Nature conservation

and

grazing management

Free-ranging cattle as a driving force for cyclic vegetation succession

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(met een Nederlandse samenvatting)

Jan Bokdam

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Alles hangt met alles samen

Alles verandert - Panta rhei (Heraclitus, ca. 500 v.C.)

Abstract

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This thesis examines the suitability of controlled and wilderness grazing as conservation management tool for open, nutrient-poor habitats. It tests the Resource-mediated Successional Grazing Cycle (RSGC) theory, which claims that free-ranging large grazers can act as driving force for successional woodland-grassland cycles. The hypotheses were that free-ranging cattle create grassland in woodland (i), deplete the nutrient pools of these grasslands (ii), induce invasion of woody pioneers because of this depletion (iii). During the subsequent woodland phase the soil nutrient pool is replenished (iv). The study was carried out in the Wolfhezerheide, The Netherlands. The vegetation was composed of 19 ha of woodland, 33 ha of grassland and 9 ha of *Calluna* heathland. The area was year-round grazed by free-ranging cattle (90 kg ha^{-1} yr^{-1}) after 1983. Atmospheric N-deposition varied from 25-60 kg ha^{-1} yr^{-1} depending on the vegetation. Vegetation change was monitored. Habitat and diet selection were quantified by 24-h observation and bite counting. On the basis of these data, nutrient balances were assessed for the whole area, the successional communities and excreta and excreta-free patches in the grassland. The results showed that cattle induced grasslawns in gaps in the heathland and woodland. They suppressed woody and tall herbaceous species in the woodland undergrowth and introduced grass seeds by dung deposition. Nutrient removal only exceeded the atmospheric inputs on excreta-free patches in the grassland for phosphorus and potassium. Nutrients were removed from these sites by off-take and gaseous excreta-N losses. Cattle also reduced the interception deposition. Nutrient depletion favoured the invasion of pioneer dwarfshrubs (*Calluna*) and trees (*Pinus sylvestris* and *Betula spp*) in the grass lawns. This result was related to the carbon-based chemical resistance of the involved woody pioneers. Cattle and wild herbivores only prevented wood encroachment on relatively nutrient-rich grasslands. Wood invasion and abandoning by the cattle induced replenishment of the soil nutrient pool. The results confirmed the RSGC hypotheses and emphasised the interaction of herbivory and plant resources as determinants of cyclic plant succession. These findings implicate that wilderness grazing may generate temporary open, nutrient-poor habitats in dry uplands, but incompleteness of the abiotic gradient, successional mosaics and herbivore assemblage will restrict the openness and soil depletion. Under these circumstances, conservation managers might prefer controlled grazing. Forced summer grazing, nutrient removal from grass lawns by housing of the animals during the night and additional removal of unwanted species seemed to mimic natural herbivory.

Key-words: biodiversity, herbivory, wilderness, non-linear dynamics, mosaic cycling, grassland, wood encroachment, forest, *Bos taurus*, *Calluna vulgaris*, *Deschampsia flexuosa.*

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Chapter 1

General introduction

Jan Bokdam

Open, nutrient-poor habitats are crucial for biodiversity. Sand lizard (Lacerta agilis) male sunbathing on a dead grass tussock. Wolfhezerheide, August 1987 (photo Maurits Gleichman).

General introduction

Large grazers as a management tool in nature conservation areas

OPEN NUTRIENT-POOR HABITATS

The ideal way to conserve populations of wild plants and animals is by protecting their pristine, evolutionary habitats (Wilson 1999). Unfortunately, this strategy can only be applied to a declining number of species and areas. This raises the question about suitable and feasible alternatives.

The rich flora and fauna of open, nutrient-poor habitats in Europe depend today mainly on semi-natural pastures (Webb 1986; Bignal, McCracken & Curtis 1994; Bal *et al.* 2001; Elligsen, Beinlich & Pflachter 1998). These grasslands and heathlands are the result of traditional pastoralism (Webb 1998). During several millennia, farmers herded their livestock in periodically flooded nutrient–rich wetlands and in nutrient-poor drained higher uplands. In both abiotic zones, pastoralism prevented sucession to woodland (Gimingham 1972; Pott & Hüppe 1991; Webb 1998; Tubbs 2001). These semi-natural pastures in the woodland domain differ from low-productive pastures in the permanent open domain (coastal zones, salt marshes, riverbanks, bogs and alpine zones) because the harsh conditions and lack of woodland-grassland mosaics in the open domain affect the species composition.

Since 1850, traditional livestock farming has gradually lost its economic and social feasibility. It has been replaced on many places by modern farming systems characterised by high energy and nutrient inputs and high outputs of products and pollution. In other areas, traditional pastures were abandoned and turned into woodland (Anonymus 1988). In the remnant open areas, often designated nature conservation areas, biodiversity is suffering from fragmentation and eutrophication (Anonymus 1988; Marrs 1993; Jefferies and Maron 1997; Bobbink, Hornung & Roelofs 1998; Bakker & Berendse 1999). Traditional pastoralism has only survived in economically marginal areas (Bignal, McCracken & Curtis 1994), in marginal climates (Schütz *et al.* 2000) and in areas with marginal land use rights (Tubbs 1986). Sustained traditional farming, as conservation strategy for open, nutrient-poor habitats, will increasingly demand financial subvention by the European Union, national governments and private nature conservation organisations. The sustainability and efficacy of such agri-environment schemes has been questioned (Baldock *et al.* 2000; Kleijn *et al.* 2001).

Nature conservation in Europe must therefore develop and test new management strategies for the conservation of nutrient-poor, open landscapes. Mechanical management may be in certain cases a suitable substitute for traditional farming (Anonymus 1988; Bakker 1989; Marrs 1993) but without marketable products this method is expensive for large areas (Werpachowski 2002). Controlled grazing using free-ranging livestock or wild herbivores, combined with minimal mechanical management is a second option for the replacement of traditional farming (Bal *et al.* 2001; Bokdam & Gleichman 2000) It has the advantage of control and marketable animal products (Kuit & Van der Meulen 1997; Prins, Grootenhuis & Dolan 2002). A third option is wilderness grazing (Baerselman & Vera 1989). This thesis examines the suitability of the last two options.

GRAZING MANAGEMENT STRATEGIES

Since 1960, cattle, horses and sheep have been increasingly used for the management of semi-natural pastures in the Netherlands (Oosterveld 1975; Thalen 1984; Bakker & Londo 1998) and abroad (Wells 1965; Welch 1997; Gordon *et al.* 1990; Bülow Olsen 1980; De Blust & Schneiders 1989; Buttenschøn & Buttenschøn 1982; Loiseau, Ignace & L'Homme 1987; Gerken & Görner 2001). During this period, traditional herding has been replaced by grazing by free-ranging livestock within fences areas, while summer grazing was changed into continuous year-round grazing. The arguments for these changes were to increase naturalness and biodiversity at to lower operational costs (Piek 1998)

Since 1975, traditional farming had been criticised as a conservation strategy, because of its 'unnatural' character and its limited conservation aims. Traditonal farming excluded competing large wild herbivores and carnivores (Van de Veen 1975). The alternative (new) wilderness strategy was launched in 1989 as a proposal for Dutch governmental conservation policy (Baerselman & Vera 1989). The strategy aimed at restoring complete herbivore and carnivore assemblages in complete abiotic gradients and successional mosaics, without human intervention. Although restoration of the pristine wilderness was, by definition, impossible, development of a so-called ‘new wilderness’ seemed to be achievable and the Dutch government accepted this (Kampf 2002). Two areas, the embanked and drained wetland Oostvaardersplassen and the dry sandy area Imbosch are actually being managed according to the wilderness concept. These areas are, however, small, incomplete and fenced, and the herbivore surpluses are (or will be) culled to prevent mass starvation and public outcry (www.minlnv.nl/grazers/).

The wilderness concept claims that complete herbivore assemblages create open habitats as components of successional mosaics in the woodland domain (Baerselman & Vera 1989; Bunzel-Drüke, Drüke & Vierhaus 1994; Bal *et al.* 2001). Such open habitats are analogous to open patches in the pre-farming woodland of W-Europe during the Atlanticum evidenced by the fossil remains of light-demanding plant and animal species (Vera 1997, 2000; Svenning 2002). Not all ecologists and conservation managers support the claims of the ‘new wilderness’ concept. Some doubt the openness in the woodland domain during the Atlanticum, and point to the incompleteness of the herbivore assemblage during that period compared to the Eemian herbivore fauna (Prins 1998). Others advocate sustained traditional farming as exclusive, original strategy (Ellenberg 1996; Pott 1998; Dierking *et al.* 2000). Experimental evidence to settle the question of the suitability of wilderness grazing in Europe is not available. The openness and low soil fertility of large grazing systems in the woodland domain in other continents have been significantly affected by man and fire (Sinclair & Norton Griffith 1979; Chase 1987; Keiter & Boyce 1991; Singer *et al.* 1998). The experiences so far suggest that, without the use of supplements or additional vegetation management, large herbivores in year-round grazing systems cannot prevent the succession of grasslands, heathlands and other unfertilised rangelands to woodland (Westerhoff 1992; Archer 1996; Pott 1998).

However, wood encroachment does not necessarily mean that open, nutrient-poor habitats disappear. They may be replaced by woodland-grassland transitions followed by nutrient-depletion. Such transitions in the past have always been attributed to man (Pott & Hüppe 1991; Ellenberg 1996). Circumstantial evidence from the New Forest (S.England) (Tubbs 2001), exclosure studies from grazed woodlands on the Veluwe (The Netherlands) (Kuiters, Slim & Van Hees 1997) and simulations (Jorritsma, van Hees & Mohren 1999) all point to the high capacity of large herbivores, especially large grazers, to suppress tree regeneration and to create grass lawns.

NEED FOR RESEARCH

The constraints and limitations of traditional farming and the potential advantages of the ‘new wilderness’ concept as a sustainable long-term conservation strategy for all native species and habitats urges the testing of its claims. In this thesis I examine the effects of cattle as creators and nutrient removers of open habitats in the woodland domain. As native typical large grazers, cattle may play a key role in controlled free-ranging systems and – as feral species – also in wilderness areas. Three conservation management questions are asked.

1. Can free-ranging cattle create and maintain open, nutrient-poor habitats in the woodland domain?
2. Can large grazers remove the actual atmospheric nutrient inputs from these open habitats?
3. How suitable are controlled grazing and wilderness grazing as strategies for the conservation of open nutrient-poor habitats?

Large grazers, plants, nutrients and vegetation succession.

LARGE GRAZERS

Large herbivorous mammals include elephants and ungulates (hoofed mammals). Taxonomists classify ungulates into odd-toed ungulates (world-wide 16 species including the non-ruminating horse and rhinoceroses) and even-toed ungulates (196 species with e.g. non-ruminating wild boar and ruminating deer, cattle, sheep and goats) (Macdonald 2001). Ecologists distinguish the functional groups large grazers (‘bulk & roughage feeders’), intermediate feeders and browsers (‘concentrate selectors’) within the large herbivorous mammals (Hofmann 1989; Macdonald 2001). Ruminant and non-ruminant large grazers co-evolved with grasses during the late Tertiary and Pleistocene periods (Stebbins 1981; McNaughton 1984). The adaptations of the large grazers involve a wide lower incisor arcade (Illius & Gordon 1987; Gordon, Illius & Milne 1996) and a long digestive tract with either a rumen or a ‘hind gut’ to allow the microbial digestion of low-digestible roughage (Hofmann 1989). Large grazers have a higher capacity to digest cell walls (van Wieren 1996) and aggregate more in nomadic herds (McNaughton 1984, Phillips 1983) when compared with the other functional large herbivore types. Large grazers seem more suitable to suppress tall herbs (‘roughage’) than the other functional types. Browsers are more selective, ingest more woody plants and live in smaller groups than grazers. The variable body size of large herbivores also has bearings on their defence strategy (‘flee, fight or hide’).

In apparent contrast to their adaptation to grasses, most species of wild cattle and spiral-horned antelopes are found in woodland habitats (Macdonald 2001). The last free-roaming Aurochs (*Bos primigenius*), the ancestor of domestic cattle (*Bos taurus*) lived in the Jaktorow Forest, Poland during the 15th and 16th century, where it consumed grasses during the summer, acorns in autumn and twigs in winter (Van Vuure 2001). Habitat use studies of domestic cattle also point to an optimal use of mosaic landscapes (Pratt *et al.* 1986; Putman 1986; Van Wieren 1988; WallisDeVries 1994).

Large grazers interact with other herbivores. They can facilitate smaller herbivores, which benefit from the high quality regrowth of lawn grasses caused through defoliation by the large grazer. Facilitation leads to association and succession (across the annual cycle) of herbivores (Bell 1970). By monopolising the regrowth, small herbivores can compete with their facilitator, even forcing it out (Edwards & Hollis 1982; Bokdam 1987; Vulink 2001; Menard *et al.* 2002). Large grazers may be helped in woodland by larger ‘bull-dozer’ herbivores such as elephants (Kortlandt 1984; Van Wijngaarden 1985). In temperate woodlands, the effects of browsers (e.g. moose and roe deer, Reimoser & Gossow 1996) and mixed feeders (deer, European bison) might favour the invasion of grasses and grazers.

GRAZED PLANTS

Plants have adapted to co-existence with large herbivores by a wide variety of strategies to reduce of the risks and to maximise the opportunities (advantages) during dispersal, establishment and during the established phase (Janzen & Martin 1982; Mc Naughton 1984; Rosenthal & Kotanen 1994; Briske 1996). Established plants may avoid defoliation by the size or the whole plant or the size of the leaves (too large or too small for the herbivore), by a short growing period (annuals) or by habitat (plants growing in inaccessible aquatic habitats, on rocks or steep slopes). Resistance (unpalatability) can be based on a low nutritional value (e.g. a high lignin content), secondary metabolites (e.g. polyphenolics, terpenes and alkaloïds), spines and other mechanical devices, or combinations of these traits (Van Genderen, Schoonhoven & Fuchs 1997; Bokdam, Cornelius & Krüsi 2001; Milchunas & Noy Meir 2002). Tolerance is by regrowth or regeneration. Perennial lawn grasses (e.g. *Deschampsia flexuosa*, *Agrostis spp*., *Poa trivialis*) tolerate defoliation and treading by regrowth, while annual herbs avoid defoliation by size and tolerate trampling by regeneration from seed. In case of extinct herbivores, characteristics may be explained by the 'ghosts of evolution past' (Janzen & Martin 1982; Barlow 2000; Howell, Kelly & Turnbull 2002).

Investment in defence competes with investment in growth or reproduction. The optimal defence hypothesis (Rhoades 1979) therefore claims that plants optimise their defence by maximising the benefit/cost ratio. 'Dual-purpose' devices are therefore profitable. They serve resource acquisition and defence. Lignin provides rigidity to stems, allowing elevated positions of leaves, but it also provides resistance against defoliation. Thorns on long shoots enable brambles and roses to climb, but they also protect them against large herbivores. The optimal defence hypothesis led to the Carbon/Nutrient Balance hypothesis (Bryant, Chapin & Klein 1983), which suggests that secondary anti-herbivore compounds will preferentially be synthesised from surplus resources that cannot be used for growth. In nitrogen-limited, low-productive sites, plants will use carbon surpluses to synthesise substances like polyphenolics (e.g. tannins) and terpenes. Plant species from shaded and nitrogen rich environments will use nitrogen surpluses for the synthesis of alkaloids (e.g. *Taxus* and *Buxus*) (Davidson 1993). Mechanical devices, based on photosynthesis products may dominate in intermediate conditions (Bokdam, Cornelius & Krüsi 2001). The inducible defence hypothesis claims that changing resource balances in the plant or the plant environment leads to changed investment in defence (Van Genderen, Schoonhoven & Fuch 1997; Mutikainen *et al.* 2000). It means that herbivores might affect the defence level of their food plants not only by defoliation but also by modifying their nutrient and light environment.

Sometimes, neighbours are decisive for survival. Resistant neighbours that provide associational resistance may protect palatable plants. Resistant plants may be defoliated when palatable neighbours providing associational palatability surround them (Huntly 1991; Olff *et al.*. 1999).

LARGE GRAZERS AND NUTRIENT CYCLING

The effects of grazing on the soil nutrient pools and nutrient cycling are complex and not well understood (Milchunas & Lauenroth 1993). Grazing means removal of nutrients, but this effect is at least partly compensated by returns in excreta. Grazing may also accelerate nutrient cycling by improving the mineralisation conditions through increases in soil temperature and through the mixing of litter with the mineral soil (Kemmers *et al.* 1997; Siepel & Van Wieren 1989). During the first years they have been introduced, large herbivores can excitate nutrient mineralisation through a temporary increase in the litter fall by trampling or defoliation (Kemmers 1996). The grazing optimisation theory suggests (over) compensation of removals by an increased primary production and litter fall and excretion (McNaughton 1983; De Mazancourt, Loreau & Abbadie 2000). Grazing can reduce the available nutrient pool not only by biomass removal, but also by shifts in the botanical composition from palatable, decomposable species to unpalatable, resistant species (Pastor *et al.* 1993). The latter group of species produces recalcitrant litter (Berendse 1990; Hobbie 1992; Grime *et al.* 1996; Pastor & Cohen 1997). Nutrients can escape from grazing systems by volatilisation of excreta N, leaching and erosion. By creating short lawns, grazing can reduce the interception of nutrients from the atmosphere and inundation water (Chapter 5).

LARGE GRAZERS AND SUCCESSIONAL VEGETATION MOSAICS

Cyclic vegetation succession is defined as a recurrent series of species or communities (‘phases’) with a specific sequence (Miles 1979). Shifting successional mosaics are composed of patches passing through the phases of the cycle in a de-synchronised way (Olff *et al.* 1999). The term ‘mosaic cycle’, coined by Remmert (1991), refers to the process and the pattern. The size and longevity of the mosaic patches depend on the size of the replaced plant and the size and type of the disturbance.

Grazing affects cyclic succession by acting as disturbance and by modifying the development in the gap. Large herbivores affect the plants directly by defoliation, treading and excretion. These influences also have indirect effects mediated by the modified plant environment (Huntly 1991; Jefferies, Klein & Shaver 1994; Bakker 1998; Olff *et al.* 1999). Grazing systems, especially self-organising ones can be very complex. Simplification requires selection of key processes and key factors. There is evidence that in temperate grazing systems with no influences from humans or fire, such key factors are large grazers and nutrients (Knapp; WallisDeVries & Van de Koppel 1998; Bakker 1998; Jefferies 1999).

Existing models of grazing systems which might be used to test the effects of grazing on cyclic vegetation succession often include effects of soil nutrients on vegetation, but they do not account for the feedback of grazing animals to nutrient availability (Coughenour 1993; Heil & Bobbink 1993; WallisDeVries & Van de Koppel 1998; Jorritsma *et al.* 1999; Van Oene, van Deursen & Berendse 1999; Kramer, Groen & Van Wieren in press). And if they do (e.g. Berendse 1985), they neglect redistribution, gaseous losses and reduction of atmospheric inputs as mechanisms.

Aim of the study and hypotheses

This thesis addresses several ecological questions:

1. Can large grazers act as driving force for successional cycles with nutrient-poor lawns as successional stage in the dry (upland) zones of the woodland domain?
2. What are the mechanisms by which large grazers drive these cycles?
3. What is the role of atmospheric nutrient inputs on these mechanisms and cycles?

I put forward the following hypotheses:

1. Large grazers can drive successional vegetation cycles with alternating later successional stages (e.g. woodland or ericoïd heath) and grass lawns.
2. These cycles are driven by
   - -creation of gaps in later successional stages by defoliation and treading;
   - -introduction of grass seeds into these gaps by dispersal in dung;
   - -depletion of the soil nutrient pool of grass lawns by biomass removal;
   - -induction of lawn colonisation by herbivore-resistant invaders;
   - -nutrient replenishment during the subsequent late-successional phase without grazing.
3. Because high nutrient inputs counteract lawn depletion, high atmospheric nutrient depositions reduce the effectiveness of large grazers as driving force for successional cycles.

Study area

The study was carried out in the nature conservation area ‘ The Wolfhezerheide’ (60 ha) (Natuurmonumenten 1996). This woodland-grassland- heathland mosaic on podzolic soils in fluvio-glacial sand is located in the Veluwe (The Netherlands) (Fig. 1). The vegetation mosaic was composed of approximately 19 ha forest, 30 ha of *Deschampsia flexuosa* grassland (also indicated as ‘grass heath’ or grass lawn), 3 ha *Molinia caerulea* grassland and 9 ha *Calluna vulgaris* heath. *Pinus sylvestris*, *Betula pendula* and *Quercus robur* dominated the woodland. From 1983 on, the area was year-round grazed by cattle (0.2 animal units ha^{-1}, 1 animal unit = 450 kg). Throughout the study period, one to three horses were allowed to graze in the area. Densities of roe deer *Capreolus capreolus* L. (2-4 km^{-2}) and rabbit *Oryctolagus cuniculus* L. (100 km^{-2}) were low. From 1984 on, a minor quantity (1-2 kg dry matter $animal^{-1}$ day^{-1}) of supplementary food (concentrates, hay or corn silage) was occasionally provided during late winter on a fixed site (0.1 ha). During the study period, the manager removed encroaching trees. The total nitrogen input by atmospheric deposition varied from 20 kg N in the short-grazed grassland to 60 kg in the woodland. For a more detailed description see Chapter 2.

Outline of the thesis

The changes in the botanical composition of grazed and ungrazed grassland and heathland communities over the first 10 years after the introduction of cattle grazing in 1983 are presented in **Chapter 2**. The results show that grazing generated dynamic grass-heather mosaics by gap formation in mature *Calluna* stands followed by grass invasion in these gaps, and by invasion of *Calluna* shrubs in short-clipped grass lawns. The invasion of *Calluna* and pioneer trees in grass lawns failed on nutrient-rich soils because of a higher grazing and browsing pressure. **Chapter 3** contains the results of the monitoring of successional replacements at the scale of plant individuals in the open grass-heather mosaics over 6 years. They show reciprocal transitions, complete heather-grass-heather cycles and important effects of browsing by heather beetles on gap formation and on the heather-grass cycle. The basic ideas underlying the Resource-mediated Successional Grazing Cycle and the potential role of alternating browsing and grazing as driving forces of cyclic succession are described in this chapter. The next chapters focus on the mechanisms behind the grazing effects previously described. They show the influences of the cattle by habitat use and diet selection and their consequences for the nutrient balance. The results of detailed 24 hour observations of the cattle over 2 years in **Chapter 4** reveal differential habitat use, which appeared to be a major determinant of lawn depletion. The results also show preferential defoliation of mid-seral trees and lawn grasses, and avoidance of lawn-invading early-seral (pioneer) trees and dwarf shrubs by the cattle. The preference for mid-seral trees points to a certain capacity of large grazers to browse and suppress saplings of shade-tolerant trees in the woodland understory. Habitat and diet selection during summer differed from that in winter, which has important bearings on the choice of the grazing season. **Chapter 5** analyses the net-offtake balances and the integrated nutrient balances for three nutrient species (N, P and K) for the whole area, for the successional habitats and for the excreta patches and excreta-free patches in the *Deschampsia* grass lawns. These results underpin the conclusions relating to lawn depletion and the capacity of cattle to compensate for atmospheric inputs. **Chapter 6** is a review of the forage quality of successional plants from wetland and upland areas during summer and winter season from grazed and ungrazed sites. It describes in broad outline the nutritional challenges faced by free ranging cattle in incomplete areas. The final tests of the ecological hypotheses are given in **Chapter 7.** Management implications are discussed in **Chapter 8**.

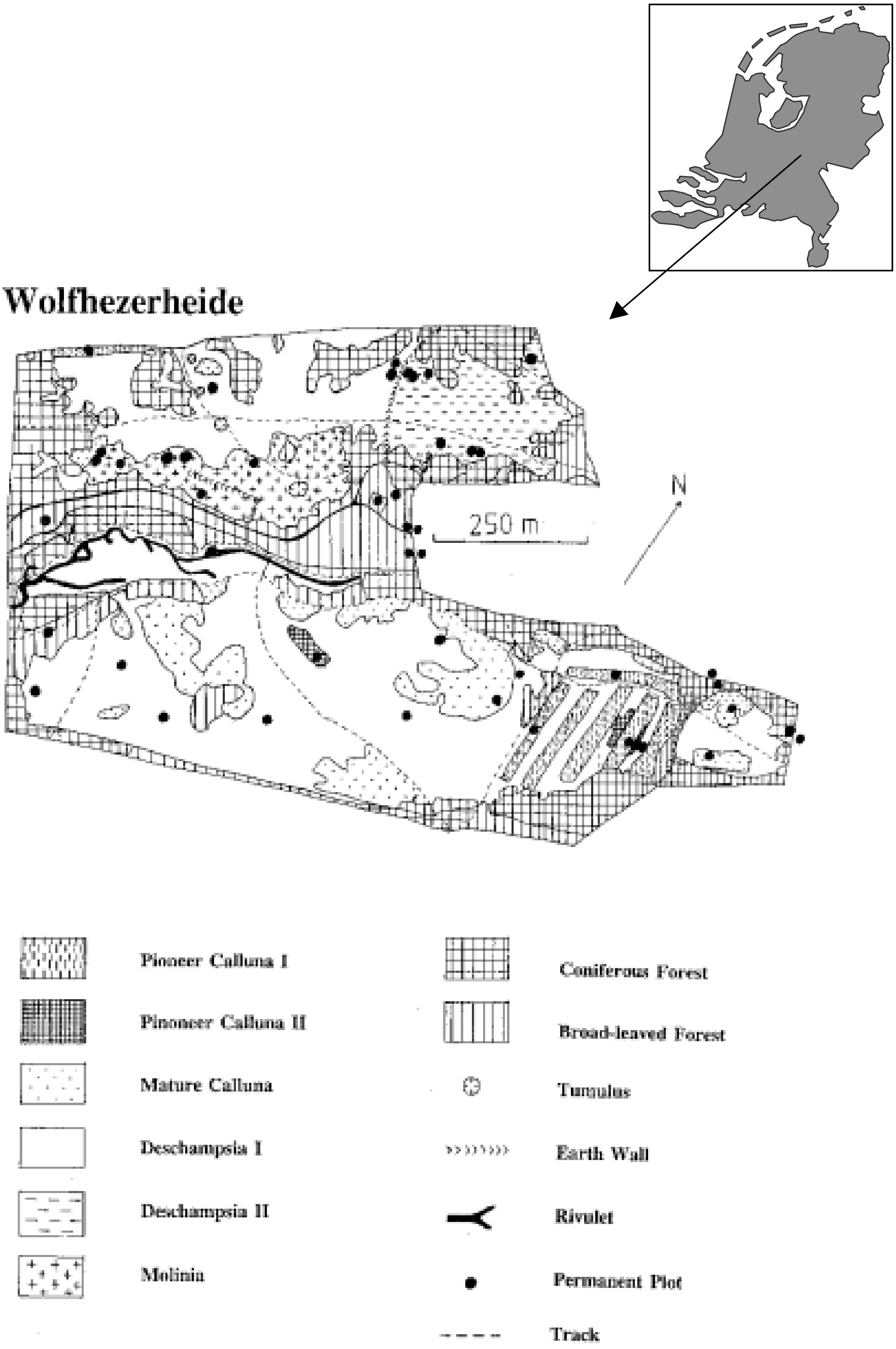

Figure 1 Geographical position and vegetation map of the study area.

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Chapter 2

Effects of grazing by free-ranging cattle on vegetation dynamics in a continental north-west European heathland

Jan Bokdam & J. Maurits Gleichman

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Grazing stimulated Calluna invasion in Deschampsia grassland on nutrient-poor podzolic soils. Wolfhezerheide, April 1983 (upper left), August 1994 (upper right) (photo Maurits Gleichman).

The cattle prevented Calluna and wood encroachment on nutrient-rich plaggen soils. Wolfhezerheide, February 1985 (lower left) and February 1995 (lower right) (photo Margaret Bokdam).

Effects of grazing by free-ranging cattle on vegetation dynamics in a continental north-west European heathland.

Jan Bokdam and J. Maurits Gleichman

Summary

Abandonment and eutrophication are major threats to traditional pastoral landscapes and their wildlife in Europe. Social and economical developments have rendered traditional pastoralism impracticable. More knowledge is needed about the effects of grazing with free-ranging herbivores, which is increasingly used as a substitute for the traditional herding system. We studied the effects of free-ranging cattle on the recovery of *Calluna* heather, tree encroachment and plant species richness in six habitats in a grass-rich Dutch heathland during a 10-year period. The habitats differed in soil fertility, initial heather-grass ratio and developmental stage of *Calluna*. Despite preferential grass defoliation, cattle grazing neither reduced grass cover in grass heath nor prevented grass invasion in heather. Grass invasion failed only in a nitrogen-poor turf-stripped *Calluna* heath. Grazing induced a substantial *Calluna* recovery in grass heaths on podzolic soils, but its recovery failed in grass heath on a phosphorus-rich medieval arable field. As a consequence, the grass/heather mosaics generated by free-ranging cattle were restricted to habitats of intermediate soil fertility. Grazing did not prevent encroachment by pine and birch. Removal by the site manager prevented conversion of 10 - 20 % of the open heathland to forest. During the first 5 years, grazing induced a significant increase in species richness in all habitats. During the second 5 years, species richness stabilised in grass heath and heather-grass mosaics and it declined in the pioneer *Calluna* heaths. We found indications of various nutrient-mediated grazing effects on the competitive balance between grass and woody pioneers. They suggest that nutrient-mediated feedback might be an important explanatory mechanism for the described vegetation mosaic cycling in heathlands. Free-ranging grazing did not remove the high atmospheric nutrient inputs of the whole area. Substantial amounts of nutrients were redistributed from the grass lawns to the forest. Free-ranging grazing combined with tree cutting appeared to be a suitable management regime for the maintenance of species-rich open heathlands with dynamic grass-heather mosaics. Without tree cutting, free ranging would have created dynamic tree-grass-heather mosaics in open heathland. Wood/pasture landscapes are fundamentally different from the open heather-dominated heathlands produced by the traditional sedentary farming system. Integrated grazing of heathland, nutrient-rich farmland and forests accelerates this change. Alternative grazing regimes are discussed.

Key-words: herbivory, biodiversity, *Calluna vulgaris*, *Deschampsia flexuosa*, mosaic cycling.

Introduction

Abandonment in conjunction with atmospheric eutrophication is a major threat to the high conservation values of European traditional pastoral landscapes (Gimingham 1972; Bignal & McCracken 1996; Osterman 1998; Webb 1998). Increased labour costs have rendered traditional herding systems economically unfeasible. Herding is increasingly substituted by more profitable free-ranging systems, using livestock or wild herbivores grazing over extensive areas. Little is known about the long-term effects of this replacement on the landscape structure and its conservation values. The design of effective grazing systems for conservation management requires predictive knowledge of the effects on biodiversity and the underlying ecological key processes and factors, e.g. vegetation succession and nutrient availability (McCracken & Bignal 1998). Long-term monitoring provides this information (Illius & Hodgson 1996; Piek 1998; Hester & Baillie 1998; Hester *et al.* 1999) and offers an opportunity for the validation of simulation models (WallisDeVries & Van de Koppel 1998). This paper assesses the effects of free-ranging cattle on the vegetation dynamics and species richness of open heathland vegetation in the Netherlands, with a special focus on nutrient-mediated mechanisms.

Inland heaths in continental NW Europe originated mainly by sedentary pastoralism and associated land use (De Smidt 1979; Pott & Hüppe 1991;Webb 1998). The daily return of the herd to the stable maximised the harvest of manure, which was essential for sustained sedentary arable farming on the nutrient-poor Pleistocene sandy sediments. After the 11th century, the manure was enriched with organic matter from ‘plaggen’ (sods) from the rangeland. This practice created ‘plaggen soils’, with a typical thick, black-brown, humic, nutrient-rich topsoil on the arable fields (Pape 1970).

Traditional sedentary herding declined in NW Europe at the beginning of the 20th century after the introduction of synthetic fertilisers and barbed wire fencing. The abandoned rangelands were transformed into fertilised farmland and forest. In the Netherlands, approximately 40 000 ha of lowland heath (5 % of the original 800 000 ha) escaped from this fate. The majority of this area is managed today as a nature reserve. An open landscape, low soil fertility and substantial heather cover are considered essential for the survival of many endangered species (Bal *et al.* 1995).

Until 1970, management was mainly restricted to the removal of encroaching trees. After 1960, the dominant heather species *Calluna vulgaris* L. and *Erica tetralix* L. were increasingly replaced by the perennial grass species *Deschampsia flexuosa* (L.)Trin. and *Molinia caerulea* (L.) Moench (Diemont 1996). Similar changes were reported from surrounding countries (De Blust & Schneiders 1989; Pott & Hüppe 1991; Bülow-Olsen 1980; Marrs, Hicks & Fuller 1986).

The grass invasion and the loss of biodiversity were attributed to increased nitrogen deposition and to abandonment by traditional livestock farming (including woodcutting, burning and turf stripping) (Diemont & Heil 1984; Anonymous 1988). Both changes were assumed to favour succession, eutrophication and acidification (Aerts 1993a,b; Bobbink, Hornung & Roelofs 1998; Bakker & Berendse 1999). Grass invasion was accelerated by a positive feedback between nitrogen availability and grass dominance (Berendse 1990, 1994). Turf stripping (removing grass, litter and nitrogen and exposing *Calluna* seeds) appeared to be an effective method for the restoration of heather dominance (Diemont & Linthorst Homan 1989; Heil & Aerts 1993). However, turf stripping has serious financial and biodiversity drawbacks (Anonymous 1988). This generated new interest in free-ranging grazing as a cheap alternative for sedentary herding and turf stripping.

The (re)introduction of grazing is hindered by lack of information on grazing management methods and their differential effects on lowland heath (Bullock & Pakeman 1997; Web 1998). Heathland grazing experiences refer mainly to British upland areas and to sheep and red deer *Cervus elaphus* L. (Gimingham 1972, 1992; Welch & Scot 1995; Hester & Baillie 1998). Moderate stocking rates are commonly recommended to prevent tree encroachment and to allow heather regeneration (Miles 1981; Gimingham 1992; Dolman & Land 1995). Overgrazing may damage the heather canopy, thus precipitating invasion by grass (Gimmingham 1992; MacDonald 1990; Hester & Baillie 1998). Undergrazing will lead to *Calluna* degeneration, shrub and tree encroachment and grass invasion (Miles 1981; Loiseau, Ignace & l'Homme 1987; Diemont 1996).

The evidence for grazing-induced heather recovery in grass heath is scarce and conflicting. Examples reported from the Netherlands with little or no heather recovery all derived from fertilised former heaths, grazed by sheep (Bakker *et al.* 1983), cattle (Wind 1980; Van den Bosch & Bakker 1990) and ponies (Van de Laar & Slim 1981). On former arable fields in the New Forest (southern England), *Calluna* and *Erica cinerea* recovery is seriously constraint by intensive defoliation and treading by cattle and ponies (J. Bokdam, personal observations). Successful heather re-establishment has been reported from unfertilised grass heaths, grazed by cattle (Jansen 1984; Van Wieren 1988; Bülow Olsen 1985; Buttenschøn & Buttenschøn 1982) and sheep or red deer (Bullock and Pakeman 1996; Welch & Scott 1995). The heather recovery in grazed unfertilised grass heaths conflicts with the sustained low heather cover in grazed wet upland grass heaths (Welch 1997) and with dramatic heather expansion after the relaxation of grazing pressure (Jones 1967; Ball 1974; Miles 1982; Anderson & Yalden 1981).

These different results of grazing in grass heaths might be attributed to differences in site (climate, management history, soil fertility, initial grass/heather ratio, heather and grass species, heather seed bank, developmental stage of heather), grazing regime (including wild herbivores) and spatio-temporal scale of observation. We hypothesised that free-ranging cattle might induce heather recovery, inhibit tree encroachment and increase vascular plant species richness in grass heath on nutrient poor soils.

The effects of grazing on vegetation tend to be explained primarily by visible, aboveground changes in the vegetation and litter structure due to defoliation and trampling. Tissue loss and modified light-profiles may be major causes of changes in establishment, growth, competitive success and longevity (Ritchie & Olff 1999). Short-term effects of dung and urine are also apparent. Long-term changes in the nutrient availability are less easy to assess (Milchunas & Lauenroth 1993). Nevertheless they might play a key role, especially in nutrient-poor environments (Berendse 1985; Jefferies, Klein & Shaver 1994; Jefferies 1999). Nutrients may affect plant production, nutritional quality, and resistance to herbivores and defoliation tolerance (Lambers, Chapin & Pons 1998; Milchunas, Lauenroth & Burke 1998). Herbivores move nutrients directly by ingestion, retention and excretion and indirectly by modifying mineralisation, dry deposition, leaching and erosion. They change pathways (De Mazancourt, Loreau & Abbadie 1998), flow rates (Pastor *et al.*. 1993) and pools (Milchunas & Lauenroth 1993). Positive nutrient-mediated feedback may stabilise or intensify the grazing pressure on grazing lawns (McNaughton 1984). Negative feedback may induce abandonment after declines in production and nutritional quality and an increase in the intrinsic resistance. A lower nutrient availability might induce higher lignin and tannin concentrations according to the carbon/nutrient ratio hypothesis (Bryant Chapin & Klein 1983; Hobbie 1992; Iason & Hester 1994). Neighbouring plants may provide associational resistance or associational palatability

(Huntley 1991; Olff *et al.* 1999; Hester *et al.* 1999).

It was hypothesised that the replacement of the traditional land use by free-ranging cattle would lead to the replacement of nutrient removal by nutrient redistribution. The induced soil fertility patterns and the free habitat choice might allow more feedback between vegetation development and use by the herbivores. This might lead to the unhindered emergence of shifting mosaics.

Material and methods

STUDY AREA AND HABITATS

The Wolfhezerheide nature reserve is situated on the Veluwe in the centre of the Netherlands, about 12 km east of Wageningen (51^o 47' N; 5^o 41'E), and owned by the Vereniging Natuurmonumenten. The grazed area (40 ha of open heathland and 20 ha of forest) covers podzolic soils in fluvio-glacial sand and cover sand, a small area of plaggen soils in cover sand, and some moist podzolic and peat soils on a valley bottom (Vrielink & Van de Hurk 1975). The plaggen soils belonged to the medieval settlement ‘Wolfheze’. Spanish soldiers destroyed it in 1585 and its arable fields were mainly used as pasture afterwards (Natuurmonumenten 1996). The annual atmospheric nutrient deposition (wet plus dry) in the open heathland accounted for about 40 kg nitrogen, 1.5 kg phosphorus and 5 kg potassium ha^{-1} (Erisman & Heij 1991). Until 1983, juvenile trees were removed from the open heathland and old heather was occasionally mown (Natuurmonumenten 1996). *Deschampsia* invasion started in about 1960 on the plaggen soil and spread between 1970 and 1980 to the dry podzolic soils (B.W.Jacobs, B. Jansen & W. Aandeweg, personal communication). Some parts of the remaining mature heather were turf-stripped in 1980, other parts were mown in 1982 (Table 1). In 1983, Deschampsia covered major parts of the open heathland. Small parts were covered by mature *Calluna*, pioneer *Calluna* and *Molinia* (Table 1).

In January 1983, the area was stocked with 17 Dutch-Friesian heifers, which from May 1983 were gradually replaced by suckling cows of various breeds. Annual stocking rates were maintained at an equivalent of approximately 0.2 animal units ha^{-1} (1 animal unit = 450 kg). Rates were c. 30 % higher in summer than in winter. During the whole study period one to three horses were allowed in the area. Late winter

Table 1. Main characteristics of 6 open heathland habitats at the Wolfhezerheide in 1983. * = established in 1984; [b] = affected by heather beetles in 1990-1991; [s] = affected by supplementary feeding.

Habitat	CI	CII	CIII	DI	DII	M
Initial vegetation (1983)	pioneer *Calluna*	pioneer *Calluna*	mature *Calluna*	Deschampsia (±tussocks)	*Deschampsia* (tussocks)	*Molinia* (tussocks)
Soil	Podzolic	podzolic	podzolic	podzolic	plaggen	podzolic, peat
Historical land use	Pasture	pasture	pasture	pasture	arable field and pasture	pasture
Previous management	turf-stripped in 1980	mown in 1982	-	-	-	-
Grazed plots, (serial numbers)	n = 3 (23, 24, 41*)	n = 2 (30, 35*[b])	n = 6 (22, 25, 26, 34*, 36*, 37*[b])	n = 7 (17, 27, 28[b] 29, 31[b], 32[b] 38*)	n = 3 (8, 11, 33[s])	n = 3 (12, 13, 14)
Ungrazed plots (serial numbers)	-	-	-	-	n = 2 (39*, 40*)	n = 2 (43*, 44*)

densities of roe deer *Capreolus capreolus* L.(2-4 km^{-2}) and rabbits *Oryctolagus cuniculus* L. (100 km^{-2}) were low. The latter value increased slightly during the study period (B.W. Jacobs, personal communication). From 1984 a minor quantity (1-2 kg dry matter animal^{-1}day^{-1}) of supplementary food (concentrates, hay or corn silage) was provided during late winter.

After 1983, the manager occasionally removed invading juvenile trees (1-2 m), mainly Scots pine *Pinus sylvestris* L. and silver birch *Betula pendula* Roth. No fires occurred. The winters of 1984-1985 and 1985-1986 were extremely cold and winter browning of *Calluna* (MacDonald 1990) was observed. Heather beetles *Lochmaea suturalis* Thomson damaged *Calluna* locally in 1991.

MEASUREMENTS

Habitats and treatments

In 1983, we located 21 5x5 m plots randomly in six habitat types in the grazed open heathland (Table 1). The habitats differed in soil, land use history, previous management and initial vegetation. In April 1984, 7 grazed plots and 4 ungrazed plots were added (Table 1). The ungrazed exclosures (ca 8x 8 m; mesh-size 5x5 cm) were constructed in the most heavily grass-dominated *Deschampsia* heath on plaggen soil and *Molinia* heath.

Plant cover and Calluna density.

Plant cover was recorded annually in August-September, using an extended point quadrat method (Goldsmith & Harrison 1976). Pins (diameter 2.5 mm) were lowered through 10 vertical holes at 10-cm intervals in a horizontal, plastic tube (diameter 5 cm, length 100 cm, 40 cm above ground level). The tube was located randomly in each plot 10 times, providing 100 pins. Hits for vascular plants (living parts only) were noted. Mosses and lichens were recorded as a group. If a species was hit more than once by the same pin, it was recorded only once. Several species per pin indicated overlap. The number of hits per species by 100 pins reflected the species cover (0-100 %). Second and third samples of 100 pins were added until the average cover remained constant (< 5 % change to the average by adding a new series). The cover of species not hit by the pins (i.e. species with a low cover or with foliage above 40 cm height) was visually estimated. Cover measurements in the ungrazed *Molinia* heath started in 1987. *Calluna* individuals were counted in the grass-heaths to assess the re-establishment rate.

Soil fertility

The soil fertility of the dry habitats was sampled during the winter 1987-1988. Samples from the A_0 (ectorganic layer, including litter, fermented horizon and humic horizon) were taken at 50 random locations within 5 m around each plot. At each location, thickness was measured on the 4 sides of a 1-dm^2 sod. The A_0 material was transported in plastic bags to the laboratory for chemical analysis. The thickness of the A_m horizon (grey-blackish mineral horizon between the A_0 and the brownish B horizon) was measured using an Edelman auger (diameter 7 cm) at eight locations around each plot. Volume samples from the A_{10} (upper 10 cm of the A_m) and from the total A_m were collected at eight locations around each plot with a gouge auger (diameter 30 mm). Samples were mixed per plot. Laboratory treatments followed Houba *et al.*. (1986). Sub-samples of the A_0 were dried at 70 ^{o}C for 7 days, grounded and sieved. Mineral soil samples were only sieved (mesh size 2mm). For all horizons, organic matter content was measured as loss-on-ignition. The pH was assessed after adding 1 M KCl-solution to the soil. Total N and P concentrations (spectro-photometrically) and total K concentration (flame-photometrically) in the soil were measured after digestion in H_2SO_4-salicylic acid-H_2O_2 and selenium. Extractable $NH4^+$-N, $NO3^-$-N, P and K in the topsoil ($A_0 + A_{10}$) were measured after digestion in 0.01 M $CaCl_2$, using a Technicon Auto-analyzer (Skalar, Breda, The Netherlands).

Calluna seed bank

To explain different rates of *Calluna* recovery, we assessed the *Calluna* seed bank in the A_0 and A_5 (top 5 cm of the A_m) in grass heath on podzolic soil (3 plots) and plaggen soil (2 plots) in June 1991. Two hundred soil samples were taken with a gouge auger (diameter 30 mm) within a 5-m distance around each plot. The A_0 (without unfermented litter) and the A_5 material were placed on perforated dishes. The dish area per plot and horizon was 1414 cm^2 and the resulting thickness of the soil material on the dishes was 1 cm for the A_0-material and 5 cm for the A_5 material. The dishes were placed in full daylight in a non-heated, ventilated greenhouse. They were kept moist and cool (< 35 °C) by daily sprinkling for 130 days (28 June – 4 November 1991). Emerging seedlings were removed with minimal soil disturbance. Their number was expressed per m^2 dish-area, approximating the density of viable seeds per unit exposed area under field conditions. Our method did not yield an estimate of the seed bank per unit volume, since the material was not stirred, dried and remoistened during the germination period (Hester, Gimingham & Miles 1991; Bruggink 1993).

Plant height

The defoliation pressure on grass and heather in the *Deschampsia* heaths on podzolic and plaggen soil was approximated by measuring the plant height of *Deschampsia* (20 random locations per plot) and *Calluna* (20 individuals or all available individuals). A perforated foam disc (diameter 10 cm; weight 8 g) was slowly lowered down a vertical measuring rod on to the plant canopy.

DATA ANALYSIS

Calluna died in some plots in 1991-1992 due to a heather beetle outbreak. This necessitated separation of affected and unaffected plots (Table 1). One of the plots in the grazed *Deschampsia* heath on plaggen soil was omitted because vegetation and soil had been severely affected by trampling and excretion during supplementary feeding at the site (Table1).

The measured data were tested for normality using a One -Sample Kolmogorov-Smirnov Test (Norusis 1993). Viable seed numbers were log-transformed. The seed bank of the A_0 as a percentage of the total seed bank was arcsine-transformed. Differences between habitats or treatments were tested using two-sample t-tests or ANOVA followed by Student-Newman-Keuls multiple comparisons. Homogeneity of variance was checked using Levene's test. Differences between time series of grazed habitats were tested using ANOVA with year as covariate. Grazing-year interactions were detected by comparing two test designs. When two-way or higher order interactions were absent, main effects were tested with a one-way ANOVA with year as covariate.

Results

SOIL FERTILITY

All habitats were very acid (Table 2). The extreme soil fertility values occurred in the pioneer *Calluna* heath on podzolic soil and in the *Deschampsia* heath on plaggen soil (Table 2). The A_0 thickness and organic matter pool were significantly lower ($P < 0.05$) in the two pioneer *Calluna* heaths than in the other habitats. The extractable nitrogen was also lower, but only significantly so ($P < 0.05$) in the turf-stripped *Calluna* heath. The grazed *Deschampsia* heath on plaggen soil differed significantly ($P < 0.05$) from the one on podzolic soil in its thicker A_m layer, higher A_0 phosphorus pool and higher extractable phosphorus. The latter value was also significantly higher in the grazed than in the ungrazed treatment ($P < 0.05$).

HEATHER AND GRASS COVER

The cover of *Calluna* and *Deschampsia* displayed different trends in the four grazed habitats on podzolic soil (Fig. 1a-d; habitat x year effect, $P < 0.001$, Table 3). In the turf-stripped pioneer *Calluna* heath (Fig. 1a) *Calluna* cover increased during the study period to nearly 90 %. This contrasted with the persistently low *Deschampsia* cover. In the mown pioneer *Calluna* heath, cover of both species increased (Fig. 1b). In the mature *Calluna* heath (Fig. 1c), *Calluna* declined initially, particularly between 1985 and 1986, but it recovered afterwards. Similar declines occurred between 1985 and 1986 in the other *Calluna* habitats. *Calluna* also recovered after the crash due to heather beetles in 1991-1992 (Fig. 1b-d). *Deschampsia* cover increased or stabilised at a high level in all *Calluna* habitats, except in the turf-stripped pioneer *Calluna* heath.

The effect of grazing on the recovery of *Calluna* differed significantly between the *Deschampsia* heath on plaggen soil and the *Molinia* heath (Fig. 1e-h; habitat x grazing interaction, $P < 0.01$, Table 4). *Calluna* recovery failed in the grazed *Deschampsia* heath on plaggen soil (Fig. 1e). In the *Molinia* heath, cover reached 20 % in 1993 (Fig. 1g). The *Deschampsia* cover in the ungrazed *Deschampsia* heath on plaggen soil declined after the tree invasion (Fig. 1f).

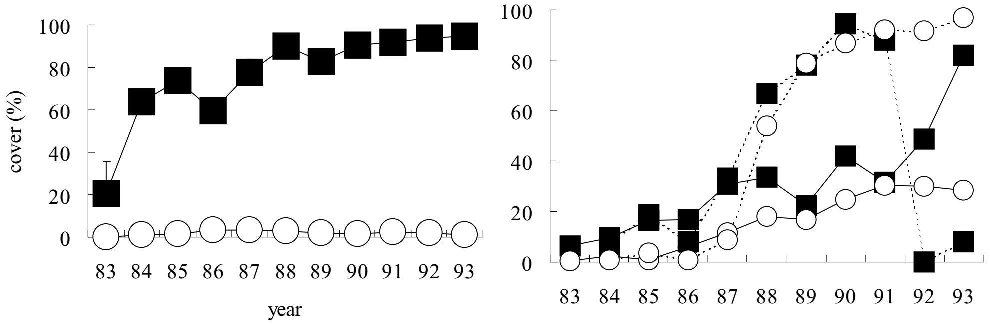
No other herbaceous species became dominant at the habitat scale. On individual plots, the non-nitrophilous species *Carex pilulifera* L., *Galium saxatile* L. and *Rumex acetosella* L. occasionally reached a 10 % cover level.

Table 2. Soil characteristics of 5 grazed and 1 ungrazed dry heathland site at the Wolfhezerheide (for site descriptions: see Table 1 and text).Values in a row with a same letter are not significantly different (One-Way ANOVA and Student-Newman-Keuls Test, $P<0.05$). A_o = Ectorganic horizon (L+F+H); A_m = humus-rich mineral horizon; A_{10} = upper 10 cm of the A_m. Extractable nutrient values concern the topsoil ($A_o + A_{10}$).

SITES (n)	Grazed turf-stripped pioneer *Calluna* heath (2)	Grazed mown pioneer*Calluna* heath (2)	Grazed mature *Calluna* heath (5)	Grazed *Deschampsia* heath (7)	Grazed *Deschampsia* heath (2)	Ungrazed *Deschampsia* Heath(2)
Soil type	podzol	podzol	podzol	podzol	plaggen	plaggen
Thickness A_o(cm)	0.10a	0.33a	1.70b	1.93b	1.97b	3.07c
Thickness A_m (cm)	31.7ac	26.5abc	30.0a	27.3a	55.5c	54.0bc
Organic matter A_o (ton ha)	-	3.5a	34.8b	33.7b	37.8b	40.2b
Organic matter A_{10} (ton.ha^{-1})	111.2b	106.4ab	94.0ab	89.6ab	82.3ab	74.2a
Organic matter A_m (ton.ha^{-1})	219.1	194.2	211.9	210.1	323.0	354.6
pH KCl A_o	-	3.09	3.00	3.06	3.14	3.14
pH KCl A_{10}	3.40ab	3.32ab	3.39b	3.40b	3.11ab	3.04a
Nitrogen pool A_o (ton.ha^{-1})	-	-	0.75	0.88	1.01	1.05
Nitrogen pool A_{10} (ton.ha^{-1})	2.27	2.28	2.04	1.99	2.01	1.90
Nitrogen pool A_m (ton.ha^{-1})	4.91	3.78	4.84	4.68	7.51	7.69
Phosphorus pool A_o (ton.ha^{-1})	-	-	0.04ab	0.04a	0.06b	0.03ab
Phosphorus pool A_{10} (ton.ha^{-1})	0.41	0.26	0.34	0.33	0.45	0.37
Phosphorus pool A_m (ton.ha^{-1})	0.87	0.55	1.01	0.93	2.36	1.94
Potassium pool A_o (ton.ha^{-1})	-	-	0.07	0.09	0.10	0.07
Potassium pool A_{10} (ton.ha^{-1})	0.99	0.88	1.01	0.92	0.93	0.92
Potassium pool A_m (ton.ha^{-1})	2.87	2.41	3.23	2.80	4.88	4.29
Extractable Nitrogen (kg.ha^{-1})	3.2a	12.8ab	36.0c	26.2bc	33.1bc	18.9abc
Extractable Phosphorus (kg.ha^{-1})	0.39a	0.46a	5.27a	3.49a	16.55b	5.38a
Extractable Potassium (kg.ha^{-1})	24.7a	24.6a	74.3b	49.8ab	58.3ab	83.3b

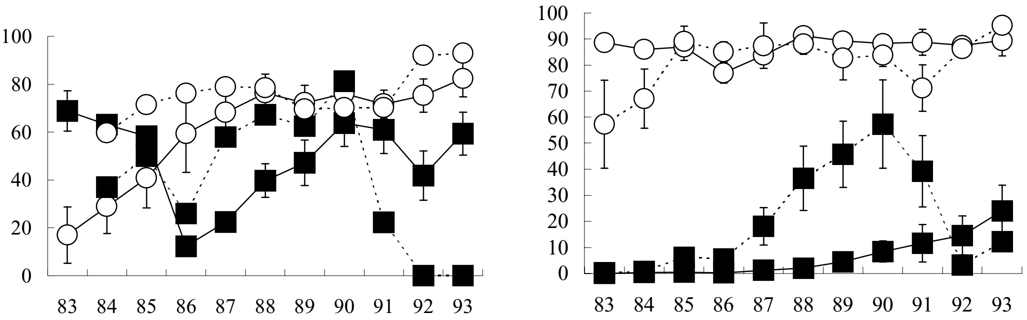
a. Grazed turf-stripped pioneer *Calluna* heath on podzolic soil

b. Grazed mown pioneer *Calluna* heath on podzolic soil



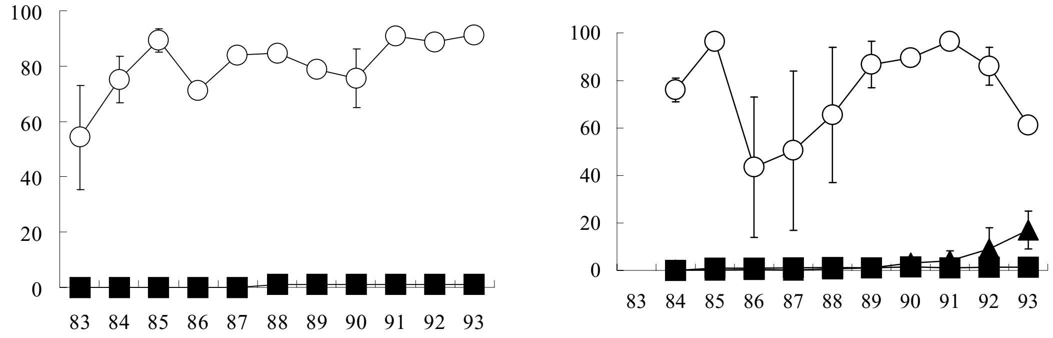
c. Grazed mature *Calluna* heath on podzolic soil

d. Grazed *Deschampsia* heath on podzolic soil



e. Grazed *Deschampsia* heath on plaggen soil

f. Ungrazed *Deschampsia* heath on plaggen soil



g. Grazed *Molinia* heath on podzolic/peat soil

h. Ungrazed *Molinia* heath on podzolic/peat soil

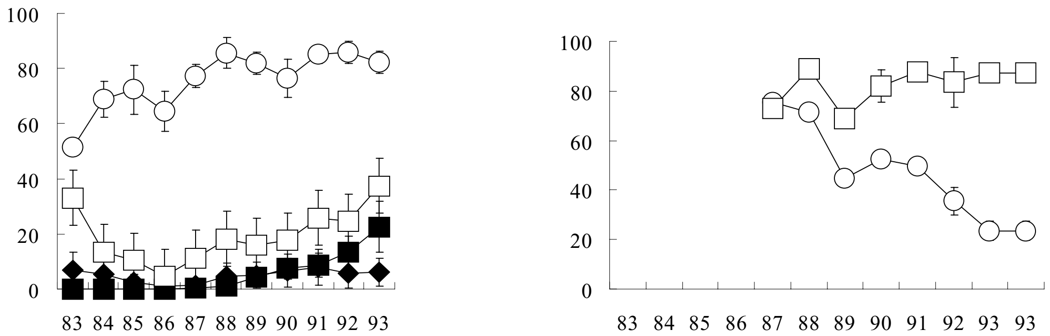


Figure 1. Cover change of potential dominant species in six heathland habitats (a-d) Grazed pioneer and mature *Calluna* and *Deschampsia* heaths on podzolic soils. (e-h) Grazed and ungrazed *Deschampsia* heath on plaggen soil and *Molinia* heath on podzolic/peat soil. Vertical bars indicate SE. ■ = *Calluna;* ◆ = *Erica*; ▲ = shrubs and trees; O = *Deschampsia*; = *Molinia*; —— = plots not affected by heather beetles; ------- = plots affected by heather beetles.

Table 3. F-values and significance levels of main effects of habitat, year and habitat x year on the cover of *Deschampsia* and *Calluna* and on the species richness in four grazed *Calluna* habitats on podzolic soils during the period 1983-1993,
(ANOVA, *** $P < 0.001$).

Response variable	d.f.	*Deschampsia* cover	*Calluna* cover	Species richness
Source of variation:				
Habitat	3	12.6^{***}	15.9^{***}	9.0^{***}
Year	1	24.8^{***}	82.5^{***}	14.0^{***}
Habitat x year	3	13.1^{***}	16.6^{***}	9.0^{***}

CALLUNA DENSITY IN GRASS HEATHS

The measured density in the grass heaths reflected the net establishment success, since plots did not contain juveniles in 1983. Between 1983 and 1990 density increased in the *Deschampsia* heath on podzolic soils significantly more than on plaggen soils (Fig. 2; ANOVA, habitat x year, $F = 4.34$; $P < 0.05$). After 1990 the rates were no longer significantly different. *Calluna* density in the grazed *Molinia* heath was also higher than in the *Deschampsia* heath on plaggen soil (ANOVA, habitat x grazing effect;
$F = 10.5$, $P < 0.01$). No significant difference occurred between the grazed and ungrazed *Deschampsia* heath on plaggen soil. In the ungrazed *Deschampsia* heath one seedling emerged, in the ungrazed *Molinia* heath none. *Calluna* density (Fig. 2) and *Calluna* cover (Fig. 1 d,e,g) were significantly correlated in 1993 ($R^2 = 0.91$).

SHRUBS AND TREES

Young trees (see the Appendix) established in the grazed treatments, but their cover remained low (<1 %), partly because of browsing and partly as a result of removal by the site manager (see the Discussion). The ungrazed exclosures displayed different results. In the ungrazed *Deschampsia* heath on plaggen soil trees started to invade after the winter of 1985-1986 (Fig. 1f). In 1993 the mean cover had reached 20 %. Tree seedlings were occasionally observed in the ungrazed *Molinia*, but they did not survive. Statistical tests were not carried out for tree cover, since the values in the grazed treatments were affected by tree removal.

The frequency of shrub and tree species remained rather constant; only birch and bramble *Rubus fruticosus* L. increased substantially (see the Appendix).

CALLUNA SEED BANK

The number of emerged seedlings from the A_0 of the grass heath on podzolic soil (1324 ± 1039 m^{-2}) and plaggen soil (96 ± 76m^{-2}) differed remarkably, but the difference was not statistically significant ($P = 0.078$; Fig. 3) due to the low number of replicates. The differences between the A_1-seed banks were less distinct: 175 ± 145 m^{-2} for podzolic soil and 89 ± 86 m^{-2} for plaggen soil (Fig. 3).

Linear regression yielded a significant relationship between the A_o-seed bank and the *Calluna* density in 1990 ($R^2 = 0.96$; n = 5; $P<0.01$; Fig. 4) and between the A_o-seed bank and the *Calluna* cover in 1990 ($R^2 = 0.95$; n = 5; $P<0.01$).

PLANT HEIGHT OF *DESCHAMPSIA* AND *CALLUNA*

Between 1991 and 1993, the average plant heights of *Deschampsia* and *Calluna* in the *Deschampsia* lawns were significantly lower on the plaggen soil than on the podzolic soil (Fig. 5; *Deschampsia*: F = 8.0, $P < 0.01$; *Calluna* F = 11.3, $P < 0.01$)

SPECIES RICHNESS

After an initial rise during the first 5 years in all grazed habitats, species richness declined during the last 5 years in the 2 pioneer *Calluna* habitats (Fig. 6a). Species richness more or less stabilised in the mature *Calluna* heath and in the other habitats (Fig. 6a,b). The effect of grazing was most clearly shown by comparing the grazed and ungrazed treatments of the *Deschampsia* heath on plaggen soils and the *Molinia* heath (Fig. 6b; Table 4, grazing x year effect, $P < 0.001$). Species richness increased in the grazed treatments from 3.0 to 8.0 (*Deschampsia* heath) and from 3.7 to 9.3 (*Molinia* heath).

It may be argued that the increase in species richness by grazing is mainly due to the introduction of dung and urine. The plant species in the plots were classified as nitrophilous species ($I_N >= 6$) and non-nitrophilous heathland species ($I_N < 6$) according to their Ellenberg's nitrogen indication value I_N ($1 =< I_N >= 9$; see the Appendix, (Ellenberg 1976). The group of non-nitrophilous herbs displayed the strongest increase in species richness, nitrophilous herbs the smallest (Fig. 7a,b). None of the 11 nitrophilous species increased by more than 10 % between 1983 and 1993. Amongst the 19 non-nitrophilous heathland species, 10 species increased more than 10 %, e.g. bramble *Rubus fruticosus* L. (0 - 48 %),

Table 4. F-values and significance levels of main effects of habitat, grazing and year and interactions on the cover of *Deschampsia*, *Molinia*, *Calluna* and on species richness in grazed and ungrazed *Deschampsia* heaths on plaggen soil and *Molinia* heaths on podzolic/peat soil, 1983-1993. (ANOVA * = $P<0.05$; ** = $P<0.01$ *** = $P<0.001$; NS=Not Significant).

Response variable	d.f.	*Deschampsia* cover	*Molinia* cover	*Calluna* cover	Species richness
Source of variation :		Decimaal plant			
Habitat	1	10.0^{**}	2.0^{NS}	6.7*	0.4^{NS}
Grazing	1	10.8^{**}	0.4^{NS}	6.9^{NS}	23.4^{***}
Year	1	1.1^{NS}	3.7^{NS}	8.1^{**}	29.5^{***}
Habitat x grazing	1	7.0^{*}	0.4^{NS}	7.2^{**}	0.9^{NS}
Rest Design 1: Habitat x year + grazing x year + habitat x grazing x year	3	5.4^{*}	2.7^{*}	11.7^{***}	10.2^{***}
Rest Design 2: habitat x year + habitat x grazing x year	2	2.1^{NS}	4.0^{*}	12.9^{***}	1.5^{NS}

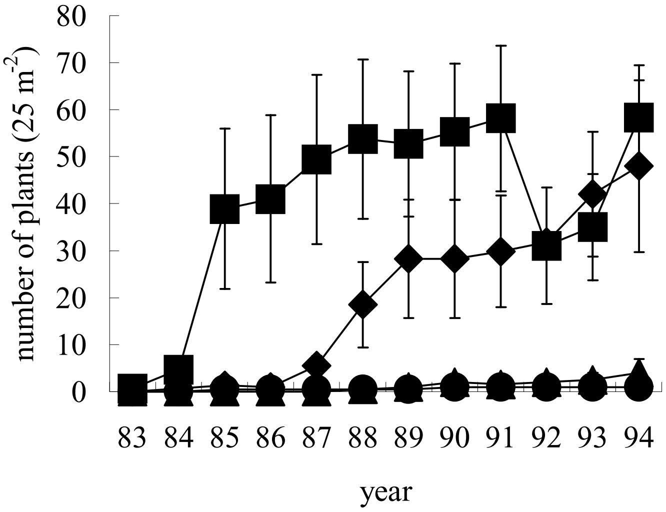


Figure 2. Re-establishment of *Calluna* from seed in grass heaths after the introduction of free-ranging cattle at the Wofhezerheide. ■ = grazed *Deschampia* heath on podzolic soil; ▲ = grazed *Deschampsia* heath on plaggen soil; ◆ = grazed *Molinia* heath on podzolic/peat soil; ● = ungrazed *Deschampsia* heath on plaggen soil. In ungrazed *Molinia* heath, no *Calluna* established. Vertical bars indicate SE.

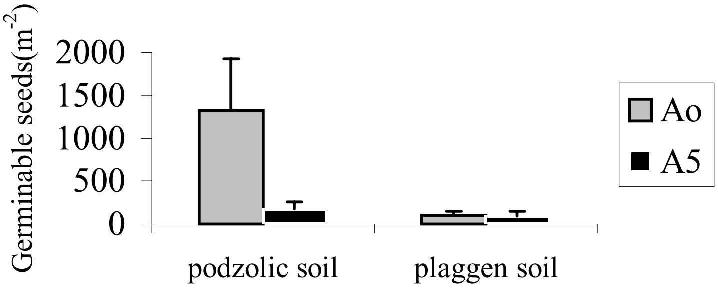


Figure 3. Seed banks of *Calluna* in the A_o and A_5 in *Deschampsia* heaths on podzolic and plaggen soils at the Wolfhezerheide (1990). Vertical bars indicate SE.

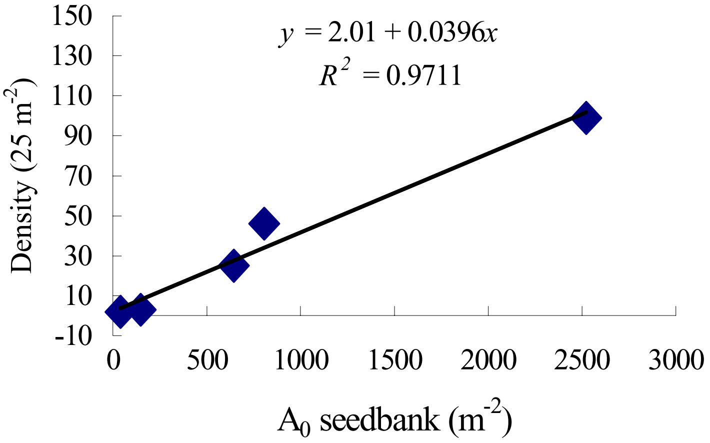


Figure 4. Linear regression of *Calluna* density after 7 years of grazing (1990) on *Calluna* seed bank in the A_0 in *Deschampsia* heaths. $y = 2.01 + 0.040x$; $R^2 = 0.97$; $P < 0.01$.

birch (29-71%) and buckthorn *Frangula alnus* Mill. (29-41%). No species disappeared from the plots (see the Appendix). Some rare species established after 1983 outside the plots (e.g. *Lycopodium clavatum* L. *and Ophioglossum vulgatum* L.).

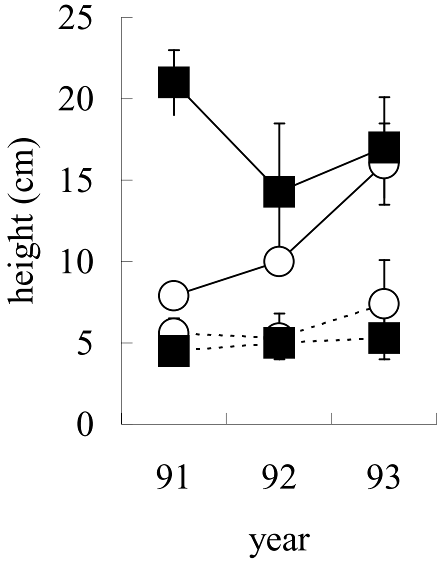


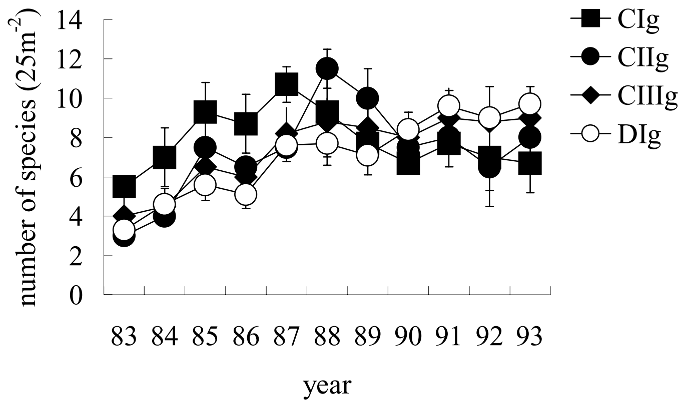
Figure 5. Plant height in late summer of *Deschampsia* (O) and *Calluna* (■) in grazed *Deschampsia* heaths on podzolic soil (——) and plaggen soil (------). Vertical bars indicate SE.

Discussion

HABITAT USE BY CATTLE

The cattle used habitats and dominant species in an uneven fashion. Timebudget studies and records of numbers of bites over 24-h periods between 1983 and 1985 (Chapter 4) showed that the cattle grazed grass preferentially during the growing season. Between November and March, *Calluna* was added to their grass diet, reaching a maximum of 50 % of all bites in January. The annual foraging pressure, based on foraging time and expressed in animal units ha^{-1}, was higher in *Deschampsia* heath (0.26) than in *Calluna* heath (0.23), *Molinia* heath (0.13) and Forest (0.10). Forest was intensively used as a shelter during the night.

a: grazed *Calluna* and *Deschampsia* heaths on podzolic soils



b: grazed and ungrazed *Deschampsia* on plaggen soil and *Molinia* heath

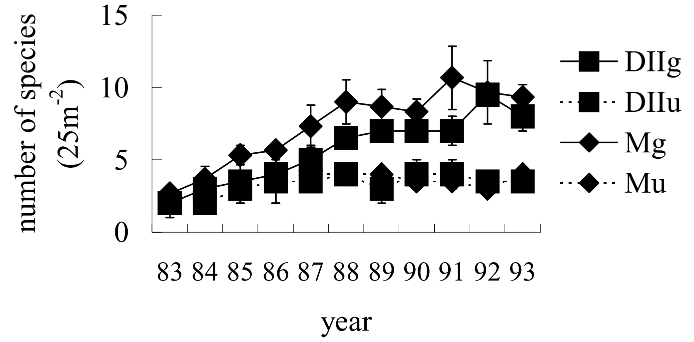


Figure 6. (a) Changes in the (vascular plant) species richness of grazed *Calluna* and *Deschampsia* heaths on podzolic soil the Wolfhezerheide. ■ = turf-stripped pioneer *Calluna* heath (CIg); ●= mown pioneer *Calluna* heath (CIIg); ◆ = mature *Calluna* heath (CIIIg); O = *Deschampsia* heath on podzolic soil (DIg). Vertical bars indicate SE.

(b) Changes in the (vascular plant) species richness of grazed (———) and ungrazed (--------) *Deschampsia* heath on plaggen soil (DII) (■) and *Molinia* heath on podzolic/peat soil (M) (◆). Vertical bars indicate SE.

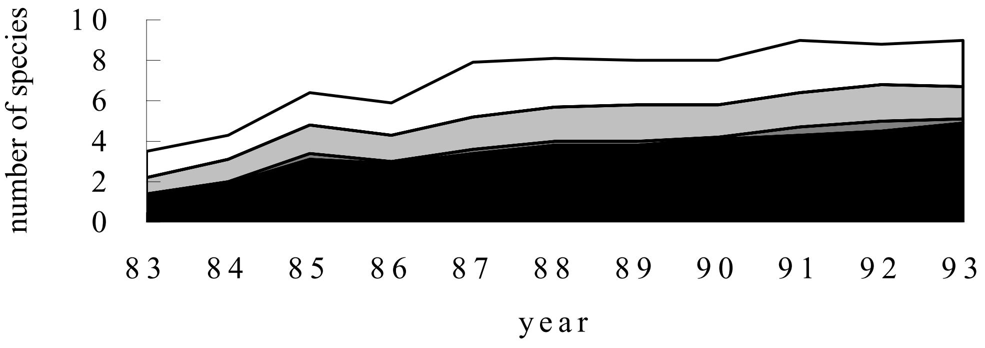
SOIL FERTILITY

Soil fertility displayed a gradient across the four habitats on podzolic soils and significant differences were found between the podzolic and plaggen soils. The increase in the amount of organic matter in the topsoil and extractable nitrogen across the podzolic soils was caused by the mechanical removal before the start of the grazing. The low amount of organic matter in the A_0 of the mown pioneer *Calluna* heath may have been due to the interrupted litter production or to litter removal by wind or run-off.

The different thickness of the A_m and extractable phosphorus level (grazed treatments only) between *Deschampsia* heaths on podzolic and plaggen soil were explained as long-lasting effects of differential use as common pasture and arable field respectively during the middle ages.

The significantly higher extractable phosphorus and (not significantly) higher extractable nitrogen in the grazed *Deschampsia* heath on plaggen soil as compared to

a. Average of 17 plots (25 m^2)



b. Species pool of 17 lumped plots (425 m^2)

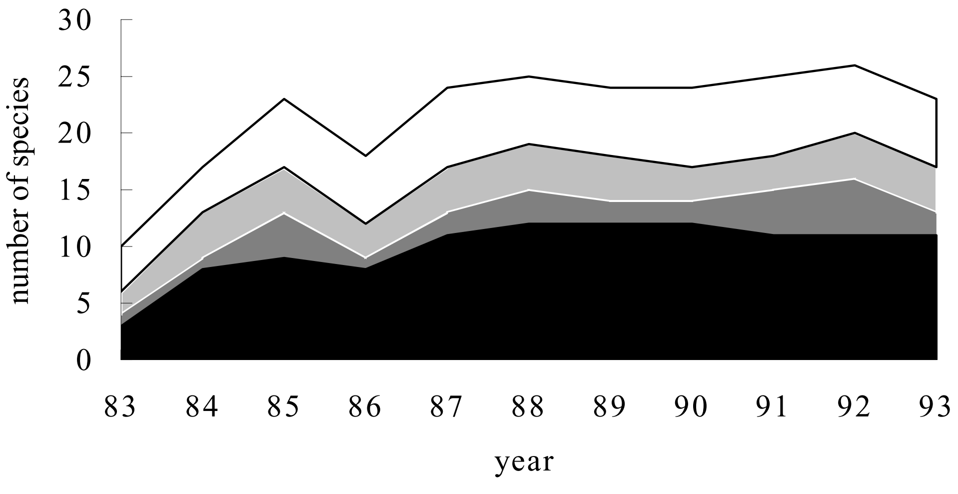


Figure 7: Changes in the (vascular plant) species richness per ecological group in open heathland after the introduction of free-ranging cattle: black = non-nitrophilous herbs; dark grey = nitrophilous herbs; light grey = dwarf shrubs; white = shrubs and trees. For ecological groups: see text and the Appendix. (a) Average of 17 plots (25 m^2); (b) species pool of 17 lumped plots (425 m^2).

the ungrazed treatment points to accelerated decomposition and mineralisation by grazing. Similar effects were found by Kemmers *et al.* (1996) in *Deschampsia* swards in pine forest.

TRANSITIONS BETWEEN GRASS AND HEATHER

Grazing did not stop the ongoing invasion of *Deschampsia* in the non-turf-stripped *Calluna* habitats (Fig. 1b,c). The failed grass invasion in the turf-stripped pioneer *Calluna* heath (Fig. 1a) was attributed to nitrogen deficiency. Ageing and accumulation of litter and nitrogen may allow *Deschampsia* to invade in the future also in gaps in this habitat. Grazing may have accelerated the grass invasion in the mature *Calluna* (Fig. 1c). The mature and degenerating stages of *Calluna* are less tolerant for defoliation and treading than the pioneer and building stages (MacDonald 1990). The prostrate growth forms, developed by layering and grazing (MacDonald *et al.* 1995) also seemed tolerant for treading.

In the grazed grass heaths, *Deschampsia* cover did not decline despite intensive defoliation (Fig. 1d,e,g). This indicates to a high tolerance of defoliation. Treading, urine scorching, and digging by rabbits and dung beetles created small gaps in the grass sward. The only declines of *Deschampsia* cover by defoliation occurred in the *Deschampsia* heath on plaggen soil, before the first measurement. Grazing of the tussocks exposed the bare inter tussock areas, which were colonised by the grass after 1983 (Fig. 1e,g). Competition by taller *Molinia* (Fig. 1h) and trees (Fig. 1f) caused all other declines of Deschampsia cover. Until 1993, *Deschampsia* was only locally suppressed by expanding *Calluna* (Bokdam 1996).

Grazing induced a significant recovery of *Calluna* in the grass heaths on podzolic and peat soils (Fig. 1d,g), but not on plaggen soils. Key mechanisms were a successful establishment from the seed bank (Fig. 5), seedling survival and expansion. Recovery included 4 phases. (i) During the lawn development phase, grazing changed the grass tussocks into a lawn by defoliation and trampling. (ii) In the heather establishment phase, the first seedlings emerged in litter gaps. They probably originated from the seed bank. During later years recruitment was also found on compacted litter and in open lawn patches. These seedlings may have derived from seed rain. Rabbits heavily browsed *Calluna* seedlings and juveniles in localised areas. (iii) During the building phase, *Calluna* plants expanded in height and width (Fig. 1a-d), despite substantial browsing by cattle and rabbits. Browsing kept the plants more or less in a prostrate or creeping growth form with adventitious roots (MacDonald *et al.*

1995). Browsing and treading may have stimulated layering and the development of adventitious roots in the moss-rich grass turf. It may have favoured also a dense canopy and increased the ability of *Calluna* to 'walk' over short-cropped grass lawns. Unbrowsed *Calluna* plants displayed the well-known classical developmental stages (Watt 1955). Layering and vegetative regeneration may have had a positive effect on the longevity of *Calluna*. Rabbits created flat, shaved *Calluna* cushions, described earlier by Welch & Kemp (1973). (iv) In the final mosaic phase, which became apparent after 5 years of grazing, *Calluna* shrubs coexisted with grass in a dynamic mosaic (Bokdam 1996).

The failure of *Calluna* to colonise *Deschampsia* lawns on plaggen soil (Fig. 1e,f, 2) was attributed to inhibition of germination, caused by the thick grass-rich A_0 (Table 2) and to intensive browsing of the young plants (Fig. 1e, 2 and 5). The inhibitory effect of the tough grass litter on the plaggen soil became obvious after a simple additional turf-stripping experiment. In two plots, each of 20 m^2, the turf was removed in 1986. The turf stripping triggered the germination of *Calluna* and resulted in a mean *Calluna* cover of 50 % by 1993. The lower plant height of *Deschampsia* and *Calluna* (Fig. 5) and the cushion form of *Calluna* confirmed the more intensive defoliation by cattle and rabbits on the nutrient-rich plaggen soil. Our findings agree with the higher grazing pressure by sheep and red deer on heather plants near grass patches (Hester & Baillie 1998; Palmer & Hester 2000). Impoverishment of the seed bank was not judged to be of great importance, since the low germinable seed density (96 m^{-2} from the A_0) did not prevent a successful recovery in the turf-stripped plots.

TREE ENCROACHMENT

Cattle browsed and suppressed all tree species (see the Appendix) except the unpalatable pine and silver birch. To maintain open heathland, the site manager had to remove several hundreds of young trees, mainly from heather stands. Without removal, 10- 20 % of the open area might have been colonised by trees (W. Aandeweg, personal communication). Similar removals are practised in other heathland areas with free-ranging cattle (Westerhoff 1992). The observed differential tree encroachment in grass and *Calluna* heaths and the frequency of bite marks suggested that pine and birch juveniles were more severely suppressed in grass lawns than in *Calluna* heaths, more on plaggen soils than on podzolic soils and more by rabbits than by cattle.

Scots pine, buckthorn, silver birch, rum cherry *Prunus serotina* Ehrh. and goat willow *Salix caprea* L. invaded in the ungrazed *Deschampsia* heath on plaggen soil

(Fig. 1f). Their establishment followed substantial *Deschampsia* die-off after a prolonged snow cover during the winter 1985-1986. The establishment after die-off and the failure of tree invasion in the vigorous ungrazed *Molinia* (Fig. 1h) suggest a threshold for tree invasion in ungrazed tall grass swards. Causal factors may be shading, small rodents and fungi. Runways and bite marks revealed the presence of small rodents in our exclosures.

Despite the increased frequency of bramble (see the Appendix), its cover remained low (< 1 %) until 1993. Nutrient deficiencies and browsing by rabbits, roe deer and horses may have checked its expansion. Cattle avoided bramble (see also Chapter 4 and 7).

During the study, more than 20 mature trees in the forest and open heathland died as a result of ageing and wind-throw. They were all replaced by grass since cattle had suppressed the shade-tolerant mid-successional pedunculate oak *Quercus robur* L. and rowan *Sorbus aucuparia* L.

SPECIES RICHNESS

The positive effect on species richness was explained by cattle-mediated seed dispersal, release from competitive exclusion by suppression of taller dominants and by increased spatial heterogeneity (Bullock & Pakeman 1997; Olff & Ritchie 1998). The nitrophilous herbs (e.g. *Poa annua* L. *and Stellaria media* (L.) Villa) occurred mainly on (old) dung patches. The increased frequency of non-nitrophilous herbs (see the Appendix, e.g. *Carex pilulifera* L. and *Potentilla ere*cta (L.) Räuschel,) was explained by improved germination conditions for seeds from the seed bank and the seed rain. The stabilisation of the species richness (Fig 6, 7) on a relatively low level may have been the result of the low pH and a failing long-distance dispersal (Bakker & Berendse 1999).

Proulx & Mazumber (1998) suggested reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. We found positive effects on poor and rich soils (Fig. 6). The decline of the species richness during the second 5 years in the most nutrient-poor *Calluna* habitats may support their theory. The decline may also be explained by out-shading of the small, light demanding heathland species by the closing *Calluna* canopy.

MOSAIC CYCLES

Cattle grazing generated shifting grass-heather mosaics in more or less homogeneous *Calluna* heaths (Fig. 1b,c) and grass heaths (Fig. 1d,g) on soils of intermediate fertility. No mosaics developed in the nutrient-poor, turf-stripped pioneer *Calluna* heath and in the nutrient-rich *Deschampsia* heath on plaggen soil (Fig. 1a,e). Diemont & Heil (1984) concluded that the sustained grass dominance in eutrophicated (non-grazed) Dutch heathlands conflicted with cyclic succession of the four classical *Calluna* stages (Watt 1955, Barclay-Estrup & Gimingham 1969) and with the *Calluna*-moss-grass cycle in fixed drifting sand (Stoutjesdijk 1959). In the Wolfhezerheide, free-ranging cattle could change the linear heather-grass transition into a heather-grass-heather cycle because invading trees were removed. Without tree removal, a heather-forest-grass-heather cycle would have been generated. Grazing acted as driving force for the cycling in two ways: (i) by inducing the invasion of grass in degenerating forest and heather; (ii) by inducing the invasion of *Calluna* and other unpalatable woody pioneers in the grass lawn after a period of exploitation and nutrient depletion.

NUTRIENT MEDIATED EFFECTS

Despite the obvious light-mediated effect of grazing on the grass invasion in ageing *Calluna* and the recovery of *Calluna* in grass heath, we may not conclude that grazing diminished the importance of nutrients for the heather-grass balance.

The nutrient requirements of *Deschampsia* and *Calluna* were apparently met in all open habitats of the study area, except in the turf-stripped *Calluna* heath. Here, nitrogen deficiency probably excluded *Deschampsia* (Table 2, Fig 1a). This result agrees with the relatively high nitrogen demand (Aerts 1993a,b; Alonso & Hartley 1998) and low phosphorus requirement (Bokdam & WallisDeVries, 1992) of this grass species. The shade tolerant *Deschampsia* was only locally restricted by shading (Fig. 1f, h).

Calluna was indirectly limited by nutrients. The relatively high nutrient availability allowed the grasses to inhibit the germination and seedling survival of *Calluna* in the grass heaths. By short-cropped lawns and gaps, cattle eliminated the nutrient-based competitive advantage of the established *Deschampsia* over the establishing *Calluna*. The grass sward on the plaggen soil with grass litter may have been more resistant to trampling, gap creation and nutrient depletion than the grass sward on the podzolic soils with *Calluna* litter. The rich *Calluna* recruitment on the turf-stripped plots on plaggen soil emphasised the essential role of gaps. Ten years of nutrient depletion in a *Deschampsia* heath at Hoog Buurlo (The Netherlands) by hay making ('defoliation without treading gaps ') did not result in any *Calluna* recovery, despite a rich seed bank (Diemont & Linthorst Homan 1989).

There is growing evidence that soil fertility may also affect the disturbance risk and longevity of *Calluna*. The more intensive browsing of *Calluna* on the plaggen soil (compared with the podzolic soil; Fig. 5) might be attributed to three nutrient-mediated mechanisms: (i) a higher nutritional value of *Calluna*, (ii) a higher intrinsic palatability of *Calluna* and (iii) a higher associational palatability, provided by a more productive and palatable grass matrix. Fertilisation with a compound fertiliser including nitrogen and phosphorus induced higher nitrogen and lower lignin concentrations in *Calluna* shoots (Iason & Hester 1993). Brunsting & Heil (1985) found a positive effect of nitrogen availability on foliage nitrogen content and the performance of the heather beetles. *Calluna* plants growing near grass patches were more intensively used than individuals at larger distances (Clarke, Welch & Gordon 1995; Hester & Baillie 1998). High nitrogen availability may also increase the risk of damage by frost and drought for *Calluna* (Berdowski 1993). The findings emphasise that *Deschampsia* and *Calluna* both are affected by nutrients, but in different ways and directions. *Deschampsia* seems to be directly limited by nutrients as resource for its performance. C*alluna* is affected indirectly and in opposite direction by the same nutrients. High levels of nitrogen increased the competitive ability of competing grasses (Aerts 1993b) and its disturbance risk. The earlier grass invasion and failing *Calluna* recovery on the plaggen soil in our study area may ultimately be attributed to the higher soil fertility when compared with podzolic soils. It shows that soil fertility pattern created by the medieval sedentary farming system may still control actual vegetation patterns.

The combination of a low phosphorus and a high nitrogen availability attributes a limiting role to phosphorus for species with a relative high phosphorus requirement Such species (e.g. bramble) might be expected to increase rapidly after phosphorus inputs (e.g. on dung patches).

A preliminary calculation revealed that the nutrient removal by defoliation exceeded the atmospheric inputs for potassium and phosphorus on intensively grazed grass lawn patches. Nitrogen inputs were nearly completely removed. As a consequence, lawn patches undergo phosphorus and potassium depletion until excreta replenish them. The calculated frequency of dung and urine deposition on these lawns was approximately once per 20-30 year, assuming no resting activities on the lawn

(Bokdam 1989). This means that nutrient depletion may have played a role in the establishment of *Calluna* in grass lawns.

At the scale of the whole grazed area, free-ranging cattle removed only a minor proportion of the atmospheric nutrient input. The animals excreted a major proportion of the ingested nutrients and redistributed a substantial amount from the grass lawns to the forest (Chapter 5).

Calluna, pine and silver birch shared many ecological traits as woody invaders in nutrient-poor grass heaths. They may be considered as a functional type (Smith, Shugart & Woodward 1997). A characterisation that would broaden the scope of hypotheses, experiments and modelling from heathlands to other grazed ecosystems (Archer 1996; Putman 1996; Vera 1997; Bokdam 1998; Prins & Olff 1998; Olff *et al.* 1999; Ritchie & Olff 1999; Van Oene, Van Deursen & Berendse 1999).

MANAGEMENT IMPLICATIONS

Continued free-ranging cattle grazing will lead to a further eutrophication of the open heathland because of ongoing atmospheric inputs and because nutrient-rich forest patches will be converted into grassland. Cessation of tree removal would lead to the restoration of a half-open wood-pasture mosaic (Pott & Hüppe 1991) This process is accelerated by integrated grazing of heathlands, arable fields, improved grasslands and forest. Eutrophication may increase in the long term the grass proportion in the open heathland. A higher soil fertility will induce a higher grazing pressure in grass lawns. It may progressively hamper the invasion of woody pioneers of nutrient-poor environments (e.g. *Calluna*, pine and birch) and change the successional pathway from a grass-heather-pine-birch-oak route to a grass-bramble-oak-beech route (Bokdam 1998).

Replacement of the actual year-round grazing by summer grazing might increase the grass consumption and favour the heather proportion in the grass-heather mosaic. Replacement of free-ranging by traditional herding (with a daily return of the herd to the stable and a daily foraging time of about 8 h) would remove about 60 % of the excreta, i.e. 40 kg nitrogen and 2.5 kg phosphorus per animal unit (or 8 kg N and 0.5 kg P ha^{-1}). Removal of the total actual atmospheric nitrogen input of the grazed area would require the replacement of all forest and heather stands by intensively used grass lawns (chapter 8). Multi-species grazing combining cattle with smaller herbivores (e.g. sheep, red deer, rabbits), might suppress shrubs and trees more effectively. Replacement of the large grazers by smaller ones may lead to dominance of coarse grasses (e.g. *Molinia, Calamagrostis epigejos* (L.)Roth) or other potential dominants that are unpalatable to smaller herbivores (see chapter 7 and 8)

We conclude that free-ranging grazing without additional management will generate dynamic tree-grass-heather mosaics in the long term. These wood-pasture mosaics are fundamentally different from the traditional heathlands in which trees and grasses were excluded by the land use. Free-ranging grazing combined with tree cutting appeared to be a suitable management regime for the maintenance of open heathlands with dynamic grass-heather mosaics. Herding, or a combination of free-ranging grazers with burning or turf stripping seems unavoidable if pure heather-dominated open heathlands are to be maintained under the present environmental conditions.

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Appendix

Frequency (%) of vascular plant species in the 17 grazed plots established in 1983 in open heathland, in 1983, 1988 and 1993. Nomenclature follows Van der Meijden (1990). The herbaceous species were arranged in nitrophilous and non-nitrophilous species according to their nitrogen indication value (N) of Ellenberg (1979) (1 = extreme nitrogen-poor environment; 9 = extreme nitrogen-rich environment. X = indifferent ? = unknown)

SPECIES (N-Ellenberg)	**1983**	**1988**	**1993**
Non-nitrophilous herbs (N-Ellenberg <6 or X)			
Agrostis capillaris (3)	0	41	71
Carex pilulifera (5)	12	65	71
Cuscuta epithymum (2)	0	12	0
Danthonia decumbens (2)	0	18	18
Deschampsia flexuosa (3)	100	100	100
Festuca ovina (2)	0	0	12
Galium saxatile (3)	0	53	88
Hypochaeris radicata (3)	0	6	6
Juncus bufonius (X)	0	6	0
Juncus effusus (4)	0	6	0
Luzula multiflora (3)	0	0	6
Molinia caerulea (2)	18	41	41

Appendix continued

SPECIES (N-Ellenberg)	1983	1988	1993
Potentilla erecta (2)	0	18	24
Rumex acetosella (2)	0	18	53
Number of non-nitrophilous herb species	3	12	11
Nitrophilous herbs (N-Ellenberg >=6)			
Cerastium fontanum (6)	0	0	6
Corydalis claviculata (?)	6	0	0
Poa annua (8)	0	6	0
Poa pratensis (6)	0	0	12
Sagina procumbens (6)	0	6	0
Stellaria media (8)	0	12	0
Number of nitrophilous herb species	1	3	2
Dwarf shrubs			
Calluna vulgaris (1)	53	95	100
Erica tetralix (2)	24	53	53
Genista anglica (2)	0	18	6
Vaccinium myrtillus (3)	0	6	6
Number of dwarf shrub species	2	4	4
Shrubs and trees			
Betula sp. (3)	29	71	71
Pinus syvestris (X)	35	71	35
Quercus robur (X)	35	18	29
Frangula alnus (X)	29	41	41
Rubus fruticosus (?)	0	18	48
Sorbus aucuparia (X)	0	23	6
Number of shrub and tree species	4	6	6
Total number of species	**10**	**25**	**23**

Species (N-value) occurring in other years: *Epilobium sp.(?), Holcus lanatus (4), Holcus mollis (3), Luzula campestris (2), Spergularia rubra (4), Chamerion angustifolium (8) Lolium perenne (7), Polygonum persicaria (7), Senecio sylvaticus (8), Solanum nigrum (8), Prunus serotina (?).*

Chapter 3

Effects of browsing and grazing on cyclic succession in nutrient-limited ecosystems

Jan Bokdam

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Walking heather. Invading Calluna vulgaris outshaded the invaded Deschampsia flexuosa lawn. The removed half of the Calluna shrub shows bare litter. Wolfhezerheide, September 1994 (photo Jan Bokdam).

Effects of browsing and grazing on cyclic succession in nutrient-limited ecosystems

Jan Bokdam

Summary

This paper deals with browsing and grazing as forces driving cyclic succession. Between 1989 and 1994 reciprocal transitions between the dwarf shrub *Calluna vulgaris* and the grass *Deschampsia flexuosa* were monitored in 9 permanent m^2 plots, each divided into 100 subplots of 10 x 10 cm in a cattle grazed grass-rich Dutch heathland on podsolic soils in which tree encroachment was prevented. Heather beetles killed *Calluna* in four of the nine plots in 1991-1992. The monitoring revealed reciprocal transitions and cycles between *Calluna* and *Deschampsia* on a subplot scale. Beetles and cattle had additional and complementary effects on the two competing species. Defoliation by beetles and trampling by cattle killed *Calluna* and favoured grass invasion. Grazing and gap creation by cattle in *Deschampsia* favoured the establishement and recovery of *Calluna.* Analysis of the causal mechanisms suggests that indirect, resource-mediated herbivory effects may be as important for the replacement processes as direct effects of defoliation and treading. Herbivory created differential light and nutrient levels in *Calluna* and *Deschampsia* gaps. Grazing and browsing improved the resource-capturing abilities of *Calluna* and its resistance to herbivory and abiotic disturbances. The emerged *Calluna-Deschampsia* cycle and its driving forces are summarised in a conceptual triangular Resource-mediated Successional Grazing Cycle (RSGC) model, a limit cycle involving herbivore-plant-plant resource interactions. It offers a deterministic equilibrium model as alternative for stochastic transitions between the meta-stable states with dominance of *Calluna* and *Deschampsia* respectively. The validity range of the RSGC model and its management implications are briefly discussed.

Key-words: *Calluna vulgaris*, cattle, *Deschampsia flexuosa*, heather beetles, heathland herbivory, meta-stability, mosaic cycle;

Introduction

Vegetation succession can be defined as the replacement of plant developmental stages, species or communities over periods of several years. It is distinguished from fluctuations generated by year-to-year variation in growth, consumption and mortality (e.g. Van Andel *et al.* 1993). Cyclic vegetation succession is defined as a recurrent series of stages, species or communities ('phases') with a specific sequence (Watt 1947; Gimingham 1972, Kershaw 1973, Miles 1979). This specific sequence is the result of ecological linkage between the phases. In the alternative non-cyclic 'carousel' succession model (Van der Maarel & Sykes 1993) specific sequences and ecological links are lacking, rendering the state of the site and its occupation independent on the preceding dominant (Herben, During & Law 2000). Shifting successional mosaics are composed of patches passing through the phases of a cycle in a de-synchronised way (Olff *et al.* 1999). The term 'mosaic cycle', coined by Remmert (1991), refers to the process and the pattern. Cyclic succession is important for nature conservation because it links dynamics, spatial heterogeneity and biodiversity (Fiedler *et al.* 1997; Scherzinger 1996). Succession may be triggered by the death of the established dominant or by the expansion of the invader. Death as well as invasion, may be driven by internal plant processes (e.g. ageing, clonal expansion), vegetation processes (competition, facilitation) or by external influences (e.g. abiotic disturbance, herbivory, management) (Van Andel *et al.* 1993).

Herbivores may have a strong and complex influence on vegetation succession and biodiversity (Huntly 1991; Bakker 1998; Olff *et al.* 1999). Therefore herbivore management is a growing issue in nature conservation (WallisDeVries *et al.* 1998 chapter 1). Defoliation, treading and excretion affect plants directly by tissue loss, mortality, regrowth and dispersal. Indirect effects include changed micro-climatic and soil conditions and cascading effects on other trophic levels (Jefferies 1999; Polis *et al.* 2000). Herbivory can modify the resource acquisition as well as the resource losses of plants. Resource acquisition may change by altered resource supplies (e.g. light, nutrients) and/or by an altered resource acquisition capacities (e.g. canopy and root structures, McNaughton 1984). Losses may be changed by a modified frequency or intensity of disturbing events (e.g. fire, herbivore assemblages or densities) or by a changed vulnerability of plants (e.g. accessibility, palatability and tolerance). In case of more than one herbivore species, their joint effects on competing plants may be cumulative or complementary, depending on their food niche overlap (Ritchie & Olff 1999). It might be argued, that the balance between browsers (with a diet of predominantly woody species) and grazers (with a predominantly herbaceous diet, Hofmann 1989; Van Wieren 1996) in the herbivore assemblage will affect the competition between herbaceous and woody plants in sites where both growthforms can be dominant.

Plant size and palatability are core traits for the outcome of competiton in grazed vegetation (Weiher *et al.* 1999). Naveh and Lieberman (1984) have described a cyclic succession model with a palatable tall grass and unpalatable low forbs. Grazing suppressed the competitively superior tall grass and shifted the dominance to the competitively inferior forbs. Cessation of grazing restored the grass dominance. It may be argued that in the inverse case with a palatable low species and an unpalatable tall species, herbivory will accelerate succession to the unpalatable tall species. Many cases of such apparently irreversible transitions to unpalatable tall herbs, shrubs and trees are known from rangelands (Dijksterhuis 1954; Archer 1994) and from grazed conservation areas in temperate climates (Piek 1998; Bokdam & Piek 1998). Restoration of the dominance of palatable lawn grasses demands the death of the unpalatable dominant and (re-) invasion by the grasses. Ageing, browsing wild 'bulldozer' herbivores (Kortlandt 1984), livestock, insects, fungal attacks, storm, fire or human intervention may break down or create gaps in tall dominants. Grass invasion in woodland gaps may, II however, fail, due to lack of seeds or soil resources. In several dry, nutrient-poor rangeland sites from which the woody dominants were removed by controlled burning, herbicides or mechanical disturbances, grass re-invasion did not take place (Fuhrmann & Crews 2001). The alternating early and late successional stages are often referred to as meta-stable states (Naveh & Lieberman 1984; Westoby *et al.* 1989; Laycock 1991; Van de Koppel *et al.* 1996). In a short grass lawn, a high herbivore load controls a low plant biomass; in a tall herbaceous or woody stage, a high plant biomass is controlling a low herbivore mass. Transitions between both appear to be unpredictable, due to the stochasticity of the causal factors and the catastrophic nature of the transition process displaying 'runaway feedback' (Naveh & Lieberman 1984). Unpredictability might also be due to an inadequate understanding of deterministic transition mechanisms.

There is a growing interest for nutrient-mediated mechanisms in cyclic succession of grasses and woody species in grazed ecosystems (Berendse 1985; Archer 1994; Krüsi *et al.* 1995; WallisDeVries & Van de Koppel 1998; Olff *et al.* 1999; Achermann 2000). Wild and domestic grazers may deplete and enrich local soil nutrient pools by offtake and excretion of dung and urine (Edwards & Hollis 1982; Achermann 2000). Erosion and leaching can be initiated by hoof-slidings, trampling and burrowing (Ellenberg 1988; Korn 1991; Milchunas & Lauenroth 1993). The most obvious effect of a changed nutrient availability is the modified outcome of competition because plants vary in their nutrient requirements (Berendse 1985; 1998;Van Oene *et al.* 1999). By changes in the litter quantity and chemistry, the changed botanical composition may amplify the grazing effect (Berendse 1994). Feed-back of grazing-induced changes in vegetation and soil to the herbivores has been largely ignored up to now. Soil fertility affects herbivory by vegetation composition, plant production, nutritional value (e.g. digestibility, protein content) and anti-herbivore resistance (Bryant *et al.* 1983; Coley *et al.* 1985; Mutikainen *et al.* 2000, Bokdam *et al.* 2001).

This paper discusses browsing and grazing as forces driving the cyclic alternation of *Calluna vulgaris*, an ericoid dwarf shrub and the grass *Deschampsia flexuosa.* The heathlands on which these two common species co-exist are temperate traditional rangelands on acid, nutrient-poor soils (Gimingham 1972; De Smidt 1975; Ellenberg 1988; Aerts & Heil 1993). Watt (1955), Barclay-Estrup & Gimingham (1969) have described cycles of pioneer, building, mature and degenerate *Calluna* alternating with lichens, bryophytes, grasses, bracken (*Pteridium aquilinum*) and other dwarf shrub species. They concluded that the cycle was controlled by intrinsic plant development of *Calluna*, allowing invasion of other species after its degeneration. *Calluna* was assumed to recover after some years spontaneously from seed. Stoutjesdijk (1959) described similar cycles of *Calluna* with *Deschampsia flexuosa* and *Molinia caerulea* in ungrazed heaths on drifting sand in The Netherlands. De Smidt (1975) emphasised the role of interactions between ageing and abiotic disturbances (fire, severe winter frost and drought), heather beetles (*Lochmaea suturalis* Thomson), local extinction of rabbits and abandonment of grazing as causal factors for *Calluna* gaps. He considered cessation of browsing by rabbits and the abandonment by livestock as ultimate causal factors for physiological ageing and subsequent replacement of *Calluna.* Implicitly, he shared the view of Gimingham (1972, 1992) that heathland management should keep *Calluna* in its building phase by sustained browsing, mowing or burning. Since 1980, atmospheric eutrophication has accelerated the shift towards grass dominance in the abandoned heathlands of continental northwestern Europe (Diemont 1996). The persistence of grass dominance cast doubt on the occurrence of *Calluna* cycles at higher nutrient levels (Diemont & Heil 1984). In ungrazed heathlands, *Deschampsia* and *Molinia* were found to persist for several decades, preventing the re-establishment of *Calluna* and other

Ericaceae (Diemont 1996). In these studies, *Calluna* died from old age and/or because of infestation by the heather beetle, a monophagous insect that create gaps of 0.1-1 ha (Brunsting 1982; Diemont & Heil 1984; Berdowski 1993). A similar replacement of *Calluna*-bracken (*Pteridium aquilinum*) cycles by a persistent dominance by bracken and Scots pine (*Pinus sylvestris*) was observed in English heathlands (Marrs & Hicks 1986). Recently, experiments in The Netherlands showed that cattle grazing could induce a substantial recovery of *Calluna* in grass-dominated heathlands on podsolic soils (Bokdam & Gleichman 2000; Heil & De Smidt 2000). Until now, little was known about the fate of these re-established *Calluna* shrubs in the face of ageing, competition by grass and heather beetles. I hypothesised that grazing and browsing by cattle might restore *Calluna*-grass cycles.

Material and methods

STUDY AREA

The study area (Wolfhezerheide) is located in the Veluwe, a dry sandy area in the centre of the Netherlands, ca. 12 km east of Wageningen (51^o 47' N; 5^o 41'E). The grazed area (40 ha of open heathland and 20 ha of forest) has mainly acid (pH $_{KCl}$ 3 - 3.5) podsolic soils that have developed on Pleistocene fluvio-glacial sand and cover sand. The annual atmospheric nutrient deposition (wet + dry) in the open heathland is ca. 40 kg nitrogen ha^{-1}, 1.5 kg phosphorus ha^{-1}and 5 kg potassium ha^{-1} (Erisman & Heij 1991). Until 1983, vegetation was managed by removal of juvenile trees and by occasional local mowing and turf-stripping. In 1983, *Deschampsia* covered major parts of the open heathland. Since January 1983, cattle have continuously (year-round) grazed the area. Annual stocking rates have been maintained at an equivalent of approximately 0.2 animal units ha^{-1} (1 animal unit = 450 kg). Rates were 30 % higher in summer than in winter. Throughout the study period 1 - 3 horses were allowed to graze in the area. Densities of roe deer *Capreolus capreolus* L. (2 - 4 km^{-2}) and rabbit *Oryctolagus cuniculus* L. (100 km^{-2}) were low and their effects the grass-heather balance in the studied plots were insignificant. From 1984 a minor quantity (1 - 2 kg dry matter animal^{-1}day^{-1}) of supplementary food (concentrates, hay or corn silage) was occasionally provided during late winter on one location. Encroaching Scots pine and silver birch (*Betula pendula*) were removed. No fires occurred. The winters of 1984-1985 and 1985-1986 were extremely cold and winter browning of *Calluna* was observed. Heather beetles damaged *Calluna* locally in 1991-1992.

MEASUREMENTS

Following the introduction of cattle grazing in 1983, *Calluna-Deschampsia* mosaics developed due to *Calluna* recovery in the *Deschampsia* grass heaths and *Deschampsia* invasion in degenerating *Calluna* (Bokdam & Gleichman 2000). In order to test the cyclic succession hypothesed, nine 1 x 1 m plots were marked in the *Calluna-Deschampsia* mosaics, using wooden pegs rising ca. 5 cm above soil level. In each plot, species dominance was estimated and recorded in 100 sub-plots of 1 dm^2 (10 x 10 cm), using a metal frame with cross-wires, laid in identical positions between the corner pegs. Recording took place in March 1989, March 1991 and November 1994 (thus covering 6 growing seasons). The species with the highest cover (projection) was considered as dominant in the subplot. If the cover of *Calluna* was more than 50 %, but lower than the cover of *Deschampsia*, *Calluna* was still noted as the dominant, since its canopy height exeeded that the canopy height of *Deschampsia*. Sub-plots with less than 10% vascular plant cover were recorded as ‘bare’. Mineral soil, litter, bryophytes or lichens covered these sub-plots. Four of the nine plots were severely attacked by heather beetles in 1991-1992.

DATA ANALYSIS

The data of the ‘treatments’ (grazing with and without heather beetles) were analysed for the periods 1989-1994, 1989-1991 and 1991-1994. Based on the values for the sub-plots, the following statistics were calculated for each plot:

- Dominance frequency (percentage of sub-plots with a certain species dominance) in 1989, 1991 and 1994;
- Dominance transition 1989-1994 (number of sub-plots with a certain transition across the indicated period, expressed as percentage of the initial (1989) number);
- Apparent constancy (number of sub-plots with the same species dominant in 1989 and 1994 expressed as percentage of the initial (1989) number);
- True constancy (number of sub-plots with the same species dominant in 1989,1991 and 1994, expressed as percentage of the initial (1989) number);
- Completed cycles (apparent constancy minus true constancy, %);

Patch longevity expressed as years was calculated as $1/\lambda$, assuming a constant extinction rate λ. On the basis of this assumption, we expected the number of patches (sub-plots) occupied from the beginning to decline exponentially $(N(t) = N(o)\ e^{-\lambda t})$ with $N(t)$ as the number of occupied patches in year t . The values for λ were assessed by linear regression of $\ln\{N(t)/N(0)\}$ versus t for all individual plots (Causton 1983).

Beetle effects on data covering the whole period were tested using One-Way ANOVA after testing the normality of the distribution with the one-sample Kolmogorov-Smirnov Test and log-transformation of percentual values. Beetle effects on the time series of dominance frequency of *Calluna* and *Deschampsia* were tested as beetle x year interaction, using a Two-Way ANOVA (GLM, Repeated Measurements, after Mauchly's Test of Sphericity, (SPSS release 8 , Norušis 1993).

Results

DOMINANCE FREQUENCY CHANGES

The mean Dominance Frequency of *Calluna* in the nine plots increased from 23 % in 1989 to 45 % in 1991 to 47 % in 1994. The value for *Deschampsia* declined from 60 % to 43 % in 1991 and 1994. *Erica tetralix* increased from 3 % in 1989 and 1991 to 7 % in 1994, bare soil declined from 13 % in 1989 to 8 % in 1991 and 2 % in 1994. Other species remained unchanged at ca. 1 %. Plots without beetles revealed a significant stronger increase in *Calluna* dominance than plots with beetles (Fig. 1, Two-Way ANOVA, $p < 0.05$); the *Deschampsia* decline was not significantly different ($p = 0.38$).

TRANSITIONS

Dominance frequency changes at plot level represent a net effect, masking dynamics at subplot scale because of opposite transitions and completed cycles at subplot level between the dates of measurement. The net increase of *Calluna* from 23 % to 47 % in the plots resulted from *Deschampsia – Calluna* transitions (53 % of the initial *Deschampsia* subplots, Table 1) and compensatory *Calluna–Deschampsia* transitions (43.4 % of the intital *Calluna* subplots) at subplot level. Apparent constancy was higher for *Calluna* (45.6 %) than for *Deschampsia* (38.3 %). Patches dominated in 1989 by *Erica tetralix* and other species changed predominantly into *Calluna,* bare soil patches into *Calluna* and *Deschampsia* (Table 1). Beetles affected these dynamics.

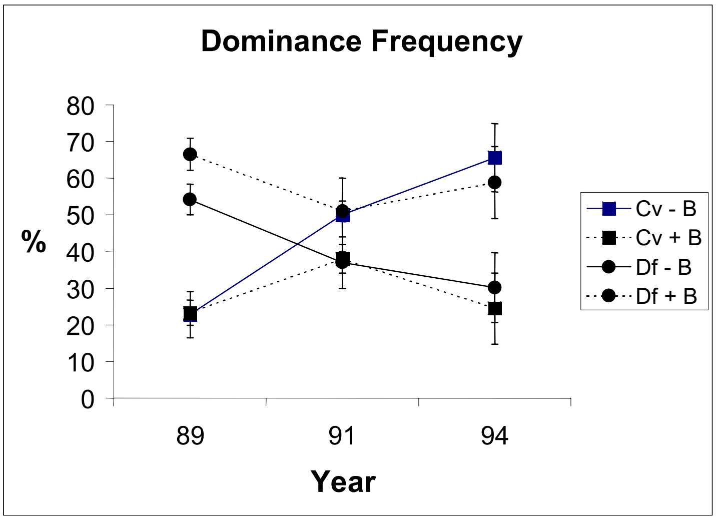

Figure 1. Dominance Frequency of *Calluna* (Cv) and *Deschampsia* (Df) in the period 1989-1994 in m² plots without heather beetles (-B) (n = 5) and with heather beetles (+B) (n = 4); vertical bars represent SE.

Apparent constancy (1989-1994) and True Constancy (1989-1991-1994) of *Calluna* were higher in the plots without beetles (61.5 and 52.7% respectively) than in the plots with beetles (25.7 and 20.4% respectively), but not significantly so ($p = 0.15$, Table 2). The apparent constancy and the true constancy of *Deschampsia* were significant lower ($p< 0.05$) in plots without beetle damage (21.7 and 11.0% respectively) if compared with plots with beetles (59.0 and 36.0% respectively). Patch longevity (Table 2) directly determines the mosaic composition. Viewed over all 9 plots, *Calluna* patches had a significantly higher longevity than *Deschampsia*, (Table 2), which is in accordance with the increased dominance frequency of *Calluna* (Fig. 1). Patch longevity of *Calluna* was lower in plots with beetles (5.6 years) than in plots without beetles (14.9 years, Table 2). Patch longevity of *Deschampsia* was significantly higher in plots with beetles than in plots without beetles. The differences are in line with the beetle effect on the mosaic (Fig. 1) It should be noted that the assessed true constancy and patch longevity values of *Calluna* in the plots with beetles are overestimations because *Calluna* recorded in 1994 in these plots concerned patches where it had died during the beetle outbreak in 1991-1992. An annual registration would have revealed these rapid beetle-induced cycles.

COMPLETED CYCLES

Completed cycles in the subplots reflected short-term and small-scaled dynamics in the heathland. Completed cycles within the study period (1989-1994) were revealed by a deviating dominant in 1991 in an apparently (1989-1994) constant sub-plot.

Table 1. Dominance Transitions 1989-1994 expressed as % age of the initial number of sub-plots in 1989; n = 9. Df = *Deschampsia flexuosa*; Cv = *Calluna vulgaris*; Et= *Erica tetralix*; Ov = Other vascular species; B = Bare (mineral soil, litter, lichens, bryophytes);[number of subplots dominated by this species in 1989].

	1994					
	Cv	Df	Et	Ov	B	Total
1989						
Cv [23.0]	45.6	43.4	5.0	0.3	5.7	100
Df [59.7]	53.3	38.2	7.0	1.1	0.4	100
Et [3.2]	82.8	17.2	0.0	0.0	0.0	100
Ov [0.7]	80.0	10.0	0.0	10.0	0.0	100
B [13.4]	45.8	45.2	5.0	2.6	1.4	100

Table 2. Apparent constancy and true constancy (expressed as % age of the number of initial sub-plots) and patch longevity (years) of *Calluna* and *Deschampsia* in plots without and with heatherbeetles, 1989-1994, ± SE; Effect of heather beetles: One-Way Anova, *=$P < 0.05$; (*) = P~`0.05. NS = not significant.

Patch	*Calluna*		*Deschampsia*	
Plots	Without beetles N = 5	With beetles n = 4	Without beetles n= 5	With beetles n = 4
Apparent	61.5 $^{\mathrm{NS}}$	25.7 $^{\mathrm{NS}}$	21.7 *	59.0 *
Constancy (%)	±15.4	±16.2	±10.0	±8.3
True	52.7 $^{\mathrm{NS}}$	20.4 $^{\mathrm{NS}}$	11.0*	36.0 *
Constancy (%)	±11.8	±17.6	±4.3	±7.2
Patch	14.9$^{(*)}$	5.6$^{(*)}$	2.8 *	6.4*
Longevity (year)	±6.1	± 4.0	±0.5	±1.1

Deschampsia patches displayed a higher percentage of completed cycles than *Calluna* patches (16 % and 7 % respectively) if viewed over all plots, but especially in the plots with beetles (23 % and 5 % respectively, Table 3). The difference between the subplot types may be attributed to the fact that *Calluna* that had invaded between 1989 and 1991 in *Deschampsia* patches was killed by heather beetles and replaced by *Deschampsia*

Table 3. Frequency of completed cycles between 1989-1994 expressed as % age of the number of initial sub-plots ± SE; Rest = *Erica tetralix* + other vascular species + bare soil. None of the differences between plots with and without heather beetles was significant ($p < 0.05$).

Completed Cycles	Plots without beetles (n = 5)	Plots with beetles (n = 4)
***Calluna* cycles**		
All	8.9 ± 6.3	5.4 ± 5.4
Calluna–Deschampsia–Calluna	8.2 ± 6.5	0.0 ± 0.0
Calluna–Rest–*Calluna*	0.7 ± 0.7	5.4 ± 5.4
***Deschampsia* cycles**		
All	10.7 ± 6.0	23.0 ± 4.2
Deschampsia–Calluna–Deschampsia	4.8 ± 3.0	3.6 ± 1.5
Deschampsia–Rest–*Deschampsia*	5.9 ± 4.4	19.4 ± 4.8

between 1991 and 1994. Mortality by heather beetles may also explain the low percentage of completed *calluna* cycles. A relatively high number of completed cycles involved alternation with 'bare' and other vascular species, particularly in *Deschampsia* cycles (19 %, Table 3). It emphasises the important role of gaps as ephemeral habitat for competition-sensitive species in heathlands.

Discussion

EVIDENCE OF CYCLIC SUCCESSION AND THE ROLE OF BROWSING, GRAZING AND NUTRIENTS.

The results provide evidence of *Calluna-Deschampsia-Calluna* and *Deschamspia-Calluna-Deschampsia* cycles in dry, grazed heathland on podsolic soils at the prevailing high atmospheric nutrient loads cycles on both dm^2 scale (Table 3) and m^2 scales (Fig.1). Despite their low Dominance frequency (Table 1), bare patches (mineral soil, litter, bryophytes, lichens), *Erica tetralix* and other vascular species (e.g. *Galium hercynicum*, *Carex pilulifera*) occurred also in completed cycles of *Calluna* and *Deschampsia* (Table 3). Their ephemeral occurrence (Table 1) reflects their great ability to invade gaps and a great susceptibility for competitive exclusion by *Deschampsia* or *Calluna*. The dominance of *Calluna* and *Deschampsia* in the successional mosaic is attributed to their competitive superiority under the prevailing environmental conditions and to the absence of taller woody species (Bokdam & Gleichman 2000). The palatable shrub and tree species *Frangula alnus*, *Sorbus aucuparia*, *Amelanchier lamarckii*, *Prunus serotina* and *Quercus robur* were suppressed by cattle browsing during the growing season. Juveniles of unpalatable *Pinus sylvestris* and *Betula pendula* were removed by the manager, since cattle avoided them during the whole year (Chapter 4).

The results confirmed that opening of the *Calluna* canopy (i.e. light) is crucial for the invasion and replacement by *Deschampsia* (Berdowski 1993). By defoliating and killing *Calluna,* heather beetles initiated or accelerated grass invasion (Fig. 1). Despite this impact, it cannot be concluded that heather beetles played a key role (sensu Begon, Townsend & Harper 1996) in the cycling, since *Deschampsia* also invaded *Calluna* gaps created by ageing, trampling and browsing by cattle, and by disturbances (Table 2-3; plots without beetles).

Cattle grazing appeared to be a true key factor for the cyclic succession, since it was crucial for the invasion of *Calluna* in *Deschampsia* patches. The design of this study – comparison of grazed mosaics with and without heather beetles on podsolic soils – excluded direct experimental evidence of grazing effects on the *Deschampsia-Calluna* transition in the study area since ungrazed control plots on podsolic soils were lacking. Ungrazed exclosures in a near-by heathland site (Hoog Buurlo) were used as control. They displayed a persistent dominance of tussocky *Deschampsia* during more than 10 year, despite a rich *Calluna* seedbank (Diemont & Linthorst Homan 1989).

Soil fertility appeared to be another key factor, because the mosaics developed only on sites of intermediate soil fertility. In *Deschampsia* on nutrient-rich plaggen soils developed in former arable fields in the study area, height growth and lateral expansion of *Calluna* seedlings failed, mainly because of the high browsing pressure (Bokdam & Gleichman 2000). Similar cases of *Calluna* inhibition by 'overbrowsing' are known from other fertilised grassland sites, e.g. reseeded areas in the New Forest (S.England) and Imbosch (The Netherlands) (Bokdam, personal observations). On turf-stripped podsolic soils in the study area with a significant lower soil fertility as compared to the non-turf-stripped podsols (Bokdam & Gleichman 2000) *Calluna* remained the dominant during more than 10 years despite canopy gaps created by browsing cattle. The failure of *Deschampsia* invasion in these gaps might be attributed to nutrient deficiency and competition by pleurocarpous bryophytes.

RESOURCE-MEDIATED EFFECTS OF BROWSING AND GRAZING.

How did grazing and intermediate soil fertility generate cyclic plant succession? The first answer is that they induced invasion of *Deschampsia* in *Calluna* and invasion of *Calluna* in *Deschampsia* by creating differential gap conditions (Fig. 2). The second answer is that the key factors had differential effects on the longevity (survival) of the two invaded species (Table 3) by the different resource concentrations in the gaps and by differential effects on resource capturing capacities and resource defence abilities of the invading species during the gap-filling process.

Gap creation is generally associated with a transfer of biomass and nutrients to the soil pool, leading to more light, a higher temperature and an increased soil nutrient pool in the gap (Borman & Likens 1979). These effects are more substantial in woody vegetation than in short-clipped grassland because of the different biomass. *Calluna* gaps displayed variable light intensities, depending on the causal gap factor, the gap size and the height and density of the surrounding vegetation. *Calluna* gaps were mostly characterised by a thick layer of accumulated, loose litter. Ageing induced a gradual increase in light and litter fall. It allowed *Deschampsia* to invade and develop sparsely below the *Calluna* canopy (Berdowski 1993). Heather beetles created an abrubt opening. They generally consume significant proportions of the canopy, but more than 50 % of the ingested dry matter (and even a higher %-age of the nitrogen) is returned into the gap as excreta and dead beetles (Brunsting 1982; Berdowski 1993). The induced light- and nutrient pulses induced and accelerated the invasion of *Deschampsia*. Sudden death by trampling, frost and drought had similar effects. The decomposition-resistant *Calluna* litter (Berendse 1994) may have delayed the nutrient transfer from the litter pool to the available pool. Increased soil temperatures, gradual invasion of decomposable *Deschampsia* litter and the trampling may have accelerated decomposition and mineralisation (Siepel & Van Wieren 1990).

In the study area*,* *Calluna* germinated in short-cropped *Deschampsia* swards in gaps with mineral soil or with compacted litter (Fig. 2, Bokdam & Gleichman 2000). Germination failed in ungrazed *Deschampsia* in the study area (Bokdam & Gleichman 2000) and in Hoog-Buurlo (Diemont & Linthorst Homan 1989). It confirmed the known shade-sensitivity of *Calluna* seedlings and the importance of gaps (Gimingham 1972). A nutrient balance (Bokdam unpubl.) and results of clipping experiments suggest that the nutrient availability in *Deschampsia* gaps was lower than in the *Calluna* gaps. The differences are mainly based on the higher off-take by herbivores and a lower dry

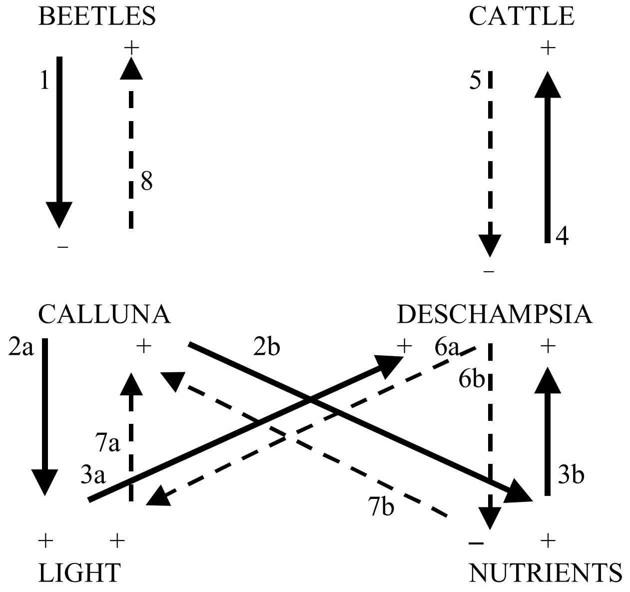

Figure 2. Hypothesised cyclic succession by alternating *Calluna-Deschampsia* (––>) and *Deschampsia-Calluna* (- - - >) transitions as emergent property of a herbivore-plant-resource system. 1: Invaded heather beetles kill *Calluna*. 2: Increased availability light (2a) and nutrients (2b) due to *Calluna* mortality. 3: Invasion of *Deschampsia* due to increased light availability (2a) and increased nutrient availability (2b). 4: Invasion of Cattle. 5: Defoliation and trampling of *Deschampsia* by cattle. 6: Increased light availability (6a) and reduced nutrient availability (6b) due to cattle grazing. 7: Invasion of *Calluna* due to increased light availability (7a) and decreased nutrient availability (7b). 8: Heather beetle invasion after *Calluna* maturation.

atmospheric nutrient deposition in grass lawns during the period preceding the gap creation. The third difference is the litter removal by treading in *Deschampsia* gaps. The annual consumption by cattle in *Deschampsia* lawns in the study area was estimated at 50 – 60 % of the above-ground production, since consumption took mainly place during the growing season (Lantinga 1985). Spatial distribution of foraging, resting and excretion behaviour revealed preferential grazing of *Deschampsia* and preferential resting in the forest. (Chapter 4,5). As a result, ca. 2/3 of the daily dung and urine excretion was deposed on resting and rumination sites outside the lawn. Dung pats and urine patches affected annually ca. 2.5 % of the lawn. It means that more than 75 % of the lawn area was still excreta-free after 10 years of grazing. It was calculated that on these excreta-free patches the losses by defoliation exceeded the gains from atmospheric deposition, resulting in a net loss for phosphorus (0.2 kg ha^{-1} yr^{-1}) and potassium (1.6 kg ha^{-1} yr^{-1}), while nitrogen maintained a small input surplus (Chapter 5). The calculated nutrient depletion agrees with measured productivity declines by clipping. In Hoog Buurlo, the annual dry matter yield of *Deschampsia* declined from ca. 3 $ton.ha^{-1}\ yr^{-1}$ to 1 $ton.ha^{-1}\ yr^{-1}$ after 9 years of annual clipping and the total amount of harvested nutrients during 9 years was roughly equal to a single turf-stripping (Diemont 1994, 1996). Litter gaps by hoof-slidings of cattle during wet wether are comparable with turf-stripped sites, irrespective of previous depletion by defoliation. In the study area, the annual *Deschampsia* production measured by monthly clipping was ca. 1.5 $ton.ha^{-1}.yr^{-1}$ in 1987/1988 (4 years after the introduction of cattle) (WallisDeVries 1989; Bokdam, unpubl.). The calculated balance (Chapter 5) and the clipping results point to soil depletion in excretion-free *Deschampsia* and to a lower nutrient availability in *Deschampsia* gaps if compared with *Calluna* gaps. They also emphasise the scale-sensitivity of the herbivore impact on the nutrient pool.

Beetles and cattle affected the resource capturing capacity of *Calluna* and *Deschampsia* by modifying their growth form. Incidental, intensive defoliation by beetles killed *Calluna,* while frequent but moderate shoot removal by cattle, rabbits and small rodents favoured clonal growth. *Calluna* plants in the study area developed flat prostrate canopies as described earlier in detail by Welch & Kemp (1973) and MacDonald *et al.* (1995). Clipping experiments showed that *Calluna* tolerates substantial shoot removal. Its productivity was not impaired by removal of 40 % of the shoots, but 80 % removal reduced the productivity by up to 66 % (Grant *et al.* 1982). The dense, flat canopies of browsed *Calluna* in the study area intercepted more than 90 % of the light (Vermaat unplublished data.). These findings suggest that moderate browsing may have favoured *Calluna* to ‘creep’ over short-grazed *Deschampsia*. Numerous adventitious roots allows creeping *Calluna* to exploit the soil resources of the invaded area. Browsing-induced creeping acted as an additional strategy to ‘jumping’ (by seed) and seems to be an advantageous phenotypic adaptation, enhancing *Calluna*’s competitive ability in small-scaled dynamic heather-grass mosaics.

The restored *Calluna-Deschampsia* cycle and patch longevity of *Calluna* in the study area may partly be attributed to decreased losses, prolonging the longevity of *Calluna*. Losses by browsing and induced clonality may have reduced losses by ageing, fire and abiotic disturbances. The spreading of erect mature branches typically marks the degeneration of unbrowsed individuals (Watt 1955). Eutrophication seems to accelerate height growth, and thus the spreading and degeneration (Berdowski 1993). It follows that nutrient depletion may have delayed this process. Clonal growth seemed to replace whole-plant mortality (partly) by modular (branch) mortality in the study area. It may have prolonged *Calluna*'s plant longevity and patch longevity. By creating low, short-clipped canopies, small herbivores (e.g. small rodents and rabbits) monopolised the dwarf-shrub lawn as food resource, reducing biomass removal and trampling damage by cattle. The trampling damage by cattle to *Calluna* in small-scaled heather-grass mosaics was also limited by preferential (walking) on the shortgrass lawn. Low gap nutrient levels may have reduced the defoliation risk of invading *Calluna*. The chemical anti-herbivore defence of *Calluna* and other evergreen *Ericaceae* is based on a low nutritional value (protein content and digestibility) and high contents of carbon-based phenolics e.g. lignin and tannins (Van Genderen, Schoonhoven & Fuchs 1996). There is growing evidence for resource-dependent protein and phenolic contents and related herbivory losses in *Calluna*. Brunsting & Heil (1985) found a positive effect of nitrogen fertilisation on foliar nitrogen content and the performance of heather beetle larvae fed on these leaves. Fertilisation with a compound fertiliser containing nitrogen and phosphorus induced higher nitrogen and lower lignin concentrations in *Calluna* shoots (Iason & Hester 1993). In the study area, defoliation of *Deschampsia* and *Calluna* was significantly lower on podsolic soils than on the more fertile plaggen soils (Bokdam & Gleichman 2000). These results suggest that nutrient depletion of *Deschampsia* may not only have stimulated *Calluna*'s invasion and longevity, but also its anti-herbivore resistance.

It is concluded that the interactions between the contrasting plants and herbivores initiated differential resource levels in *Calluna* and *Deschampsia* gaps. These conditions, and especially the differential gap nutrient levels, could act as important determinants of the gap-filling processes in the studied plots due to the intermediate soil fertility level of the podsolic soils. At more extreme high and low soil fertility levels in the plaggen and turf-stripped podsolic soils in the study area, nutrient levels overruled the grazing effect. Cattle played its key role mainly by creating gaps in the dominant *Deschampsia* with sufficient light and decreased soil fertility. The differential gap conditions in *Calluna* and *Deschampsia* constituted the legacy by which the soil-plant-herbivore systems controlled their succession. Gap conditions provided the ecological link and the clue for the switch between the succeeded and the succeeding species, fulfilling the criterium for cyclic succession.

RESOURCE-MEDIATED SUCCESSIONAL GRAZING CYCLE (RSGC).

The cyclic succession of *Calluna* and *Deschampsia* might be typified as a Resource-mediated Successional Grazing Cycle (RSGC) because of the key roles of grazing and differential gap resource levels. Successional grazing cycles differ from annual and intra-annual cycles by the successional replacement of the foodplants. The RSGC desscribes the behaviour of a resource-plant-herbivore subsystem with two resources, two plant species and two herbivores (Fig. 2). It should be noted that the model is still hypothetical. The necessary testing might be facilitated by the following summary of the essentials.

The RSGC can be represented by a triangle (Fig. 3). The sides reflect the building and degeneration phases of *Calluna* and the lawn phase of *Deschampsia*. The RSGC acts as a limit-cycle (Begon, Townsend & Harper 1996). At the angles, the cycle is reaching limits of maximum *Calluna* biomass, maximum and minimum soil nutrient pool respectively. Infestation by heather beetles and other disturbances are most probable in the mature and nutrient saturated *Calluna* (Berdowski 1993), invasion by *Deschampsia* and cattle during the degeneration phase. Because of nutrient depletion *Deschampsia* production declines, the grazer moves on, allowing *Calluna* to re-invade. Abandonment by cattle and *Calluna* invasion may display positive feed-back. Nutrients accumulate in the biomass and soil pool during the building and mature phases of *Calluna* (Berendse 1998*)*. During degeneration, nutrients of biomass pool are transferred to the soil pool, from which they are absorbed by *Deschampsia* and subsequently harvested and exported by the grazer (cattle). The biomass maximum and the longevity of the building phase depend on the growth rate and herbivory; the biomass minimum on the degeneration and replacement rate of *Calluna* by grass. The upper limit of the soil nutrient pool is determined by the input of plant litter, the lower limit by the net off-take by grazing and other losses. Losses by erosion and leaching may strongly vary according to slope, uptake capacity of the vegetation and retention capacity of the soil (e.g. Cation Exchange Capacity). The soil depletion rate and the browsing pressure on invading *Calluna* are important determinants of the lawn longevity.

Nutrients play a crucial role in the model by modifying many of the plant-herbivore interactions. External inputs will change the cycling rate, not the cycle, unless critical thresholds are surpassed. Fertilisation may prolong the *Deschampsia* phase and shorten the *Calluna* phase by accelerating its height growth, maturation and nutrient saturation. When nutrient inputs exceed or equal the losses during the *Deschampsia* phase, the soil nutrient pool is not depleted and the RSGC is running out of its validity range. On fertilised, highly productive lawns, grazing may continue at a high intensity level, preventing the expansion of germinated *Calluna* by browsing and trampling. In such lawns, alternative successional pathways with other woody species and other resistance mechanisms may occurr (e.g. *Rubus, Ulex, Rosa, Prunus spinosa)* (Bokdam *et*

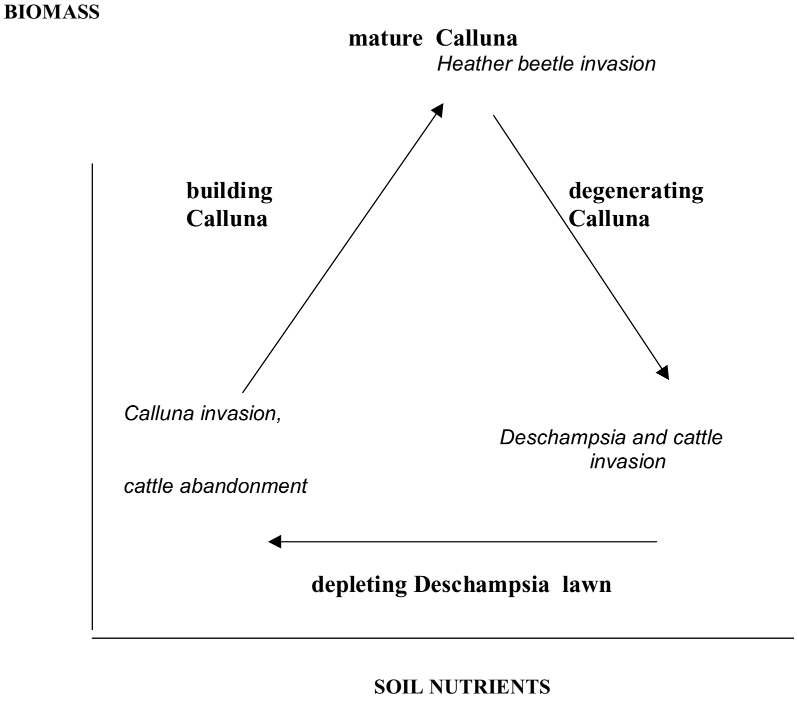

Figure 3. Conceptual model of the Resource-mediated Successional Grazing Cycle of *Calluna* and *Deschampsia.*

al. 2001). Nutrient depletion by additional losses may shorten the lawn phase and prolong the dwarf-shrub phase. Intensive browsing of *Calluna* (e.g. by rabbits, herded livestock or mowing) may create a long-lasting dwarf shrub lawn if gaps with a replenished soil nutrient pool are prevented. If the soil is depleted by the browsing or by additional fires, erosion and management mimicking these natural influences (e.g. mowing, burning, turf-stripping), *Calluna* cycles with bare soil, litter, lichens and bryophytes might emerge. Examples of such *Deschampsia*-free *Calluna* cycles occur in blown-out areas in drifting sand landscapes browsed by mouflon, red deer and rabbits in the Hoge Veluwe National Park (Bokdam, personal observations).

In the demostat model of Naveh & Lieberman (1984), grazing drove a cycle of a palatable grass and unpalatable smaller forbs. The RSGC model deals with the inverse situation. Transitions between meta-stable states are often considered as highly stochastic due to unpredictable vegetation disturbance and herbivore crashes (van de Koppel *et al.* 1996, Huisman *et al.* 1999). The RSGM proposes a resource-mediated equilibrium mechanism for plant – herbivore systems. The meta-stable states have different resource levels, dominant plants and herbivore assemblages (herbivory pressures). The states act as patch in a mosaic with a shifting configuration. The composition (patch proportions) may remain constant by opposite, compensatory transitions as long as the herbivore load and the nutrient pool of the whole mosaic (area) remain constant.

The hypothesised RSGC might be valid across a broader range of spatial scales, plants and herbivores in nutrient-limited environments. The studied sub-plots and plots constituted mosaics at community scale ($25 m^2$, Bokdam & Gleichman 2000). Patterns of *Calluna*-dominated and *Deschampsia*-dominated areas of larger size (> 1 ha) in the study area reflected soil fertility patterns due to differential land use and management history (Bokdam & Gleichman 2000). Grazing-induced transitions between *Molinia caerulea* and *Erica* and related mosaics occurred in the study area (Bokdam & Gleichman, 2000 Fig 1 e-f; Bokdam personal observations). The RSGC-model may generate qualitative predictions of effects of different herbivores, herbivores management strategies (e.g. free-ranging vs. herding, summer grazing vs. winter grazing) and additional vegetation management. These variables will affect the cycling rate and related mosaics, according to the resulting habitat use, diet selection, treading pressure and nutrient redistribution patterns. The model suggests that heathland restoration and maintenance require different grazing regimes. Restoration of *Calluna* in *Deschampsia* grass-heaths will be maximised by large grazers with preferential grass diets, displaying large-scale spatial segregation of foraging and resting habitats and a high hoof pressure. Heavy browsing or trampling in this stage would impair the establishment and lateral expansion of *Calluna*. Moderate browsing may favour the clonal growth of *Calluna*. Restoration success may therefore increase with body size: heather beetle < small rodents < rabbits < sheep < red deer < horses < cattle. Maintenance of *Calluna* will be maximised by moderate browsing (by rabbits, sheep or red deer) if the soil nutrient pool remains at a low level. Browsing will delay ageing and favour vegetative regeneration and *Calluna* re-establishment in *Deschampsia*-free gaps, but uneven defoliation and nutrient redistribution will inevitably lead to small-scaled mosaics with local grass invasion. Cattle and other large grazers might accelerate this process, leading to heather-grass mosaics, while large-scaled homogeneous, even-aged *Calluna* requires machines and fire.

The RSGC-model, linking herbivory and soil fertility to vegetation succession and biodiversity may become a useful tool for conservation managers. Implementation requires further testing of its validity range and quantification (Berendse 1985; Van Oene *et al.* 1999).

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Chapter 4

Free-ranging cattle as opportunistic exploiters of a successional woodland-grassland-heathland mosaic

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Cattle as opportunistic exploiters. Frangula alnus (photo) and other woody and herbaceous understory species were suppressed by consumption, trampling and head-rubbing. Wolfhezerheide, July 1987 (photo Maurits Gleichman).

Free-ranging cattle as opportunistic exploiters of a successional woodland-grassland-heathland mosaic

Jan Bokdam, J. Maurits Gleichman, Sipke E. VanWieren & Michiel F. WallisDeVries

Summary

Large herbivores are increasingly used as a conservation management tool. Using herbivores in this way requires knowledge of their habitat and diet preferences. We studied the habitat and diet preferences of cattle in woodland-grassland-heathland mosaics using direct observations and bite counts from three study areas. The aim was to test differential preferences for successional habitats and species (grasses, early and mid-seral woody species) as causal factors driving cyclic succession. Our results provided evidence for differential habitat preference during foraging and non-foraging. Foraging time was spent predominantly (83 %) in open communities, non-foraging time mainly (56 %) in woodland, despite a low proportion (33 %) of this habitat in the mosaic. The findings implicated a substantial nutrient redistribution from lawns to woodland. *Deschampsia flexuosa* was the dominant species in the diet. This grass species and a group of other ”short grasses” (i.a *Holcus spp*, *Agrostis capillaris)* were significantly selected. *Molinia caerulea* was consumed during summer only. Mid-seral shrubs and trees (e.g. *Quercus robur, Sorbus aucuparia, Frangula alnus* and *Prunus serotina*) were selected, especially during summer, but not significantly so. *Rubus fruticosus* was the exception and was avoided. The early-seral dwarf shrubs *Erica tetralix and Calluna vulgaris* (during summer only) and trees *(Pinus sylvestris* and *Betula spp)* were avoided. The opportunistic use of the mosaic components suggests that successional mosaics with at least woodland and grassland are optimal habitats for cattle. The results confirmed that cattle may act as a driving force for mosaic cycling but they also revealed variation in the palatability within successional species groups of grasses, early-seral and late-seral woody species. Cattle can suppress palatable woody undergrowth in woodland and create and deplete lawns until resistant shrubs or trees invade. Implications of the findings for the use of cattle as a conservation tool are briefly discussed.

Key-words: nature conservation, cyclic vegetation succession, grazing, browsing, habitat preference, diet selection, soil nutrients.

INTRODUCTION

Livestock and wild herbivores are increasingly used as a management tool in nature conservation areas (Oosterveld 1975; Bakker 1989, 1998; Gordon *et al.* 1990; Severson & Urness 1994; VanWieren 1995; Piek 1998). Their use as a tool presumes a key role of herbivores in the functioning of ecosystems and requires knowledge of their habitat and diet preferences (Coughenour 1991). Open, nutrient-poor habitats are important for biodiversity and in many areas traditional extensive livestock grazing is continued or reintroduced (Gimingham 1992; Bignal, McCracken & Curtis 1994; WallisDeVries, Bakker & VanWieren 1998, Bokdam & Gleichman 2000). Livestock grazing as a management policy is challenged by the wilderness grazing policy (Bunzel-Drüke, Drüke & Vierhaus 1993/1994; Vera 1997, 2000; Svenning 2002). Cattle, horses and other grazers may play an important role in both strategies, either as livestock or as feral species. We studied the habitat and diet preferences of free-ranging cattle as a determinant for open, nutrient-poor habitats in successional woodland-grassland- heathland mosaics.

The effects of grazing on plant succession depend on the involved herbivores (Hoffman 1989, Gordon, Illius & Milne 1996), plant species (Briske 1996; Bakker 1998; Bullock *et al.* 2002; Milchunas & Noy Meir 2002), and environmental factors e.g. soil fertility, fire and man (Ormerod 2002). Openness is the result of replacement of woodland by short vegetation and by prevention of re-invasion of trees. Replacement of woodland by grassland requires tree mortality, suppression of woody undergrowth and grass invasion. In W-Europe, mature trees are rarely killed by large herbivores. They usually die by ageing, storm, fire, insects, fungi or cutting by man. But many large herbivores are able to suppress woody undergrowth (shrubs, saplings) and to introduce grass seeds. Common undergrowth species on nutrient-poor acid soils that are suppressed are the mid-seral *Quercus spp, Sorbus aucuparia*, *Frangula alnus, Prunus serotina* and *Vaccinium myrtillis* and late-seral species *Fagus sylvatica, Ilex aquifolium and Taxus baccata* (nomenclature follows Van der Meijden 1990).

Openness of grassland or heathland habitats may be lost by invasion of early-seral trees (P*inus sylvestris, Betula* spp) (Gimmingham 1992). These early-seral woody species differ from the mid-seral ones by smaller seeds, anemochorous (in stead of zoochorous) dispersal, smaller seedling, higher requirements for light and lower requirement for nutrients and moisture (Bazzaz 1979; Ellenberg *et al.* 1992). Diet selection (Putman 1986; Van Wieren 1996) and plant chemistry (Bokdam &

WallisDeVries 1992; Van Genderen, Schoonhoven & Fuchs 1996) suggest that early-seral woody species – being more resistant than mid-seral ones – might be able to outcompete ungulates.

Herbivores can create or maintain nutrient-poor soils by net nutrient removals (offtake > return) and by secondary losses due to volatilisation, erosion, leaching, etc., if the losses are not compensated by inputs (fertilisation) or by accelerated cycling (Milchunas & Lauenroth 1993; Frank, Kuns & Guido 2002). Net removal is enhanced by differential habitat use (foraging and non-foraging in different habitats) redistributing nutrients from foraging habitats to resting habitats. Cattle and other social large ruminants are superior nutrient movers. Their consumption is aggregated and they spend less time foraging and more time on resting sites than non-ruminants (e.g. horses) (Arnold & Dudzinski 1978). Large herbivores with large home ranges may transport nutrients over longer distances.

Until now, models predicting grazing effects on vegetation succession have been predominantly based upon differential defoliation of established plants and competitive displacement for light (Coughenour 1993; Jorritsma *et al.* 1997; Vera 1997, 2000; Van Oene, Van Deursen & Berendse 1999, Groot Bruinderink *et al.* 1999; Olff *et al.* 1999). Differential dispersal and establishment and effects mediated by changing soil fertility have either been ignored or incompletely included. Recently, long-term botanical changes in sub-alpine pastures grazed by red deer (Krüsi *et al.* 1995; Schütz *et al.* 2000) and wood encroachment in *Deschampsia* heaths grazed by free-ranging cattle (Bokdam 1996; Bokdam & Gleichman 2000) were attributed to lawn nutrient depletion. Differential habitat and differential diet preference (preference for mid-seral woody species, avoidance of early-seral species) have recently been integrated in a conceptual Resource-mediated Successional Grazing Cycle (RSGC) model (Bokdam, Cornelius & Krüsi 2001; Bokdam 2001). The name refers to grazing as the driving force for successional grazing cycles (as opposed to circadian, intra-seasonal and annual grazing cycles, Drent & Van der Wal 1999) and to mediation by nutrients and light. The RSGC model (Fig 1) plots biomass (and light availability) on the y-axis and soil nutrients (total or available pools) on the x-axis. The three essential grazing influences to be tested in this paper are (i) suppression of mid-seral woody undergrowth species, (ii) soil nutrient depletion of the grass lawn and (iii) avoidance of early-seral dwarf shrubs and trees invading in the nutrient-depleted grass lawn.

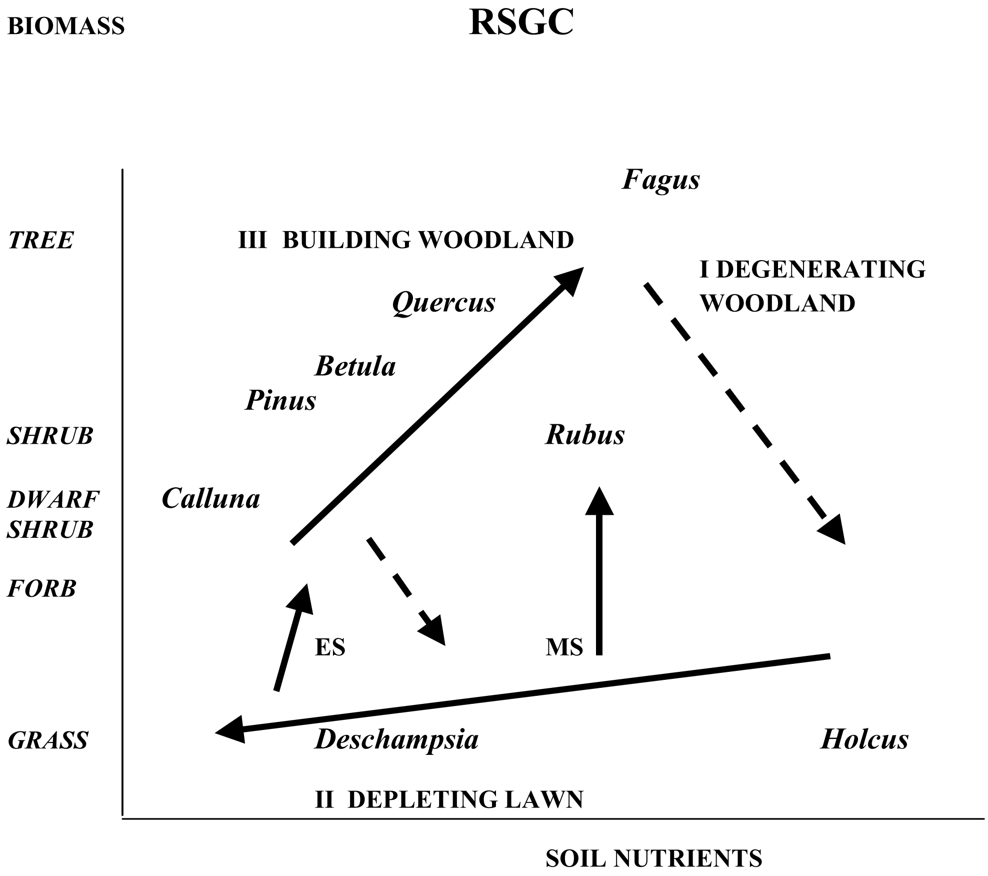

Figure 1: Resource-mediated Successional Grazing Cycle (RSGC). During woodland degeneration (I) soil fertility increases by input of nutrients in dead biomass and increased mineralisation. Grazers facilitate the establishment of grass lawns by suppressing mid-seral woody undergrowth (MS), grass seed dispersal, defoliation and treading. Nutrient and light availability increase. During the lawn stage (II) the soil nutrient pool is depleted by biomass removal. Nutrients ingested on the grazing lawns are excreted in non-foraging habitats. Nutrient depletion followed by reduced food production, food quality and grazing intensity enhance the invasion of light demanding unpalatable early-seral (ES) dwarf shrubs (*Calluna vulgaris, Erica tetralix)* and trees (*Pinus sylvestris* and *Betula pendula*). Abandonment by the grazer initiates a new woodland phase and nutrient replenishment (III).

Domestic cattle (*Bos taurus*) are generally considered to be typical grass consumers and grassland exploiters. This suggests a low pressure on browse (woody food plants). The adaptation of cattle to grasses and grasslands involve a wide lower incisor arcade (Illius & Gordon 1987), an adapted digestive tract (Hofmann 1989), a high capacity to digest cell wall material (Van Wieren 1996) and an aggregative behaviour (McNaughton 1984, Phillips 1983). Although grazers ('Grass & Roughage

Feeders' sensu Hofmann 1989) co-evolved during the Tertiary and Quaternary with grasses (Stebbins 1981; McNaughton 1984) actual wild cattle and spiral-horned antelope species are predominantly found in woodland habitats with varying proportions of grasses (Sinclair, Cock & Hall 2001; Hall & Underwood 2001). The last free-roaming Aurochs (*Bos primigenius*) also lived in woodland (Jaktorow Forest, Poland, 15-16th century) and were reported to consume grasses during summer, acorns in autumn and twigs in winter (Van Vuure 2001). It may be assumed that habitat choice and woody diets of these wild species have been affected by predators. This assumption would imply that domestication, breeding and selection since 9000 years BP (Clutton-Brock 1999) might have enforced the preference of cattle for open landscapes and grasses.

Studies on free ranging domestic cattle in woodland-grassland mosaics do not confirm this hypothesis but point to a sustained opportunistic use of woodland and grassland across foraging and non-foraging periods, seasons and environmental conditions (Arnold & Dudzinski 1978; Senft, Rittenhous & Woodmansee 1985 a,b; Pratt et al 1986; Putman 1986; Bokdam 1987; Van Wieren 1988; Phillips 1993; WallisDeVries 1994). The average composition (± sd) of 121 diets of free-ranging cattle, mainly from North America showed 72 (± 25) % grass (and graminoids), 15 (± 16) % forbs (dicotyledonous herbs) and 13 (± 21) % woody plants ('browse') (Van Dyne *et al.* 1980). In some cases, the low browse content may have been due to a low availability. Ten out of the 121 diets contained > 50 % browse. It suggests that domestic cattle might be capable of creating and maintaining openness by browsing.

Cattle select not only between but also within the broad categories of grasses, forbs and browse (Van Dyne *et al.* 1980; Putman 1986). Based on empirical observations, pasture plants of W-Europe have been ranked in 10 classes of Forage Value ranging from –1 (poisonous and avoided), 0 (without any value, avoided) to 8 (highest quality, strongly preferred) (Klapp 1965).

Our aim was to test the following hypotheses:

1. Cattle display differential habitat preference. They prefer grassland to non-grassland (woodland and heathland) during foraging and prefer woodland to open habitats during non-foraging.
2. Cattle display diet preferences. They prefer lawn grasses to woody species, and prefer mid-seral to early-seral woody species.

MATERIAL AND METHODS

DEFINITION OF PREFERENCE AND ATTRACTIVENESS

Preference is an animal trait, referring to the probability that the animal will choose an item (habitat, plant or site) from a specified range of alternatives. Selection refers to the processes that are involved. Attractiveness (or palatability) is a plant trait, referring to the probability that this plant will be chosen by a specified herbivore from a specified range of alternatives. Preference and palatability are variable in space and time, because herbivores and plants change (Provenza 1996). Preference and palatability should ideally be assessed by the choices made under *ad libitum* conditions. Under field conditions with limited availability, preference and palatability are approximated by selection indices (relative use /relative availability) (Van *Dyne et al.* 1980; Loehle & Rittenhouse 1982; Senft *et al*. 1985 a,b).

STUDY AREAS

The study areas Wolfhezerheide, Doorwerthse Heide and Imbosch (Table 1) are located on the Veluwe, a dry fluvio-glacial moraine and aeolian cover sand area with (mainly) podzolic soils and drifting sand, in the centre of the Netherlands. The successional woodland-grassland-heathland mosaics developed from heathland by spontaneous succession, by tree planting and by grass invasion due to eutrophication after abandonment by pastoralists at the beginning of the 20th Century. The openness of the remaining heathland area was maintained by removal of encroaching trees and occasional and local mowing and turf stripping (Bokdam & Gleichman 2000). At the Wolfhezerheide, the *Deschampsia* habitat (*Deschampsia flexuosa cover* > 75 %) had become the dominant habitat by 1983. In *Calluna* habitats there was > 25 % cover of *Calluna vulgaris*. Pure *Calluna* stands were in the building phase after restoration by turf stripping and mowing. Degenerate *Calluna* was being invaded by grasses. In January 1983, cattle were introduced as a management tool for the restoration of *Calluna* and the suppression of colonising trees. Annual stocking rates have been maintained at an equivalent of approximately 0.2 animal units ha^{-1} (1 animal unit = 450 kg) until 1993. Rates were 30 % higher in summer than in winter. From 1984 on, a minor quantity (1-2 kg dry matter animal^{-1} d^{-1}) of supplementary food (concentrates, hay or corn silage) was occasionally provided during late winter at a fixed location to prevent starvation. Throughout the study period 1-3 horses were occasionally allowed in the area. Densities of roe deer *Capreolus capreolus* L. (2-4 km^{-2}) and rabbit *Oryctolagus cuniculus* L. (100 km^{-2}) were low. The winter of 1984-1985 was cold by Dutch standards. Since 1970, no fires occurred in the study area.

The Doorwerthse Heide (28 ha) is situated adjacent to the Wolfhezerheide. The successional mosaic included less woodland and *Molinia* habitat and more *Calluna* heath compared to the Wolfhezerheide. Cattle were introduced into this area in April 1989 as part of an experiment to compare the carrying capacity of nutrient-poor and nutrient-rich landscapes for cattle (WallisDeVries 1994, Table 1).

The Imbosch is located at 20 km East of the other two areas. A small herd of cattle was introduced in December 1982 to study vegetation changes and animal performance (Van Wieren 1988). The area was mainly covered by pine forest with an understory of *Deschampsia*, *Vaccinium myrtillus* and *V. vitis-idaea.* The open terrain (ca. 10 %) was covered by *Deschampia, Calluna* and *Vaccinium vitis-idaea* (Table 1).

DATA COLLECTION

Habitat use and bite counts in the Wolfhezerheide were assessed from summer 1983 until summer 1985 by direct visual observations at 10-minute intervals during 24-h observation periods. The data set, composed of 52 24-h periods, covered 2 years and involved 3 study animals. Habitat, geographical position and behavioural activity (foraging or non-foraging) of the study animals were noted. During 1 minute in each interval, bites per plant species were counted. The study animal was considered to be representative of the whole herd.

In the Doorwerthse Heide 5 study animals were used. Their diet was assessed by bite counting during 1994-1996, 6 phenological periods per year (May, July, September, November, January and March), each with 3 sampling days (daylight period only) (WallisDeVries 1994). In the Imbosch the habitat use and diet composition was assessed in 1983 by visual bite counting at 10-minute intervals during 24-h periods using one cow as the study animal (Van Wieren 1988).

Table 1: Main characteristics of the study areas.

GRAZED AREA	**WOLFHEZER HEIDE**	**DOORWERTHSE HEIDE**	**IMBOSCH**
REFERENCE	Bokdam & Gleichman 2000	WallisDeVries 1994	Van Wieren 1988
SOIL	Dry-moist, coarse-fine sand, podsolic and plaggen soils	Dry, coarse-fine sand podsolic soils	Dry, coarse-fine sand, podsolic soils
SURFACE (ha)	60	28	173
SUCCESSIONAL HABITATS (%)			
Woodland	32	9	90
Deschampsia habitat	49	51	Open habitat 10
Molinia habitat	4	1	
Calluna habitat	14	36	
Other	1	3	
SPECIES COVER (layer < 1.80 m, %)			
'Short grasses'	0.6	0.7	1
Deschampsia	78.8	55.4	50
Molinia	4.2	0.9	0.1
Calluna	8.1	32.6	2
Erica	2.2	2.4	0.1
Vaccinium myrtillus	0.7	0.0	6
Early-Seral trees (major species)	4.4 (*Pinus, Betula*)	5.1 (*Pinus, Betula*)	2.1 (*Betula*)
Mid-Seral trees (major species)	0.3 (*Sorbus aucuparia, Prunus serotina, Quercus robur, Frangula alnus*)	2.9 (*Prunus serotina, Quercus robur*)	0.1 (*Quercus robur, Sorbus aucuparia*)
Other (major species)	0.9	0.0	38.6 (*Vaccinium vitis-idaea*)
HERBIVORE ASSEMBLAGE, CATTLE			
Breed (sex and age)	Dutch-Friesian (heifers)	Meuse-Rhine-Yssel MRY (steers)	Scottish Highland (mixed)
Introduction	January 1983	April 1989	December 1982
Number of animals (Stocking rate, au ha^{-1})*	14 (0.2)	5 (0.18)	10 (0.06)
Study period	May 1983-May 1985	April 1989-July 1991	January-December 1983
Observation method	24-h, direct, 1 animal	Daylight, direct, 5 animals	24-h, direct, 1 cow
Other herbivores	1-3 horses, roe deer, rabbits	roe deer, rabbits	Red deer, wild boar, roe deer, rabbits

*1 au (animal unit) = 450 kg

DATA ANALYSIS AND STATISTICS

The observations in the Imbosch did not distinguish between habitats (plant communities) in the open landscape. Therefore we used only the 24-h data of the Wolfhezerheide for testing the differential habitat hypothesis. The 52 24-h data were pooled and monthly averages were calculated. Seasonal, half-year and annual averages were calculated as averages of 3, 6 and 12 monthly values respectively. Seasons were defined as winter (December-February), spring (March-May), summer (June –August) and autumn (September-November). Foraging Time in habitat type i (FT_i) was transformed into Relative Foraging Time (RFT_i) by dividing FT_i by the total foraging time of that day TFT. An identical procedure was followed for Non-Foraging (NF) and Occupancy (Foraging + Non-Foraging). The habitat Selection index for Foraging (SF_i) was calculated as $SF_i = RFT_i / RA_i$ in which RA_i = Relative Area of habitat type i (Loehle & Rittenhouse 1982). Selection indices for Non-Foraging (SNF) and Occupation (SO) were calculated in a similar way.

We used the diet of the Wolfhezerheide to compare habitat use with diet at species level. This diet also allowed distinction of successional forage classes "other short grasses" (including the lawn species with a low cover), early-seral trees and mid-seral trees (Table 1). These classes allowed us to use the data of the three study areas for testing of preferences for these forage classes. The number of bites per plant species per day (B_j) was transformed into the Relative number of Bites (R B_j). Diet selection indices for species j (S_j) were calculated as $S_j = R\ B_j/RC_j$ in which RC_j = Relative Cover of species j in the vegetation. The Relative Cover values of plant species (Table 1) were assessed by stratified sampling. Vegetation was classified according to the dominant species, mapped and the area of each type on the map was assessed. For each type, the relative cover of each plant species was assessed in relevees using an extended Point Quadrat method in the Wolfhezerheide (Bokdam & Gleichman 2000) and visual estimates in the other two areas (WallisDeVries 1994; Van Wieren 1988).

The combination of daylight observations from the Doorwerthse Heide with 24-h observations from the other two areas introduced a minor bias. Nocturnal grazing in the latter two areas was restricted to the winter months (September-April) and rarely exceeded 1 h. Monthly data for the Doorwerthse Heide were obtained by intrapolation of the data of the 6 phenological periods.

Habitat selection in the Wolfhezerheide and diet selection in the three study areas were assessed by testing S-values for deviation from 1, using One-Sample T-tests after logtransformation and testing for normal distribution using Kolmogarov-Smirnov. A significant deviation from 1 means preference or avoidance. Differences between the S-values of diet components were tested using GLM Repeated Measures with *post hoc* multiple comparisons, with diet components as between-subject factor and the 12, 6 or 3 months as within-subject factors in case of annual, half-year and seasonal S-values respectively, and three areas as replicates (SPSS release 9).

RESULTS

HABITAT SELECTION

The habitat use by the study animals was considered to be representative of the herd. The heifers remained together (< 50 m from each other) for more than 95 % of the observation time, using obvious visual, vocal and olfactory communication.

Foraging started around or shortly after sunrise and ceased around sunset. Night grazing occurred between September and April, predominantly as one bout of <1 hour. During the day, foraging alternated with non-foraging. Within non-foraging periods rumination alternated with sleep (no rumination, closed eyes and a head-in-flank position, Phillips 1993).

Over the year, the heifers foraged 452 minutes 24-h $^{-1}$ (7,5 hour or 31 % of the time) (Fig. 2). The residual non-foraging time (988 minutes, 16.5 hour or 69 % of the time) was used for rumination, walking, sleeping, social activities, drinking, etc. Foraging time showed a bi-modal distribution with peaks in spring (April: 580 minutes 24-h $^{-1}$) and autumn (October: 545 minutes 24-h $^{-1}$) and minimum values in mid-winter (January: 405 min 24-h $^{-1}$) and in mid-summer (June: 380 minutes 24-h $^{-1}$) (Fig. 2a). Non-foraging time varied in a complementary way (Fig. 2b).

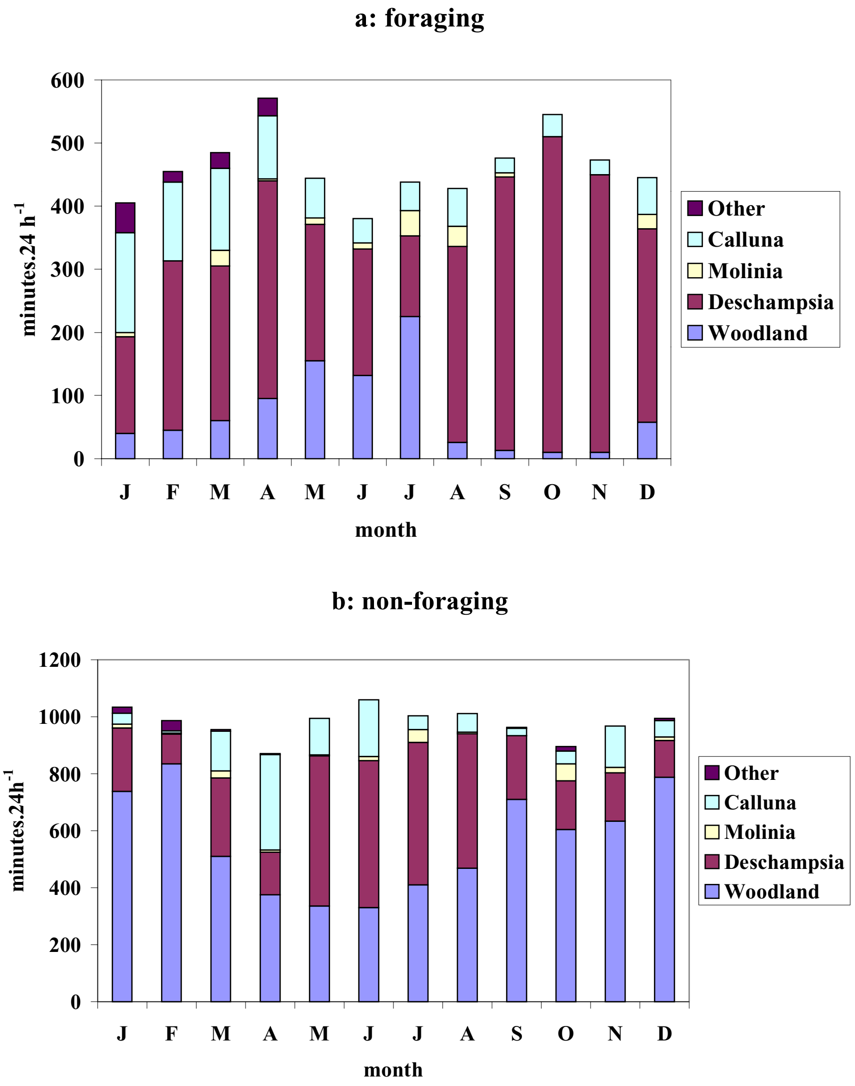

Figure 2. Habitat use during foraging (a) and non-foraging (b) by free-ranging cattle at the Wolfhezerheide (1983-1985)

The circadian rhythm of the Dutch-Friesian heifers at the Wolfhezerheide was very similar to that of other cattle breeds, sexes and age classes in the New Forest (Pratt *et al.* 1986), Imbosch (Van Wieren 1988) and other areas (Phillips 1993). Highland cattle in the Imbosch also grazed on average 6-7 hours, with maximum values of 8-9 hours in spring and autumn and minimum values of 5-6 hours in mid-summer and mid-winter (Van Wieren 1988).

The animals spent 57 % of their time in open area. The open habitats were strongly preferred for foraging, while woodland (forest) was used for non-foraging (Figs 2a,b). Viewed over the whole year, 278 minutes (62 % of the Total Foraging Time) were spent in *Deschampsia* habitat, 73 minutes (16 %) in *Calluna* habitat, 14 minutes (3 %) in *Molinia* habitat, 77 minutes (17 %) in woodland and (2 %) in 'other habitats'. Non-foraging time was mainly spent in woodland (558 minutes, 56 % of the Total Non-Foraging Time). *Deschampsia* habitat (307 minutes, 31 %), *Calluna* habitat (102 minutes, 10 %), *Molinia* habitat (14 minutes, 1 %) and other habitats (7 minutes, <1 %) were less used.

The animals displayed differential habitat selection. *Deschampsia* habitat was significantly selected, while forest was avoided as foraging habitat (Fig. 3). For non-foraging, woodland was significantly selected and *Deschampsia* habitat and *Molinia* habitat avoided (Fig. 3). For *Calluna* habitat none of the S-values deviated significantly from 1. For occupancy (presence) woodland was significantly selected.

The seasonal S-values displayed a similar pattern to the seasonal use values. Foraging in *Deschampsia* habitat peaked in early spring (S = 1.2) and in autumn (S = 1.9), in *Molinia* habitat in mid-summer (S = 2) and in *Calluna* habitat during winter (S = 2.5). Forest was avoided as foraging habitat during the whole year, except during early summer. Non-foraging in forest peaked during the winter half-year and in the *Calluna* habitat during spring. Despite a lower use during all summer months, forest remained selected (S>1) as non-foraging habitat.

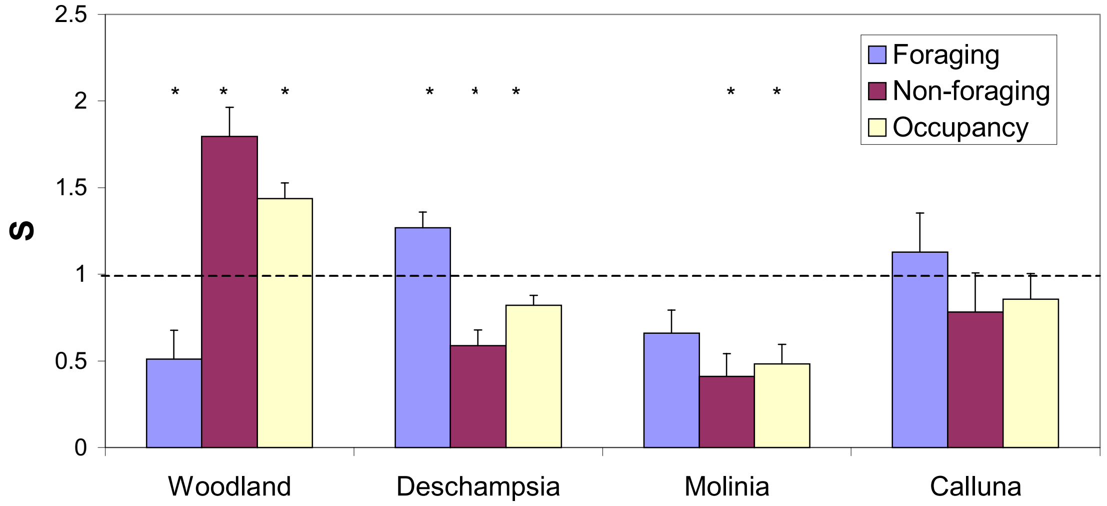

Figure 3. Annual values of habitat selection (Sa) during foraging, non-foraging and occupancy (presence) by free-ranging cattle in the 4 major habitats of the Wolfhezerheide (1983-1985). * = significant selection or avoidance (One-Sample T-test, deviation from 1, *P*<0.05).

DIET SELECTION AT SPECIES LEVEL AT THE WOLFHEZERHEIDE

The annual average number of bites at the Wolfhezerheide was 22,993 24-h^{-1}. The monthly averages showed a bi-modal curve, with maxima in April (32,834 24-h^{-1}) and October (31 ,708 24-hr^{-1}) and minima in January (16,032 24-h^{-1}) and August (16 156 24-h^{-1}) (Fig. 4a) . *Deschampsia* was the major diet species in all months, except in January when it was exceeded by *Calluna*. The proportion of *Deschampsia* peaked in spring (93 % in May) and in autumn (99 % in November). These peaks coincided with peaks in the number of bites (Fig. 4a) and in the foraging time (Fig. 2). Other plant species displayed maxima between the *Deschampsia* peaks. *Molinia caerulea*, the 'short grasses' *(Holcus lanatus, Carex pilulifera* and *Agrostis capillaris* (Fig. 4b), *Vaccinium myrtillis* (Fig. 4c) and the mid-seral tree species (*Prunus serotina, Frangula almnus, Sorbus aucuparia and Quercus robur* (Fig. 4e) peaked during the mid-summer depression of *Deschampsia*. Other species reached their maximum diet proportions during winter: *Calluna vulgaris* during early winter (Fig. 4c), *Erica tetralix* (Fig. 4c), *Pinus sylvestris* and *Betula spp* (Fig. 4d) during late winter.

The corresponding peaks in the S-values were for *Deschampsia* 1.16 (May) and 1.26 (November), *Molinia* 4.80 (July), the short grasses 20.70 (June), *Vaccinium* 2.31 (June), the mid-seral trees 28.46 (June), *Calluna* 7.72 (January), *Erica* 2.46 (March), *Betula spp and Pinus sylvestris* 0.37 (March).

DIET SELECTION, AVERAGE OF THREE AREAS

The seasonal pattern in the diet selection at the Wolfhezerheide allowed to distinguish functional types (forage classes): lawn grasses (*Deschampsia* and other short grasses), tall summer-green grass (*Molinia caerulea*), early-seral trees (*Pinus sylvestris* and *Betula spp*) and mid-seral trees (*Quercus, Sorbus, Frangula, Prunus serotina*). Despite different breeds, stocking rates and vegetation mosaics (Table 1), the seasonal diet selection values (S) were similar in the three areas, as may be concluded from the low standard errors (Fig. 5 a,b). The high error (and underlying deviation) of the summer S-values of *Molinia* was mainly due to variation between the months. *Molinia* showed high S-values in July (Doorwerthse Heide 15, Imbosch 39 and Wolfhezerheide 5) and low values in August (Doorwerthse Heide 8, Imbosch 4 and Wolfhezerheide 1). This decline is attributed to the low digestibility of this summer-green grass after the

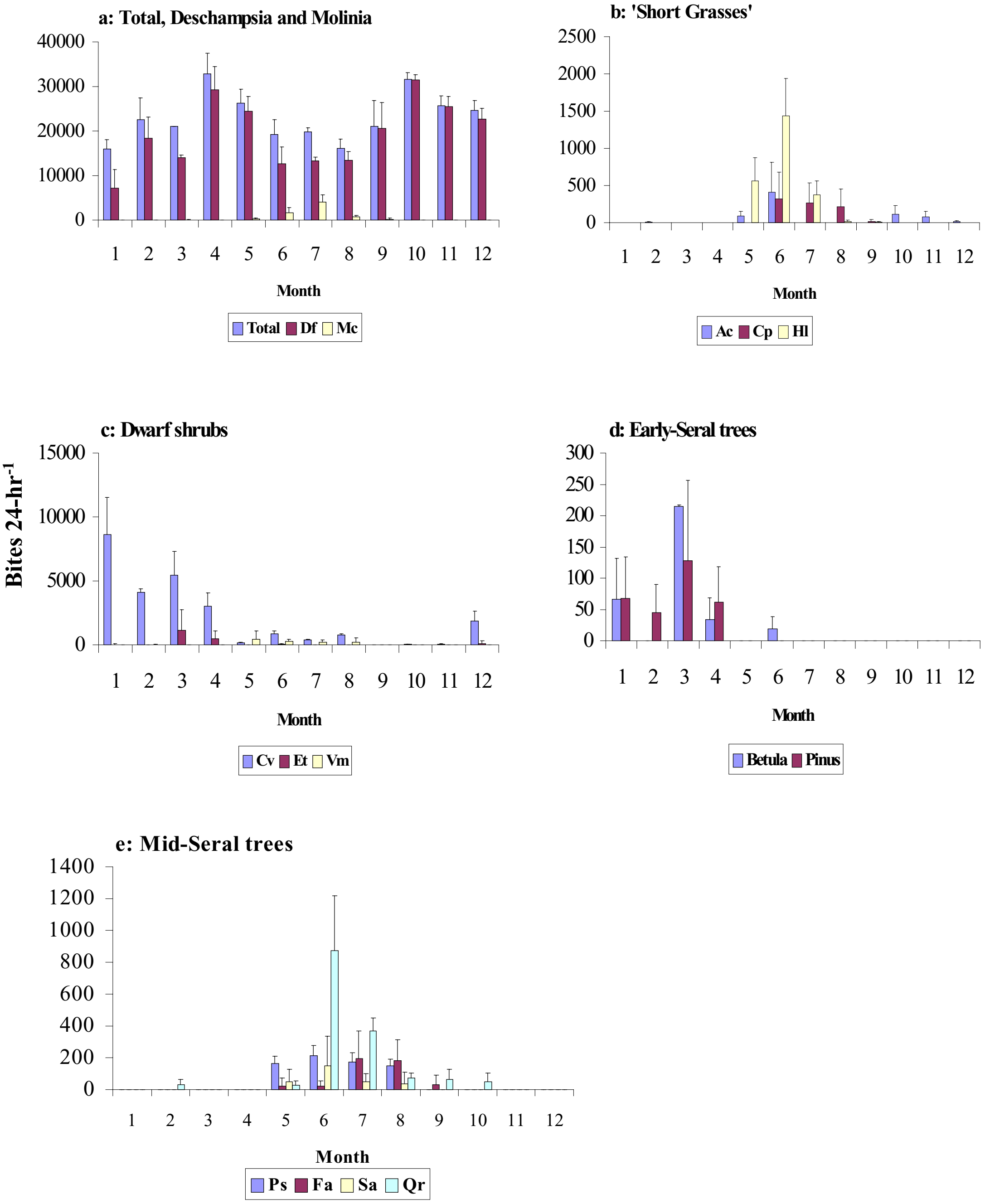

Figure 4. Monthly diet composition (bites 24-h^{-1}) of free-ranging cattle at the Wolfhezerheide (1983-1985). a: Total number and dominant grasses. Df = D*eschampsia flexuosa,* Mc = *Molinia caerulea* ; b: short grasses. Ac = *Agrostis capillaris* , Cp = *Carex pilulifera,* Hl = *Holcus lanatus*; c: dwarf-shrubs. Cv = *Calluna vulgaris,* Et = *Erica tetralix* and Vm = *Vaccinium myrtillus*; d: early-seral trees. *Betula spp* and *Pinus sylvestris*; 4e: mid-seral trees. Ps = *Prunus serotina*, Fa = *Frangula alnus,* Sa = *Sorbus aucuparia* and Qr = *Quercus robur.*

flowering (Chapter 6). The relatively low values in the Wolfhezerheide are explained by the few horses that competed with cattle for *Molinia*.

The annual S-values revealed significant ($P<0.05$) selection for the lawn grasses and avoidance for 3 components. "Short grasses" (4.20) and *Deschampsia flexuosa* (1.45) were significantly preferred. *Erica* (0.11) and the early-seral trees

C

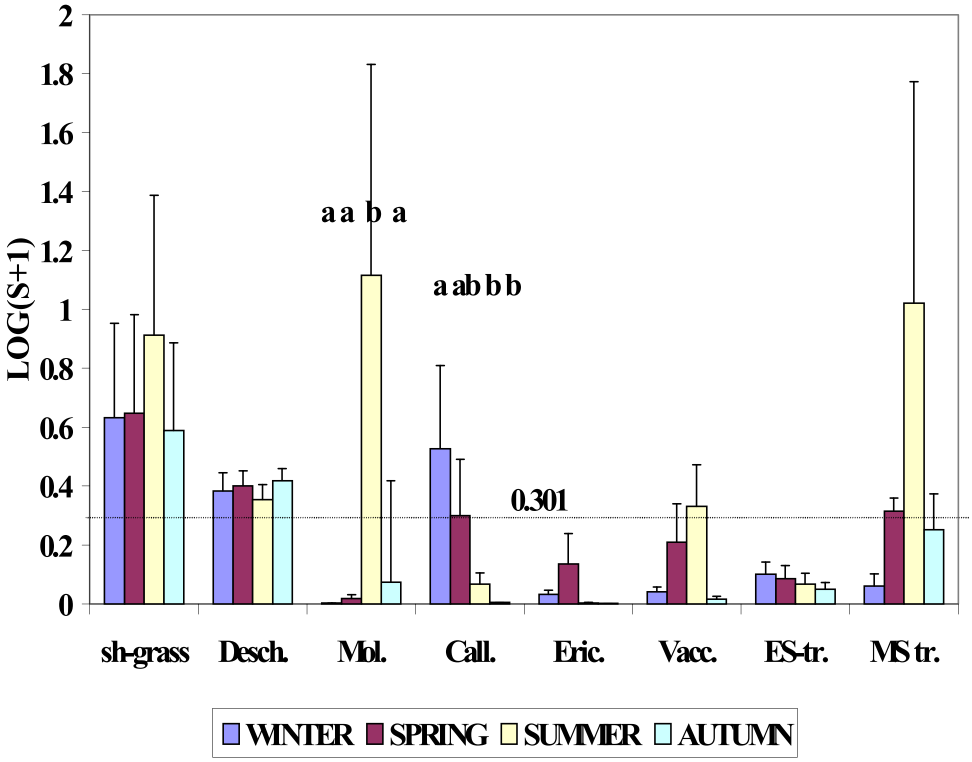

Figure 5. Seasonal variation of selection (S) of successional diet components by free-ranging cattle in woodland-grassland-heathland mosaics. Average values of the Wolfhezerheide, Imbosch and Doorwerthse Heide. Diet components: short grass (*Agrostis capillaris, Holcus lanatus, Carex pilulifera*), *Deschampsia flexuosa, Molinia caerulea, Calluna vulgaris, Erica tetralix, Vaccinium myrtillus*, early-seral (ES) trees (*Pinus sylvestris* and *Betula spp*) and mid-seral (MS) trees (*Prunus serotina*, *Frangula alnus*, *Sorbus aucuparia* and *Quercus robur).* Winter = December-February; Spring = March-May; Summer = June-August; Autumn = September-November. S = (proportion in diet)/(proportion in vegetation); S = 1 (no selection) corresponds with Log (S+1) = 0.301. Different letters indicate significantly different seasons (GLM Repeated Measures, *P*<0.05).

(*Betula spp* and *Pinus sylvestris*, 0.19) and *Vaccinium myrtillus* (0.48) were significantly avoided (S<1, *P*<0.05, Table 2). S-values of *Molinia caerulea* (3.07), *Calluna* (0.88) and mid-seral trees (2.88) were not significantly deviating from 1, probably due to large variations across the year and between the areas (see next section). Multiple comparisons revealed significant differences between the preferred and avoided species, but also between short grasses and *Molinia* and between short grasses and mid-seral trees (Table 2a).

The differences between species in the summer diets showed the same pattern as in the whole year diet, except for *Vaccinium myrtillus*, which was not significantly avoided during summer (S=0.86) (Table 2b). Short grasses (summer: 5.43), *Deschampsia* (1.42), *Molinia* (6.13), *Vaccinium myrtillus* (0.86) and mid-seral trees

Table 2. Significance of differences between the Diet Selection Indices (S) of 8 major diet components (average of three areas). ShGr = Short Grasses; Df = *Deschampsia flexuosa*; Mc = *Molinia caerulea*; Cv = *Calluna vulgaris*; Et = *Erica tetralix*; Vm = *Vaccinium myrtillus*; EST = early-seral trees and shrubs; MST = mid-seral trees and shrubs. Bold = preferred species (S >1, *P*< 0.05); *Italic* = avoided species (S <1, *P*< 0.05). GLM Repeated Measures and multiple comparisons LSD * = *P*<0.05, ** = *P*<0.01, *** = *P*<0.001, values between 0.1 and 0.05 are added between parentheses.

a: annual values (Sa)

Diet component	**ShGr**	**Df**	Mc	Cv	*Et*	*Vm*	*EST*	MST
Sa	4.20	1.45	3.07	0.88	0.11	0.48	0.19	2.88
ShGr								
Df	-							
Mc	*	-						
Cv	**	(0.09)	-					
Et	***	*	(0.09)					
Vm	**	*	-	-	-			
EST	**	*	-	-	-	-		
MST	*	-	-	-	-	-	-	

b: summer half-year values (Ss)

Diet component	**ShGr**	**Df**	Mc	*Cv*	*Et*	Vm	*EST*	MST
Ss	5.43	1.42	6.13	0.09	0.01	0.86	0.13	5.54
ShGr								
Df	(0.08)							
Mc	-	-						
Cv	**	*	*					
Et	***	*	**	-				
Vm	**	-	*	-	-			
EST	**	(0.06)	*	-	-	-		
MST	(0.06)	-	-	(0.07)	*	-	(0.08)	

(5.54) were apparently more selected during the growing season than during winter. Summer half-year S-values of *Calluna* (0.09), *Erica* (0.01) and early-seral trees (0.13) were on the contrary lower than the annual S, indicating that they were more avoided in summer than in winter. The strong contrasts between mid-seral trees and early-seral trees (both annual and summer half-year S values, Table 2a,b) were not significant (*P*=0.297 and *P*=0.08 respectively). The lack of significance was probably due to relatively low S-values for mid-seral trees on the Doorwerthse Heide (mainly *Prunus serotina).*

The multiple comparison also revealed significant differences between diet components (Table 2a,b) and between seasons (Fig 5). Short grasses and *Deschampsia* were selected during the four seasons, while *Molinia*, *Vaccinium myrtillus* and the mid-seral trees were mainly consumed within the summer half-year (May-October). *Calluna, Erica tetralix* and the early-seral trees were avoided until (late) winter. Summer (June-August) values of *Molinia* differed significantly from all other seasons. Selection of *Calluna* during the winter was significantly higher than selection in summer and autumn (Fig. 5).

Multiple comparison yielded significant differences between the annual S-values of preferred short grass and *Deschampsia* on the one hand and the avoided dwarf shrubs (*Calluna*, *Erica, Vaccinium*) and early-seral trees (*Betula* and *Pinus*) on the other hand (Table 2a). Summer half-year values yielded significant contrasts between typical summer diet species (*Molinia, Vaccinium* and mid-seral trees *Quercus robur, Sorbus aucuparia, Frangula alnus* etc.) on the one hand and the typical winter diet species (dwarf shrubs and early-seral trees) on the other hand (Table 2b).

DISCUSSION

DIFFERENTIAL HABITAT PREFERENCE

Our results from the Wolfhezerheide provided evidence for differential habitat use and preference. Foraging time was spent predominantly (83 %) in open communities, a minor proportion (17%) was spent in woodland, which was significantly avoided during this activity (S<1, Fig. 3). Non-foraging time was spent mainly (56 %) in the significantly preferred woodland (S>1, Fig. 3). Viewed over all activities, woodland was the preferred habitat (Fig. 3)

The preference for open habitats during foraging concerned only the *Deschampsia* habitat (62 % of the average grazing time, S >1). *Molinia* was not significantly selected, probably because of its short period of use from June-August, which is probably due to the short growing season and the rapid loss of quality after flowering (WallisDeVries 1989). The *Calluna* habitat was mainly used during winter. Its annual S value surpassed 1, but not significantly so (Fig. 3). It should be noted that part of the foraging time in this habitat was used to eat the *Deschampsia* growing between *Calluna* shrubs (Fig. 4a). The high winter S-value of *Calluna* as food plant is explained by its relatively high winter quality (Bokdam & WallisDeVries 1992) and depletion of the *Deschampsia* habitat. Similar seasonal foraging patterns of cattle across grassland and heathland habitats were found in the New Forest (Pratt *et al.* 1986) and Imbosch (Groot Bruinderink & Lammertsma 2001). The peak of foraging in the forest from May until July (Fig. 2a) was attributed to lower densities of flower stalks of *Deschampsia flexuosa* compared with *Deschampsia* outside the forest, a small amount of fallen pine needles in the grass and 'flushing' mid-seral woody species. Thermo-regulation during hot sunny summer days may also have stimulated grazing in the forest. It follows that the foraging preference for open landscapes if compared to forest was not based on openness as such, but on food availability. This conclusion confirms the findings of Senft *et al.* (1985a,b). It means that open landscape and lawns dominated by unattractive species (e.g. *Nardus stricta, Calluna, Erica*) may be abandoned in favour of woodlands with a superior food availability. Hence, the use of open landscapes is opportunistic.

Non-foraging in forest peaked during the winter half-year (Fig. 2) pointing to shelter as a major determinant, especially during winter and other times when conditions were harsh. The lower use in summer (Fig 2) was due to resting during the night in open communities. Resting during the day still took place in woodland. Scottish Highland cattle in the Imbosch also spent more non-foraging time in forest during winter (69 %) than in summer (57 %) (Van Wieren 1988). Winter night camps in the Wolfhezerheide were exclusively located in pine forest. Occasional measurements during late nights at 10 cm above soil level revealed during winter up to 4 ^{o}C higher temperatures in pine forest than in neighbouring open grassland habitats, probably because of differential radiation losses. It suggests that thermo-regulation, especially energy retention (Murray 1991) was a major factor controlling non-foraging habitat selection, but a possible influence of predation prevention cannot be excluded. The commonly observed sheltering of livestock under trees during hot days and cold nights confirms this conclusion (Arnold & Dudzinski 1978). Differential habitat preference therefore seems to be directly explained by the hierarchy of functions during foraging and non-foraging. More detailed explanation by identifying all factors and quantifying gains and losses is beyond the scope of this paper. The findings indicate a substantial nutrient redistribution from lawns to woodland.

DO CATTLE PREFER GRASSES TO WOODY SPECIES?

The selection of *Deschampsia flexuosa* and 'short grasses' during the whole year (Table 2a, Fig. 4a,b) confirmed the hypothesised preference of cattle for lawn grasses. The preference for *Molinia* (nearly significantly, *P* = 0.06) was restricted to the summer period. *Nardus stricta* and *Danthonia decumbens* (included in other species) seemed to be avoided during the whole year, showing that the preference of cattle for grasses did not cover all species.

Woody plants contributed substantially to the cattle diets because of the winter consumption of *Calluna*. The high summer half-year and annual S-values (5.54 and 2.88 respectively) of mid-seral trees reflected cattle's high preference for these speices during summer. The low proportion in the diet was attributed to the low availability. When *Deschampsia* and *Calluna* are scarce, cattle may shift in winter to trees and shrubs. Woody species in the diet of Scottish Highland cattle in a woodland habitat in Kootwijkerveen shifted from 25 % (mainly Oak) in May-June to ca. 60 % (coniferous and deciduous species) in February (Groot Bruinderink *et al.* 1997).

Because of the important difference between the S-values of mid-seral and early-seral woody species (Table 2a,b) the testing of woody species as a whole against the lawn grasses was not meaningful. The S-value of the preferred short grasses exceeded the S-values of the preferred mid-seral woody species only for the whole year, but not for the summer period alone (Table 2a,b). Short grasses and mid-seral woody species had similar low proportions in the vegetation (Table 1), and therefore similar high potential maximum S-values. The S-value of *Deschampsia* (1.45) was lower than the S-values for mid-seral woody species, but in this case the comparison is not meaningful because the maximum S-value of *Deschampsia flexuosa* – in the case of a 100 % *Deschampsia* diet – can never exceed 1.73. This bias of different ceilings in the S-value only occurs when we compare preferred species (S>1) with highly different proportions in the available forage. The significant difference between the S-values of preferred grasses and avoided early-seral woody species therefore confirmed the hypothesised difference between these functional groups. The results agree with the general shift in the diets of many ungulates from grass during the growing season to woody species during winter (Van Dyne *et a.* 1980).

DO CATTLE PREFER MID-SERAL WOODY SPECIES TO EARLY-SERAL SPECIES ?

The results pointed to a general preference of mid-seral to early-seral woody species, but there were exceptions. The leaves and stems of the typical mid-seral *Rubus fruticosus* were strongly avoided by cattle although consumption of fruits was occasionally observed after 1985. The differences between the S-values of mid-seral trees and early-seral trees were not significant (Table 2a,b). The avoidance of the early-seral *Erica*, *Calluna* (during summer), *Vaccinium vitis-idaea, Betula spp* and *Pinus* (Table 2,3) are explained by resistance based on phenolics and terpenes (Van Genderen, Schoonhoven & Fuchs 1996).

FORAGE CLASSES.

The results allowed the discrimination of 4 forage classes, which were linked to the successional groups of the RSGC. The allocation of species to forage classes that emerged from our study agreed in general with the Forage Values attributed to pasture species by Klapp (1965). These values (-1 = poisonous; 0 = avoided, no value, 8 = highest value) are added in brackets.

Year-round forage. Defoliation-tolerant perennial short grasses and graminoids with a bi-modal growth curve (Behaeghe 1979) and wintergreen tillers with a low winter production and relatively high quality (WallisDeVries 1989; Bokdam & WallisDeVries 1992). *Agrostis capillaris (5), Festuca rubra (4/5), Holcus lanatus (4), Holcus mollis (3), Carex pilulifera (1)* and *Deschampsia flexuosa (3*).

Summer forage. Defoliation-tolerant perennial tall summer-green grasses (and graminoids) and deciduous woody plants, with a uni-modal growth curve, over-wintering by buds at or below soil level or at woody branches. *Molinia caerulea (2), Quercus robur, Sorbus aucuparia, Frangula alnus* and *Vaccinium myrtillis (0*).

Winter forage. Moderately defoliation-resistant and defoliation-tolerant winter-green woody species. *Calluna vulgaris (0*). Cattle lose weight when only feeding on this species (Bokdam & WallisDeVries 1992).

Non-forage. Defoliation-resistant herbaceous and woody species (dwarf shrubs and tree saplings) with a moderately-low defoliation tolerance which are avoided during the whole year. Substantial consumption might induce disorder (Forsyth 1979; Van Genderen, Schoonhoven & Fuchs 1996). *Erica tetralix (0)*, *Juncus effusus (1),* *Nardus stricta* (2), *Danthonia decumbens* (2), *Vaccinium vitis-idaea (0)*, *Rubus fruticosus, Betula pendula, Pinus sylvestris*). Often colonising grazing lawns. In general vulnerable to intensive defoliation (or mowing) and trampling. Inaccessible species ('avoiders' with an annual life cycle, small stature, prostrate growth form, epiphytes, aquatic plants, etc.) and trees with canopies above the browse line (200 cm) are also non-forage.

Absence or depletion of year-round and summer forage may induce the consumption of winter forage (e.g. *Calluna*) during summer. Depletion of year-round and winter forage during winter may force large grazers to consume low-quality remnants of summer forage and non-forage species, with potentially dramatic effects on the animal's performance and health. Summer forage remnants (e.g. *Molinia, Phragmites*) have a very low nutritional value in winter (Bokdam & WallisDe Vries 1992; Vulink 2001). Adding year-round forage (e.g. by supplementation or access to farm grassland) leads to the avoidance of winter forage and non-forage species. Suppression of non-forage species by grazing requires "forced'' defoliation by hungry animals (Vulink 2001), eventually supported by adjusted supplementation at the end of the day.

SUPPORT FOR RSGC -THEORY

The results confirmed the key-role of cattle hypothesised in the RSGC-theory: preferential defoliation of mid-seral woody species, differential habitat preference causing soil nutrient depletion in grass lawns and avoidance of early-seral woody species. The different spatial scales and magnitudes of the nutrient redistribution will be presented in Chapter 5.

Preferential defoliation of mid-seral woody species facilitating the establishment of grasses was demonstrated for all mid-seral woody species, except *Rubus.* This thorny species can therefore initiate an alternative successional pathway to mid-seral woodland (Bokdam 1998; Olff *et al.* 1999). Suppression of *Rubus* prolongs the lawn and depletion process.

The resistance of early-seral dwarf shrubs and trees to grazing explains why cattle are ultimately out-competed on nutrient-poor soils by woody plants. More selective smaller domestic and wild herbivores (e.g. sheep, goats, rabbits) with access to younger and shorter plants and plant parts might be able to delay the invasion by

Calluna or other lawn invaders (Grant *et al.* 1987; Bokdam & Gleichman 2000). The relatively high forage quality and acceptability of the winter-green *Calluna*, in the absence of preferred food items, explains its use as winter forage. Browsing of '*Calluna*- lawns' might prolong the soil depletion process.

Cattle acted as soil nutrient croppers, using lawn grasses as an interface. Depleted lawn nutrient pools are replenished during the next successional phase (heathland or woodland). The exploitation of the accumulated nutrient capital is very similar to the exploitation by human shifting cultivators. The grazers establish grass lawns instead of arable fields. Both grazers and man abandon the exploited site after soil nutrient depletion and/or invasion by weeds.

In the study areas, domestic cattle were shown to be a woodland-grassland mosaic species, using the woodland for resting and the glades for foraging. Cattle in the Wolfhezerheide spent 43 % of their total time in woodland, which covered 32 % of the area (Table 1). In the Imbosch, the occupancy of woodland was 63 % (Van Wieren 1988). The relatively low availability of woodland in the Wolfhezerheide resulted in a significant selection of this successional stage (S = 1.3) in this area. The high availability of woodland in the Imbosch (90 %) explains the avoidance (S = ca. 0.7). These findings point to optimal use and suggest that woodland-grassland mosaics are optimal cattle habitats. They offer better food than pure woodland and better shelter than pure grassland. If so, cattle improve their own habitat (self-facilitation) by creating woodland-grassland mosaics.

Opportunistic, selective exploitation is explained by Optimal Foraging theory (see WallisDeVries 1994). Optimal Foraging requires frequent updating of the animal's information about the spatial distribution of food, water and shelter by so-called 'patrolling' or 'sampling' (WallisDeVries 1994; Provenza 1996). Sampling allows animals not only to discover and adapt to intra-seasonal and annual changes, but also to adapt to successional changes. Moving to new woodland gaps and lawns and abandoning depleted patches are advantageous for the animals and keep the mosaic shifting.

MANAGEMENT IMPLICATIONS

For a more extensive treatment of implications of the RSGC for the management of woodland-grassland-heathland mosaics we refer to Chapter 8 and Bokdam (2002).

Grazing management requires clear targets and understanding of the consequences of the choice of the grazed area and the herbivore assemblage to be used. Both groups of variables affect the habitat and diet selection. Year-round free-ranging cattle on a pure *Calluna* heath will lead to mosaics with grassland patches and woodland (*Pinus* and *Betula*) and eventually *Rubus* (Bokdam & Gleichman 2000), but might require supplementary feeding (WallisDeVries 1994). Adding woodland or fertilised grassland to the grazed heathland stimulates differential habitat use and mosaic development. Adding fertilised grassland will reduce the foraging pressure on low-productive lawns and heathland in the mosaic. Adding other herbivore species may favour openness by the increased defoliation pressure on the woody species and herbaceous plants (Palmer & Hester 2000).

Openness and soil poverty are maximised by maximising the removal of biomass and nutrients (i.e. foraging) and minimising the return (excretion, non-foraging activity). This has been practised since pre-history in W-Europe by traditional livestock farming moving biomass and nutrients from the lawns (pastures) to barns and arable fields. This system created a fixed mosaic landscape with no or little woodland. Unpalatable non-forage trees and shrubs invading pastures were suppressed by pasture management, while winter forage was used during summer. In free-ranging and wilderness grazing systems, woodlands function as a natural 'barn'. Free ranging large grazers, re-cycling the excreted nutrients by creating lawns in the woodland, act as shifting cultivators in a dynamic landscape.

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Chapter 5

Free-ranging cattle as nutrient movers in a successional woodland-grassland-heathland mosaic.

Jan Bokdam

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Redistribution was more important for soil nutrient depletion than body retention. Wolfhezerheide, March 1984 (photo Maurits Gleichman).

Free-ranging cattle as nutrient movers in a successional woodland-grassland-heathland mosaic.

Jan Bokdam

Summary

Large herbivores are increasingly being used as a management tool for maintaining biodiversity associated with open landscapes and low soil fertility. Optimisation therefore requires predictive knowledge of the effects of grazing on vegetation and soil. This paper tests the hypothesis that large grazers can create open, nutrient-poor habitats by depleting the total and available nutrient pool of grass lawns occurring as stage and component of successional mosaics on acid, sandy soils. Comparing grazed and ungrazed sites, grazing effects were calculated as Net Offtake (offtake – excretion) and as Integrated Balance ({atmospheric deposition + excretion + weathering} – {offtake + gaseous excreta losses}). These balances were assessed for the whole grazed area, for the mosaic components *Deschampsia flexuosa* grass heath, *Calluna vulgaris* heath and woodland, and for dung, urine and excreta-free patches within the most intensively grazed *Deschampsia heath*s. Atmospheric deposition in the study area was high. The Net Offtake was based on measured habitat use, the other effects on assumptions derived from published data. Grazing was year-round by free-ranging cattle (stocking rate 0.2 au.ha^{-1}) receiving salt licks and a small amount of winter supplements. Body Retention (as % of the ingested nutrients) was low for N (4.9), K (1.1) and Mg (2.5), moderate for Na (14.1) and high for P (23.1) and Ca (34.3). Net Offtake from the whole area was low (N: 0.4, P: 0.2, K: -0.1, Na: - 0.2, Ca: 0.3 and Mg -0.004 kg ha^{-1} yr^{-1}). Negative values were caused by inputs from supplements, drinking water and salt licks. The cattle moved substantial amounts of nutrients from lawns to forest by differential habitat use. Foraging pressure was high on *Deschampsia heath* (0.26 au ha^{-1}) and low in forest (0.10 au ha^{-1}). Foraging use contrasted with non-foraging and occupancy, the latter being rather low in *Deschampsia* (0.17 au ha^{-1}) and high in forest (0.29 au ha^{-1}). Net N Offtake from *Deschampsia heath* was 7.0 kg ha^{-1}

yr^{-1} while N was imported into woodland (-3.1 kg N ha^{-1}). Redistribution was maximal at patch scale (e.g. Net N Offtake of 18.8 kg N ha^{-1} on excreta-free *Deschampsia lawns*, -367.8 kg N ha^{-1} on dung patches and -432.3 kg N ha^{-1} on urine patches). The annual dung and urine covered area in *Deschampsia* was low (ca. 2.5 %), leaving > 75 % excreta-free after 10 years of grazing. Grazing reduced the interception of atmospheric N for the whole area by 5.2 kg ha^{-1} yr^{-1} and in grass lawns by 9.6 kg ha^{-1} yr^{-1} by reduction of the vegetation height. The assumed gaseous losses of excreta-N (40 %) corresponded with 6.6, 5.3 and 9.4 kg N ha^{-1} yr^{-1} for the whole area, for *Deschampsia heath* and for forest respectively. According to the conservative values of the Integrated Balance, the cattle had depleted the P and K pools on excreta- free *Deschampsia lawns* by 0.2 and 1.6 kg ha^{-1} yr^{-1} respectively. It was therefore concluded that nutrient depletion may have played a role in the assessed encroachment of *Calluna* and pioneer trees (*Pinus sylvestris* and *Betula pendula*) in the *Deschampsia heath*. The results confirmed that large grazers can reduce soil fertility in grass lawns, one of the key-mechanism of the Resource-mediated Successional Grazing Cycle theory.

Key-words: Cyclic vegetation succession, soil fertily, large herbivores, grazers, nutrient redistribution, nutrient cycling.

Introduction

The aim of this paper is to assess the effects of free-ranging cattle on the nutrient balance of a successional mosaic under high atmospheric nitrogen input and to test the hypothesis that cattle can deplete the soil nutrient pools of grass lawns in such mosaics.

Large herbivores are increasingly being used as a tool for management and restoration of biodiversity (Bakker 1989; WallisDeVries, Bakker & Van Wieren 1998). Grazing management requires clear targets and adequate understanding of the role of herbivores in the functioning of grazing systems (Jefferies 1999). The major management variables are the herbivore assemblage and the grazed area.

Open nutrient-poor habitats are essential for many endangered wild plants and animals (Marrs 1993; Bakker & Berendse 1999). Traditional pastoralists exploiting domesticated native grazers have maintained these habitats for several millennia. In W-Europe, low-productive pastoral landscapes have almost completely disappeared through intensification and abandonment (Bignal & McCracken 1996; Webb 1998). The relicts are managed as conservation areas, often by grazing (Piek 1998). Undesired succession, eutrophication and loss of biodiversity in these relicts are attributed to an increase in nutrient inputs, fragmentation and inadequate grazing (Gimingham 1992; Bakker & Berendse 1999; Bokdam & Gleichman 2000). Traditional pastoral landscapes have survived only in economically marginal areas (Bignal, McCracken & Curtis 1994), on marginal soils (Pott & Hüppe 1991), in marginal climates (Schütz *et al.* 2000) and under marginal land use rights (Tubbs 1986). Maintenance of biodiversity in economically and socially non-viable traditional pastoral systems might appear unfeasible in the future European Union (Bignal, McCracken & Curtis 1994). Nature conservation should therefore test alternatives: mechanical management (Bakker 1989), new extensive farming systems (Bignal & McCracken 1996; Bokdam & Gleichman 2000) and ‘new wilderness’ (‘natural’) grazing systems with wild and feral herbivores without human intervention (Baerselman & Vera 1989; Wood 2000).

Because of its far-reaching consequences, the revolutionary new wilderness concept is actually causing fierce debate. It claims that free-ranging wild and feral herbivore assemblages can create open, nutrient-poor habitats as part of shifting successional mosaics (Vera 1997, 2000; Svenning 2002). Experiences so far suggest that free-ranging herbivores can delay but not prevent succession from short vegetation to woodland. Without the help of abiotic factors (low temperature, salt, wind, flooding, drought, fire) or man (cutting, burning, herbivore supplementation), open habitats are sooner or later colonised by woody plants, despite – or perhaps because of – high grazing pressures (Westerhoff 1992; Archer 1996; Pott 1998; Bokdam & Gleichman 2000). Encroachment does not necessarily mean that the openness is lost, as losses by succession can be balanced by the creation of new grasslands in degenerating and disturbed woodland. The simultaneous occurrence of wood encroachment on existing lawns and the creation of new lawns in woodlands can only partly be explained by associational resistance by light-demanding shrubs in the lawn (Olff *et al.* 1999). It has been argued that lawn soil nutrient depletion might play also a role in the encroachment by resistant woody pioneers, e.g. *Calluna vulgaris*, *Pinus sylvestris* and *Betula pendula* (Bokdam 1998; Bokdam, Cornelius & Krüsi 2001; Chapter 4).

Effects of grazing on the total and available soil nutrient pools of grasslands are complex, variable and sometimes opposed in time and space (Watkin & Clements 1978; Clark, Cole & Bowman 1980; Till 1981; Milchunas & Lauenroth 1993). Mechanisms include direct influences (consumption, excretion, treading) and indirect influences (plant species replacement and changes in the total herbivore assemblage, vegetation, precipitation, percolation, runoff and susceptibility to fire, etc.) on the different nutrient flows (Fig. 1) (Frissel 1978; Floate 1981; De Mazancourt & Loreau 2000). Influences and flows display feedback and cascades to other trophic levels (Jefferies, Klein & Shaver 1994; Jefferies 1999). Without inhibition by grazing, primary and secondary vegetation succession may lead to an accumulation of biomass, soil organic matter and nutrients (Berendse 1990; Olff, Huisman & Van Tooren 1993; Leuschner 1993). Potential input flows are weathering, atmospheric deposition, microbial fixation or other external inputs (Fig 1). In W-Europe, atmospheric deposition has become a major source of nutrients in nature conservation areas on dry, mineral-poor soils (Bakker & Berendse 1999).

Consumption removes potential litter and mineralisable nutrients, but this effect may be compensated by returns in excreta and by increased mineralisation rates of the residual litter and excreta input. According to the grazing optimisation theory, herbivory will enhance primary production, litter fall and quality (McNaughton 1983, 1984; De Mazancourt & Loreau 2000; Sirotnak & Huntly 2000). Grazing may also accelerate nutrient cycling by improving abiotic mineralisation conditions such as soil temperature, soil moisture and pH (Kemmers *et al.* 1997; Siepel & Van Wieren 1990). Long-term observation is required to distinguish between acceleration and excitation.

During the first years after introduction, large herbivores can also excitate nutrient mineralisation by a temporary increase in the litter fall by trampling, death by defoliation or reallocation of carbo-hydrates from roots to shoots (Holland & Detling 1990; Kemmers *et al.* 1996). Grazing can also decelerate mineralisation by decreased litter input, redistribution of excreta (O'Connor 1981) and by shifts in the botanical composition from palatable, decomposable species to unpalatable, resistant species producing recalcitrant litter (Hobbie 1992; Grime *et al.* 1996; Pastor & Cohen 1997; Berendse 1998).

Measured effects originate mostly from experiments in grassland under high stocking rates. In woodland-grassland mosaics, net offtake from grassland may be increased by differential habitat use, moving nutrients from the grazed grass lawn to the resting sites in woodland (Weeda 1979; O'connor 1981; Bakker *et al.* 1983; Chapter 4). For cattle and other animals without active latrine behaviour (Edwards &

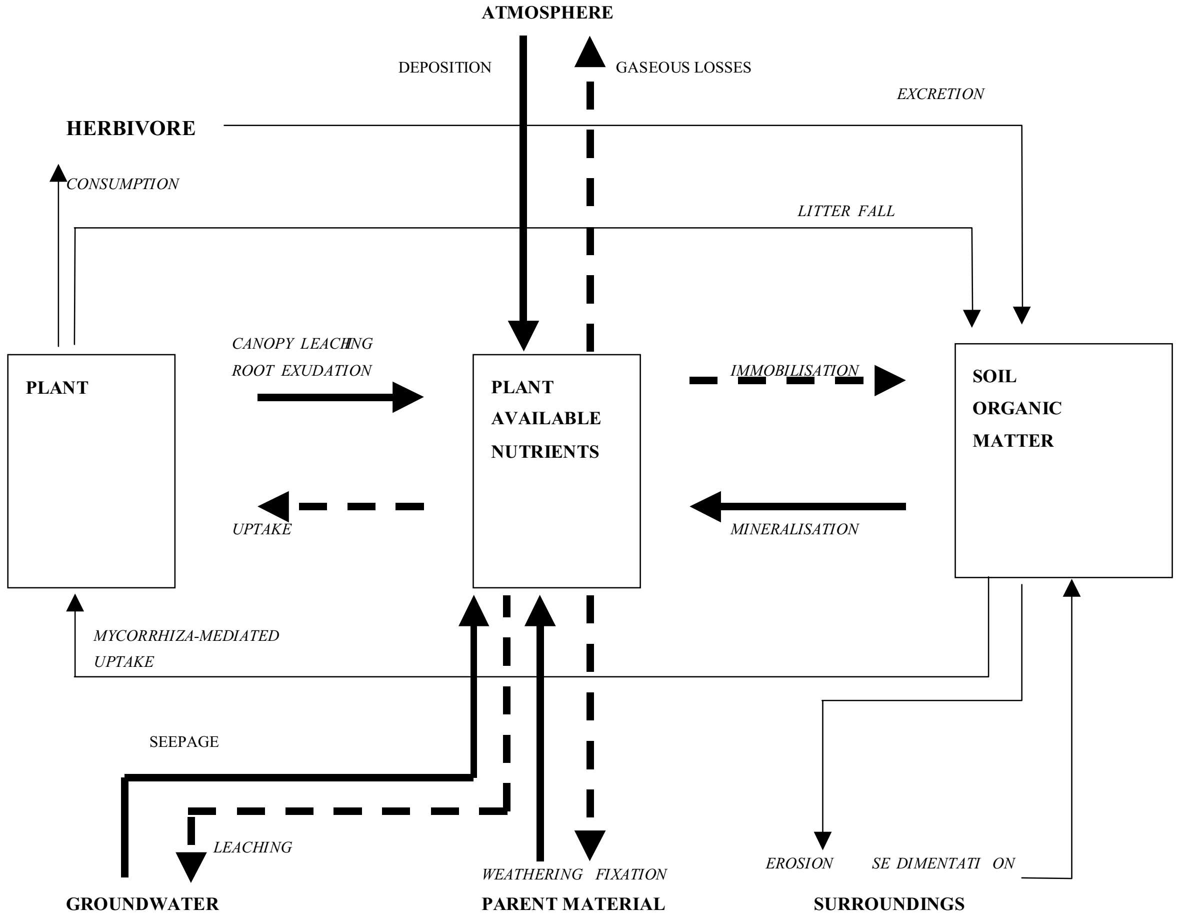

Figure 1 External and internal flows of the Plant/Soil Nutrient Pool in the study area. Bold arrows indicate gains and losses of the anorganic Plant Available Nutrient Pool.

Hollis 1982) excretion is proportional to occupancy (Arnold & Dudzinski 1978).

Models predicting grazing effects on vegetation might be used to test cyclic succession. Unfortunately, these models often include effects of nutrients on the vegetation, but they rarely account for feedback of grazing to soil nutrient availability (Coughenour 1993; Heil & Bobbink 1993; *WallisDeVries* & Van de Koppel 1998; Jorritsma, Van Hees & Mohren 1999; Van Oene, Van Deursen & Berendse 1999; Kramer, Groen & Van Wieren in press). Even when they do (e.g. Berendse 1985) they ignore redistribution, gaseous losses and reduction of atmospheric inputs. Recently, soil nutrient depletion has been put forward to explain wood encroachment on grazing lawns grazed by red deer (*Cervus elephus* L.) (Krüsi *et al.* 1995, Achermann 2000) and cattle (*Bos taurus*) (Bokdam 1996; 1998; 2001). The Resource-mediated Successional Grazing Cycle (RSGC) theory proposed by Bokdam, Cornelius & Krüsi (2001) and Bokdam (2001) focusses on the reciprocal interaction between grazers and soil nutrients. The RSGC theory claims that grazers can create grass lawns in woodland gaps because of the high availability of light and nutrients and that these lawns are encroached by woody plants because of soil nutrient depletion.

Material and methods

STUDY AREA

The Wolfhezerheide (60 ha) is located in the southern part of the Veluwe, a dry sandy area in the centre of the Netherlands, about 12 km east of Wageningen (51^o 47' N; 5^o 41'E). The soil is mainly acid (pH $_{KCl}$ 3-3.5) and podzolic, developed in Pleistocene fluvio-glacial sand and cover sand. In 1983, the successional vegetation mosaic included 19 ha forest, 30 ha of *Deschampsia flexuosa* heath, 3 ha *Molinia caerulea* heath and 9 ha *Calluna vulgaris* heath (Table 1). Plant nomenclature follows Van der Meijden (1990). Before 1983, encroaching shrubs and trees had been removed by the manager, some small parts being mown (in 1982) and turf-stripped (in 1980). In 1983, *Deschampsia flexuosa* covered most parts of the open area and also occurred in the undergrowth of the forest. In January of that year, heifers were introduced for year-round continuous (24-h) grazing. After 1985, they were gradually replaced by suckling cows, but the annual stocking rate was maintained at 0.2 animal units ha^{-1} (1 animal unit = 450 kg). Stocking rates in summer were 30 % higher than in winter. Throughout

Table 1. Distribution of foraging and occupancy across successional habitats in the Wolfhezerheide, based on 52 24-h observations during the period 1983-1985. 1 au (animal unit) = 450 kg; * = mainly supplements

SITE	SURFACE		FORAGING PRESSURE	OCCUPANCY PRESSURE
	ha	%	au ha^{-1}	au ha^{-1}
Whole Area	60.43	100	0.20	0.20
Communities				
Forest	19.30	31.94	0.10	0.29
Deschampsia	29.85	49.40	0.26	0.17
Molinia	2.63	4.35	0.13	0.10
Calluna	8.55	14.15	0.23	0.18
Supplementary feeding site	0.1	0.1	1.98 *	1.53

the study period, 1-3 horses were allowed to graze in the area. Densities of roe deer *Capreolus capreolus* L. (2-4 km^{-2}) and rabbit *Oryctolagus cuniculus* L. (100 km^{-2}) were low. From 1984 on, a minor quantity (1-2 kg dry matter $animal^{-1}$ d^{-1}) of supplementary food (concentrates, hay or corn silage) was occasionally provided during late winter on a fixed site (0.1 ha). Encroaching Scots pine *Pinus sylvestris* and silver birch *Betula pendula* were removed by the manager. Following the introduction of cattle in 1983, *Calluna* invaded in the heavily grazed *Deschampsia lawns*. These *Calluna* plants were taller and covered a greater area in the nutrient-poor podzolic soils than in the (relatively) nutrient-rich plaggen soils (Bokdam & Gleichman 2000), where they appeared to be more intensively grazed. *Deschampsia* invaded gaps in grazed *Calluna* stands, except on the turf-stripped sites. The results suggest that grazing favoured *Calluna* invasion in *Deschampsia* by creating nutrient-poor gaps through the depletion of the soil nutrient pool during the lawn phase, and favoured *Deschampsia* invasion in mature *Calluna* by creating nutrient-rich gaps after a period of non-grazing and nutrient accumulation (Bokdam & Gleichman 2000; Bokdam 2001).

NET OFFTAKE AND INTEGRATED NUTRIENT BALANCE

Effects of grazing on nutrient pools can be assessed by monitoring soil chemistry and indicative plant species, and by assessing input/output balances. The last method is applied in this paper. Comparing ungrazed and grazed conditions, grazing effects on the total nutrient pool of the plant-soil compartment were calculated as Net Offtake (Offtake–Excretion) and as Integrated Balance, which included atmospheric deposition, excretion and weathering as input and offtake and gaseous N losses from excreta as output. Input by N-fixation, seepage and sedimentation and output by denitrification (gaseous losses of non-excreta-N), K-fixation by parent material, P-precipitation, leaching and erosion were ignored. Both types of balances were assessed for N, P, K, Na, Ca and Mg, for the whole area, for the successional communities (forest, *Deschampsia*, *Molinia* and *Calluna* vegetation), for the supplementary feeding site and for individual patches (excreta-free patches and dung and urine patches) in the *Deschampsia* community. Whole area values for dry atmospheric deposition and gaseous losses were obtained by area-weighted averaging of community values.

ESTIMATION OF PARAMETER VALUES

The used parameter values are summarised in Tables 1-2. Between 1983-1993, the average stocking rate was 91.6 kg cattle ha^{-1} or 0.2 au ha^{-1} (1 animal unit corresponds with 450 kg Live Weight (LW)). The herd ingested nutrients from the vegetation (offtake), drink water, saltlicks and supplements. The annual average Dry Matter Intake (DMI) of cattle was calculated as 365 * 0.021 * 450 = 3449 kg DM au^{-1} yr^{-1}. The value for the daily DMI value per kg LW (0.021) was derived from worldwide averages for cattle (Van Dyne *et al.* 1980). The Annual DM Offtake, calculated as Intake – supplements, was 3381 kg DM au^{-1} yr^{-1} or 676 kg ha^{-1}. Nutrient Offtake was calculated as DM Offtake * Diet Nutrient Concentrations. Diet Nutrient Concentrations were derived from published studies in the study area and comparable heathlands (Bokdam & WallisDeVries, 1992; WallisDeVries 1989; 1996) (Table 2). Drinking water consumption was estimated at 30 l au^{-1} d^{-1} (Van Dyne *et al.* 1980). Nutrient concentrations in drinking water were derived from Van der Hoek (unpublished data). Saltlicks contained 38 % Na (product information) and the animals consumed 2 kg Na au^{-1} yr^{-1} (based upon the quantity supplied by the manager). Offtake was allocated to communities according to the annual foraging time (see Table 1; Chapter 4).

Excretion by the herd for the whole study area was calculated as Intake – Body Retention. Body Retention includes nutrients retained in the carcass and the gut. Carcass Nutrient Retention is the product Carcass Live Weight Gain * Carcass

Table 2. Nutrient concentrations in the components of Intake and Body Weight Increment of free-ranging cattle on the Wolfhezerheide.

NUTRIENTS	N	P	K	Na	Ca	Mg	Ref.
COMPONENTS							
INTAKE							
Offftake (% of DM)	2.15	0.14	0.93	0.02	0.16	0.09	1
Supplement (% of DM)	2.15	0.14	0.93	0.02	0.16	.09	1
Salt lick (% of DM)	-	-	-	38.0	-	-	2
Drinking-water (mg l^{-1})	traces	traces	0.13	0.13	0.16	0.04	3
BODY WEIGHT GAIN							
Carcass (% of Live Weight)	2.56	0.80	0.20	0.15	1.4	0.05	4
Gut-fill (% of wet fill)	0.52	0.05	0.26	0.018	0.07	0.07	5

Nutrient Concentration (Table 2). Gut fill Nutrient Retention is the product Gut fill Live Weight Gain * Gut fill Nutrient Concentration. Average Body Live Weight Increment in the study area was 160 kg au^{-1} yr^{-1}, according to measured weight increments of heifers in the study area (Bokdam & Van Wieren 1985) and growing steers on a comparable heathland (WallisDeVries 1992; 1996). Carcass Live Weight Increment was assumed to cover 85 % of the Body Live Weight Increment, the rest being Gut Fill Increment (Agricultural Research Council 1980). Gut Fill Nutrient Concentration was assumed to be the average of diet and dung (values from the Imbosch, Van Wieren not published). Carcasses from mineral-poor heathlands might be expected to have lower nutrient concentrations. WallisDeVries (1992; 1996, unpublished data), comparing cattle from heathland and flood plain grassland, studied the relation between their LW gain and rib-bone chemistry. He found a significant (50 %) lower LW gain but only a 10 % lower P-concentration in rib-bone ash in the heathland group. Nutrient species were partitioned over dung and urine according to Church (1969), Lantinga *et al.* (1987) and Betteridge, Andrewes & Sedcole (1986) (Table 2). Excretion was partitioned over the communities according to the measured occupancy (Chapter 4; Table 1). Excreta-free areas were calculated by assuming 10 defaecations and 10 urinations per animal unit per day and affected areas of 0.15 m^2 for a dung patch and 0.3 m^2 for a urine patch. These assumptions were based on the observations in the study area (Chapter 4) and literature (Watkin & Clements 1978).

For gaseous excreta-N losses, a rate of 40 % of the excreted N was assumed.

This loss rate included direct gaseous N-losses from the animal, which may cover 12 % of the ingested N (Church 1969). The rate of 40 % gaseous losses may vary in reality between 20 and 60 % (Weeda 1979; Vertregt & Rutgers 1988). For Dutch pastures Vertregt & Rutgers (1988) found 50 % total N-loss from dung, partitioned over volatilisation (13 %), chemo-denitrification (25 %) and leaching (12 %). Immobilisation counted for 30% and apparent recovery for 20 %. For urine total N-loss was 60 %, partitioned over volatilisation (13 %), denitrification (25 %) and leaching (22 %). Immobilisation was 25 %. Only 15 % of the excreted N were recovered as plant uptake. These results refer to fertilised pastures and summer season, but the N-rich *Deschampsia* diets may have produced similar dung and urine composition (Table 2). Urine scorching was a common feature in the study area during summer.

For input from weathering, rate values for fine and coarse textured leptic podzols in the Netherlands were used, as suggested by De Vries (1991): K = 2.6; Na = 1.6; Ca = 1.6 and Mg = 0.4 kg ha $^{-1}$ yr^{-1}.

Atmosperic bulk deposition in the study area was estimated by interpolation using regional values (see Appendix 1) and best professional judgement (Van der Eerden, personal communication). Reduction of the interception deposition by reduction of the vegetation height had an important indirect grazing effect (Table 3). Total Atmospheric Deposition is the sum of Bulk Deposition (as measured in open-air funnels) and True Interception Deposition (throughfall + stemflow – bulk deposition – canopy exchange) (Fangmeier *et al.* 1994). True interception deposition may be estimated by multiplying the bulk deposition with the (true) I/B ratio (Interception/Bulk deposition ratio, De Vries 1991). This true I/B ratio is mainly a function of the Leaf Area Index and winter greenness (Van Dam *et al.* 1990; Heil 1988; Heil *et al.* 1988; Fangmeier *et al.* 1994; Bobbink, Heil & Scheffers 1990; De Vries 1991; Berendse, Aerts & Bobbink 1993). Heil (1988) and Van Dam *et al.* (1990) found a linear relationship between the Leaf Area Index (LAI) and the interception of sulphur and ammonium-N in grasslands. Many interception studies comparing stem flow and throughfall with bulk deposition fail to account for canopy exchange (adsorption of ammonium N and release of cations) (Bobbink, Heil & Raessen 1990; 1992). The true I/B ratios used in this study for the successional habitats (Table 3) were estimated by interpolation of the available data (see Appendix 1) after correction for canopy exchange by best professional judgement where necessary (Bobbink, personal communication). For this interpolations we used approximated LAI values (Fliervoet, personal communications) The true I/B values for the forest in the study

Table 3. Approximations of bulk deposition and true Interception/Bulk Ratio's for 6 nutrients in successional communities on acid dry nutrient-poor sandy soils in the Wolfhezerheide, 1983-1993.

NUTRIENTS	N NOx	N NHy	N tot	P	K	Na	Ca	Mg
BULK DEPOSITION (kg ha^{-1} yr^{-1})	5	11	16	0.6	3	15	5	2
True INTERCEPTION/BULK ratio								
Pine Forest (LAI = 5-8)	2.2	2.5	2.3	2.0	1.5	0.8	1.3	1
Deciduous Forest (LAI = 4-6)	1.8	2.0	1.9	1.8	1.0	0.6	0.8	0.7
Calluna Heath (LAI = 3-5)	1.2	1.7	1.5	1.2	0.6	0.3	0.6	0.4
Tall Grassland (LAI = 2-6)	1.0	1.4	1.2	1.4	0.6	0.3	0.6	0.4
Short Grasslawn (LAI = 0.5-2)	0.5	0.7	0.6	0.7	0.3	0.2	0.3	0.2
Pioneer/ bare litter (LAI = 0-1)	0.2	0.3	0.3	0.3	0.1	0.1	0.1	0.1
Bare Sand (LAI = 0)	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0

area were obtained by averaging the values for coniferous and broad-leaved forest (Table 3). Differences in the interception between edges and core areas of the mosaic patches were neglected.

Results

NET OFFTAKE BALANCE

Offtake represented > 95% of the Intake for all nutrient species, except Na (Table 4). Drinking water provided 8% of the Na Intake, saltlicks 46%. Body Retention efficiency (as percentage of the Intake) varied strongly across nutrient species. It was low for N (4.9%), K (1.1 %), Mg (2.5%) and high for Na (14.1%), P (23.1%) and Ca (34.3%). A low retention implicated a high excretion percentage (of the ingested amounts). These excretion percentages varied from 99 % (K), 97 % (Mg), 95 % (N), 86 % (Na), 77 % (P) to 66 % (Ca). The low retention efficiency implied a low Net Offtake for the grazed area as a whole (Table 4). The negative Net Offtake values for K, Na and Mg were caused by the introduced supplement, drinking water and salt licks.

Offtake and excretion were unevenly distributed across the successional mosaic

Table 4. Nutrient balance of year-round, free-ranging cattle on the Wolfhezerheide. Intake, Offtake, Retention, Excretion, Retention Efficiency and Net Offtake, 1983-1985. 1 au (animal unit) = 450 kg.

	NUTRIENTS (kg au^{-1} yr^{-1})					
	N	P	K	Na	Ca	Mg
INTAKE						
Offtake	**72.7**	**4.7**	**31.4**	**0.7**	**5.4**	**3.0**
Supplements	1.5	0.1	0.6	0.0	0.1	0.1
Drinkwater	0.0	0.0	0.1	0.1	0.2	0.0
Salt licks	0.0	0.0	0.0	0.8	0.0	0.0
Total Intake	**74.2**	**4.8**	**32.2**	**1.6**	**5.7**	**3.1**
RETENTION						
in 160 kg body weight increment						
Carcass increment (136 kg)	3.5	1.1	0.3	0.2	1.9	0.1
Gut increment (24 kg)	0.1	0.0	0.1	0.0	0.0	0.0
Total retention	**3.6**	**1.1**	**0.3**	**0.2**	**1.9**	**0.1**
EXCRETION						
Dung	21.2	3.7	4.8	0.1	3.7	3.1
Urine	49.4	0.1	27.1	1.2	0.1	0.0
Total excretion	**70.6**	**3.7**	**31.9**	**1.4**	**3.8**	**3.1**
RETENTION AND NET OFFTAKE EFFICIENCY						
RETENTION EFFICIENCY						
[Retention as % of Intake]	**4.9**	**23.1**	**1.1**	**4.1**	**34.3**	**2.5**
NET OFFTAKE (Offtake – Excretion)						
Kg au^{-1} yr^{-1}	2.1	1.0	-0.4	-0.7	1.6	-0.02
Net Offtake as % of Offtake	2.9	21.2	1.4	-103.0	30.4	-0.9

(Fig. 2). Cattle realised the highest offtake in the preferred *Deschampsia heath* (1.3 * average of the whole area), the lowest in the avoided forest (0.5 * average, Fig. 2). Offtake levels in *Calluna* (Fig. 2) and *Molinia* heath (data not presented) were intermediate. The value in *Calluna* heath exceeded that in *Molinia*. Offtake from the supplementary feeding site was not taken into account since the natural vegetation was heavily trampled. Offtake from excreta patches was assumed to equal that from the community. Forage around dung patches was only temporally avoided and a higher production and consumption may have compensated the avoidance period afterwards.

Excretion was also unevenly distributed across the successional communities (Fig. 2) but its pattern appeared to be complementary to the Offtake pattern. Forest attracted most excreta per unit area (1.5 * whole area average), which was almost twice that on *Deschampsia lawns* (0.8 * whole area average) and three times as much as in *Molinia* heath (0.5 * average value). Nutrient deposits on dung patches (387 kg N ha^{-1}, 67 kg P ha^{-1} and 87 kg K ha^{-1}) and urine patches (451 kg N ha^{-1} and 247 kg K ha^{-1}) approximated or exceeded annual manuring levels on farmland.

The annually dung-affected area (= covered area + edge zone influenced by diffusion and root transport) per animal unit was 365 * 10 * 0.15 m^2 = 547 m^2 au^{-1} yr^{-1}. For urine, this value was 913 m^2 au^{-1} yr^{-1}. Dung and urine together covered 1460 m^2 au^{-1} yr^{-1}, if overlap is ignored. It follows that the annually excreta-affected area on *Deschampsia lawns* was 0.17 * 1460 = 248 m^2 ha^{-1}, composed of 93 m^2 ha^{-1} dung-affected and 155 m^2 ha^{-1} urine affected areas. The annually excreta-free lawn area was

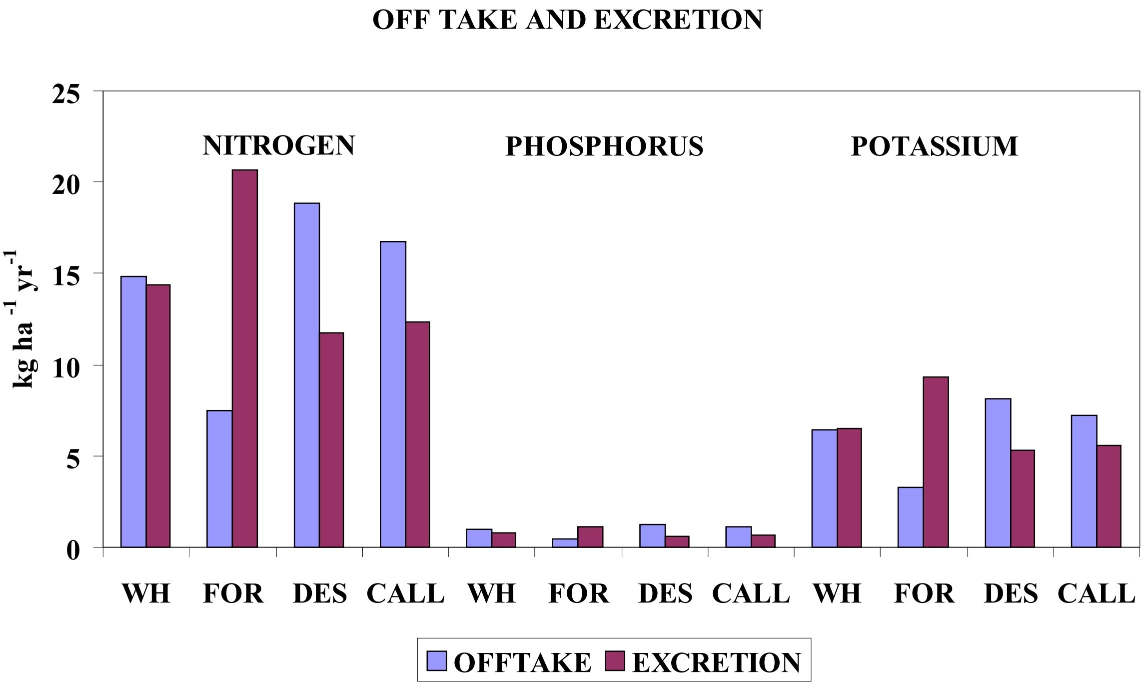

Figure 2. Offtake and Excretion of nitrogen, phosphorus and potassium in the whole area and in the components of the successional mosaic. WH = Whole area of the Wolfhezerheide; FOR= forest; DES = *Deschampsia flexuosa* grasland; CALL = *Calluna vulgaris* heath. For Net Offtake (Offtake – Excretion) from the whole area per animal unit, see Table 3.

97.5 %. This means that in 1993, 10 years after the introduction of grazing, 75 % of the sustained *Deschampsia* lawn was still excreta-free. This figure is a conservative estimation, since some overlap will occur between dung and urine and between years. N and K pulses in dung or urine will occur once per 40 years on *Deschampsia lawns*, P pulses (exclusively in dung) once per 106 years.

Because of the complementary distribution of offtake and excretion, Net Offtake varied strongly across the communities (Fig. 2) . The pattern showed exports from *Deschampsia* and *Calluna* communities to forest for all nutrient species. Net N-Offtake varied from 7.0 kg ha^{-1} in the *Deschampsia lawns* and 4.4 kg ha^{-1} in *Calluna* to –13.1 kg ha^{-1} in Forest.

At patch scale, Net N-Offtake varied from 18.8 kg ha^{-1} on excreta-free *Deschampsia lawns* to -367.8 kg ha^{-1} on dung patches and -432.3 kg ha^{-1} on urine patches. For P these values were 1.2, -65.5 and 0.2 kg ha^{-1} respectively, and for K 8.1, -79.2 and -239.3 kg.ha^{-1} respectively. These results emphasise the relatively small influence of Offtake on excreta patches.

INTEGRATED BALANCE

The transformation of tall, tussock grass heaths into short-grazed grass lawns reduced the total N-deposition by 9.6 kg (27 %) from 35.2 to 25.6 kg ha^{-1} in *Deschampsia* and *Molinia* heaths (Table 3). Interception in forest and on *Calluna* heath was assumed to have remained unchanged since their LAI values were not substantially changed by grazing. The reduction in the grass heaths reduced the deposition for the whole area from 40.5 to 35.3 kg.ha^{-1} (13 %). Grazing had similar reducing effects on the deposition of other nutrient species.

The 40 % gaseous excreta-N loss corresponded with 5.7 kg N ha^{-1} for the whole area, 8.3 kg N ha^{-1} for forest, 4.7 kg N ha^{-1} for the *Deschampsia* habitat, 2.8 kg N.ha^{-1} for *Molinia*, 4.9 kg N. ha^{-1} for the *Calluna* community, 43.15 kg N ha^{-1} for the suppletion site, 171.7 kg N ha^{-1} for dung patches and 240.4 kg N ha^{-1} for urine patches.

The comparison of the integrated balances of grazed and ungrazed conditions (Fig. 3a-c) showed a substantial grazing effect. Grazing reduced the annual (mainly airborne) surplusses for the whole area, for the communities (except for forest) and for the excreta-free patches. The reduction of the N-surplus increased with decreasing scale (Fig. 3a). The N-reduction was 13 kg ha^{-1} yr^{-1} for the whole area, 25 kg ha^{-1} yr^{-1} for the *Deschampsia* community to 33 kg ha^{-1} yr^{-1} for the excreta-free area in

Deschampsia. The other nutrient species (Figs 3b,c) displayed similar trends. Despite the high grazing pressure, the integrated balances of the most intensively grazed lawn (*Deschampsia*) still displayed surpluses for N (11.1 kg ha^{-1} yr^{-1}), P (0.22 kg ha^{-1} yr^{-1}) and K (2.54 kg ha^{-1} yr^{-1}). This was caused by the high atmospheric inputs and returns in the excreta. Depletion of the soil nutrient pool, by removal of the annual inputs and a part of the stored nutrients, occurred only in the excreta-free patches in *Deschampsia* for P (-0.2 kg ha^{-1} yr^{-1}) and K (-1.6 kg ha^{-1} yr^{-1}). Because of their lower Offtake values, excreta-free patches in *Molinia* and *Calluna* heaths maintained small surpluses for P and K.

Discussion

LAWN DEPLETION

The depletion for P and K in the grazing lawns shown by the integrated nutrient balances (Fig 3a-c) are the results of conservative calculations. The calculations did not account for seasonality in the offtake, leaching of soil and excreta nutrients and effects of horses and other herbivores. The value for *Calluna* heath may have been overestimated because of the season effect. The applied Dry Matter Intake rate for cattle (0.021 kg kgLW^{-1} d^{-1}) was confirmed in a nearby cattle grazing experiment (*WallisDeVries* 1994). However, the value varied between 0.03 kg kgLW^{-1} d^{-1} in summer and 0.015 kg kgLW^{-1} d^{-1} in winter, corresponding with +40 % to –30 % of the annual average. In both study areas, the grass lawns of *Deschampsia* and *Molinia* were predominantly defoliated during the growing season, while *Calluna* was exclusively consumed during winter (Chapter 4). It means that during summer dry matter offtake, diet nutrient concentration (Bokdam & WallisDeVries 1992; WallisDeVries 1996), body weight increment (Bokdam & Van Wieren 1985; WallisDeVries 1994) and body retention were higher than during winter. The net offtake by the horses may roughly be estimated at 15 % of that of the cattle, if simply based on body weight. Ignoring their effect contributed especially to the underestimation of the net offtake from grass lawns because the horses consumed during summer predominantly *Deschampsia* and *Molinia*. Putman (1986) found in the New Forest 78 % habitat overlap and 96 % diet overlap between ponies and cattle (Putman 1986) and these ponies also displayed differential habitat use (Edwards & Hollis 1982; Pratt *et al.* 1986).

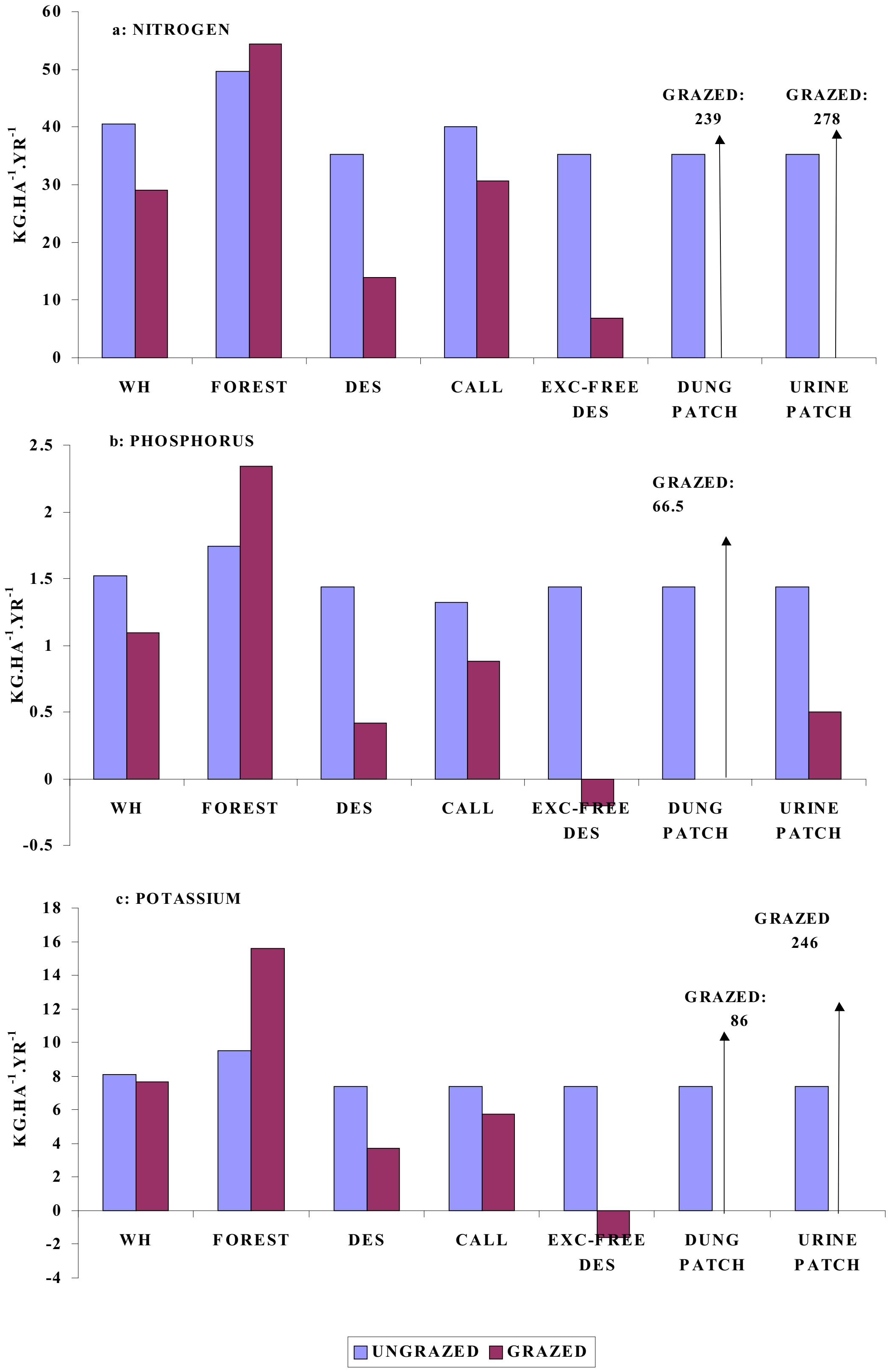

Figure 3. Integrated nutrient balances under ungrazed and grazed conditions for the whole area (WH), successional habitats and patches within *Deschampsia flexuosa* grass lawns, for nitrogen (a), phosphorus (b) and potassium (c). WH = Whole area of the Wolfhezerheide; FOR= forest; DES = *Deschampsia flexuosa* grassland; CALL = *Calluna vulgaris* heath; EXC_FREE DES = excreta-free patches in the *Deschampsia flexuosa* grassland.

Leaching of excreta and soil nutrients was not taken into account in the calculations because of a lack of reliable data. It may be argued that plant uptake, soil absorption and microbial immobilisation were insufficient to prevent leaching, especially for mobile N and K on excreta patches and patches where root systems were damaged by scorching or trampling. Furthermore, the soil retention capacity in the study area may have been saturated by high atmospheric inputs, especially of N, in forests (De Vries *et al.* 1995) and on *Calluna* heaths (Berdowski 1993; Bobbink & Heil 1993). The constant total N-pool measured under ungrazed *Molinia* heath under a high N-deposition level (Berendse 1990) also points to N leaching. A coarse soil texture favours percolation. Precipitation surpluses in the short lawns may have exceeded 400 mm yr^{-1} reported for heathlands and the 200 mm yr^{-1} for forests (De Vries 1991). The typical large nutrient pulses in dung and urine patches (Fig. 3a-c) may also have increased the risk of leaching. The (calculated) nutrient concentrations in the dung in the study area (1.80 % N, 0.30 % P, 0.31 % Ca and 0.26 % Mg) agreed roughly with values measured in the dung from Scottish Highland cattle in the nearby Imbosch (2.26 % N, 0.34 % P, 0.25 % Ca and 0.23 % Mg, Van Wieren unpublished data).

The residual K surplus in *Deschampsia* community (3.7 kg ha^{-1} yr^{-1}, Fig. 3c) would have disappeared through the leaching of 30 % of the total K input (11.8 kg ha^{-1} yr^{-1}, composed of weathering, atmospheric input and excreta) or 70 % of the excreta K input (5.3 kg ha^{-1} yr^{-1}). Smit (2000) found 30% reduction of the extractable K pool in the topsoil of grazed, apparently excreta-free *Deschampsia lawns* under forest on inland dunes and she attributed this loss partly to leaching. Loss of the residual N surplus in *Deschampsia* (13.9 kg ha^{-1} yr^{-1}) would have required leaching of 37 % of the total N input (37.4 kg ha^{-1} yr^{-1}). N-fixation, seepage, sedimentation, erosion and denitrification of soil N (Fig. 1) had little effect on the results, because of the low proportion of *Leguminosae* in the vegetation, the free drainage and aeration of the soil and the flat topography (Bokdam & Gleichman 2000). For a general discussion of uncertainties in the nitrogen cycle, the reader is referred to Kroeze *et al.* (in press).

On the basis of the results and the discussed bias, I conclude that the free-ranging cattle depleted the total P and K pools and perhaps also the total N-pool of the excreta-free grass lawns. The cattle probably also depleted the *Deschampsia* lawn as a whole for K. Grazing accelerated the ongoing eutrophication of the woodland for all nutrient species. For the grazed area as a whole, cattle compensated for none of the airborne nutrient surpluses.

REDUCED NUTRIENT AVAILABILITY

Did grazing also reduce nutrient availability for plants in the excreta-free *Deschampsia* lawn? Offtake obviously reduced the influx of litter and thus mineralisable nutrients. Gaseous losses and reduced atmospheric inputs also concerned available nutrients. Initially, these reductions may have been compensated by excitation. During the first 5 years of grazing, litter input in the grass lawns was obviously increased by the trampling and fragmentation of *Deschampsia* and *Molinia* tussocks (Bokdam & Gleichman 2000). The last dead tussocks disappeared after 5 years of grazing. It suggests that long-term deceleration effects may have been masked by excitation for at least 5 years. In 1988 (after 5 years of grazing) the topsoil of the grazed *Deschampsia* lawn on plaggen soils (covered by strongly developed tussocks in 1983) contained significantly more extractable P but not significantly more extractable N or K, when compared with ungrazed exclosures (Bokdam & Gleichman 2000; Chapter 2). Smit (2000) found after 5 years of cattle grazing in a *Deschampsia* vegetation under Scots pine a significant reduction of the above ground biomass, a 1.6 times reduction of living root mass and a reduced extractable K-pool. Similar changes were measured in coastal dune grassland (Kooyman & Smit 2001). Bülow-Olsen (1980) found also a reduced extractable K pool in a *Deschampsia* heath topsoil after 5 year of grazing, but increased extractable amounts of P, Ca and Mg. These results may be explained by excitation followed by differential leaching.

Increased soil temperature and pH, and the excreta may have sustainably accelerated the mineralisation rates. However, a permanently increased litter input by a sustainable increased primary production as suggested by McNaughton (1983) and Frank, Kuns & Guido (2002) is unlikely in our acid, nutrient–limited study area. Several studies on comparable sites revealed a reduced (aboveground) production as a result of grazing and clipping. Ten years of (annual) experimental clipping mimicking excreta-free lawns reduced the annual dry matter yield of *Deschampsia* and *Molinia* heaths on podzolic soils dramatically from 3 to 1 ton DM ha^{-1} yr^{-1} (Diemont 1996). Kooyman & Smit (2000) found a 1.5-4.1 times reduction in aboveground grass production in dry grasslands on sandy soils as a result of grazing. During a 40-years period of (summer) grazing in unfertilised grassland paddocks on clay in the Ossekampen, The Netherlands (Van der Werf, unpublished data) the above ground production first declined and then stabilised. These results point to the establishment of an equilibrium between external inputs and removals in case of controlled summer grazing.

The higher initial soil fertility and excitation may explain the delay in the invasion of *Calluna* and pioneer trees in the *Deschampsia lawns* on plaggen soils if compared to sites on podzolic soils (Bokdam & Gleichman 2000; Chapter 2 and 7). A re-assessment in 2001 of the soil nutrient pools in 12 plots on podzolic soils invaded by *Calluna* since 1983 revealed significantly increased organic matter and total N, P and K pools. However, there were lower available (extractable) pools for the three elements when compared with 1988 (Scherpenisse 2002). The increased proportion of *Calluna* in vegetation and soil litter may explain the opposite trends in total and extractable pools. *Calluna* might be able to deplete the extractable pool to a lower level than *Deschampsia*. Also, *Calluna* litter decomposes more slowly than grass litter (Berendse 1990).

HIERARCHY OF MECHANISMS.

The quantification of influences and nutrient flows allowed a comparison of the hierarchy of mechanisms across spatial scales and nutrient species.

The effect of redistribution increased with decreasing scale. From the whole area, cattle ‘removed’ 13 kg N ha^{-1} yr^{-1} (31 % of the N surplus in the ungrazed situation), composed of body retention (1 kg), reduced atmospheric deposition (6 kg) and gaseous excreta-N losses (6 kg). It revealed the minor role of body retention for N-removal under conditions with a high atmospheric input and a low production. On the scale of the successional habitats, redistribution became a dominant mechanism. The N removal from the *Deschampsia* community (25 kg ha^{-1} yr^{-1}) was composed of net offtake (10 kg), reduced atmospheric deposition (10 kg) and gaseous losses (5 kg). Differential habitat use accounted for 40 % of the removal. At patch scale, redistribution was even more important. The reduction in N surplus on the excreta-free *Deschampsia* lawn (33 kg ha^{-1} yr^{-1}) consisted of net offtake (23 kg or 70 %) and reduced atmospheric deposition (10 kg).

The differences between nutrient species were related to their mobility and metabolic function. Removal by body retention from the whole area was more important for P than for N. The removed amount of P (0.51 kg ha^{-1} yr^{-1}) consisted of body retention (0.28 kg or 55 %) and reduced atmospheric deposition (0.23 kg). In the *Deschampsia* community, the P reduction of 1.22 kg was composed of net offtake (0.8

kg or 66 %) and reduced atmospheric deposition (0.42 kg). On the excreta-free *Deschampsia* lawn, offtake (1.22 kg) represented 75 % of the total removal of 1.62 kg P ha^{-1} yr^{-1}, which turned the surplus of ungrazed lawns (1.44 kg ha^{-1} yr^{-1}) into a deficit. These findings agree with small-scale net P removal up to 1 kg ha^{-1} yr^{-1} by red deer in sub-alpine grasslands in the Swiss National Park (Achermann 2000). The differences between N and P in the study area were caused by differences in the initial surpluses, mobility, animal requirement and retention, and by uneven excretion in dung and urine. The absence in urine increased the P-free period in lawns to more than 100 years, which points to a prolonged period of P-limitation in excreta-free lawns.

The results illustrate the complexity of the effects of grazing on nutrient cycling in grazed ecosystems and explain the apparently conflicting results from different studies (Milchunas & Lauenroth 1993). A major conclusion to be drawn is the insignificance of body retention when compared to redistribution, gaseous losses, reduced atmospheric interception and (probably) leaching. Unfortunately, conclusions about the effectiveness of grazing for nutrient removal have often been based on retention only. The results also show that nutrient redistribution is a major explanation for the effects of grazing on vegetation dynamics and they stress the necessity to incorporate nutrient redistribution in spatially explicit models of vegetation dynamics in grazed ecosystems at community scale.

Redistribution also plays a dominant role at the scales of hoof prints and permanent excreta-free sites. Both types of micro-sites were not included in this study despite their importantance for biodiversity. Hoof sliding acts as small-scale turf stripping, creating nutrient-poor gaps in the vegetation and litter layer. Permanent excreta-free lawn patches emerge where sites are accessible for the mouth but inaccessible for hoofs and excreta, e.g. on the edges of inaccessible slopes, hummocks, ant hills, wet places, rocks, spiny shrubs and areas under and along-side fences. Such permanent excreta-free lawns are important nutrient-poor habitats for plants and animals that are vulnerable to eutrophication and treading (Bokdam & Piek 1998). Mowing mimics permanent excreta-free lawns.

RSGC THEORY

The results supported the RSGC-theory. In the study area, cattle depleted only the P and K pools of excreta-free parts of the grass lawns – and perhaps also the K-pool of grass lawns as a whole – because of the high atmospheric inputs. Under natural low atmospheric input levels and a same primary production based on a mineralising soil organic matter pool, grazing would have depleted the grass lawns as a whole for all nutrients. It follows that grazers can deplete whole grass lawns, unless high inputs prevent the depletion. The results imply that nutrient depletion may have contributed to the observed establishment and expansion of pioneer dwarf shrubs (e.g. *Calluna vulgaris*, *Erica tetralix*) and trees (*Pinus sylvestris*, *Betula pendula*) in the grass lawns of the study area (Chapter 2).

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Appendix 1. Reference values for Atmospheric Bulk Deposition, Apparent Interception/Bulk Ratio and True Interception/Bulk Ratio in seral communities for 6 nutrients.

NUTRIENT SPECIES	NOx-N	NHy-N	N-tot	P	K	Na	Ca	Mg	Ref.
BULK DEPOSITION (kg ha^{-1}yr^{-1})									
Netherlands ('78-'82)	6.4	13.1	19.5	0.9	3.2	18.4	7.5	2.7	1
Netherlands (NL,'86-'87, 984 mm)	6.0	13.0	19.0	0.9	9.9	18.2	6.5	2.9	2
Coast	5.5	7.5	13.0	0.4	5.1	34.5	5.8	4.3	2
North	6.2	13.4	19.6	1.0	12.5	16.7	6.2	3.1	2
Central	6.3	15.2	21.5	1.3	8.5	17.1	6.2	2.4	2
South	5.8	13.5	19.3	0.9	10.8	12.6	7.4	2.2	2
Limburg (South)(4/'86-4/'88)	6.2	10.8	17.0	1.9	3.9	7.8	22.8	3.4	3
Hackford (Central)(4/'81-4/'84)	7.6	16.7	24.3	0.3	2.0	20.2	15.6	5.0	4
Speuld (Central)(1/'87-1/'89)	5.1	9.3	14.4	-	0.7	10.8	5.0	3.3	5
Kootwijk (Central)(1/87-1/89)	5.0	10	15	-	0.7	10.2	4.6	2.9	5
Assel (Central)(8/'88-10/'89)	5.3	13.5	18.8	-	-	-	-	-	6
Elspeet (Central)(4/'89-4/'90)	5.4	11.8	17.2	-	-	-	-	-	6
NW-Gelderland (Central)89,93.	4.5	9.1	13.6	-	1.6	11.0	2.0	1.2	7,8
S-Gelderland (Central)'89,'93.	4.6	10.6	15.2	-	1.6	11.5	2.4	1.0	7,8
APPARENT INTERCEPTION/BULK RATIO'S									
Coniferous forests									
Netherlands	1.5	4.1	3.3	1.2	2.5	2.4	1.9	2.5	2
Coastal Area	2.2	3.2	2.8	2.3	7.2	5.1	4.3	6.2	2
North	1.0	3.5	2.7	0.7	1.5	1.6	0.8	1.1	2
Central	1.5	3.7	3.1	1.8	2.9	1.3	1.9	1.8	2
South	1.9	5.0	4.0	1.0	2.6	2.7	2.4	2.9	2
Speuld	1.1	2.3	1.9	-	25.7	1.0	2.3	1.4	5
Kootwijk	1.0	1.9	1.6	-	21.6	0.7	1.9	1.3	5
Deciduous forest									
Hackford a	0.8	1.5	1.3	6	20.6	0.3	0.8	1.3	4
Hackford b	0.9	1.5	1.3	8	22.0	0.2	0.6	1.2	4
Hackford c	0.6	1.0	0.8	8	16.8	0.1	0.5	1.1	4
Hackford d	0.9	1.9	1.6	7	22.8	0.7	2.4	2.4	4
Tall Grassland									
Maartensdijk (Motorroad verges)				8-11					9
Houten (Motorroad verges)				2-25	1-18				9

Appendix continued

NUTRIENT SPECIES	NOx-N	NHy-N	N-tot	P	K	Na	Ca	Mg	Ref.
TRUE INTERCEPTION/BULK RATIO'S									
Coniferous forest									
Speuld	1.2	3.2	2.5	-	1.7	1.0.	1.5	0.9	5
Kootwijk	1.1	2.6	2.1	-	1.1	0.7	1.2	0.7	5
Netherlands	2.1	2.2	2.1	-	1.0	0.5	1.1	0.8	8
Deciduous forest									
Netherlands	1.9	1.8	1.8	-	0.9	0.5	0.9	0.7	8
Ericoid Heathland									
Assel	0.2*	0.8	0.6	-	-	-	-	-	6
Elspeet	1.4	1.6	1.6	-	-	-	-	-	6
Artificial (Assel)	0.6	0.3	-	-	0.1	-	0.7	0.5	6,10
Netherlands	1.2	1.8	1.6	-	0.3	0.3	0.6	0.5	8
Tall Grassland									
Artificial (LAI=3), Motorroad verges	1.5	2.5	-	2-5	2-10	-	-	-	9
Brachypodium	0.9	0.9	0.9	1*	1.9	0.6	1.8	1	3

References:

1.Median values of 27 rain water monitoring sites of VEWIN (Van de Meent, Van Oosterwijk & Aldenberg 1984)

2.Average of 13 selected coniferous forest monitoring sites, distributed over the regions Coast (n=2), North (n=4), Central (n=3), South (n=4) (Houdijk 1990: 17; Houdijk & Roelofs 1991)

3. Chalk grassland dominated by *Brachypodium pinnatum* (peak biomass = 2.3 ton /ha; Van Dam 1990: 97)

4. 4 Oak (Quercus robur) forest sites (van Breemen, Visser & Pape 1988: 114)

5. 2 Douglas fir (Pseudotsuga menziesii) sites (Van der Maas & Pape 1990:5; Van Breemen & Verstraten 1991: 307)

6. 2 Heathland monitoring and experimental sites (Bobbink, Heil & Raessen 1990 and 1992; Van Breemen & Verstraten 1991: 296).

7. Calculated values of NOx and NHy-depositon in 1989 for 2 (selected from a total of 20) "acidification regions" nearest to the Wolfhezerheide (Erisman & Heij 1991: 76)

8. Calculated values of P and Base Cations depositions in 1993 for 2 (from a total of 20) "acidification regions" nearest to the Wolfhezerheide (Erisman & Bleeker 1994: 32, 34, 62)

9. Artificial canopies (LAI=3) in motorway roadsides (Bobbink , Heil & Scheffers 1990:26)

10. Bobbink (unpublished data)

Chapter 6

Forage quality as limiting factor for cattle grazing in isolated Dutch nature reserves

Jan Bokdam & Michiel F. WallisDeVries

Conservation Biology (1992), **6**, 399-408. Also as chapter in *Wildlife and Forests. Readings from Conservation Biology* (1995) (ed D. Eherenfeld), pp.134-143. Blackwell, Cambridge, USA.

During late winter and snow periods, the manager provided a minor amount of hay. Wolfhezerheide, January 1985 (photo Maurits Gleichman).

Forage quality as limiting factor for cattle grazing in isolated Dutch nature reserves

Jan Bokdam & Michiel F. WallisDeVries

Summary

Most Dutch nature reserves are small, isolated fragments of former semi-natural landscapes. Cattle and other domestic large herbivores are increasingly (re-)introduced in nature reserves as a tool for vegetation management and as an ecological substitute for extinct wild herbivores. The performance of cattle in these single-landscape areas appears to be seriously limited by a combination of inadequate forage and habitat isolation. Animals cannot move seasonally between different landscape types. The forage quality of three landscape types was compared. Quality parameters were organic matter digestibility and contents of the macronutrients nitrogen (N), phosphorus (P), potassium (K), sodium (K), calcium (Ca) and magnesium (Mg). In landscapes of low fertility insufficient concentrations were found for P, Na, Ca and Mg. However, because the assumed maintenance requirements for cattle are possibly overestimates, the prediction of deficiencies for the animals remains uncertain. In landscapes of intermediate fertility, the level of Na is deficient for most of the year. Winter digestibility is inadequate in vegetation remaining ungrazed until winter, whereas in grazed vegetation the quantity of easily-digestible forage is insufficient to satisfy quantitative intake requirements. In landscapes of high fertility, the mineral supply is adequate, but low digestibility in winter will lead to energy shortage. Insufficient forage quality seems to preclude sustained year-round grazing in each of the three landscape types.

Single-landscape areas constitute seasonal habitats for cattle, suitable for summer or winter grazing only. Connection of complementary landscapes is essential to create complete year-round habitats for cattle and other large herbivores. The restoration of linkage of summer and winter range by the creation of corridors is the most natural solution. Seasonal grazing with controlled migration or transportation of the herd between winter and summer range reserves is a second-best alternative involving less interference than year-round grazing with supplementation.

Key-words: nature conservation, grazing management, cattle, carrying capacity, herbivore nutrition, landscape fragmentation, migration.

Introduction

Migration by large herbivores between contrasting landscapes and ecotopes is a common feature in natural grazing systems, as well as in traditional 'transhumance' pastoral systems around the world. The ecological significance of these horizontal and vertical movements has been emphasized repeatedly by animal ecologists (Bell 1970; Baker 1978; Sinclair 1983; McNaughton 1987, 1988, 1990). Landscape ecologists have stressed that isolation of summer and winter ranges will impose serious constraints on the performance and survival of wild and domestic herbivores (Zonneveld 1983; Forman & Godron 1986). The case described in this paper supports this view.

Most Dutch nature reserves are small (10-1000 ha), isolated fragments of former semi-natural landscapes, comprising only one single landscape zone. Daily movements and seasonal migration by terrestrial animals between these reserves and their surrounding matrix area are inhibited by barriers such as fences, motorways, railways, canals, ditches and agricultural areas.

Since 1970, extensive grazing (i.e. grazing at low stocking rates) has become an important tool in the management of nature conservation areas in the Netherlands. Large herbivores such as cattle, ponies and sheep have been (re-)introduced in hundreds of nature reserves in order to maintain or to increase their conservation value and restore ecological processes associated with herbivory.

At first, grazing was applied as a continuation of former traditional pastoral land use. It was considered to be an essential factor for spatial heterogeneity and biological richness of semi-natural landscapes. Later, large herbivores were also introduced as a more natural as well as a cheap method for controlling vegetational succession, substituting mechanical techniques such as tree felling, shrub clearance, hay making and turf cutting.

More recently, domestic large herbivores have also been introduced in nature reserves as essential components of more natural, complete ecosystems. Cattle and ponies are considered as ecological substitutes for their extinct ancestors. In the Netherlands, this approach of grazing is part of a new conservation policy, called wilderness or 'nature development' (Baerselman & Vera 1989). It is aimed at the creation of biological corridors in the landscape and at the restoration of more natural, self-regulating ecosystems with little or no human interference. In view of the objective of self-regulation, there is a strong preference for year-round grazing without food supplementation which, in the long run, should lead to dedomestication. The incorporation of livestock into the fauna of nature reserve has potential drawbacks. As soon as livestock becomes an aim instead of a tool, problems may arise such as overgrazing (to increase financial benefit) and eutrophication (due to the introduction of food supplements).

Several experiments on year-round grazing with semi-wild and domestic cattle were started after 1983 in various single-landscape nature reserves. In all cases at least part of the animals appeared to need supplements to prevent starvation during winter (Drost 1986; de Bie & Bokdam 1987, 1989) or to cure mineral deficiencies (van Wieren 1988). This outcome suggests that the energy and/or mineral content of the available forage in many, if not all, landscape types might be insufficient for yearlong survival of cattle.

The objective of this paper is to give a general view of the nutritional quality of the available forage for cattle in the semi-natural landscapes of the Netherlands and to examine the effects of single-landscape habitats on cattle performance and survival. Implications of these findings are discussed, followed by management recommendations and suggestions for future research.

Methods

Dutch landscapes have been classified into three broad types based on soil fertility, which is strongly related to geomorphology and hydrology (Table 1). Dominant plant species and vegetation types, as main potential food sources for cattle, have been indicated. For the nomenclature of plants we refer to van der Meijden *et al.* (1983).

Low and high fertility landscapes both cover large areas in the Netherlands. Intermediate fertility landscapes are relatively scarce (Fig. 1) but often occupy a key position in gradients between high and low fertility landscapes.

The available forage quality data for the three landscape types orginate from the Databank of the Department of Nature Conservation and from a number of Dutch studies (Dirven 1984; Koorevaar 1986; van Wieren 1988; Vulink & Drost', unpublished).

Table 1. Geomorphological features and major forage plant species of the three basic landscape types in the Netherlands.

Landscape type	Geomorphological features	Major forage plant species
Low soil fertility	Pleistocene cover sand and sandy fluvio-glacial sediments, inland dunes and oligotrophic peat with a low pH	Herbaceous: *Deschampsia flexuosa, Molinia caerulea* Woody: *Calluna vulgaris, Vaccinium myrtillus, Pinus sylvestris, Betula pendula, Betula pubescens, Quercus robur*
Intermediate soil fertility	Coastal dunes, loess areas, natural levees in river valleys, sandy-loamy Pleistocene fluvio-glacial sediments	Herbaceous: *Agrostis capillaris, Festuca rubra,* Woody: *Prunus spinosa, Crataegus monogyna, Quercus robur, Fagus sylvatica, Carpinus betulus, Hedera helix*
High soil fertility	Holocene fluvial and marine sand and clay, eutrophic peat	Herbaceous: *Poa spp., Lolium perenne, Agrostis stolonifera, Trifolium spp., Cirsium arvense, Urtica dioica, Phragmites australis, Calamagrostis epigejos,* Woody: *Salix spp., Populus*

A distinction was made between summer (May-October) and winter (November-April). A further subdivision would confuse the broad view we are aiming at.

Grassland, as the major forage resource for cattle, was emphasized. Data from grazed and ungrazed patches in grassland vegetation have been treated separately because of the different quality levels. Data from tall herbs and woody species have been included in the analysis because of their potential importance as forage in more natural landscapes with a progressed vegetation succession, but it should be noted that some species are unpalatable to cattle (e.g. Pinus sylvestris, Cirsium arvense).

All data concern samples of above-ground material from vegetation, species and plant parts which were considered to be potential cattle forage. Samples of herbaceous plants were clipped at 2 cm above ground level or hand-plucked. The inclusion of litter was avoided. In the case of woody species, terminal parts of 10 cm length of the current year's shoot were collected.

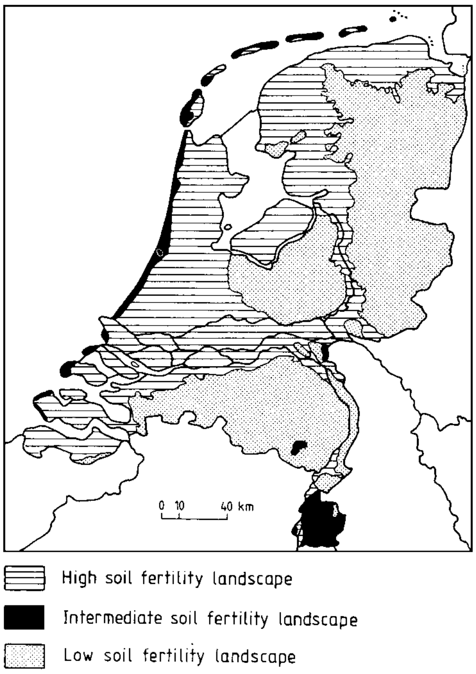


Figure 1. Geographical distribution of the three basic landscape types in the Netherlands.

Parameters of nutritional quality have been restricted to energetic value and the macronutrients nitrogen (N) and the macrominerals phosphorus (P), potassium (K), sodium (Na), calcium (Ca) and magnesium (Mg). The energetic value was assessed as the *in vitro* organic matter digestibility following Goering & Van Soest (1970), using rumen fluid of steers fed on hay. The data were transformed into *in vivo* organic matter digestibility values and further into multiples of maintenance requirements for cattle. Macronutrients were determined as total element contents, following the automated routine procedures of the Department of Soil Science and Plant Nutrition of the Agricultural University (Walinga *et al.* 1988).

The requirement levels for N and the macrominerals have been taken from the Agricultural Research Council (ARC 1980). The maintenance level for organic matter digestibility has been estimated at 50%, based on Van Soest (1982) and ARC (1980).

Forage quality was considered to be deficient when the seasonal mean value of a quality parameter was below the maintenance requirement level.

Results

Table 2 shows the ranges and average values for digestibility, N and macro-minerals. In general, the ranges between minimum and maximum values represent the seasonal variation within the summer and winter period. In summer quality levels decrease from May to October. During winter, the lowest quality is found in late winter (February-March).

LOW FERTILITY LANDSCAPES

Deschampsia flexuosa is the major grassland species of dry low fertility landscapes. Little difference was found between grazed and ungrazed vegetation. Digestibility was quite high in both periods and only fell below maintenance level during periods of severe frost in the absence of snow. N and K were present in sufficient concentrations, but P, Na, Ca and Mg rarely or never met the maintenance level (Fig. 2).

A comparable outcome was found for the dominant grass species *Molinia caerulea*, from moist and wet low fertility landscapes, during summer. The aerial parts of this species die off completely in November; their digestibility and nutrient content then fall far below maintenance requirements. As *Molinia caerulea* was never consumed in significant amounts during winter, this season has been omitted in the results.

Woody plants such as the dwarf shrub *Calluna vulgaris* and the two deciduous tree species of the genus *Betula* generally had a moderate or low digestibility during both periods. Their mineral content, especially Ca and Mg, was higher than for the grasses. Digestibility and mineral content of *Vaccinium myrtillus* was similar to *Calluna vulgaris* (Bokdam unpublished data; van Wieren 1988).

INTERMEDIATE FERTILITY LANDSCAPES

Agrostis capillaris/*Festuca rubra* grassland is considered as characteristic for this landscape type. Winter digestibility was higher in grazed than in ungrazed vegetation due to the presence of more stem and standing dead material in the latter vegetation. All nutrient concentrations, except for Na, were higher in the grazed vegetation (WallisDeVries 1989).

Table 2. Dietary maintenance requirements of cattle and forage quality of major plants from three basic landscape types in the Netherlands. Means and (minimum - maximum) ranges of digestibility (OMD, % of organic matter) and macronutrient content (% of dry matter). Summer: May-October; Winter: November-April. (n) = number of study areas involved in the values. Seasonal means and ranges are based on monthly values from the study areas. No subdivision has been made between summer and winter season and between grazed and ungrazed, and no mean has been given, when data were few or incomplete.

	OMD	N	P	K	Na	Ca	Mg
MAINTENANCE REQUIREMENT	50	1.2	0.22	0.6	0.07	0.25	0.17
FORAGE QUALITY			**Low fertility landscape**				
Deschampsia flexuosa (n=3)[1,2,3]							
Grazed, summer	75.5	2.12	0.10	1.23	0.03	0.14	0.09
	(70-80)	(1.27-3.8)	(0.07-0.16)	(0.65-1.95)	(0-0.5)	(0.12-0.17)	(0.07-0.13)
Grazed, winter	57.4	2.24	0.12	0.56	0.02	0.10	0.08
	(48.1-69)	(1.78-2.66)	(0.06-0.21)	(0.38-0.90)	(0-0.03)	(0-0.19)	(0.04-0.11)
Ungrazed, summer	65.6	1.66	0.16	1.28	0.03	0.18	0.08
	(46-77.3)	(1.25-2.19)	(0.08-0.25)	(0.53-2.13)	(0-0.05)	(0.06-0.28)	(0.04-0.10)
Ungrazed, winter	53.9	2.19	0.18	0.72	0.01	0.18	0.13
	(43-68.1)	(1.39-2.70)	(0.09-0.24)	(0.55-0.94)	(0-0.02)	(0.12-0.24)	(0.10-0.14)
Molinea caerulea (n=2)[2]							
Grazed, summer	65	1.94	0.09	1.0	0.02	0.15	0.10
	(56-72.9)	1.17-2.70)	(0.06-0.15)	(0.71-1.47)	(0-0.04)	(0.09-0.21)	(0.06-0.13)
Ungrazed, summer	58.5	1.86	0.08	1.06	0.02	0.14	0.10
	(38.6-69.5)	(1.1-2.93)	(0.04-0.13)	(0.7-1.37)	(0-0.04)	(0.10-0.19)	(0.07-0.11)
Calluna vulgaris (n=2)[1,3]							
year-round	42	1.33	0.07	0.41	0.04	0.41	0.14
	(27.3-49.0)	(1.18-1.50)	(0.03-0.07)	(0.18-0.66)	(0.01-0.06)	(0.3-0.51)	(0.06-0.22)
Betula spp. (n=2)[1,.3]							
year-round	(30-63)	(1.4-3.3)	(0.08-0.29)	(0.3-1.0)	(0.03-0.08)	(0.28-0.44)	(0.1-0.1)

Table 2. Continued

	OMD	N	P	K	Na	Ca	Mg
				Intermediate fertility landscape			
Agrostis capillaris/Festuca rubra grassland (n=3)[1,2]							
Ungrazed, summer	62.6	2.11	0.19	1.61	0.04	0.28	0.13
	(52.2-76.6)	(1.0-5.19)	(0.08-0.37)	(0.8-2.84)	(0.01-0.11)	(0.08-0.47)	(0.1-0.21)
Ungrazed, winter	49.5	2.15	0.17	0.76	0.02	0.26	0.08
	(41.6-60.3)	(1.41-3.4)	(0.13-0.24)	(0.32-1.95)	(0-0.05)	(0.12-0.43)	(0.04-0.14)
Prunus spinosa (n=1)[1]							
year-round	36.1	1.44	0.16	0.76	0.05	0.59	0.1
	(26.1-45.6)	(1.04-1.88)	(0.11-0.22)	(0.47-1.39)	(0.02-0.07)	(0.48-0.7)	(0.08-0.13)
				High fertility landscape			
Poa spp. /Lolium perenne/Agrostis stolonifera grassland, (n=7)[1,4,5,6,7]							
Grazed, summer	78.2	2.88	0.41	1.85	0.37	0.78	0.23
	(70.9-84.1)	(2.36-4.10)	(0.36-0.49)	(0.98-2.23)	(0.25-0.57)	(0.37-1.34)	(0.17-0.29)
Grazed, winter	44.8	2.4	0.26	1.0	0.13	0.65	0.16
	(32.8-56.7)	(1.3-4.8)	(0.10-0.47)	(0.22-2.51)	(0.06-0.2)	(0.45-0.85)	(0.12-0.19)
Ungrazed, summer	66.6	2.03	0.28	1.63	0.21	0.47	0.24
	(56.3-81.3)	(1.48-4.15)	(0.2-0.4)	(.96-2.08)	(0.06-0.30)	(0.28-0.85)	(0.11-0.39)
Ungrazed, winter	36.1	1.8	0.18	0.69	0.1	0.36	0.17
	(23.9-50.2)	(1.2-2.9)	(0.11-0.36)	(0.14-2.07)	(0.05-0.18)	(0.23-0.57)	(0.1-0.3)
Urtica dioica/Cirsium arvense/Atriplex hastata (n=3)[1,7]							
summer (year-round for OMD)	(19-81.9)	(1.3-5.7)	(0.35-0.93)	(2-4.2)	(0.01-1.2)	(1.4-6.4)	(0.3-0.58)
Phragmites australis (n=2)[7]							
summer (year-round for OMD)	(26.1-81)	(1.6-3.6)	(0.2-0.38)	(1.5-2.6)	(0.02-0.08)	(0.2-0.5)	(0.1-0.1)
Salix spp (n=1)[7]							
year-round	(25-50)	(1.3-2.6)	(0.15-0.25)	(0.6-1.7)	(0.05-0.15)	(0.4-0.6)	(0.1-0.22)

1. Bokdam (unpublished data); 2. WallisDeVries (1989); 3. Van Wieren (1988); 4. Bal (1989); 5. De Bie & Bokdam (1987,1989); 6. Korevaar (1986); 7. Vulink & Drost (unpublished data).

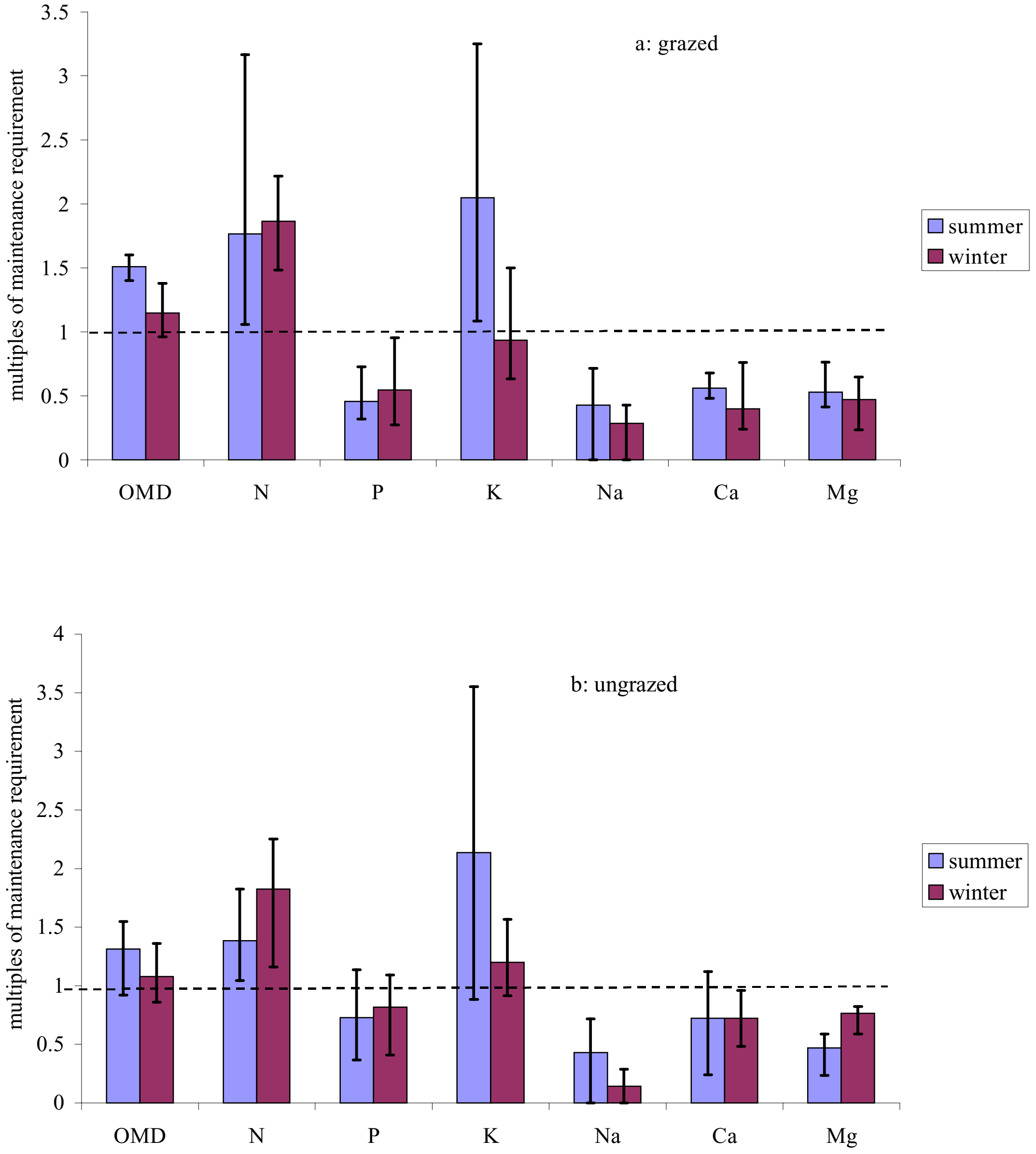


Figure 2. Average and minimum-maximum range of forage quality of grazed (a) and ungrazed (b) *Deschampsia flexuosa* grassland in summer and winter, expressed as multiples of maintenance requirements for OMD (Organic Matter Digestibility) and macronutrients.

Digestibility in the ungrazed vegetation fell below maintenance requirement during winter (Fig. 3). This was not observed in the grazed vegetation, but it might occur during spells of heavy frost, when even the wintergreen *Festuca rubra* dies back. Intake rates by cattle may be very low in the grazed vegetation, due to the reduced sward biomass (WallisDeVries 1989).

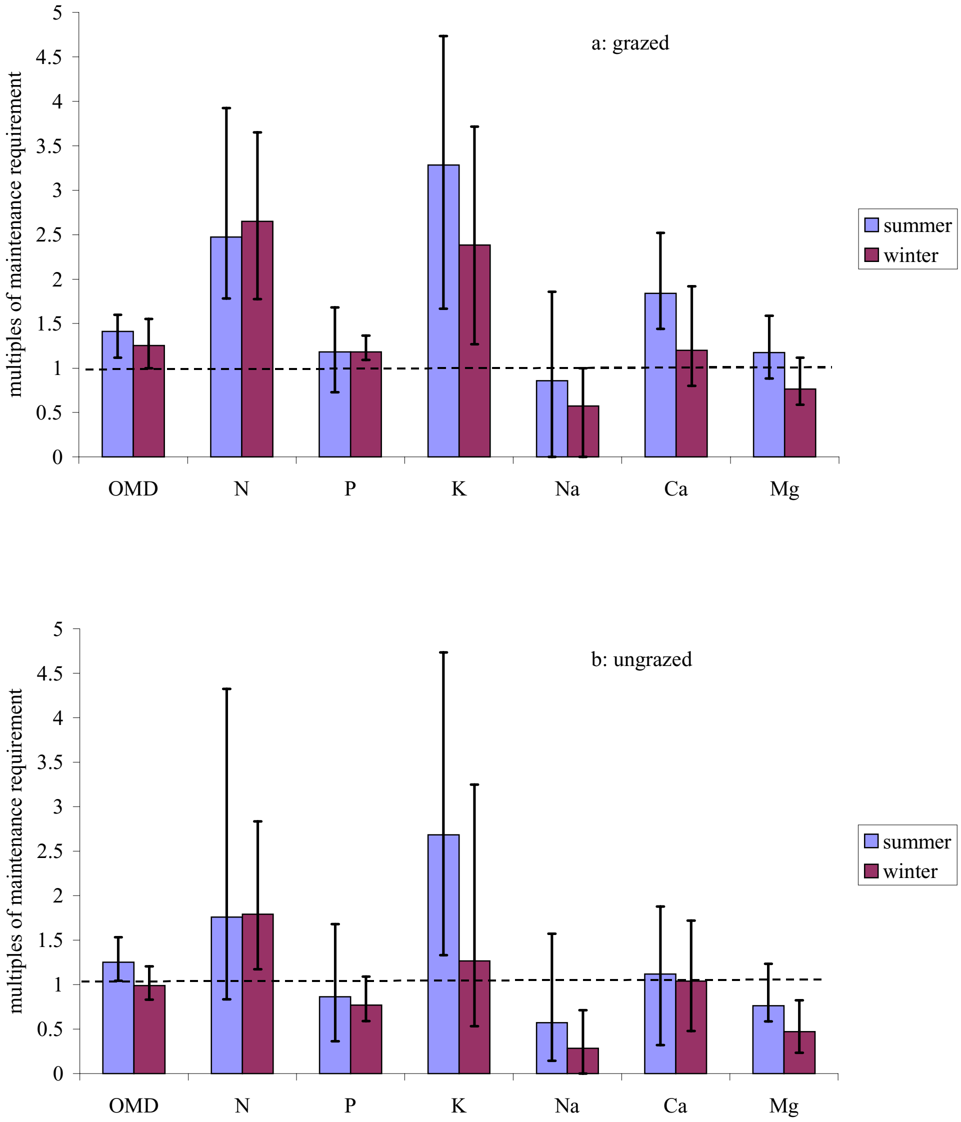


Figure 3. Average and minimum-maximum range of forage quality of grazed (a) and ungrazed (b) *Agrostis capillaris/Festuca rubra* grassland in summer and winter, expressed as multiples of maintenance requirements for OMD (Organic Matter Digestibility) and macronutrients.

Among the macro minerals, Na was deficient for most of the year with the exception of mid-summer; only traces were found in winter. P and Mg were generally deficient in the ungrazed vegetation, while Ca was present in marginal or sufficient concentrations in the grazed vegetation (Fig. 3).

The shrub *Prunus spinosa* had a low digestibility throughout the year. Its mineral content is comparable to that in *Agrostis capillaris/Festuca rubra* grassland.

HIGH FERTILITY LANDSCAPES

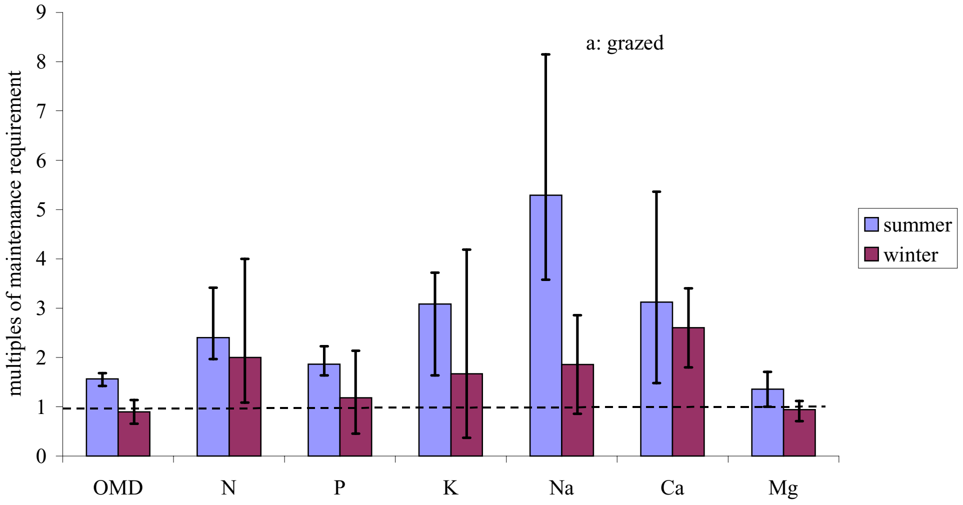
Domimant and representative species in high fertility grasslands are *Lolium perenne*, *Poa spp.* and *Agrostis stolonifera*. As to the differences between grazed and ungrazed grassland vegetations, the same pattern as in the intermediate fertility landscape occurred, with highest digestibility and nutrient content in the grazed vegetation (Fig. 4).

In summer, no deficiencies for any quality parameter were found, but during winter depressed nutrient contents and a very low digestibility occurred in grazed as well as in ungrazed vegetation. The die-back in the aerial parts of grasses was generally more severe than in any of the other landscape types. Early regrowth may have a high quality but tiller length and biomass limit the intake by cattle.

For tall herbs from drained sites such as *Urtica dioica*, *Cirsium arvense* and *Atriplex hastata*, the same remarks apply as for the grasses. Summer energy content was even higher than in grasses, but digestibility of dead, standing winter material was far below maintenance requirements. New shoots, produced in early spring, are of excellent quality however (Vulink & Drost, unpublished data).

An important forage species from moist and wet sites in high fertility landscapes is *Phragmites australis*. Digestibility and macromineral contents were sufficient during summer. During winter, digestibility was far below maintenance requirement. Digestibility of *Salix* shoots hardly reached the maintenance requirement level, even in summer.

Indeed, de Bie & Bokdam (1987 and 1989) found in a study on embanked tidal flats that cattle needed energy supplements during winter to prevent starvation. Drost (1986) found similar results in a study on cattle in the Ysselmeerpolders.



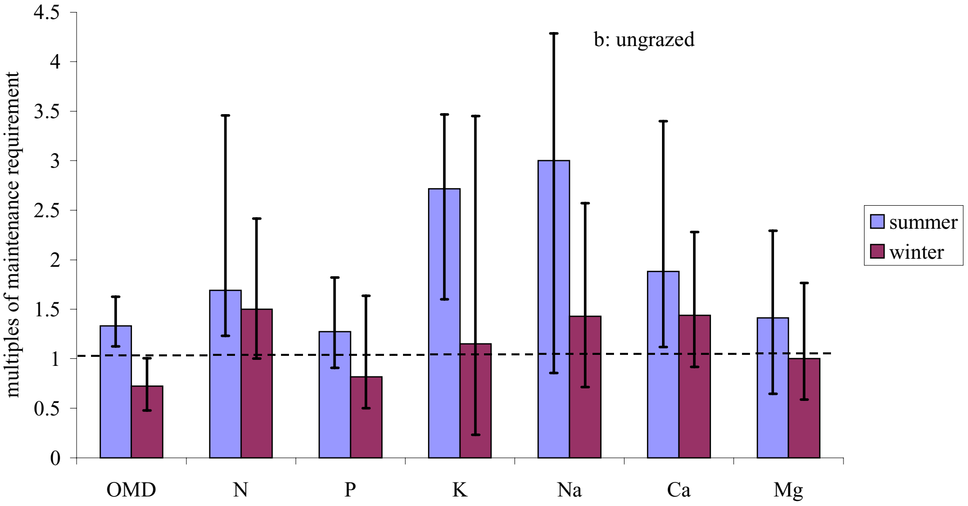


Figure 4. Average and minimum-maximum range of forage quality of grazed (a) and ungrazed (b) *Lolium perenne/Poa spp./Agrostis stolonifera* grassland in summer and winter, expressed as multiples of maintenance requirements for OMD (Organic Matter Digestibility) and macronutrients.

Discussion

The summer values of grasslands of high and intermediate fertility landscapes of this study are comparable to the values of corresponding individual species given by Dirven (1984). For *Molinia caerulea*, higher concentrations of Na (0.09 %), Ca (0.30

%) and Mg (0.18 %) were reported by the same author in early summer. As his material derived from unfertilised hayfields on minerotrophic peat soils (Dirven, personal communication) these data were not used for the calculation of the low fertility grassland values.

The data presented also show a close similarity to data from studies of comparable vegetation and from studies of the same species from other countries of northwestern Europe. We refer to Buttenschøn & Buttenschön (1982) for Denmark and to Thomas *et al.* (1945); Rawes (1963), Grant *et al.* (1963, 1978), Robertson & Davies (1965), Rawes & Welch (1969), Milne (1974), Moss & Miller (1976), Brasher & Perkins (1978), Miller (1979), Moss *et al.* (1981), Hodgson & Grant (1981) and Armstrong & Hodgson (1986) for Great Britain. The observed similarity suggests that the forage quality values observed in the Netherlands apply to the wider region of northwestern Europe.

In view of the use of the results for the assessment of the carrying capacity for year-round cattle grazing, some remarks should be made with respect to the selected parameters and to the interpretation of the compiled data set.

This survey has been focused on energy and macronutrients. Insufficient data are available for trace elements, which are potentially of equal importance to the herbivore. Deficiencies in cobalt, selenium, iodine and possibly copper seem likely in the low and intermediate fertility landscapes (Russell *et al.* 1956; Hartmans 1974; Van Soest 1982; Langlands 1987; de Bie & Bokdam 1989). In the high fertility landscape induced copper deficiency may occur on marine sediments through the inhibition of copper absorption by high molybdenum and sulphur concentrations, heavy metals and by a high alkalinity (Russell *et al.* 1956; ARC 1980).

Other plant characteristics may also act as limiting factors for animal performance. We may point to toxic substances, structural digestion inhibitors such as lignin, and morphological structures such as spines and hairs. We do not expect that these factors will change the overall picture emerging from this review. Toxic plants and morphologically unpalatable plants are rarely dominant in the vegetation types concerned and they are usually avoided by cattle.

The composition of diets actually selected by the animals will be different from the reviewed analysed simulated diets. However, this is not expected to greatly change the interpretation. Even green leaves (which provide the highest food quality) of *Deschampsia flexuosa* and *Molinia caerulea* usually have deficient mineral contents (WallisDeVries 1989). Furthermore, in the high fertility landscape the possibility of selecting green leaves in winter is probably too limited for cattle to reach an acceptable digestibility value and a sufficient intake level.

The levels of maintenance requirement used in this paper are open to discussion. Suttle (1987) pointed to the lack of understanding of the mineral requirements of herbivores. It is well known that the requirement standards vary between authors and between different editions. Most recent publications use lower levels than earlier ones. Little (1980), for instance, demonstrated that diet concentrations of 0.12% P met the growth requirements of beef cattle; this compares with the estimated minimum levels found by van Wieren (1988). He observed in a low fertility landscape apparent P and Ca deficiency in free-ranging Highland cattle supplemented only with NaCl. Not all of the animals were equally affected.

It is clear that in animal husbandry, from which the requirement standards originate, the tendency will be to play safe and to include even the higher requirements of less efficient animals in order to ensure a high productivity of the entire herd. In the case of extensive grazing in nature reserves the survival and maintenance of a population as opposed to production is the central issue. This would suggest a policy of using the existing variation between individuals and breeds in order to select animals with low requirements for the limiting nutrients. In the long run, this may result in cattle populations with lower requirements.

However, three factors complicate this discussion. Firstly the use of diet concentrations to express requirements is not an ideal approach. It presupposes a constant food intake and absorption. Both factors, however, vary depending on digestibility and on the rate of food passage, thus biassing the requirement estimates. Secondly, the use of body reserves has not been taken into account. Cattle may use a considerable amount of fat during winter. A weight loss of up to 30% without a fatal loss of condition was reported for Highland cattle by van Wieren (1988). Little is known about the potential use of mineral reserves. A rapid build-up of reserves during a short period of adequate mineral supply might suffice to bridge a longer period of shortage. Suttle (1987) remarks that adult sheep and cattle may draw on skeletal P and Ca reserves for extended periods. Thirdly, various additional non-forage sources may be exploited for minerals in low fertility landscapes. Drinking water is one of these. Lecomte & Le Neveu (1986) found concentrations of 0.17 g Ca l^{-1} in up-welling groundwater. They suggested that water uptake could possibly explain the fact that no signs of Ca deficiency were observed in free-ranging Highland cattle. Soil consumption is another known way of obtaining minerals, which may contribute substantially to the animal's mineral balance (Kreulen & de Jager 1984, McDowell 1985). Bones, excreta and even live animals may provide a source of Ca and P. Bone chewing has been observed frequently in association with shortage of these minerals (McDowell 1985). Predation on seabird chicks by sheep and red deer has been recorded in the mineralogically poor environment of the Isle of Rhum (Scotland) (Furness 1988). Consumption of rabbit faeces and rabbit corpses by cattle has repeatedly been observed in mineral-poor heathlands by the authors. However, there are as yet no indications that these non-food sources contribute substantially to the mineral balance of cattle in the situations concerned.

Finally, non-forage factors governing carrying capacity such as inundation, a weak soil, snow cover and diseases have not been taken into consideration. The first two factors periodically exclude grazing in wet high fertility landscapes, especially on floodplains and peatland during late winter and spring.

Conclusions

In dry low fertility landscapes digestibility of the main herbaceous forage plants is adequate for maintenance, except for short periods of heavy frost. In moist low fertility landscapes digestibility is inadequate during the whole winter. In both types, minerals (primarily Na and Ca, but also P, Mg and possibly a number of trace elements) seem in short supply and may lead to serious deficiencies. Woody plants will probably not contribute sufficiently to the mineral balance of cattle. Their low digestibility does not allow a sufficient intake.

In intermediate fertility landscapes the mineral supply is better, but Na and certain trace elements may still be limiting. Winter digestibility is inadequate in ungrazed vegetation. In grazed vegetations digestibility meets maintenance requirement but it is doubtful whether the low biomass and sward height permit a sufficient intake rate to cover the animal's energy demand during the winter period.

In high fertility landscapes the mineral supply will not pose any problem, although in some areas induced Cu deficiency may be expected. A more serious problem is the lack of forage with adequate digestibility during winter. The insufficient energy supply may last for a period of up to four months, which seems to be too long to be compensated by body reserves.

In each of the three landscape types sustained year-round cattle grazing seems to be precluded by insufficient forage quality. Each type should therefore be considered as an incomplete habitat for cattle, in which survival is at risk. The intermediate fertility landscape seems to offer the least unfavourable environment.

Contrasting landscape types, particularly the low fertility landscape and the high fertility landscape, constitute complementary sources of energy and macronutrients for cattle. In combination, the two contrasting landscape types offer a nutritionally complete habitat. High fertility landscapes are suitable as summer range only and low fertility landscapes as winter range. The position of the intermediate fertility landscape type seems to be intermediate, as its name suggests. The question remains open whether the storage capacity of cattle for minerals during summer in high fertility landscapes will be sufficient for survival during winter in low fertility landscapes.

The results of this study also support the view, that the spatial distribution of resident and migratory large herbivores is strongly regulated by the available forage quality (McNaughton 1988, 1990).

Management Recommendations

Seasonal migration, either spontaneously or controlled, between contrasting high and low fertility landscapes or ecotopes does seem the most natural and most promising management solution for the nutritional constraints cattle are faced with under year-round grazing. The emerging pattern of forage quality of the different landscape types and seasons stresses the need for an evaluation of the actual grazing management regimes in Dutch nature reserves. In single-landscape reserves, seasonal grazing by cattle should be considered as more natural than year-round grazing with supplementary feeding.

Future Research

The validity of the recommendations presented in this paper concerning the incomplete and seasonal habitat character of isolated landscapes and ecotopes for cattle and similar large herbivores should be thoroughly tested. Appropriate research should include actual diet quality, forage intake and animal performance in different single landscape types and landscape combinations throughout the year. Comparable studies are desirable for all other important large domestic and wild herbivores in Dutch nature reserves, such as ponies, sheep, red deer and wild boar. These species all receive food supplements during a part of the year in most reserves.

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Chapter 7

Free-ranging cattle as a driving force for resource-mediated successional grazing cycles: a synthesis

Jan Bokdam

By suppressing woody and tall herbaceous undergrowth and introducing grass seeds, cattle generated new grass lawns in woodland (photo Jan Bokdam).

Free-ranging cattle as a driving force for resource-mediated successional grazing cycles: a synthesis

Jan Bokdam

Introduction

This chapter synthesises the results from the previous chapters in answer to the questions raised in the general introduction about the effects of free-ranging grazers on openness and soil fertility in the woodland domain. First, I recapitulate the claims of the Resource-mediated Successional Grazing Cycle theory. I then summarise the evidence for these claims found in the study area, using some new data on the ongoing *Calluna* and *Rubus* invasion. I also add evidence from other areas in Western Europe with a long grazing history. Lastly I examine different successional pathways and micro-cycles in the lawn, and discuss the variation in the life strategies and anti-herbivore resistance strategies of lawn invaders across successional stages and C/N gradients.

What's in a name? Claims of the RSGC hypothesis

The RSGC-model hypothesises that free-ranging large grazers act as a driving force for successional mosaic cycles in the woodland domain by creating, depleting and abandoning grass lawns. These lawns, composed of lawn grasses, herbs and dwarf shrubs constitute the open, nutrient-poor habitats so essential for biodiversity (Chapter 1). The RSGC is a limit cycle with a grazed lawn alternating with a successional phase without grazing. The duration of the grazing lawn period is limited by the depletion of the essential soil resources (nutrients) of the lawn grasses. These resources are replenished during the later successional phase without grazing. Re-invasion of grazers and grasses in gaps with a high light and nutrient supply in this taller vegetation initiates the start of a new grazing period (Fig.1).

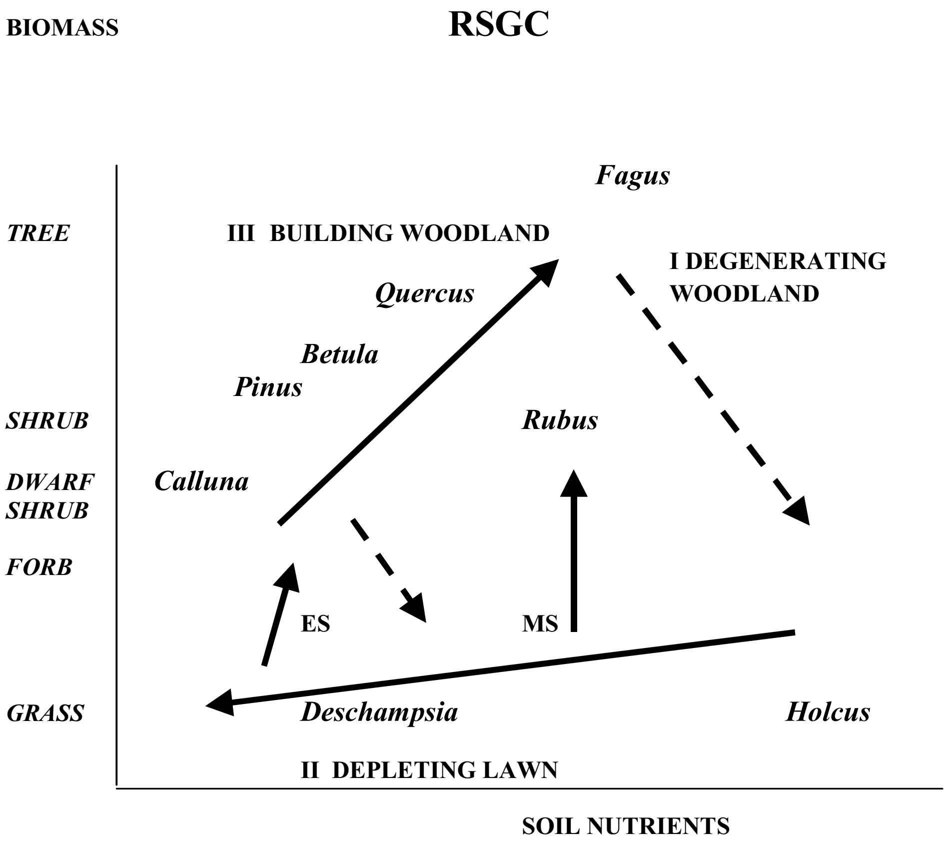

Figure 1: Resource-mediated Successional Grazing Cycle (RSGC). During woodland degeneration (I) soil fertility increases by input of nutrients in dead biomass and increased mineralisation. Grazers facilitate the establishment of grass lawns by suppressing mid-seral woody undergrowth (MS) and forbs (tall herbs), grass seed dispersal, defoliation and treading. Nutrient and light availability increases. During the lawn stage (II) the soil nutrient pool is depleted by biomass removal. Nutrients ingested on the grazing lawns are excreted in non-foraging habitats. Nutrient depletion followed by reduced food production, food quality and grazing intensity enhance the invasion of light demanding unpalatable early-seral (ES) dwarf shrubs (*Calluna vulgaris, Erica tetralix)* and trees (*Pinus sylvestris* and *Betula pendula*). Abandonment by the grazer initiates a new woodland phase and nutrient replenishment (III).

This thesis examines nutrients and light as resources mediating successional grazing cycles in the woodland domain, with cattle as grazers. Therefore, four claims are tested:

- cattle create grass lawns in later successional stages (i);
- cattle deplete the soil nutrient pool of these grass lawns (ii);
- nutrient depletion induces replacement of lawn grasses by unpalatable taller species (iii);
- the lawn nutrient pool is replenished during the period of succession after abandonment by the grazer (iv).

Evidence from the Wolfhezerheide

Chapters 2-5 provide evidence that free-ranging cattle created depleted and abandoned grass lawns as stage in the successional woodland-grassland-heathland mosaic of the study area. They also show that the proportion, size, longevity, degree of nutrient depletion and distribution of the lawns are sensitive to nutrient levels, which were affected by the historical land use, former management and the grazers.

CREATION OF GRASS LAWNS

The establishment of grass lawns requires nutrients, light and seeds. In most communities in the study area, mineralisation of plant litter, atmospheric deposition and excreta supplied sufficient nutrients, except in the turf-stripped *Calluna* (Chapter 2). Cattle allowed light onto the woodland floor by suppressing taller plants in the undergrowth that acted as competitors for light: late and mid-seral shrubs and trees and tall herbs and grasses (e.g. *Molina*) (Chapter 4). Cattle did not kill mature trees, but horses killed the few *Ulmus* trees in the forest and some *Sorbus* trees in the open heathland by bark peeling. All other tree gaps were the result of storms. Death by ageing was rare because of the young age of the canopy trees (< 80 year). In the lower *Calluna* dwarf shrub, cattle created gaps by trampling, but the main reasons for gaps were ageing and death caused by plagues of heather beetles (Chapter 2). High nutrient inputs probably accelerated death by ageing and beetle plagues (Berdowski 1993).

The dispersal of grass seeds by cattle (Klapp 1965; Heady 1975; Bakker 1998) was not quantified in the study area. *Deschampsia* was already locally present in the woodland undergrowth before the introduction of cattle in 1983. Subsequently, other species of lawn grasses invaded the woodland by germination on dung patches. Their frequency in the open lawn also increased after 1983 (Chapter 2, Appendix). The importance of seed dispersal by cattle to woodland gaps became more obvious after the adding of farm grassland to the study area in 1993. After that year, *Lolium perenne, Poa annua, Poa pratensis, Phleum pratense, Agrostis capillaris, Plantago major, Taraxacum vulgare* and *Polygonum aviculare* were frequently found on dung.

SOIL NUTRIENT DEPLETION IN GRASS LAWNS.

Cattle reduced the total and available P and K pools in the excreta-free grass lawns of the study area despite the high atmospheric inputs (Chapter 5). Under naturally low

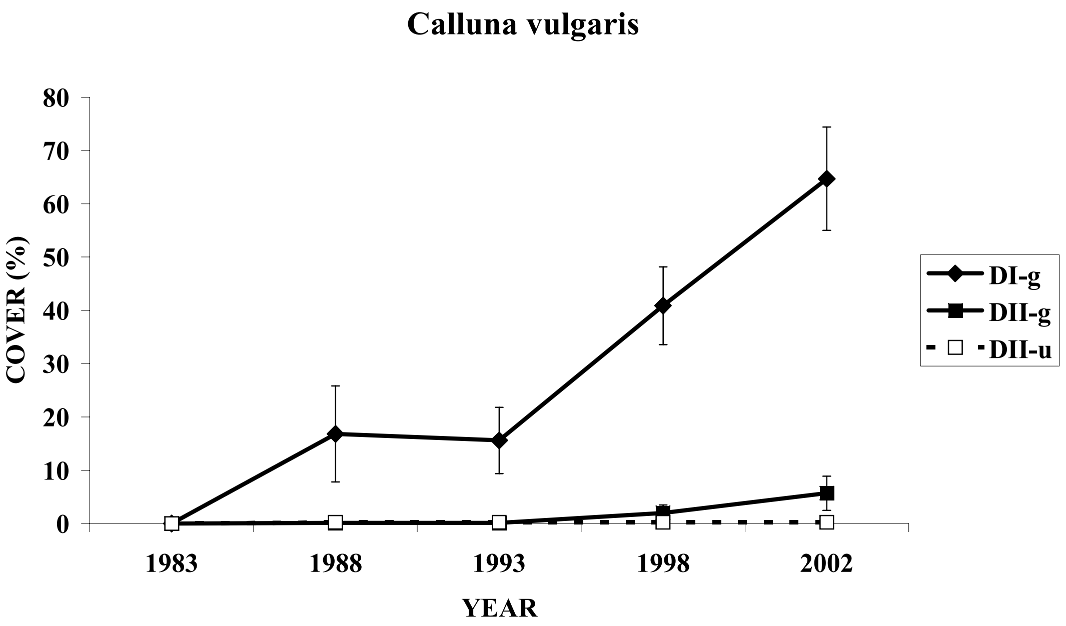

Figure 2. Cover of *Calluna vulgaris* in grazed and ungrazed successional stages of the mosaic cycle, 1983-2002. DI-g = *Deschampsia* lawn on podsolic soil, grazed; DII-g = *Deschampsia* lawn on plaggen soil, grazed; DII-u = *Deschampsia* lawn on plaggen soil, ungrazed.

levels of atmospheric input, cattle would have depleted the grass lawn as a whole. The depletion was the net effect of off-take, body retention, redistribution, gaseous losses and reduced dry deposition (Chapter 5).

Defoliation reduced the biomass of *Deschampsia*, but not its cover as measured with the Point Quadrat method (Chapter 2). Cover declined only locally after shading by expanding *Calluna* (Chapter 3). I did not measure changes in the productivity of *Deschampsia*. Measurements by other authors revealed a decline after 5 years of summer grazing (Kooijman & Smit 2001).

INVASION OF WOODY PLANTS IN GRASS LAWNS.

Cattle induced and allowed lawn invasion by *Calluna* and/or pioneer trees on all soils, except on the relatively nutrient-rich plaggen soils. Here they suppressed the few seedlings (Chapter 2; Fig. 2). Bite counting (Chapter 4) and bite marks revealed that cattle, horses, rabbits and roe deer contributed to this suppression on the relatively fertile lawns. On the relatively nutrient-poor podzolic soils, cattle did not browse the woody pioneer trees (*Pinus* and *Betula*), but they suppressed the mid-seral woody species (*Quercus*, *Sorbus*, *Frangula, Prunus serotina*, *Amelanchier lamarckii* (Chapter

4). After 1993, the increase of *Calluna* continued on all soils, but the increase was most dramatic on the podzolic soil (Fig. 2).

The failure of *Calluna* and pioneer trees to encroach on the nutrient-rich lawn was primarily attributed to associational palatability provided by *Deschampsia*. The higher production and quality of the lawn grass on the nutrient–rich soil may have induced a higher grazing pressure by cattle, horses and rabbits and a higher risk for woody invaders to be browsed and trampled (Chapter 2).

REPLENISHMENT OF THE SOIL NUTRIENT POOL

Total and available soil nutrient pools usually increase during secondary succession (Odum 1971; Berendse 1990; Leuschner 1993). An assessment in the study area covering 1988-2001 showed a significant increase in total N in the *Deschampsia* lawn on podzolic soils invaded by *Calluna* after 1983 (Scherpenisse 2002).

CIRCULAR MODEL

The same investigation also showed a significant decrease in extractable N and P in these *Deschampsia-Calluna* sites (Scherpenisse 2002). Findings suggested that a circular model might be more suitable for the available nutrient pool, than the proposed triangular model (Fig.1). A circular model represents a gradual transition from mature to degenerating woodland and woodland gaps. In cases of gaps by disturbance, a sharp angle may be maintained. If the available nutrient pool already declines before the woodland biomass has completely disappeared from the gap (e.g. by leaching of nutrients from mineralised litter, Borman & Likens 1979), then the right lower angle may also be gradual. The transition from lawn to woodland (the left lower angle) may be curved if the nutrient availability increase lags behind the biomass build-up. Pioneer plants from nutrient-poor sites might be able to deplete the available soil nutrients to a lower level than lawn grasses. Delayed mineralisation of recalcitrant, tannin-rich *Calluna* litter (Berendse 1990) may also contribute to a curved angle.

Evidence from other grazed areas

Formally, the data of the Wolfhezerheide cannot be used to test the RSGC because they induced the model (Chapter 3). Therefore I have also used additional evidence from other areas. Testing of the whole model requires monitoring of vegetation dynamics, soil fertility and grazing pressure during a whole cycle, e.g. a period of more than 20 years for a short heather-grass cycle or a period longer than 200 years for a tree-grass-heather cycle. Such data are probably non-existent. But parts of the model may be tested over shorter time periods by assessing the interactive effects of grazers and nutrients on lawn creation, lawn depletion and lawn succession.

NEW FOREST (SOUTH ENGLAND)

This area provides rich circumstantial evidence for the effects of free-ranging grazers on lawn creation, lawn depletion and wood encroachment in depleted lawns. The grazing history of this woodland-grassland-heathland mosaic (ca. 25.000 ha) dates back to at least medieval times (Tubbs 2001). The actual herbivore assemblage includes free-ranging cattle and horses, red deer, fallow deer, sika deer and roe deer (Putman 1986). Parts of the dry (upland) zones were temporarily used as arable field during World War II and reintegrated in the grazed area in the late 1940's after reseeding with grasses (Putman 1986; Tubbs 2001).

Gaps in the 'ornamental' (degenerating) beech and oak woodlands are invaded by lawn grasses (e.g. *Festuca rubra, Agrostis capillaris*). The palatable *Quercus, Fraxinus* and *Sorbus* only regenerate when protected by resistant spiny shrubs or fences. Woodland undergrowth (e.g. *Taxus, Ilex*), gap invading tree saplings, shrubs (*Prunus spinosa, Crataegus*), bracken (*Pteridium aquilinum*) and coarse grasses are more or less suppressed by consumption and trampling. The presence of typical woodland ground flora, remnants of the undergrowth and the presence of brown earth soils point to a relatively recent woodland-grassland transition (Tubbs 2001).

The extremely low production and species composition of old lawns point to nutrient depletion by grazing (Tubbs 2001). The free ranging cattle and ponies display differential habitat use (Pratt *et al.* 1986; Putman 1986), the proportion of excreta-free lawns being enhanced by the latrine behaviour of the ponies (Edwards and Hollis 1982). *Calluna* locally invades acid grass lawns in forest gaps (Bokdam personal observation).

The New Forest also provides circumstantial evidence for nutrient-dependent wood encroachment in grazing lawns. There is little invasion and expansion by Ericaceous dwarf shrubs (*Calluna vulgaris, Erica cinerea*), gorse (*Ulex europaeus*), bracken (*Pteridium aquilinum*), bramble (*Rubus*), pine (*Pinus sylvestris)* and silver birch (*Betula pendula*) on the short-cropped reseeded grasslands, but neighbouring unfertilised sites are heavily occupied. The tree and shrub encroachment in the heathlands is counterbalanced by cutting and burning, while mowing, sweeping and herbicide spraying is practised to control bracken (Westerhoff 1992).

JUNNER KOELAND (THE NETHERLANDS)

The decline in woody lawn invaders since 1967 in the Junner Koeland also points to a nutrient-dependent wood invasion in grass lawns. The nature reserve Junner Koeland (50 ha) is a former common pasture area for herded cattle. It is located in a dry, sandy flood plain of the Overijsselse Vecht (Sloet van Oldruitenborgh 1982; Bokdam 1987). The density and cover of *Crataegus monogyna*, *Rosa spp*, *Calluna vulgaris*, *Juniperus communis*, *Betula pendula* and *Pinus sylvestris* have been declining since 1967 (Bokdam unpublished data). Established plants died through ageing, browsing by cattle and rabbits and by trampling. They were replaced by grass or bare soil. Re-establishment almost completely failed. Rare exceptions were seedlings found in inaccessible micro-sites and exclosures.

This decline in woody invaders is attributed to an overall eutrophication, increased production and increased grazing and browsing pressure. The large rabbit population in the area occasionally surpassed 1500 (on 50 ha) during the 1980s (Bokdam 1987; Gleichman unpublished data). The assumption of eutrophication is based on floristic changes and the changed nutrient balance. Inputs from the atmosphere (Chapter 5) and from flooding have increased since the 1950's. Traditional herding, involving housing at night and at midday has already been replaced by continuous (24-h) grazing (0.7 animal unit ha^{-1}) in the early 1900s. The vegetative expansion of *Prunus spinosa* fluctuated since 1967 as a result of temporary cattle exclosures and fluctuations in the rabbit density.

VELUWE (THE NETHERLANDS)

The woodland-grassland-heathland-bare soil mosaic of the National Park the Hoge Veluwe (5000 ha) is grazed by ca. 250 red deer, 250 mouflon, 100 wild boar and a small roe deer population (Smit, Bokdam & WallisDeVries 1998). This assemblage suppresses *Quercus* and *Sorbus* in the understory of all woodlands. These palatable species only cross the upper browsing line when fenced. The height growth of *Fagus sylvatica* is delayed. The open heathlands are colonised by *Pinus sylvestris* and *Betula* *pendula* and volunteers (‘Pine-weeders’) remove annually thousands of saplings of these species. Heavily grazed *Deschampsia* lawns are obviously much less encroached and on the intensively grazed fertilised seeded grasslands (‘game pastures’) wood invasion fails completely.

Selective suppression of deciduous trees by red deer and roe deer has already been described before for other forest sites on the Veluwe (Fanta 1982; Kuiters, Slim & Van Hees 1997). Simulation using the FORGRA model also suggests that cattle and horses (even at low densities of 1-3 animals km^{-2}) can prevent tree regeneration in these woodlands on sandy soil (Jorritsma, Van Hees & Mohren 1999).

Pathways and micro-cycles

ALTERNATIVE SUCCESSIONAL PATHWAYS

Any tall plant species with sufficient resistance can induce a successional pathway in a grazed lawn. The common pioneer species *Calluna*, *Erica*, *Pinus* and *Betula* often associate with *Empetrum nigrum*, *Juniperus communis*, *Genista spp* and *Ulex spp*. Non-leguminous spiny and thorny lawn invaders (*Crataegus*, *Rosa*, *Rubus, Prunus spinosa*) seem to be restricted to more base-rich and fertile lawns. In the depleted lawns and heathlandsof the study area, nitrophilous species (e.g. *Urtica dioica*, *Senecio jacobaea*, *Rumex obtusifolius*, *Solanum nigra*) were restricted to excreta patches.

ATMOSPHERIC DEPOSITION AND *RUBUS* ENCROACHMENT

Rubus encroachment is a growing phenomenon in conservation areas in the Netherlands. In the study area, this thorny mid-seral shrub emerged as a lawn invader after 1983 in the grazed open heathland (Chapter 2, Appendix; Fig. 3). Its expansion accelerated after 1993, especially in the *Deschampsia* lawns on podzolic soils with a high *Calluna* recovery. *Rubus* provided associational resistance to palatable and grazing-sensitive tree and shrub species (e.g. *Quercus*, *Sorbus*, *Frangula alnus*).

The establishment of *Rubus* in the open grass lawns and *Calluna* heath in the study area after 1983 is explained by enhanced germination in the short lawns and lawn gaps created by the cattle. Ungrazed *Deschampsia* on plaggen soil was the only site where *Rubus* did not become established (Fig. 3). Its expansion was attributed to the increased nutrient availability as a result of the blanket of atmospheric nutrients and the local dung and urine depositions. *Rubus fruticosus* is zoochorous and has a persistent seed bank (Thompson, Bakker & Bekker 1997; Ferris & Simmons 2000). Its anti-herbivore defence includes thorns and tannins (van Genderen, Schoonhoven & Fuchs 1996). The long, thorny stems that allow *Rubus* to climb suggest that this species is merely a woodland gap invader and not a grazing lawn invader. The sudden increase (Fig.3) followed after the adding of 6 ha fertilised farm grassland to the woodland-grassland-heathland mosaic in 1993. The productive farm grassland attracted much of the grazing pressure from cattle and horses, and reduced the browsing pressure on *Rubus* in the heathland.

The expansion of *Rubus* was apparently limited by nutrients and browsing. Stem height in the heathland ranged between 50-70 cm. On eutrophicated sites (dumps of removed saplings and (illegal) garbage), height exceeded 100 cm and the shrubs seemed wider and more vital. *Rubus* was unevenly browsed during its life cycle. Seedlings mixed with grass were ingested by cattle and horses. Rabbits and roe deer browsed also leaves from taller stems.

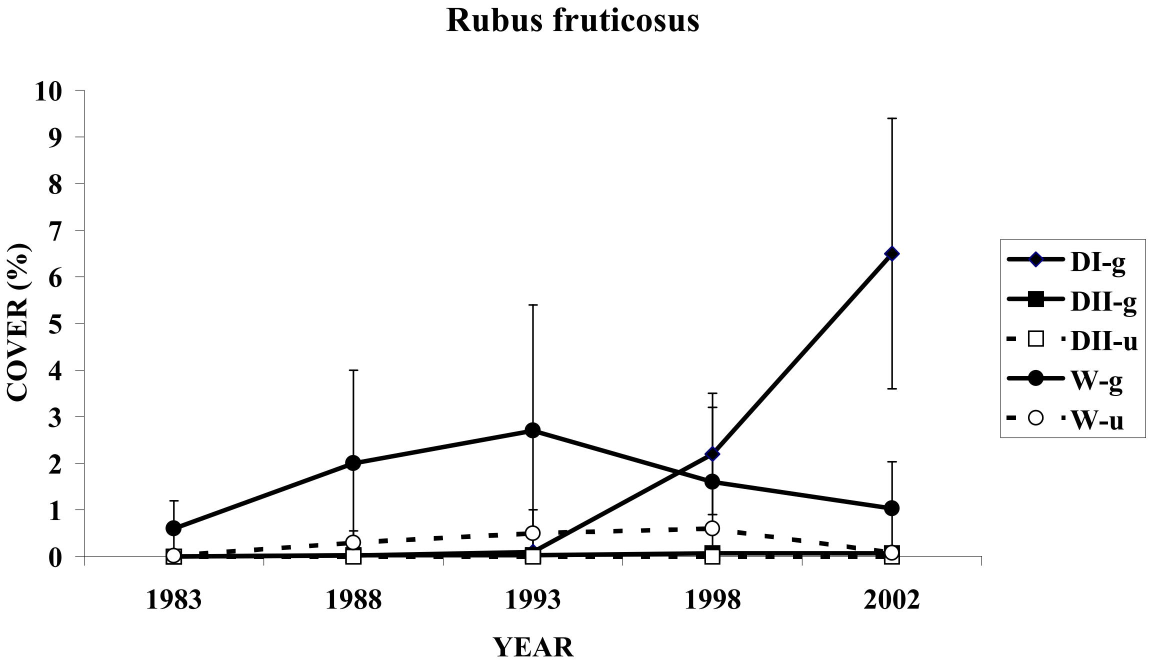

Figure 3. Cover of *Rubus fruticosus* in grazed and ungrazed successional stages of the mosaic cycle, 1983-2002. DI-g = *Deschampsia* lawn on podsolic soil, grazed; DII-g = *Deschampsia* lawn on plaggen soil, grazed; DII-u = *Deschampsia* lawn on plaggen soil, ungrazed (not accessible for roe deer and rabbits); W-g = Woodland, grazed; W-u = Woodland, ungrazed (but accessible for roe deer and rabbits).

The relatively stronger increase of *Rubus* in *Deschampsia* lawns with a high *Calluna* cover (Fig. 3) suggests an effect of associational resistance provided by *Calluna*. It emphasises the importance of browsing as limiting factor for *Rubus* expansion. It may therefore be expected that the ongoing eutrophication will further enhance this invader in the near future, so that a crash in the rabbit or cattle population might trigger an explosive *Rubus-Quercus* expansion. So far, the manager removed more than 30 *Quercus* trees from *Rubus* shrubs to keep the landscape open. Replacement of the *Calluna* pathway by the *Rubus* pathway will have consequences for the biodiversity.

The *Rubus* pathway meets the requirements of the RSGC. Its establishment and expansion in the study area was preceded by depletion and gap formation in the *Deschampsia* lawn and favoured by *Calluna* establishment.

MICRO-CYCLES IN THE LAWN AND BIODIVERSITY

Sustained prevention of lawn succession stimulated micro-cycles: small-scale successional changes (or fluctuations sensu Rabotnov (1974)) of short duration at plant scale. These micro-cycles involve replacement of lawn grasses by small herbs and bare soil (Chapter 3; Watt 1981). Small herbs replacing lawn grass are usually inaccessible for the mouth of the large grazer and tolerant to treading (e.g. *Galium hercynicum, Hieraceum pilosella*, *Hypochaeris radicata*, *Aira spp*, *Ornithopus perpusillum*) (Chapter 2, appendix). Similar micro-cycles and micro-mosaics occur in dune grasslands (Weeda, Doing & Schaminée 1996), limestone grasslands (Rosén 1982) and flood plain grasslands (Sykora, Schaminée & Weeda 1996). It may be argued that the alternation between lawn grasses and small inaccessible herbs or bare soil may also be driven by depletion and replenishment of soil resources (Rietkerk *et al.* 1996).

On dry sandy soils, treading easily creates bare soil patches Annuals and non-vascular plants invading such patches tolerate trampling by producing numerous spores and seeds (e.g. *Polytrichum piliferum*, *Erophila verna*, *Spergularia media*). Eroded patches may initiate certain successional pathways (e.g. *Juniperus communis*). Sustained intensive grazing and trampling on dry sandy soils may lead to autonomous erosion enlarging small eroded patches into eroded landscapes. For a discussion of the role of grazing and resources involved in cycles of grassland and eroded soil on larger scale and their stochastic dynamics, the reader is referred to Laycock (1991) and Rietkerk *et al*. (1996).

Micro-mosaics composed of lawn grasses, tall invaders, small herbs and bare patches are nested in the larger-scaled woodland-grassland-heathland mosaic. The high species-richness of such nested, shifting mosaics (Schertzinger 1991; Pott & Hüppe 1991; Schütz *et al*. 2000; Tubbs 2001) contrasts dramatically with the green deserts of the modern agricultural landscape (Kleijn *et al*. 2001).

Anti-herbivore defence across the grazing cycle

OPTIMAL DEFENCE

The plant species in the study area displayed a wide range of life strategies. Their variation across the successional stages and related C/N gradient was in agreement with the Optimal Defence theory (Rhoades 1979; Chapter 1). Mature large deciduous trees avoided defoliation and treading because of their size, but their seedlings and saplings and deciduous shrubs in the understory appeared to be sensitive. The tussocks of *Molinia* and *Deschampsia* and the erect form of *Calluna* in open heathland were also sensitive to defoliation and treading (Chapter 2). As adapted clonal growth form, however, these species and other lawn grasses (*Holcus spp* and *Agrostis capillaris*) tolerated defoliation and treading. All tall invaders in the grazing lawns were defoliation resistant woody pioneers. Resistant tall herbs were restricted to more nutrient-rich micro-sites (Senecio jacobaea, Urtica dioica). Small perennial and biennial herbs (e.g. *Galium hercynicum, Hypochaeris radicata*) avoided defoliation by their low stature and tolerated treading by the tensile strength of their stems and leaves. Annuals (e.g. *Spergula morisonii, Spergularia rubra, Ornithopus perpusillum*) and Bryophytes participating in the lawn erosion micro-cycle avoided defoliation by size and tolerated trampling by regeneration. Lichens on nutrient-poor sand and litter may decline by grazing since these plants are vulnerable to treading because of their low growth rate (Aptroot & Van Herk 2001). *Calluna* emerged as a flexible species. It displayed a great phenotypic plasticity and acted as pioneer on bare soil and compacted litter, as grazing-tolerant lawn-invading creeping clonal shrub and as erect subclimax species (Chapter 2).

OPTIMAL RESISTANCE

The intrinsic resistance of the lawn invaders across the C/N gradient in the study area supported the CNB-hypothesis (Chapter 1, Bryant, Chapin & Klein 1983; Van Genderen, Schoonhoven & Fuchs 1996). The resistance varied from C-based chemical resistance at open, nutrient-poor sites with high C/N values (*Pinus*, *Betula*, *Calluna*), to CN-based mechanical resistance (*Genista*, *Rubus*) or chemical resistance (*Senecio jacobaea* and *Sambucus nigra*) on sites with intermediate C/N values, to N-based chemical resistance (*Solanum nigrum*) on shaded sites with low C/N values.

Induced resistance (phenotypical change of the resistance) was not studied, but it might partially have explained the encroachment of *Calluna* and pioneer trees in the oligotrophicating grass lawns and the establishment of *Sambucus* in the eutrophicating resting sites in woodland. Oligotrophication increasing the C/N ration may have increased the concentrations of the polyphenolics in *Calluna* and terpenes in *Pinus* and *Betula*, while eutrophication by excretion might have increased the concentrations of the cyanogeneous glycosides in *Sambucus nigra* (Chapter 1). The multiple resistance of *Rubus* (by tannins and thorns) point to a flexible strategy and a capacity to colonise sites across a broad range of C/N values.

Neighbours also appeared to be important. Associational palatability was considered as the most important mechanism preventing wood encroachment in the nutrient-rich grass lawns. To cross the upper browse line, *Quercus* and *Sorbus* depended completely on associational resistance provided by *Rubus*.

Ecological conclusions

1. Free-ranging cattle can create and deplete grass lawns as temporary open, nutrient-poor habitats in the woodland domain. Because of this capacity, cattle can act as a driving force for Resource-mediated Successional Grazing Cycles (RSGC's). Because of their habitat and diet overlap with cattle, horses have probably a similar capacity. The proportion, size, longevity, depletion level and spatial distribution of the created lawns depend on the grazed area and herbivore assemblage.
2. Light and nutrients play an important role in the RSGC. Nutrient accumulation may induce gaps and favour the establishment of lawn grasses. Nutrient depletion may limit the longevity of lawn grasses by inducing wood encroachment. It means that nutrient inputs also affect the RSGC.

3. Nutrients and light (carbon) not only act as resources for plant growth but also as resources for chemical and mechanical anti-herbivore defence. Changes in the C/N ratio can enhance or reduce the defence of lawn invaders. A better quantitative understanding of these relationships may improve the prediction of grazing and nutrient input effects on vegetation succession.
4. Different herbivore guilds and species exploit different successional habitats and plant species. The RSGC provides a framework for more comprehensive successional herbivory cycles. It may be argued that more diverse herbivore assemblages ("mixed grazing") will increase the longevity and potential depletion level of the lawn (see Chapter 8).
5. The basic explanation for the RSGC is the combination of optimal foraging by large grazers with the optimal defence by the grazed plants. The RSGC theory links co-evolution (the 'arms-race') to co-existence (the 'battle'). Plant resources (the 'battleground') appeared to be crucial for the outcome of this battle.

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Chapter 8

Grazing as a conservation management tool for open, nutrient-poor habitats

Jan Bokdam

Abandoned farmland may substitute lacking natural nutrient-rich grasslands. Addition of these attractive grasslands ('graasweiden') may reduces the summer grazing pressure and accelerate succession on the dry nutrient-poor soils. The photo shows former farmlands grazed since 1993 and colonised by the Common Ragwort (Senecio jacobaea). Wolfhezerheide, July 1999 (photo Jan Bokdam).

Grazing as a conservation management tool for open, nutrient-poor habitats

Jan Bokdam

Introduction.

Grazing management requires unequivocal targets and an adequate understanding of the grazing system. In the previous chapters I discussed the effects of free-ranging cattle and tested the RSGC-model. This chapter focuses on the use of cattle and horses as large grazers for the conservation of open, nutrient-poor habitats in uplands. Cattle and horses may have similar effects on the successional vegetation mosaic cycle (Kuiters & Slim in press) They display a substantial habitat and diet overlap (Putman 1986; Vulink 2001; Menard *et al.* 2002). Uplands are higher grounds beyond the influence of flooding, and characterised by a low natural external nutrient input. After exploring the effects of the herbivore assemblage and the characteristics of the grazed area as management variables, I compare the suitability of wilderness and controlled grazing as alternative grazing management strategies. The conclusions are summarised at the end.

Herbivore assemblage

LARGE GRAZERS

Large grazers are the most important guild in herbivore assemblages used for the conservation of open, nutrient-poor habitats, because they can create grasslands in the woodland domain and deplete their soil nutrient pool. Large grazers act as shifting cultivators, harvesting accumulated nutrients from lawns. Lawn grasses act as interface (Chapter 7). Large grazers create lawns by suppressing woody undergrowth, tall herbs and coarse grasses (Chapter 4). The name 'bulk and roughage feeder' (Hofmann 1989) perfectly describes their function. Intermediate feeders, browsers and small herbivores also can suppress woody plants by consuming seeds, seedlings, saplings, bark and roots, but they generally avoid coarse grasses. Examples are red deer-*Phragmites* (Vulink 2001), Red deer-*Molinia* (Ball 1974; Gordon 1988; NP Hoge Veluwe, Bokdam, personal observation), red deer-*Calamagrostis epigejos* (NP Hoge Veluwe and Fontainebleau, personal observation), European bison- *Calamagrostis epigejos/*tall sedges (Bialowieza, personal observation). Additional evidence for this exclusive ability of large grazers may be derived from the cases in which coarse grasses invaded short grass lawns after the cessation of grazing (Bakker 1998). A second important contribution of large grazers is the dispersal of grass seeds into the woodland gaps (Klapp 1965; Bakker 1998). Dispersal by intermediate feeders and small herbivores might be less effective because these guilds tend to avoid the seed-containing standing hay. Cattle might also be superior to horses in this respect.

Large grazers are excellent lawn depletors. They combine high offtake levels (up to more than 60 % of the annual aboveground production, Van Dyne *et al.* 1980) with the export of excreta nutrients to resting areas and the induction of additional losses (Chapter 5). Large grazers may be succeeded as exploiters by intermediate feeders (Gordon 1988; Chapter 5) and other herbivores (Chapter 2). Nutritious early growth in late winter and early spring even meets the requirements of the highly selective browser roe deer.

Large grazers may accelerate the germination and establishment of woody invaders in grass lawns by generating gaps by their hoof prints. Large grazers can prevent the expansion and height growth of unpalatable species by mixing them with grass in their bites. Associational palatability is therefore an important mechanism. Facilitated smaller herbivores may be more appropriate for the depletion of grazing lawns with a low production and vegetation height, but they may more easily avoid unpalatable invaders.

DIVERSITY

Diversity of the herbivore assemblage may favour openness and soil depletion. Herbivores may have additional and complementary effects on competing plant species (Ritchie & Olff 1998). Diversity leads to competition, facilitation, association and succession in the herbivore guild. The effects of “mixed grazing” are therefore more than the sum of the effects of individual species. Large herbivores can facilitate smaller succeeders by acting as ‘bulldozer’ (Kortlandt 1984; Van Wijngaarden 1985) or as mowing machine removing unpalatable tall and coarse grasses. Intermediate feeders and browsers can facilitate large grazers by creating tree gaps, suppressing woody undergrowth in woodlands (Chapter 4; Putman 1996; Kuiters, Slim & Van Hees 1997) and woody invaders in grass lawns (Chapter 2).

Lawn nutrient depletion by large grazers is limited by a decreasing foraging efficiency at declining vegetation height. Red deer depleted low productive lawns with fine-leafed grasses in a sub-alpine woodland-grassland mosaic (Achermann 2000). Large grazers, especially cattle, facilitate and may be succeeded by smaller herbivores with a superior ability to harvest short-clipped, low productive lawns (e.g. horses, sheep, goats, deer, rabbits and hares). These herbivores might deplete the vegetation and soil nutrient pool of the lawn to a lower level, but it must be added that smaller herbivores may be less effective as nutrient movers. Central place foragers such as rabbits exploit small home ranges around burrows. By foraging and by excretion on latrine sites, they create smaller-scaled depletion-replenishment mosaics within the lawns created by the large grazers.

Facilitated intermediate feeders and small herbivores may out-compete large grazer by cropping the lawn to such a low level that it becomes inaccessible to them, during winter only or during the whole year. Cattle are susceptible to competitive exclusion by horses (Edwards & Hollis 1982; Vulink 2001; Menard et al. 2002), red deer (Gordon 1988) and rabbits (Bokdam 1987). Competitive exclusion may force large grazer to accept less attractive forage offered by the latrine area’s of the competitor (Edwards & Hollis 1982), lawn invaders (Chapter 4), later successional stages (Chapter 4 and next section). They also may be forced to shift to less favourable landscape zones (Chapter 7).

DENSITY AND SEASON

Density and season are key variables to maximise off-take and to suppress unpalatable plants. Short- cropping during the whole year maximises the annual harvest. Offtake rates decline with decreasing biomass and may reach maintenance levels, below which the animal will loose weight and starve. The offtake season may be prolonged by supplementation. Full supplementation may create bare soils because of trampling. Winter grazing removes fewer nutrients because of litter fall during the growing season and the lower nutrient concentration in aged forage. Year-round grazing at high densities creates in autumn and winter hungry herbivores willing to consume unattractive species. Examples are the consumption during late winter of *Ilex* and *Ulex* by ponies in the New Forest (Tubbs 1986; Putman 1986), *Sambucus* by cattle in the Oostvaardersplassen (Vulink 2001; Gresnigt & Vermeulen 2002) and the consumption of woody pioneers in the study area (Chapter 4).

Characteristics of the grazed area

COMPLETENESS OF THE ABIOTIC AND SUCCESSIONAL GRADIENT

The delimitation of the grazed area is a very important management variable because it affects the terrain use, diet and nutrient and seed distribution by the animals. The consequences of a restricted gradient become apparent through studies of large grazers in complete gradients (Putman 1986; Bokdam 1987) and studies in contrasting abiotic zones (WallisDeVries 1994) and successional stages. A complete abiotic gradient includes mineral wetland and dry upland, but it may also include peatland and permanent open domains with salt marshes, coastal areas, riverbanks or alpine zones. Each abiotic zone contain more or less complete successional series.

Complete landscapes can host more complete and divers herbivore assemblages and food chains than incomplete landscapes. The population density of large grazers can be higher because the animals can escape starvation by moving to other zones or successional habitats in times of shortage and harsh conditions. During the growing season, large grazers generally prefer fertile grasslands in permanent open domains and wetlands because of the superior forage quantity and quality (Chapter 6). Dry, nutrient-poor grasslands, heathlands and woodland are relatively more attractive as winter habitat because of winter-green forage, less deep snow, superior shelter and dry resting sites (Putman 1986; WallisDeVries 1994; Aerts 1995; Chapter 6). Food and shelter in the summer habitats may be depleted or inaccessible during winter.

In a complete abiotic gradient with a complete herbivore assemblage at high densities, forage depletion and competition may force large grazers, especially cattle, to leave the nutrient-rich wetland zone before the end of the growing season. This ‘overflow’ favours offtake and openness in the dry upland, depletes the winter forage, which may lead to winter mortality. The magnitude of the overflow effect will therefore be restricted. Because of the overflow, uplands surrounded by wetland such as river dunes and borders along river valleys will probably become the most open and nutrient-poor parts of the wooded upland.

The completeness of the successional mosaic affects the lawn depletion process. If the grazed area covers only grassland, all excreted nutrients remain in the grass lawn, unless the animals are removed at night to a barn. Under harsh climates in montane and coastal regions, grazers accumulate excreta on sheltered sites. Redistribution within the grass lawn may delay or even prevent lawn depletion, since the nutrient removal will be restricted to body retention, gaseous losses and leaching. Under the actual atmospheric input, nutrient-poor grasslands will eutrophicate and nutrient-rich grasslands will remain nutrient-rich (Bokdam & Piek 1998).

EXTERNAL NUTRIENT INPUTS

Successional grazing cycles as described in the RSGC theory may be considered as rotational nutrient harvests at a successional time scale. It enables large grazers to survive in ecosystems with a low external nutrient input and a low average nutrient availability. They ‘scavenge the peaks’. Accumulation during the non-grazing period may be essential to allow lawn grasses and grazers to invade after the creation of a gap. Nutrient depletion limits the lawn phase and induces woodland recovery. High external nutrient inputs preventing lawn depletion and wood invasion may lead to ‘eternal’ lawns (or to lawn succession through other mechanisms and pathways).

Because of the high atmospheric input, cattle depleted in the study area only the excreta-free-lawns for P and K and – perhaps – the whole grass lawn for K. They did not prevent the shift of the whole area to a higher soil fertility level. This eutrophication will continue until saturation is reached (Chapter 5). It means that the average soil fertility of the open areas will also gradually increase. A reduction of the atmospheric input may shift the system gradually back to a lower, more natural, level. At low inputs, net offtake alone may remove the input under controlled grazing. In Mols Bjerg (E-Jutland, Danmark), summer grazing by cattle removed the P-input of 1 kg ha^{-1} yr^{-1} from a grass heath area by body retention only (Bülow-Olsen 1980).

Complete removal of the inputs demands continuous harvesting, and hence openness by intensive grazing or mowing. Removal of the complete atmospheric input in the study area by grazing would require replacement of the actual successional mosaic by a homogeneous grass lawn or even by excreta-free lawn conditions. This would implicate mowing (once or twice a year) or intensive grazing by herding or mechanical substitutes.

Grazing management strategies

NEW WILDERNESS

Wilderness aims at the conservation of biodiversity by restoring complete landscapes with natural processes and complete, self-organising herbivore and carnivore assemblages (Van de Veen 1975; Baerselman & Vera 1989; Bal *et al.* 2001; Kampf 2002). Local extinction may be compensated by re-invasion from the regional population (Groot Bruinderink 2002). The claim of the wilderness strategy for openness in woodland was based on the assumed openness during the pre-farming Atlanticum (Vera 1997, Chapter 1). The capacity of cattle to create and maintain temporary grass lawns in the woodland domain evidenced in this thesis (Chapter 7) is supporting this claim.

This study also showed that the proportion, patch size, duration and soil fertility in the open lawns may be influenced by many other factors. Quantitative predictions therefore remain speculative. The only wilderness grazing experiment in the Netherlands (the Imbosch) recently begun and the actual successional mosaic is still very much a result of the historical land use and management. The incomplete abiotic gradient, the age of the woodland, the added farmland and the culling (see Chapter 1) affect the terrain use of the herbivores and bias the potential natural mosaic development.

Predictions of the openness and soil depletion rate might also be based on habitat and diet preferences of the large grazers and the RSGC model. These predictions point to more openness in the wetland zone than in the dry upland zone because of the higher production and higher summer quality of grass lawns in the former zone (Chapter 6). A high pressure in the uplands requires a large nutrient-rich wetland “hinterland” and a high density to guarantee overflow. The ratio between summer and winter areas determines therefore the openness in the higher areas.

Grazers confined to mineral poor landscapes (e.g. Imbosch, Veluwe) may suffer water and mineral deficiencies (Chapter 6; WallisDeVries 1996) and their density may remain low (e.g. Imbosch 0.03-0.05 au ha^{-1}). The natural solution is to restore the connection between upland and wetland (Chapter 6; Anonymus 2000). The supply of drinking water, mineral licks and supplementary feed might also cure the problem and lead to higher grazing pressures and more openness. In the past, conservationists sometimes refused supplementation as conservation management because it conflicted with the non-intervention principle. Abandoned farmland is now proposed to substitute lacking nutrient-rich grassland (Chapter 6; 'graaasweiden', Anonymus 2000). Without sustained fertilisation, such farmland will display succession to woodland, in the same way as other grass lawns derived from woodland. After soil nutrient depletion the former farmland will be colonised by invaders with a CN and C- based resistance from neutral and acid soils (*e.g. Senecio jacobaea, Crataegus Rosa, Rubus, Calluna, Betula, Pinus*). For a sustained functioning as substitute for nutrient-rich wetland grassland, sustained fertilisation is required, mimicking nutrient inputs by flooding. This solution has been practised since ca.1960 in the NP the Hoge Veluwe ('game pastures', see Chapter 7).

Grazers confined to wetlands (mineral and/or peat) face a serious challenge to survive the winter because of the lack of energy food and cover and because of the flooding (Chapter 6; WallisDeVries 1994, 1996). The availability of palatable soft wood species (e.g. *Salix* and *Populus*) and hard wood (*Fraxinus*, *Ulmus*) may increase the carrying capacity of wetlands during winter. If a connection with uplands is excluded, summer grazing is a more natural solution than supplementation. Grasslands in embanked, drained mineral wetland (e.g. Oostvaardersplassen) are functionally fertile upland lawns. When grazed as part of a successional mosaic their high initial soil fertility may decrease on the long term, inducing invasion by lawn invaders known from chalk grassland. Crashes in the herbivore densities by diseases, culling or escapes through broken fences will allow recovery of defoliation-sensitive species.

CONTROLLED GRAZING

Controlled grazing offers the most reliable strategy for open, nutrient poor habitats. The area grazed, herbivore assemblage, density, season and supplementation are all under control. Openness and low soil fertility will be maximised by high levels of biomass consumption and nutrient removal.

Controlled grazing might also aim to imitate traditional farming or to mimic wilderness. Traditional livestock farming have included nomadic, transhumance and sedentary systems. Domestication, herding and sedentarisation transformed wild nomadic and migratory grazers into resident central-place foragers. Livestock farming systems used to maximise the harvest of animal products (meat, milk, wool). After the combination with arable farming, livestock farmers were urged to collect manure and additional organic matter from the rangeland. These removals may have contributed to the replacement of wood-pasture landscapes by open, tree-less *Calluna* heathlands and drifting sands (for references see Chapter 2). Livestock farmers used uplands as summer range in order to allow the wetlands to be used for haymaking. Barns replaced woodland as night camp and as winter habitat. Housing of livestock facilitated the milking and collection of manure greatly. It means that traditional sedentary livestock farmers generated a very intensive grazing pressure, which may not have had an equivalent in natural systems on this scale.

Controlled grazing may also mimic wilderness by introducing self-organising free-ranging large grazers. The manager may also mimic (locally) extinct large herbivores by making tree gaps in woodland, suppressing woody undergrowth to stimulate lawn development in woodland and by suppressing wood encroachment in lawns to prolong their longevity. Seed dispersal and scarification by extinct herbivores may be another lost wilderness processes to be imitated. It should be noted that much of this type of substitutive management requires more reliable references.

Despite the differences between wild large herbivores and traditional farmers there appears to be much similarity in their influences and effects on upland systems. This similarity may originate from the fact that herbivores and farmers were both optimal exploiters of natural vegetation and nutrient resources in an upland ecosystem without external nutrient inputs. Both developed a shifting harvesting system. Sedentary farmers exploiting manured permanent arable fields mark the transition from a shifting to a fixated landscape mosaic. It suggests that nomadic and transhumance systems are better approximations of wilderness than sedentary livestock farming. The latter system is certainly more appropriate for the maintenance of large-scale openness and extremely over-exploited and nutrient-poor heathland and drifting sand. It may be assumed that the wild flora and fauna is still genetically adapted to shifting successional mosaics. The investigation of the links between the life cycles of target species and the successional vegetation mosaic cycles in their habitats might therefore be very rewarding for nature conservation.

Conclusions

1. The Resource-mediated Successional Grazing Cycle model may be used for the prediction of the effects of grazing management variables on the successional vegetation mosaic in nutrient-limited uplands.
2. Quantitative models predicting the effects of grazing on vegetation succession should integrate the feedback between herbivory and the plant resources.
3. Large grazers are a key component of herbivore assemblages used for open, nutrient-poor habitats in uplands. Herbivore diversity and density also favour these habitats.
4. High nutrient inputs favour openness because they prevent oligotrophication and wood encroachment
5. Even under the actual atmospheric inputs, wilderness grazing can create temporary open, nutrient-poor habitats in uplands. Their proportion, patch size, longevity, soil fertility and spatial distribution depend on the grazed area and herbivore assemblage.
6. Complete grazed areas with incomplete herbivore assemblages and/or low herbivore densities favour woodland dominance in the upland zone.
7. Controlled grazing can be used to mimic traditional farming and to imitate wilderness systems.
8. Controlled grazing is the most reliable method to create and maintain large open, nutrient-poor habitats in incomplete ecosystems.

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Summary

Conservation management questions

Low-productive grasslands, heathlands and open sand areas are crucial habitats for many threatened plants and animals. These habitats were created and maintained in the past by traditional farmers, who used them as pasture for herded livestock, but also as a source of wood, winter forage, game, litter and sand. Since the middle of the 19th century, traditional farming has declined in W-Europe, and pastures have been intensified or abandoned and replaced by woodland. The biodiversity in the remnant areas is constrained by further intensification and abandonment, and by eutrophication through atmospheric nutrient inputs. By loosing its economic and social viability, traditional farming has become dependent on financial incentives and EU policy, which have made its long-term future as conservation strategy questionable.

Therefore nature conservation is searching for suitable alternative management strategies to conserve open, nutrient-poor habitats. Mechanical management may be a suitable substitute to conserve open, nutrient-poor habitats, but unmarketable harvested products limit its economic feasibility. Other alternatives are controlled grazing by free-ranging livestock combined with minimal mechanical interventions and “new wilderness”. In the latter concept, self-organising feral livestock and wild herbivores must guarantee the future of open, nutrient-poor habitats without human help. The suitability of controlled grazing and wilderness grazing and their effects are incompletely understood and much debated. Can free-ranging large grazers create and maintain open, nutrient-poor habitats in nature conservation areas in mineral-poor drained upland areas? Have controlled grazing and wilderness grazing different roles to play in these aims?

The RSGC theory

In this thesis, I will examine the Resource-mediated Successional Grazing Cycle (RSGC) theory. According to this theory, large grazers can act as a driving force for successional vegetation cycles with alternating ungrazed woodland (or other tall vegetation) and grazed grassland. The reciprocal transitions are mediated by shifts in the availability of plant resources, especially light and nutrients. A complete cycle passes through 4 phases. During the first phase the large grazers create a grass lawn by generating a gap in the canopy and undergrowth of the woodland, and by introducing grass seeds in the gap. Sustained defoliation leads in the second phase to depletion of the soil nutrient pools of the grass lawn. Because of this depletion, grazing-resistant taller species invade in the low-productive lawn and the large grazers abandon the patch (third phase). During the last phase the nutrient pool is replenished during the ungrazed woodland succession phase. The RSGC theory was tested for cattle, because as native large grazers, cattle will play a key role in future controlled and wilderness grazing strategies in Europe. The following ecological questions were addressed:

- Can free-ranging cattle create grass lawns in woodlands and heathlands?
- Can free-ranging cattle deplete the soil nutrient-pools of these grass lawns?
- Does lawn nutrient depletion induce the invasion of grazing-resistant plants?
- Does abandonment and succession lead to replenishment of the nutrient-pool?

The research

These questions were studied in the Wolfhezerheide (60 ha), a conservation area situated in the South Veluwe (The Netherlands) and owned by the *Vereniging Natuurmonumenten.* The successional vegetation mosaic was composed of woodland (19 ha), grassland (33 ha) and heathland (9 ha). The soil consisted of acid fluvio-glacial and aeolian sandy deposits with podzolic soils. A small area of the grass lawn was situated on a relatively nutrient-rich plaggen soil, which developed in medieval arable fields through sustained manuring. The woodland canopy was dominated by *Pinus sylvestris*, *Betula pendula* and *Quercus robur,* while the undergrowth was made up of *Sorbus aucuparia*, *Frangula alnus*, *Prunus serotina* and *Quercus robur*. The *Deschampsia flexuosa* and *Molinia caerulea* grasslands developed after the degeneration of unmanaged *Calluna vulgaris* heathland. Some *Calluna* sites were turf-stripped in 1980 and others were mown in 1982. For three years from 1983, the area was grazed by free-ranging Dutch Friesian heifers (stocking rate ~ 90 kg ha^{-1} yr^{-1}). After 1985 these were replaced by suckling cows of variable breeds. The herbivore assemblage included further 1-3 horses, some roe deer and about 100 rabbits. The cattle had natural open water, salt licks (NaCl) and received a minor quantity of supplements during late winter. The manager removed the encroaching *Pinus* and *Betula* from the heathland. The annual atmospheric nitrogen deposition varied from 25 kg ha^{-1} yr^{-1} in the short-grazed grassland to 60 kg ha^{-1} yr^{-1} in the woodland.

During the period 1983-1993, vegetation changes at community scale were monitored by an annual assessment in grazed and ungrazed woodland, grassland and heathland, using plots of 25 m^2 and an extended Point Centred Quadrat method (**Chapter 2**). Changes at individual plant scale were measured by annual records of the dominant plant species in microplots of 100 cm^2 arranged within plots of 1 m^2 in *Deschampsia/Calluna* mosaics during the period 1989-1994 (**Chapter 3**). The habitat and diet selection were investigated between 1983 and 1985 using direct visual 24-hr observations to quantify foraging and non-foraging activities of the cattle in the various habitats (**Chapter 4**). Net offtake and integrated nutrient balances were calculated over the whole study area, for the successional habitats and for the excreta and excreta-free patches within the *Deschampsia* lawns. These balances were based on the terrain use data and on the best approximations of nutrient fluxes (**Chapter 5**). A review of the forage quality for cattle across abiotic and successional gradients in the Netherlands was added to show the differential nutritional challenges large grazers are facing in different habitats and seasons (**Chapter 6).**

Results

The vegetation monitoring (**Chapter 2**) showed that the free-ranging cattle created shifting heather/grass mosaics. *Deschampsia* invaded gaps in *Calluna*, while *Calluna* invaded short-grazed *Deschampsia* lawns. The mosaic did not develop either on turf-stripped *Calluna* sites (because of the failure of *Deschampsia* invasion) or on the plaggen soils (because of the suppression of *Calluna* by cattle on the relatively nutrient-rich soils). The cover of mid-seral trees *Quercus, Sorbus aucuparia* and

Prunus serotina below the browse line (1.80 m) and the tall grass *Molinia caerulea* decreased over the whole area, favouring the expansion of the lawn grass *Deschampsia flexuosa*. Unpalatable pioneer trees (*Pinus* and *Betula*) invaded open habitats, especially *Calluna* heath. Their invasion onto the plaggen soils was suppressed by the cattle and other herbivores. These findings pointed to light (gaps), nutrients (soil type) and grazers as determinants of the replacement of woody plants by *Deschampsia* and as determinant of the replacement of grasses by *Calluna* and pioneer trees. The replacements at plant scale in the microplots (**Chapter 3**) confirmed the reciprocal transitions between *Calluna* and *Deschampsia*, and even revealed completed cycles. *Deschampsia* and *Calluna* were also replaced by small vascular species (e.g. *Galium hercynicum*, *Carex pilulifera),* lichens, mosses, litter and bare mineral soil.

The habitat and diet study (**Chapter 4**) portrayed cattle as opportunistic exploiters of successional mosaics. Foraging was mainly in open habitats (83%) and non-foraging mainly in woodland (56%). This differential habitat use pointed to a substantial nutrient transport from the open foraging habitat to the resting sites in woodland. The lawn grass *Deschampsia* was the dominant diet component. Together with other lawn grasses (e.g. *Agrostis capillaris*, *Holcus* spp) it was significantly selected as a food plant throughout the year. The cattle selected summer-green mid-seral trees and shrubs (*Quercus, Sorbus*, *Frangula alnus* and *Prunus serotina*) and the summer-green grass (*Molinia caerulea*) only during the growing season. The winter-green *Calluna* was substantially consumed during the winter. The cattle avoided the pioneer trees, the thorny mid-seral *Rubus fruticosus* and the dwarf shrub *Erica tetralix* during the whole year, although they browsed them slightly during (late) winter. These results confirmed the major role of cattle as powerful consumers of woody understory species and weak inhibitors of woody pioneers such as *Calluna* and the pioneer trees. The only exception was the grass lawn on the nutrient-rich soil. There was circumstantial evidence for browsing by roe deer and rabbits on the mid-serial understory trees and lawn invaders. However, the herbivore assemblage as a whole was not able to prevent wood invasion in the open habitats on the podzolic soil.

The nutrient balance of the grazed area and successional habitats (**Chapter 5**) revealed a minor nutrient retention in body weight increment. Differential habitat use had a major influence on the nutrient balance of open habitats, but volatile N-losses from excreta and reduction of the dry atmospheric input were also important. The integrated nutrient balance showed a reduced surplus for the whole area, an increased surplus for woodland and strongly reduced surpluses for the *Deschampsia* and *Calluna* habitats. The excreta-free parts of the *Deschampsia* lawns were the only sites where the cattle successfully depleted the soil nutrient pools of phosphorus and potassium. Without atmospheric deposition, the cattle would have depleted the pools of all nutrient species for the whole grass lawn.

Chapter 6 shows that the carrying capacity of wetland areas and dry upland areas for year-round grazing cattle is limited by different food quality traits. Mineral wetlands offer year-round food with a high mineral content, but the digestibility, quantity and accessibility might limit survival of the cattle during winter. Mineral-poor dry uplands with winter-green grasses and dwarf shrubs offer a relatively higher digestible food in winter. Year-round grazing in uplands may, however, be limited by low mineral concentrations. Cattle confined to upland areas may risk deficiencies of sodium, phosphorus, calcium and magnesium, while in wetlands, cattle might starve through energy deficiency during winter. The natural solution is to (re-) connect the complementary single-zone landscapes.

Ecological conclusions

The results from the study area and additional evidence from other areas broadly support the four hypotheses of the RSGC theory (**Chapter 7**). Did free-ranging cattle create grass lawns in the woodland? They created gaps in dwarf shrub canopies by trampling, but appeared to be unable to kill mature forest trees. Canopy gaps in woodland depended on ageing of the trees and wind-throw. Nevertheless, cattle facilitated lawn grass by suppressing all woody and tall herbaceous undergrowth species, except *Rubus*. There was good circumstantial evidence that cattle also introduced grass seeds in the woodland gaps by dung deposition. Nearly all trees that died between 1983 and 1993 were replaced by grass lawns. *Rubus* invaded some gaps.

Did cattle deplete the nutrient pools of grass lawns under the actual atmospheric deposition? Because of the high atmospheric inputs, the cattle were able to deplete the nutrient pools only on excreta-free sites in the grass lawns, and only for phosphorus and potassium. The nitrogen pool maintained a small surplus. The calculated balances were conservative estimates and neglected leaching. It means that the whole grass lawn might have been depleted for potassium by the grazing cattle. At natural lower deposition levels, the cattle would have depleted the grass lawns as a whole for all elements. A more diverse herbivore assemblage and higher densities might have stimulated the creation and depletion of grass lawn.

Did nutrient depletion induce the replacement of lawn grasses by unpalatable woody species? Cattle induced the establishment of pioneer woody plants in all lawns. The assemblage of cattle and other herbivores was only able to suppress the expansion of these pioneers on the nutrient-rich plaggen soil. On the nutrient-poor podzolic soils the grasses and grazers were outcompeted by the woody pioneers, which disposed of anti-herbivore chemicals based on carbon surplus (polyphenolics, terpenes), and a pioneer with thorns (*Rubus*). The dramatic expansion of *Rubus* after 1993 was attributed to the ongoing atmospheric eutrophication and local deposits of excreta, in combination with the loss of browsing pressure after the connection of the poor heathland to attractive farm grassland in 1993.

Was the lawn nutrient pool replenished after the invasion of unpalatable species? Comparison of the soil nutrient pools in 1988 and 2001 of grass lawns on podzolic soils invaded by *Calluna* revealed that these total nutrient pools had increased.

Summarising, it was concluded that cattle – as typical large grazers – fulfilled most of the functional roles put forward in the RGGC concept. In pristine wilderness, their functioning might have been complemented by larger and smaller herbivores, especially by “bulldozer” herbivores creating gaps in woodland and by smaller herbivores enhancing the longevity and depletion of the grazing lawns. It was suggested that the RSGC might be enlarged to a Resource-mediated Successional Herbivory Cycle.

Management implications

The major implications of the ecological conclusion with respect to grazing management are discussed in **Chapter 8.** Wilderness seems to be a suitable strategy for temporary open, nutrient-poor habitats in uplands as part of complete successional mosaic cycles. The required grazing pressure in the upland demands grazed areas with complete abiotic and successional gradients, complete herbivore assemblages and unrestricted population growth. A large fertile wetland “hinterland” guarantees high winter densities of nomadic grazers in the uplands. Food depletion in the wetland may initiate overflow during summer, inducing summer grazing in the upland. Uplands surrounded by mineral wetlands (e.g. river dunes and coastal dunes) and borders along wetlands will be the most open parts of the upland. Grazing of complete abiotic gradients (or areas with heathlands and nutrient-rich farmland) by incomplete herbivore assemblages or populations at densities below the carrying capacity will reduce the grazing pressure in the uplands and change it from a year-round to a winter grazing pressure. During winter, large grazers select winter-green grasses and dwarfshrubs in the upland and they avoid residues of summer-green species with a low forage quality (e.g. *Molinia*). A shift from summer to winter grazing may therefore induce a reversal of the competitive balance of winter-green dwarfshrubs (e.g. *Calluna*) and the summer-green *Molinia.*

When the open, nutrient-poor habitats required by identified target species are not met, or when the aims of cultural historical open landscapes are not fulfilled by the wilderness strategy, managers can shift to (additional) controlled grazing. Controlled grazing is a powerful tool for the conservation of open, nutrient-poor habitats in dry uplands. It can force summer grazing in uplands by restricting the grazed area (1), increasing the grazing pressure by herding, fencing or adjusted supplementation (2). It can force soil nutrient depletion by housing the animals at night (3) and remove unwanted species and nutrients by additional mechanical management (4). Controlled grazing can therefore be used to mimic traditional farming or to substitute lost natural herbivory influences and processes.

Samenvatting

Natuurbeheer en begrazing

Schrale graslanden, heidevelden en stuifzanden herbergen veel soorten wilde planten en dieren. Ze zijn daarom erg belangrijk voor het natuurbeheer. Deze open, voedselarme gebieden zijn grotendeels in het verleden ontstaan en onderhouden door traditionele veehouders, die ze exploiteerden als onbemeste weide en als leverancier van wintervoer, brandstof, strooisel, zand en andere nuttige producten. In west-Europa is hun oppervlakte al vanaf het midden van de 19-de eeuw teruggelopen, enerzijds door bemesting en intensivering, anderzijds door verlating en bosvorming. Het kleine areaal dat bewaard bleef wordt nu als natuurgebied beheerd. Maar ook in deze natuurgebieden wordt de biodiversiteit van deze habitats bedreigd door te weinig begrazing en te veel meststoffen uit de lucht. Een zelfde ontwikkeling bedreigt nu de half-natuurlijke weiden in oost-, centraal-, en zuid-Europa. Het proces van intensivering en verlating is hier na 1990 in een stroomsversnelling geraakt door de politieke ontwikkelingen. Vergelijkbare veranderingen kunnen zich in de toekomst ook buiten Europa voordoen.

Het einde van de traditionele veehouderij dwingt de natuurbescherming om naar nieuwe beheersvormen te zoeken. Nabootsing van het oude boerenbedrijf is zeer kostbaar. Maaien, plaggen en andere vormen van mechanisch beheer vervangen maar ten dele de kleinschalige invloeden van grazende dieren. Deze maatregelen zijn bovendien vaak te duur voor toepassing op grote oppervlakten omdat er geen markt is voor de geoogste producten. Ook aan branden kleven ecologische en praktische bezwaren. De overblijvende alternatieven zijn gestuurde begrazing met vrij-grazend (niet-gehoed) vee binnen een raster (‘*ranching*’) en ongestuurde ‘wildernis’ begrazing. In dit laatste concept moeten inheemse grote grazers (runderen en paarden) als vervangers van hun uitgestorven wilde voorouders samen met de aanwezige wilde herbivoren en zonder hulp van de mens voor openheid en een voedselarme bodem zorgen. De geschiktheid van wildernisbegrazing voor dit doel wordt echter betwijfeld. De verwachting dat wilde grote herbivoren open plekken creëren in bos is tot nu toe slechts gebaseerd op de aangetoonde aanwezigheid van lichteisende planten en dieren in bossen tijdens het Atlanticum voor de komst van de landbouw (ca. 7000-5000 jr. voor heden). Ook is het onzeker of, in welke mate, en op welke wijze de vrij levende grote herbivoren deze open plekken voedselarm kunnen maken, mede gezien de huidige neerslag van meststoffen uit de lucht. Deze vragen vormden het vertrekpunt voor dit proefschrift.

De *RSGC*- theorie

In dit proefschrift wordt de '*Resource-mediated Successional Grazing Cycle'* (*RSGC*) theorie getest. Volgens deze theorie fungeren grote grazers zoals runderen en paarden als drijvende kracht achter successiecycli in de vegetatie, waarbij bos, grasland en heide elkaar in de loop van de tijd vervangen. Doordat plekken in het begraasde gebied in verschillende stadia van de cyclus verkeren ontstaan dynamische mozaïeklandschappen. Volgens de *RSGC* theorie ontstaan deze dynamische mozaïeken niet alleen door de directe inwerking van vraat, tred en excretie op de planten zelf, maar ook door hun effecten op de *resources* (bronfactoren) van de plant, met name licht en voedingstoffen (nutriënten). De graascycli zoals de *RSGC* theorie ze beschrijft bieden een nieuwe mechanistische verklaring voor cyclische vegetatiesuccessie en mozaïekontwikkeling in begraasde landschappen.

Een graascyclus omvat vier fasen. Tijdens de eerste fase creëren grazers een weide ('graasgazon') in een bos of heide. Ze maken gaten in het kronendak, onderdrukken de de ondergroei en introduceren graszaden via mest. In de tweede fase wordt de bodem onder de ontstane graasgazons verschraald door een netto afvoer van nutriënten. Tijdens de derde fase raakt de weide als gevolg van deze verschraling gekoloniseerd door onsmakelijke dwergstruiken en bomen. De grote grazers verlaten de plek zodra ze elders betere foerageermogelijkheden vinden. Tijdens de daaropvolgende vierde fase met onbegraasde heide of bos herstelt de nutriëntenvoorraad zich, zodat na verloop van tijd een nieuwe graascyclus kan beginnen.

De theorie is getest voor runderen, omdat deze inheemse grote grazers in de toekomst een prominente rol kunnen spelen in de nieuwe vormen van begrazing. De volgende ecologische vragen werden daarom onderzocht.

-Kunnen vrij-grazende runderen weiden creëren in bos?

-Kunnen vrij-grazende runderen deze weiden verschralen bij de huidige atmosferische depositie?
-Leidt verschraling tot invasie van dwergstruiken en bomen in de weiden?
-Herstelt de nutriëntenvoorraad in de bodem zich tijdens een heide- of bosfase?

Het onderzoek.

Vanaf 1983 is onderzoek verricht naar deze vragen op de ‘Wolfhezerheide’ (ca. 60 ha), een natuurgebied van de Vereniging Natuurmonumenten op de Zuid Veluwe. Het successiemozaïek in dit studiegebied omvatte 19 ha bos, 33 ha grasland en 9 ha heide. De bodem bestond uit droog fluvio-glaciaal grindrijk zand en dekzand met holtpodzolen. Een kleine oppervlakte werd in beslag genomen door enkeerdgronden van de voormalige middeleeuwse nederzetting Wolfheze. De belangrijkste bosbomen in het studiegebied waren Grove den (*Pinus sylvestris*), Ruwe berk (*Betula pendula*) en Zomereik (*Quercus robur*). In de bosondergroei domineerden Zomereik, Lijsterbes (*Sorbus aucuparia*), Vuilboom (*Frangula alnus*) en Amerikaanse vogelkers (*Prunus serotina*). Al deze soorten kwamen in 1983 ook voor als spontane opslag in het open terrein. De beuk (*Fagus sylvatica*) was vertegenwoordigd met enkele oude vrijstaande exemplaren. Bochtige smele (*Deschampsia flexuosa*) en Pijpenstrootje (*Molinia caerulea*) domineerden in de graslanden, die na 1960 waren ontstaan door vergrassing van heide. Struikheide (*Calluna vulgaris*) was de belangrijkste soort in de niet-vergraste heide. Voorafgaand aan de introductie van de begrazing waren kleine gedeelten van de heide geplagd (in 1980) en gemaaid (in 1982). In januari 1983 werd jaarrond begrazing met vrij-grazende runderen geïntroduceerd, met een veebezetting van ca. 90 kg^{-1} ha^{-1} jr^{-1}. Daarmee werd de Wolfhezerheide een van de eerste heide gebieden in Nederland met runderbegrazing. Aanvankelijk betrof het Fries-Hollands jongvee (pinken), maar vanaf 1985 werd geleidelijk overgestapt op zoogkoeien van andere rassen. Ook liepen er afwisselend 1-3 paarden in het gebied. De dichtheid van reeën en konijnen was laag. De runderen beschikten het hele jaar over open water en likstenen (keukenzout). In de late winter werden de runderen en paarden in beperkte mate bijgevoerd. De beheerder verwijderde regelmatig opslag van Grove den en Berk uit het open gedeelte. De totale atmosferische stikstofdepositie (bulk- en interceptie) varieerde van 25 kg^{-1} ha^{-1} jr^{-1} in de kort afgegraasde weiden tot 60 kg^{-1} ha^{-1} jr^{-1} in het bos.

Tussen 1983 en 1993 werden de vegetatieveranderingen geregistreerd d.m.v. jaarlijkse opnames met een punt-kwadraat methode in permanente kwadraten van 25 m^2 verspreid over de successiestadia in het begraasde gebied en in exclosures (niet voor het vee toegankelijke plekken). Na 1993 werd de opnamefrequentie teruggebracht tot 1 keer per 5 jaar. Tussen 1989 en 1994 werden in het open gebied ook veranderingen op het schaalniveau van de plant (10 x 10 cm^2) geregistreerd. Om de invloeden van de runderen op de vegetatie en de nutriëntenvoorraad in de bodem vast te stellen werd van 1983 tot 1985 het terreingebruik en het dieet van de dieren onderzocht d.m.v. 24-uurs zichtwaarnemingen. De hoeveelheid en verdeling van grazen en niet-grazen (lopen, herkauwen, slapen etc.) binnen het begraasde gebied vormde de basis voor de berekening van de netto opname (opname-excretie) van stikstof, fosfor en kalium voor het gebied als geheel, voor de successiestadia en voor de excretie-vrije delen en mest- en urine plekken binnen het Bochtige smele grasland. Deze netto-opname balansen werden vervolgens uitgebreid tot integrale nutriëntenbalansen door er de aanvoeren uit de atmosfeer en bodemverwering en de verliezen door stikstofvervluchtiging uit mest en urine aan toe te voegen. Deze laatste stromen werden berekend op basis van literatuurgegevens en schattingen door experts. Ook werd het dieet vastgesteld door het aantal happen per voedselplant te tellen. De resultaten hiervan werden vergeleken met resultaten van dieetonderzoek aan runderen op de Imbosch en de Doorwerthse heide. Om een beeld te krijgen van de verschillen in voedselkwaliteit tussen droge voedselarme gebieden en natte, voedselrijke gebieden werd een literatuurstudie verricht naar de verteerbaarheid en mineralengehaltes van belangrijke soorten uit deze milieus.

Resultaten

Uit de monitoring van de vegetatieveranderingen bleek dat de runderen in het open gebied op de podzolen met een middelmatige voedselrijkdom dynamische gras-heide mozaïeken creëerden. Ze stimuleerden zowel de vestiging van Bochtige smele in de oude heide als de vestiging van Struikheide in de kort-afgegraasde graasgazons door gaten te maken in de bestaande vegetatie. Gras-heide mozaïeken bleven uit op de relatief voedselarme en voedselrijke gronden. In de heide op de arme geplagde podzolen bleef vestiging van gras uit, waarschijnlijk vooral door gebrek aan voedingstoffen. Op de voedselrijke enkeerdgronden met Bochtige smele grasland hielden de runderen, samen met de paarden en wilde herbivoren, de uitbreiding van de weinig talrijke Struikheideplanten tegen door vraat en tred. Dit laatste bleek uit de geringere planthoogte van Bochige smele en Struikheide op deze enkeerdgronden in vergelijking met die op de podzolen. De half-schaduw soorten Zomereik, Lijsterbes, Vuilboom en Amerikaanse vogelkers werden in het hele gebied, zowel in de bosondergroei als in het open terrein, onderdrukt. De lichteisende pionier boomsoorten Grove den en Ruwe berk daarentegen slaagden er wel in om zich te vestigen in de voedselarme heide en het heide-gras mozaïek op de podzolen, maar niet op de voedselrijke enkeerdgronden. Hier werd de groei van deze pionier bomen – net als bij Struikheide – door de herbivoren onderdrukt. Dit bleek uit de vestiging van deze boomsoorten in de (niet-begraasde) exclosures op de enkeerdgronden tussen 1983 en 1993 (**Hoofdstuk 2**). Monitoring van micro-plots op de holtpodzolen (**Hoofdstuk 3**) bevestigde dat grassen en heide elkaar afwisselden. Door de massale sterfte van Struikheide door insecten (heidehaantjes) konden zich zelfs complete gras-heide-gras cycli voltrekken binnen de 6 jaar van de monitoringsperiode. Bochtige smele en Struikheide wisselden behalve met elkaar ook af met kleine kruiden zoals Liggend walstro (*Galium saxatile*), Pilzegge (*Carex pilulifera*), korstmossen, bladmossen, en met strooisel en minerale grond.

Het habitat- en dieetonderzoek (**Hoofdstuk 4**) toonde aan dat de vrij grazende runderen hun leefgebied selectief en opportunistisch gebruikten. De dieren foerageerden gemiddeld over het hele jaar ongeveer 7-8 uur per etmaal. Deze graastijd werd voornamelijk (83 %) besteed in open terrein. Voor niet-foerageren (herkauwen, slapen, lopen, etc) kozen de dieren daarentegen vooral het bos uit (56 %). Dit gedifferentieerde terreingebruik veroorzaakte een belangrijke nutriëntenstroom van grasland naar bos. De dieren vraten het hele jaar bij voorkeur korte grassen, vooral Bochtige smele, maar ook Witbol (*Holcus spp*) en Gewoon struisgras (*Agrostis capillaris*). Loofbomen (behalve Berk) en Pijpenstrootje werden alleen in de zomerperiode meer dan gemiddeld gevreten. Deze resultaten wezen er op dat runderen door middel van zomervraat niet alleen de houtachtigen en hoge grassen in bosondergroei onderdrukten maar ook hun vestiging en uitbreiding in open weiden verhinderden. Struikheide werd overwegend in de winter gegeten. Dopheide (*Erica tetralix*), Grove den, Berk en Braam (*Rubus fruticosus*) bleven vrijwel onaangeroerd.

Alleen aan het einde van de winter werd een beetje van deze onsmakelijke soorten gevreten. Deze selectie verklaarde het oprukken van de lichteisende houtachtige pioniers in het open terrein en de onderdrukking van de halfschaduw boomsoorten in het hele gebied als gevolg van begrazing.

Uit de berekende netto-opname van de kudde (**Hoofstuk 5**) bleek dat de dieren maar een klein deel van de opgenomen voedingstoffen gebruikten voor hun lichaamsgroei. Het grootste deel verliet het lichaam weer als mest en urine. Dit betekent dat de verplaatsing van nutriënten van vraat- naar excretieplekken en van graas- naar rustgebieden een veel groter effect hadden op de verschraling van de weiden dan de afvoer in lichaamsgroei. De integrale nutriëntenbalansen toonden aan dat de runderen het bestaande nutriëntenoverschot in het studiegebied als geheel enigszins reduceerden, maar niet verwijderden. In de weiden werd het overschot veel sterker teruggebracht, en mogelijk voor kalium volledig verwijderd. Alleen op de excretie-vrije plekken in de graasgazons bleek de integrale balans duidelijk negatief voor fosfor en kalium. Met andere woorden, hier voerden de dieren meer af dan er uit de lucht (en voor kalium ook door verwering) werd aangevoerd. De bodem werd dus voor deze elementen verschraald. Door de kleine oppervlakte (ca. 2.5 %) die jaarlijks door mest en urine werd beïnvloed was na 10 jaar nog > 75 % van het Bochtige smele grasland excretie-vrij, en dus verschraald. Het feit dat vrij-grazende runderen ook onder de huidige atmosferische depositie de bodem onder weiden in het studiegebied locaal verschraalden betekent dat deze bodemverschraling een rol kan hebben gespeeld bij de kolonisatie van deze weiden door Struikheide, Grove den en Berk.

De resultaten in **Hoofdstuk 6** suggereren dat de geschiktheid voor jaarrondbegrazing met runderen in voedselrijke natte gebieden (*wetlands*) en voedselarme hogere gronden door verschillende voedselkwaliteitsfactoren wordt gelimiteerd. Op de voedselrijke gronden was de voedselkwaliteit in het groeiseizoen hoog, maar in de winter daalde de verteerbaarheid door de stagnerende groei, sterfte en verrotting van oud materiaal. Op droge, voedselarme gronden bleef de verteerbaarheid in de winter relatief hoog, maar waren de mineralengehaltes het gehele jaar laag. Op grond van deze verschillen kon worden voorspeld dat voedselrijke graslanden vooral als zomergebied fungeren voor grote grazers en de droge voedselarme gronden als wintergebied. De aantrekkelijkheid als wintergebied berust niet alleen op de wintergroene grassen en dwergstruiken, maar ook op de veiligheid voor hoog water, beschikbaarheid van droge ligplekken en – in geval van bos – beschutting tegen extreme weersomstandigheden en geringere sneeuwbedekking. De relatief hoge winterkwaliteit op voedselarme gronden gold niet voor alle plantensoorten. Pijpenstrootje bleek als zomergroen gras een typische zomervoedselplant te zijn die in de herfst haar kwaliteit verliest en daardoor in de winter wordt gemeden. Dit leidde tot de conclusie dat natte voedselrijke en droge, voedselarme landschapszones elkaar aanvullen. Alleen samen vormen ze jaarrond een draagkrachtig leefgebied voor runderen. Gebieden met een intermediaire bodemvruchtbaarheid namen een tussenpositie in.

Ecologische conclusies

In **Hoofdstuk 7** zijn de vier *RSGC*-hypotheses getest met behulp van de onderzoeksresultaten uit het studiegebied en aanvullende informatie. Uit het onderzoek bleek dat vrij-grazende runderen in staat zijn om heide en bos om te vormen tot weide mits de bodemvruchtbaarheid voldoende is. De runderen maakten door vraat en vertrappping wel gaten in de oudere heidevegetatie, maar ze bleken niet in staat om grote bomen te doden. Voor gaten in kronendak van het bos waren ze afhankelijk van sterfte door veroudering en windworp. De runderen onderdrukten daarentegen wel de schaduwtolerante bomen en struiken (behalve Braam) en hoge grassen in de bosondergroei waardoor de korte (gazon)grassen bevorderd werden. Runderen stimuleerden de invasie van deze grassen door verspreiding van graszaden in hun mest. Vrijwel alle bomen die in de periode 1983-1993 in het studiegebied stierven werden vervangen door grasgazons. Zonder grote grazers, korte grassen en voldoende nutriënten zouden vegetatiesuccessiecycli ontstaan zonder een weidefase.

Verschraalden de vrij-grazende runderen de weiden bij de huidige atmosferische depositie? Door de aanvoer van meststoffen uit de lucht bleef de verschraling van de graasgazons beperkt tot de excretievrije plekken en tot fosfor en kalium. Wanneer met de onderschattingen in de balans rekening wordt gehouden kan worden geconcludeerd dat begrazing waarschijnlijk de kaliumvoorraad van het gehele grasland verlaagde. Bij vermindering van de atmosferische bemesting kan het grasland als geheel ook voor andere elementen verschralen. Voor het bosgebied betekende de aanvoer van mest en urine op de rustplekken een extra eutrofiëring naast die uit de lucht. Voor het studiegebied als geheel werd berekend dat begrazing het jaarlijkse stikstofoverschot van 50 kg ha^{-1} met 13 kg ha^{-1} verminderde. Hiervan werd 1 kg vastgelegd in lichaamsgroei, 6 kg verdween door vervluchtiging uit mest en urine en 6 kg kwam voor rekening van een verminderde interceptie (droge depositie). Het proces van voedselverrijking werd dus niet gestopt op het schaalniveau van het hele begraasde gebied. In de toekomst zal daardoor een evenwicht ontstaan op een hoog niveau tussen de aanvoerstromen en de verliezen.

De veronderstelling dat verschraling de invasie van onsmakelijke houtachtige pionier soorten in de begraasde weiden stimuleert werd bevestigd door de combinatie van de resultaten van de nutriëntenbalans en de vegetatiemonitoring. De hypothese werd ook ondersteund door de gebleken licht- en nutriëntenafhankelijke anti-herbivoor strategieën van de betrokken pioniers. De nutriëntenbalans toonde aan dat begrazing (delen van) de weiden in het bos-grasland mozaïek verschraalde. De snellere invasie door pioniers zoals Struikheide, Grove den en Berk op voedselarme bodems in vergelijking met voedselrijke bodems werd niet alleen in het studiegebied maar ook elders vastgesteld. Deze houtachtige pioniers van voedselarme habitats verdedigen zich tegen vraat met op koolstof gebaseerde anti-vraatstoffen (polyphenolen en terpenen) (*intrinsic defence*). Verschraling en toename van de hoeveelheid licht betekent een toename van de *C/N* balans in het plantmilieu en de plant. Dit zou geleid kunnen hebben tot hogere concentraties van deze anti-vraatstoffen in deze pioniers *(‘inducible defence’*). Tenslotte verlaagt verschraling de productie en voedingswaarde van de weidegrassen, wat in het geval van grazers die zowel grassen als houtachtigen vreten niet alleen tot een geringere graasduur leidt maar ook tot minderr kans op vraat en vertrapping van opslag van struiken en bomen (afname van de ‘*associational palatability*’ en vervanging door ‘*associational resistance’*). De toename van de induceerbare resistentie door verschraling geldt waarschijnlijk niet voor Braam omdat deze zijn verdediging (mede) baseert op dorens die stikstof en mineralen bevatten. Braam vestigde zich na de start van de begrazing in 1983 in het open terrein van het studiegebied maar de bedekking nam pas sterk toe na 1993. De vestiging werd toegeschreven aan de verbeterde kiemingskansen voor zaden uit de persistente zaadbank dankzij open getrapte plekken in het grasland. De spectaculaire toename van de bedekking vanaf 1993 in het open gebied werd verklaard door de verminderde zomergraasdruk door de grazers sinds dat jaar als gevolg van de aankoppeling van voedselrijke landbouwgrond en door de toenemende bedekking van Struikheide, die jonge Bramen bescherming tegen vraat door konijnen en reeën bieden.

Leidde successie naar heide en bos tot herstel van de bodemnutriëntenpool? Uit literatuuronderzoek bleek dat de totale en beschikbare hoeveelheden in het algemeen toenemen in de loop van de successie. Uit bodemkundig onderzoek in het studiegebied bleek dat tussen 1988 en 2001 in de grasgazons die geleidelijk met Struikheide waren dichtgegroeid de totale voorraden van stikstof, fosfor en kalium waren toegenomen. De extraheerbare voorraden waren echter afgenomen, mogelijk doordat Struikheide de beschikbare voedingsstoffenvoorraad sterker kan uitputten dan Bochtige smele en doordat nutriënten in moeilijk afbreekbaar Struikheidestrooisel langzaam beschikbaar komen.

Beheerskundige conclusies

De hoofdconclusie luidde dat grote grazers in bosgebieden op de hogere gronden tijdelijke open, voedselarme graslanden en heiden kunnen creëren als fase in hun graascyclus. De ligging, oppervlakte, levensduur, nutriëntenbeschikbaarheid en botanische samenstelling van de open habitats zullen afhangen van het begraasde gebied, het begrazingsseizoen en het herbivorenbestand. In **Hoofdstuk 8** werden deze beheersvariabelen behandeld.

Het voedselkwaliteitsonderzoek suggereerde dat jaarrond begrazing zonder menselijke hulp een complete eco-hydrologische gradiënt (bodemcatena) vereist. Beperking van het begraasde gebied tot het droge, arme deel kan mineralengebrek (natrium, fosfor, calcium en magnesium) veroorzaken. Bij jaarrondbegrazing in het droge deel van de catena, zoals in het studiegebied, wordt het wintervoer (gedeeltelijk) al in de zomer geconsumeerd, waardoor er ’s winters een energietekort kan ontstaan. Om dit te voorkomen moet de dichtheid laag worden gehouden. De ontbrekende mineralen kunnen worden aangevuld door likstenen met een brede mineralensamenstelling, aankoppeling van voormalige bemeste landbouwgronden (‘graasweiden’) of door (locale) bemesting. In het geval van jaarrondbegrazing in een geïsoleerd voedselrijk, periodiek overstroomd *wetland* moet het wintergebied worden vervangen door een bedijkt gedeelte of een terp, met meer of minder energiebijvoedering. Een alternatief is zomerbegrazing, waarbij de dieren elders of in een stal overwinteren.

De perspectieven voor open, voedselarme habitats in het droge voedselarme deel van de catena lijken bij wildernisbegrazing in complete landschappen beperkt. De resultaten van de dieetselectie (**Hoofdstuk 4**) suggereren voor de onderdrukking van zomergroene houtachtigen, kruiden en grassen op droge voedselarme gronden zomerbegrazing nodig is. De wintergroene soorten kunnen ook door winterbegrazing onderdrukt worden. In complete landschappen zal bij wildernisbegrazing de zomerdruk van grazers op de droge voedselarme gronden afhankelijk zijn van overloop uit de zomergebieden. Deze overloop kan een gevolg zijn van voedselschaarste en concurrentie in het zomergebied, maar ook van predatiedruk. Een soortenarm herbivorenbestand, een geringe dichtheid en afwezigheid van predatoren zullen de overloop tot de winter beperken en de kans op openheid in het voedselarme deel van de catena verkleinen. Door het uitsterven van ‘bulldozer-herbivoren’ zoals olifanten zijn grazers voor gaten in het kronendak nog meer afhankelijk geworden van de ouderdom van de bomen, abiotische factoren (storm, brand) en insecten. In complete landschappen met wildernisbegrazing zullen de hogere gronden in of langs de voedselrijke zones (b.v. kust- en rivierduinen, randzones van het Pleistoceen) de grootste kans maken om open en voedselarm te worden. Bestaande grootschalige heiden en stuifzanden in de kernen van droge arme gebieden zullen de grootste kans maken om dicht te groeien met bos.

Graasweiden (aangekoppelde bemeste landbouwgronden) die in incomplete droge, voedselarme landschappen het natuurlijke zomergebied vervangen vertragen het dichtgroeiproces mits de herbivoordichtheid wordt aangepast. Na stopzetting van de bemesting zullen ook graasweiden verschralen en uiteindelijk in bos veranderen. Een blijvende functie als graasweide vereist voortgaande (lichte) bemesting.

In sommige gebieden zal de voor belangrijke doelsoorten of cultuurhistorische doelen vereiste openheid en voedselarmoede op de hogere gronden onvoldoende door wildernisbegrazing gerealiseerd worden. In die gevallen kan wildernisbegrazing vervangen of aangevuld worden met gestuurde begrazing. Successieremming en nutriëntenafvoer kunnen worden vergroot door beperking van het begraasde gebied, zomerbegrazing, uitbreiding van het herbivorenbestand met exotische grazers (schapen, geiten), forcering van de begrazingsdruk door hoedebeweiding of tijdelijke inrastering en door aanvullend vegetatiebeheer. Gestuurde begrazing kan zowel wildernisbegrazing als traditionele veehouderij systemen nabootsen. Voorwaarde is wel dat er betrouwbare referenties voorhanden zijn. Gestuurde begrazing levert in het algemeen beter verkoopbare (dierlijke) producten op en levert een aantrekkelijker landschap voor het publiek dan mechanisch beheer

Dankwoord

Dit proefschrift zou er niet geweest zijn zonder de bijdragen van veel collega's, vrienden en familie. Het is daarom een beetje misleidend dat alleen mijn naam op de voorkant prijkt. Het geeft een gevoel van de circusacrobaat in een chinese pyramide, die op de schouders van anderen even alle aandacht trekt.

In de eerste plaats wil ik mijn promotor Frank Berendse bedanken. Hij stimuleerde mij om dit proefschrift met de resultaten van het Wolhezerheideonderzoek af te ronden. Voor zijn vertrouwen en motivatie ben ik hem dankbaar. Hij gaf mij ook de ruimte om te schrijven en voorzag mij van zorgvuldig en nuttig commentaar. Han Olff ben ik zeer erkentelijk voor zijn hulp bij de dataverwerking van en commentaar op het tweede hoofdstuk, maar meer nog voor zijn bijdrage aan mijn theorievorming over herbivorie. Onze plant-herbivoor werkgroep functioneerde helaas kort, maar ze heeft in ieder geval nu ook met dit proefschrift een spoor nagelaten. Ook de discussies met Herbert Prins, Frans Vera, Chris Geerling, Rory Harrington, Reiner Cornelius, Bertil Krüsi, Karle Sykora, Wim Braakhekke, Harmke van Oene, Ruben Smit, Liesbeth Bakker, mijn co-auteurs Maurits Gleichman, Sip van Wieren en Michiel WallisDeVries en de doctoraalstudenten waren waardevol. Diegenen die hielpen bij het veld- en laboratoriumwerk in eerdere periodes van het onderzoek werden al met name in de betreffende hoofdstukken vermeld. De bibliotheekmedewerkers Fried Kampes en Jan Roesink stonden steeds klaar om mij te helpen. Het Engels verbeterde aanzienlijk door de adviezen van Margery Rigg-Lyall. Harmke van Oene, Toos van der Garde, Ruben Smit en Herman van Oeveren dank ik voor hun hulp bij het persklaar maken van het manuscript.

Het is goed om ook even iets verder terug te blikken. Het waren Maurits Gleichman en Harm Piek (Vereniging Natuurmonumenten) die in 1983 het monitoringsvoorstel voor de Wolfhezerheide lanceerden in de toenmalige vakgroep Natuurbeheer onder leiding van Claus Stortenbeker. Door exclosures, experimentele ingrepen en procesgericht onderzoek groeide het monitoringsproject snel uit tot een beheerskundig onderzoek. Mijn fascinatie voor grote herbivoren en begrazingsbeheer werd in die periode gevoed door het BON (Begrazings Overleg Nederland, met o.a. Piet Oosterveld, Pieter Slim, Jan Bakker, Harm Piek, Thies Oomes en Ger Londo, Maurits Gleichman en Claartje Sloet van Oldruitenborgh), het Maliproject (Chris Geerling en Steven de Bie), het Imbosch project (Harm van de Veen en Sip van

Wieren), bezoeken aan het New Forest (Rory Putman en Colin Tubbs) en Denemarken (Merita en John Buttenschøn). Op hun beurt raakten veel heidebeheerders uit Nederland en daarbuiten door hun bezoek aan de Wolfhezerheide overtuigd van de mogelijkheden (en beperkingen) van runderbegrazing op vergraste heiden.

Mijn pyramide heeft nog een derde laag. Mijn ouders en overige familie dank ik voor wat ze mij door *nature and nurture* hebben meegegeven. Het boerenwerk en de omgang met vee bij de familie Bokdam en de veldervaring opgedaan tijdens de jachtdagen bij de gastvrije familie Jansen in Vriezenveen zijn terugkijkend erg bepalend geweest voor mijn studie- en loopbaankeuze.

Ten slotte, mijn *act* zou jammerlijk mislukt zijn zonder de steun van Margaret. Ik draag daarom dit proefschrift met liefde op aan haar en onze kinderen.

Curriculum vitae

Jan Bokdam werd geboren op 26 mei 1946 te Almelo als zoon van Johannes Bokdam en Magdalena Jansen. In 1963 slaagde hij voor zijn eindexamen HBS-B aan het Christelijk Lyceum in diezelfde plaats. In datzelfde jaar begon hij zijn studie aan de toenmalige Landbouwhogeschool te Wageningen, waar hij in 1970 het ingenieursdiploma Tropische Houtteelt kreeg uitgereikt. Zijn afstudeervakken waren tropische houtteelt, natuurbeheer, plantensystematiek en –geografie van de tropen en tropische bodemkunde. Tijdens zijn verlengde praktijktijd (1967-1968) onderzocht hij de vaatplantenflora en zoogdierenfauna van het Parc National du Comoë in het noord-oosten van Ivoorkust. Van hieruit werden plantenverzamelreizen gemaakt naar aangrenzende west-Afrikaanse landen. De collecties uit deze en de volgende periode maken deel uit van Herbarium Vadense. Van 1970 tot 1974 werkte hij als docent plantkunde en bosecologie aan de Faculté des Sciences van de Université Nationale du Zaire te Kisangani. Tijdens deze periode maakte hij studiereizen naar de Ruwenzori, de vulkanen in oost- Zaire en enkele nationale parken in oost-Afrika. Na een tijdelijk aanstelling als wetenschappelijk medewerker bij het Laboraratorium voor plantensystematiek en -geografie van de Landbouwhogeschool te Wageningen trad hij in 1976 in dienst bij het Staatsbosbeheer (Dienstvak Natuurbehoud, Noord-Brabant). Daar werkte hij als ecoloog o.a. aan inrichtings- en beheersplannen voor landinrichtings- en natuurgebieden zoals het Dommeldal en de Brabantse Biesbosch. In 1980 werd hij aangesteld als wetenschappelijk medewerker in de vakgroep Natuurbeheer van de Landbouwhogeschool . Momenteel verzorgt hij als universitair docent in de leerstoelgroep Natuurbeheer en plantenecologie van Wageningen Universiteit cursorisch onderwijs in de systeem-en landschapsecologie en het natuurbeheer en begeleidt hij leeronderzoek, stages en extern gefinancierde onderzoeksprojecten. De resultaten van zijn eigen lange-termijn onderzoek naar effecten van begrazing op de flora en vegetatie van natuurgebieden en onderliggende systeemecologische mechanismen zijn gepubliceerd in nationale en internationale tijdschriften en congresverslagen. Een deel ervan is nu gebundeld in dit proefschrift. Daarnaast fungeert hij als adviseur voor terreinbeherende natuurbeschermingsorganisaties.