomassaproduktie concentreerden in een smalle zone grenzend aan de akker. Laagblijvende soorten werden daarentegen voornamelijk gevonden in een zone op aanzienlijke afstand van de akker (hoofdstuk 4). De produktiviteit van de hoge soorten resulteerde in een grote stijging van de biomassa produktie van de gehele vegetatie dichtbij de akker. Deze stijging werd waarschijnlijk gesubsidieerd door nutriënten uit de akker, aangezien waargenomen werd dat de wortels van planten uit de akkerzoom een flink stuk de akker ingroeiden. De abundantie van de twee belangrijkste, in de nieuwe vegetatiestroken voorkomende akkeronkruiden (de meerjarige soorten *Cirsium arvense* en *Elymus repens*) werd sterk en statistisch significant gereduceerd door het bij aanleg van de stroken inzaaien van een concurerende vegetatie.

In 1994 en 1995 werden de effecten onderzocht die het aanleggen van de vegetatiestroken (beschreven in hoofdstuk 4) had op het gewas in de buitenste meters van de akker. De resultaten, weergegeven in hoofdstuk 5, tonen aan dat onder normale omstandigheden (dus zonder nieuw aangelegde strook) de gewasopbrengsten in de buitenste meters van de akker over het algemeen lager zijn en er meer onkruiden voorkomen dan in het centrum van het perceel. De gewasopbrengst naast de vegetatiestroken waren, drie jaar na aanleg van de stroken, significant lager dan de opbrengsten verkregen naast de controle randen waar geen vegetatiestroken waren aangelegd. Echter, niet de hoeveelheid onkruiden maar de biomassaproduktie van de belendende vegetatiestrook bleek negatief gecorreleerd te zijn met de gewasopbrengsten in de rand van de akker. Dit duidt erop dat in deze gewasranden de concurrentie van de zoomvegetatie grotere nadelige gevolgen had dan de concurrentie van onkruiden.

Hoofdstuk 6 bouwt voort op de waarneming in hoofdstuk 4 dat planten in akkerzomen een deel van de nutriënten kunnen bemachtigen die een boer zijn gewas toedient. Een reeks van experimenten toonde aan dat de biomassaproduktie van de zoomvegetatie verhoogd kan worden door nutriënten die verkregen zijn uit de naastgelegen akker. In de onderzochte, door gras gedomineerde zomen was dit effect echter beperkt tot de 0.2 m het meest nabij de akker. Een vergelijking tussen individuele soorten leerde dat klonale soorten (waaronder *Cirsium arvense* en *Elymus repens*) en niet-klonale soorten even efficient waren in het bemachtigen van nutriënten uit de akker, maar dat de biomassaproduktie van vooral de hoog opgroeiende soorten significant toenam indien hun wortels vrij toegang hadden tot de akker.

Een belangrijk aspect bij het herstel van soortenrijke akkerzoomvegetaties is de vestiging van (nieuwe) soorten in de zomen als de groeiomstandigheden eenmaal verbeterd zijn. In hoofdstuk 7 werden de vestigingskansen van zes ecologisch uiteenlopende, meerjarige graslandkruiden onderzocht in de eerste drie jaar van een secundaire successie (vergelijkbaar

met die in de vegetatiestroken van hoofdstuk 4). Over het algemeen waren hoog opgroeiende, vroeg-successionele soorten erg succesvol op de kale grond van het eerste jaar van de successie, maar slaagden zij er nauwlijks in zich te vestigen in de twee oudere stadia. Dit werd voornamelijk veroorzaakt door een significante afname in de opkomst en groei van de kiemplanten. Gemeten in uiteindelijk geproduceerde biomassa waren de laat-successionele soorten minder succesvol op de kale grond van het eerste jaar van de secundaire successie. Deze soorten waren echter wel in staat om zich te vestigen in de latere successie stadia doordat de opkomst niet significant lager was of niet tot verwaarloosbaar lage aantallen werd teruggebracht in de oudere successiestadia. Bovendien werd de groei van de kiemplanten van laat-successionele soorten minder sterk geremd in de oudere stadia van de successie dan die van de vroeg-successionele soorten. De resultaten tonen aan dat de vestiging van (veelal ongewenste) hoog opgroeiende, vroeg-successionele soorten verhinderd of aanzienlijk geremd kan worden door de aanwezigheid van een goed ontwikkelde meerjarige vegetatie.

De moderne landbouw leunt zwaar op het gebruik van chemicaliën zoals kunstmest en pesticiden. Emissies van herbiciden en onzorgvuldig kunstmeststrooien kan de vegetatiesamenstelling van akkerzomen aanzienlijk beïnvloeden. De in hoofdstuk 8 beschreven experimenten werden uitgevoerd in twee verschillende vegetatietypen en in de kas en toonden aan dat drift van zowel kunstmest als herbicide de vegetatiesamenstelling in belangrijke mate kan verstoren. Het toedienen van zowel kunstmest als herbicide benadeelde voornamelijk de laagblijvende soorten in de vegetatie. De effecten van kunstmest op soortenrijkdom, biomassa produktie en de abundantie van individuele soorten waren echter veel sterker en consistenter dan die van de herbicide. De experimenten illustreren bovendien dat de resultaten van bio-assay toetsen voor herbiciden slecht naar veldomstandigheden vertaald kunnen worden.

In hoofdstuk 9 werd de ecologie van de klonale soort *Elymus repens*, het voornaamste in akkerzomen groeiende akkeronkruid in het onderzoeksgebied, nader onderzocht. De groei en morfologie van deze rhizoomvormende soort werd bepaald in relatie tot (i) de aanwezigheid van kale grond in zijn directe omgeving en (ii) de produktiviteit van zijn groeiplaats. De resultaten toonden aan dat *Elymus repens* in staat was te anticiperen op het contrast in nutriëntenrijkdom dat ontstond tussen de kale en de met vegetatie begroeide plekken in zijn omgeving. Dit gebeurde door rhizomen selectief de kale plekken te laten binnengroeien. Op deze manier concentreerde de soort zijn biomassa in plekken waar voor hem gunstige groeiomstandigheden heersten. Bemesting (hoge produktiviteit van de habitat) resulteerde slechts in een algemene toename van de groei van rhizomen, hetgeen uiteindelijkleidde tot de produktie van meer knoppen en scheuten.

Gewasgroei in de rand van de akker is over het algemeen minder goed dan in het centrum van de akker en de omstandigheden zijn daardoor gunstiger voor de groei van onkruiden. Indien het gebruik van herbiciden in deze rand uitgesloten wordt, kunnen deze akkerranden mogelijk als toevluchtsoord dienen voor bedreigde akkeronkruidsoorten. De in hoofdstuk 10 gepresenteerde resultaten illustreren dat, naast het gebruik van herbiciden, ook het gebruik van meststoffen uitgesloten dan wel beperkt zou moeten worden, willen de akkerranden voldoen als habitat voor levensvatbare populaties van zeldzame akkeronkruidsoorten. Bemesting heeft een betere ontwikkeling van het gewas tot gevolg waardoor het meer licht onderschept. De afgenomen lichtval door het gewas resulteerde vervolgens in een significante afname van de groei van zowel zeldzame als algemene onkruidsoorten.

Dit proefschrift sluit af met een hoofdstuk dat de resultaten van de voorgaande

hoofdstukken integreert en bediscussieert. Hierin wordt gesteld dat drie factoren sleutelrollen hebben gespeeld bij de achteruitgang in soortenrijkdom en het voorkomen van akkeronkruiden in akkerzoomvegetaties. (1) De directe toepassing van herbiciden in akkerzomen. (2) Het hedendaagse type maaibeheer in akkerzomen waarbij het maaisel niet wordt afgevoerd. (3) Grondbewerkingsaktiviteiten die gaten creëren in de zoomvegetatie. Een duurzame onderdrukking van onkruiden in akkerzomen kan verkregen worden door het regelmatig en consistent maaien van de vegetatie waarbij het maaisel wordt afgevoerd. Dit zou minstens één keer per jaar moeten gebeuren. Daarnaast moet het op grote schaal creëren van kale grond in akkerzomen vermeden worden. Dit type beheer zal niet alleen tot onderdrukking van onkruidsoorten leiden maar tevens tot het ontstaan van een soortenrijke(re) zoomvegetatie. Een goed in de bedrijfsvoering inpasbare methode wordt voorgesteld waarbij het maaisel van de zoomvegetatie gedeponeerd wordt op de buitenste meters van de akker. Voor- en nadelen van deze methode worden bediscussieerd en aandachtspunten voor verder onderzoek worden aangeduid.

Curriculum vitae

David Kleijn werd geboren op 30 juni 1968 te Oostzaan. Hij behaalde het VWO diploma (Atheneum) in mei 1986 aan de OSG Rooswijk te Zaandijk. Aansluitend startte hij de studie Plantenveredeling aan de Landbouwuniversiteit in Wageningen. Tijdens de doctoraalstudie doorliep hij een tweetal vakken Plantenveredeling alsmede stages (ook Plantenveredeling) in Syrië en Indonesië. Hij besloot zijn studie met een bijvak Onkruidkunde. Hierin vond hij zijn draai in het onderzoek pas echt goed zodat hij, na in augustus 1992 te zijn afgestudeerd, in januari 1993 begon als assistent in opleiding bij de toenmalige vakgroep Vegetatiekunde, Plantenoecologie en Onkruidkunde van de Landbouwuniversiteit in Wageningen. Na verplaatsing van de leerstoel Onkruidkunde naar de vakgroep Theoretische Produktie-ecologie in 1994, zette hij het onderzoek aan die vakgroep voort. Zijn onderzoek spitste zich toe op de factoren die de soortenrijkdom en de veronkruiding van akkerzoom vegetaties (permanente vegetatie langs akkers) bepalen. De resultaten van dit onderzoek, onder leiding van de promotoren prof. dr. M.J. Kropff en prof. dr. F. Berendse, zijn vastgelegd in dit proefschrift. Van 1 januari-1 april 1997 en van 1 juli tot 1 september 1997 is hij betrokken geweest bij het opzetten van de cursussen 'Inleiding Agro-ecologie' en 'Agro-ecology'. Vanaf 1 oktober 1997 is hij tijdelijk werkzaam bij de leerstoelgroep Natuurbeheer en Plantenecologie, waar hij een projectvoorstel over agrarisch natuurbeheer voorbereidt.