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Regeneration of mixed deciduous forest in a Dutch forest-heathland, following a reduction of ungulate densities

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Abstract

The conversion of single-species coniferous forest stands into mixed stands by promoting the natural regeneration of indigenous broadleaved tree species was studied in a forest-heathland on the Veluwe, in the central part of the Netherlands. Red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) had a large impact on regeneration dynamics, as was established by comparing 20 pairs of fenced and unfenced plots (40 × 40 m) during a 10-year period. A fivefold reduction of total herbivore biomass to 500 kg per km^2, resulted in a strong increase of shrub and tree sapling numbers in all vegetation types. However, height growth of the most palatable broadleaved tree species was still strongly impeded. Under the present-day grazing pressure, Scots pine (*Pinus sylvestris*) and beech (*Fagus sylvatica*) will become the dominant canopy species in the forests in the near future. It is argued that the most browse-sensitive woody species such as pedunculate and sessile oak (*Quercus robur* and *Q. petraea*) will successfully regenerate, only if temporal and spatial variation in browsing pressure is allowed to occur.

Keywords: Browsing pressure; *Capreolus capreolus*; *Cervus elaphus*; Conversion management; Forest-heathland; Regeneration dynamics; *Sus scrofa*

1. Introduction

Nature conservation values of forest stands on the Veluwe in the central part of the Netherlands are, as in many other countries of northwest Europe (Mosandl and Kleinert, 1998; Peterken, 1999), nowadays promoted by conversion of even-aged single-species stands into mixed stands with indigenous broadleaved tree species dominating the canopy. Timber production and hunting are no longer primary management goals. Non-indigenous species, such as Douglas fir (*Pseudotsuga menziesii*), Norway spruce (*Picea abies*) and Japanese larch (*Larix decidua*), planted as even-aged stands in the first half of the last century, are gradually being removed. Further, small canopy gaps of one to three times mean tree-height are created by group selection harvesting (Kuper, 1994), promoting the natural regeneration of broadleaved species. Birch–oak (Betulo–Quercetum) and beech–oak (Fago–Quercetum) are the natural forest communities (Fanta, 1986; Stortelder et al., 1999).

For successful regeneration of broadleaved species, the prevailing browsing pressure by ungulates is a decisive factor (Kuiters et al., 1996). Ungulate species such as roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) are well known for their retarding effect on shrub and tree invasion on heathlands (Webb, 1990; Bullock and Pakeman, 1997; Bokdam and Gleichman, 2000) and on natural regeneration in forests throughout Europe (Gill, 1992; Chytry and Danihelka, 1993; Groot Bruinderink and Hazebroek, 1996; Nolan et al., 1998; Moore et al., 1999). By selective browsing, herbivores may promote changes in forest tree composition (Putman, 1996). Peterken and Tubbs (1965) showed evidence that a contemporary woodland structure in the New Forest (UK) reflects past fluctuations in deer and livestock population levels. Putman et al. (1989) found significant recovery of tree regeneration in an oak–beech woodland following experimental protection from high browsing pressure by deer and ponies in an exclosure-study. The same effect was observed in an oak–birch woodland by Pigott

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(1983), after exclusion of sheep grazing. Beaumont et al. (1995) reported an increase in regeneration of native pinewood in Scotland after red deer density was reduced from 12 to 5 head per km^2.

Less cited in literature is that ungulates may also promote woody plant encroachment, especially in grasslands. By grazing and trampling dense grass sward vegetation can be opened, favouring the germination and establishment of certain woody species (Miles and Kinnaird, 1979; Harmer, 1995; Olff et al., 1999; Scott et al., 2000). Thereby large herbivores have an impact on the cyclic succession of grassland into shrub- and woodland and *vice versa* (Vera, 2000). A sudden exclusion of grazers often leads to a rapid development of the ground vegetation, which prevents the regeneration of most tree species. In their review on large herbivore grazing and the conservation of upland woodlands, Mitchell and Kirby (1990) concluded that control of browsing rather than the complete removal is generally a desirable option, but that little data are available in literature to support this hypothesis. There is a need for more information on the differential effects of intensity and timing of grazing and browsing on woodland dynamics (Kuiters and Kirby, 1999).

The aim of this study was to examine the regeneration of mixed deciduous forest in an intensively managed forest-heathland at the Veluwe under conversion management, after a major reduction of ungulate densities. For the restoration of natural forest communities, it is crucial to understand how the most browse-sensitive species such as silver birch (*Betula pendula*), pedunculate oak (*Quercus robur*) and sessile oak (*Q. petraea*) recover, following a relief from heavy browsing. By the assessment of tree regeneration before and after reduction of ungulate numbers and comparing this with the regeneration in fenced plots (exclosures), we were able to ascertain whether natural forest communities with broadleaved tree species dominating the forest canopy will have a chance to successfully regenerate in the near future.

2. Study area and research method

2.1. Study area

The Veluwe is a 900 km^2 forested area in the central part of the Netherlands (52°00′–52°30′ N, 5°20′–6°10′ E). Overexploitation of the area for centuries by domestic stock grazing, wood cutting and litter removal, as in many other countries of northwest Europe (Pott and Hüppe, 1991), had changed the area into one of extensive drift-sands and heaths around 1850. In the second half of the nineteenth century, grazing by sheep was strongly reduced and afforestation of former drift sand and heathland started. Nowadays, the area is mainly covered by woodland and patches of heathland, with pine-plantations covering ca. 60% of the total area. Indigenous forest communities, i.e. birch–oak forest on sandy soils (Betulo–Quercetum) and beech–oak forest (Fago–Quercetum) on loamy sand, cover only small areas. Dry heath is present in 5–8% of the total area and, at many locations, has been recently invaded by grasses such as wavy hair-grass (*Deschampsia flexuosa*) and purple moor-grass (*Molinia caerulea*), as a result of increased levels of atmospheric nutrient deposition (Heil and Aerts, 1983; Diemont, 1996).

The study was conducted in the 'Staatsdomein bij Het Loo', a 1250-ha forest-heathland, in the central part of the Veluwe (Fig. 1), managed by Het Loo Royal Forestry. Soil types are predominantly brown podzols, developed on a parent material of Pleistocene loamy sand. Mean annual precipitation is 790 mm $year^{-1}$ and average annual temperature is 9.4 °C, with a minimum in January of 2.5 °C and a maximum in July of 16.4 °C. Two-thirds of the area was covered by forest stands, mainly Scots pine (*Pinus sylvestris*), but pedunculate oak, sessile oak, beech (*Fagus sylvatica*), red oak (*Quercus rubra*), Norway spruce, Japanese larch and Douglas fir were also present. Understorey vegetation was in most stands dominated by bilberry (*Vaccinium myrtillis*), cowberry (*V. vitis-idaea*), wavy hair-grass, purple moor-grass, and locally, bracken (*Pteridium aquilinum*). Only in beech stands was herbaceous cover lacking. Several woodland clearings were present, varying in size from 0.3 ha to 2.5 ha. The remaining third consisted of dry heath, dominated by heather (*Calluna vulgaris*) and cross-leaved heath (*Erica tetralix*). It has been invaded by wavy hair-grass and purple moor-grass and till 1987 was managed by periodic mowing and controlled burning in a small-scale mosaic.

The area supported populations of red deer, roe deer and wild boar in a total density of ca. 14 animals km^{-2} (Table 1). Before 1986 fallow deer (*Dama dama*) and mouflon (*Ovis musimon*) also inhabited the area. The whole area was fenced and ungulate numbers were maintained at a more or less stable level by yearly culling.

2.2. Management

Since 1987, improvement of conservation values has been the main management objective in the area, with timber production and hunting of only secondary importance. Changes in management included:

1. conversion of single-species stands, mostly conifers, into mixed deciduous stands by promoting natural regeneration processes;
2. clearing stands of non-indigenous species such as red oak, Douglas fir, Norway spruce and Japanese larch;

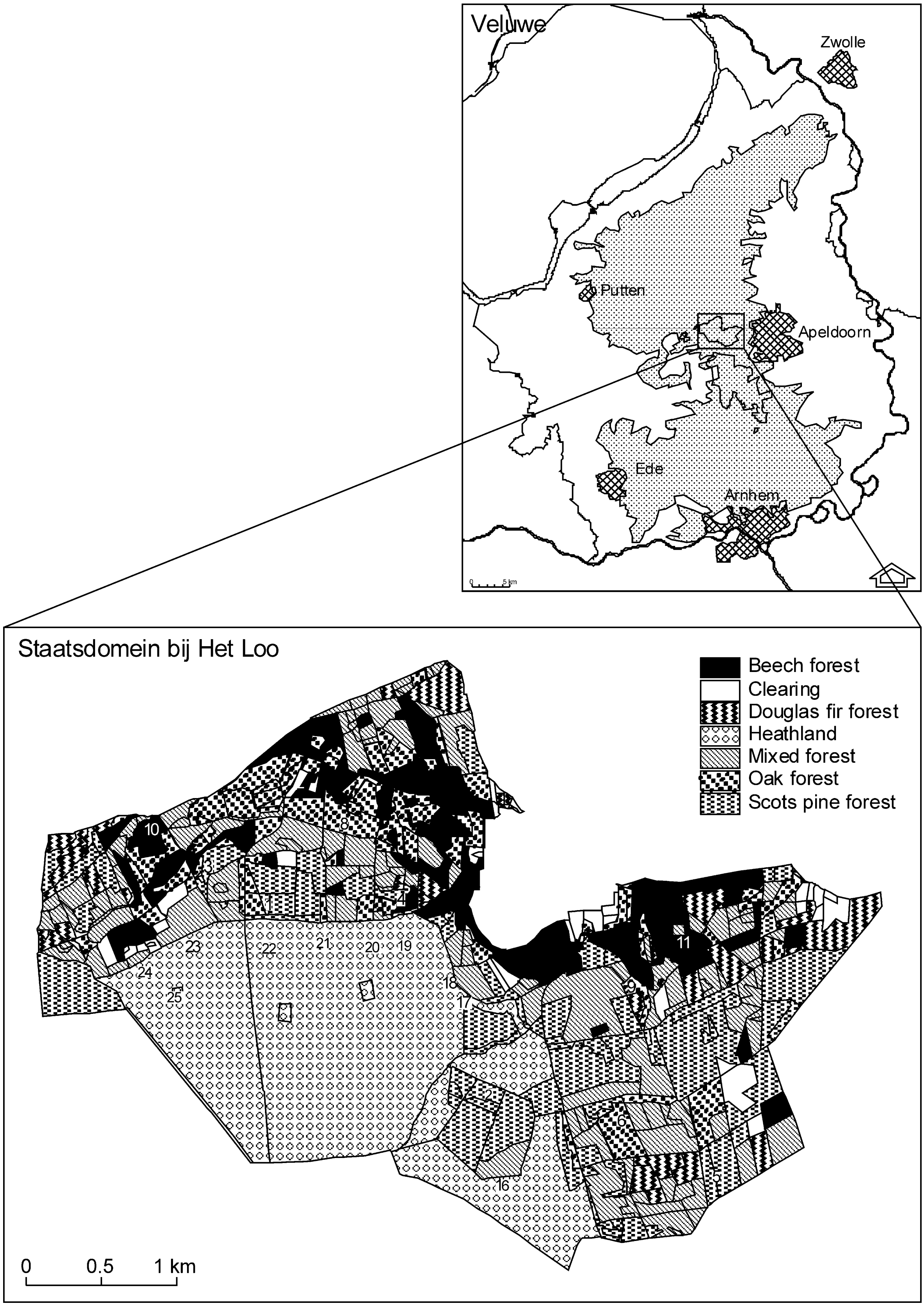

Fig. 1. Site map of the 'Staatsdomein bij Het Loo' on the Veluwe, and the location of the unfenced and fenced plots (1–5: plots in Scots pine stands; 6, 8 and 9, plots in oak stands; 10–11, plots in beech stands; and 16–25, plots on heathland).

Table 1
Ungulate densities (head km^{-2}) and related herbivore biomass (kg km^{-2}) in the research area in the periods before and after 1987

Ungulate species	1978–1986		1987–1998	
	Number (km^{-2})	Weight (kg km^{-2})	Number (km^{-2})	Weight (kg km^{-2})
Red deer	9.6	624	4.8	312
Wild boar	32.0	1,280	2.4	96
Roe deer	2.0	28	6.4	90
Fallow deer	8.0	416	–	
Mouflon	6.4	240	–	
Total	58.0	2,588	13.6	498

3. creation of small gaps in the even-aged stands to promote heterogeneity in canopy structure;
4. experimental cessation of active management (mowing, burning) on a part of the heathland;
5. an 80% reduction of the grazing pressure by the ungulate populations, by removing fallow deer and mouflon, and reducing numbers of red deer and wild boar (Table 1);
6. cessation of supplementary feeding of the ungulates;
7. cessation of culling roe deer.

2.3. Fencing and data collection

In the winter of 1987/1988, a series of 20-paired fenced (exclosures) and unfenced plots was installed in the five most dominant vegetation types, i.e. heathland ($n=10$), Scots pine forest ($n=5$), oak forest ($n=3$) and beech forest ($n=2$; Fig. 1). The number of plots was chosen in accordance with the relative area of each vegetation type in the total study area. For the beech-forest the survey of one pair of plots (nr. 11, Fig. 1) was stopped after windthrow in the winter of 1990 partly opened the canopy in the fenced plot and prevented any further comparison between the fenced and unfenced plot. The plots on heathland were all situated at the edge of the heathland where active management ceased in 1985, and within 200 m distance from the adjacent Scots pine stands or mixed stands with Scots pine and oak.

Each exclosure consisted of a 40 × 40 m quadrat, with a 2-m tall fence. Only small mammals like rabbits (*Oryctolagus cuniculus*), voles and mice were able to pass through the fences. An unfenced control plot of similar size and comparable vegetation cover, marked only at the corners, was established ca. 20 m from each fenced plot. Although higher densities of small mammals or ungulates near the fenced plots might have caused edge effects, there was no evidence for this. The forest stands were generally too small and too heterogeneous in canopy cover to permit the use of buffer zones of several hundred metres between fenced and unfenced plots.

Fenced and unfenced plots were surveyed for tree regeneration at the start of the study (winter of 1987/1988). This was repeated every 3–4 years, in the winter of 1990–1991, 1993–1994 and 1997–1998. Number and height of seedlings and saplings of shrubs and trees were determined with a linear transect of 10 × 56 m across the diagonal of each plot. The threshold height level for seedlings to be counted was 10 cm. The height classes used were 10–25 cm, 26–50 cm, 51–100 cm, 101–150 cm, 151–200 cm and 201–500 cm. In 1994, tree invasion on the heathland was quantified in relation to the distance from the forest edge. Number and height of seedlings and saplings were assessed on ten 8×350-m transects.

2.4. Data handling

The number of seedlings and saplings (young trees reaching a height of >1.5 m) counted on a transect in each plot was expressed as number per ha. Mean height was determined by calculating the weighted mean of number × mean height per height class. For the height class of 201–500 cm, the true mean height was taken, because the height of each sapling in this class was exactly determined.

Two-way analysis of variance was applied to test for differences in tree density among unfenced and fenced plots and among years for each vegetation type. Statistical tests were carried out on ^{10}log-transformed data, i.e. sapling number and mean height (Sokal and Rohlf, 1995). Changes in the mean height of the regeneration with time were described by a linear regression model. We also attempted to predict the future species composition of the unfenced and fenced plots by identifying the species composition of the largest cohort (i.e. height classes 5 and 6), consisting of saplings >1.5 m.

3. Results

3.1. Tree invasion on heathland

After active management of heathland ceased in 1987, a rapid invasion of mainly Scots pine was observed in 30% of the plots. In 1987, at the start of this study, mean tree density amounted to 300–400 stems ha^{-1} (Fig. 2). Variation among plots was high, with some having no regeneration, whereas in other plots mean tree density increased beyond 5000 stems ha^{-1}. The establishment of young trees was related to the distance from the edge of adjacent forest (Fig. 3). It showed a maximum at 20–30 m and rapidly decreased with increasing distance. Beyond 350 m no Scots pine saplings were observed. Other woody species that regenerated in low densities in the fenced plots were rowan

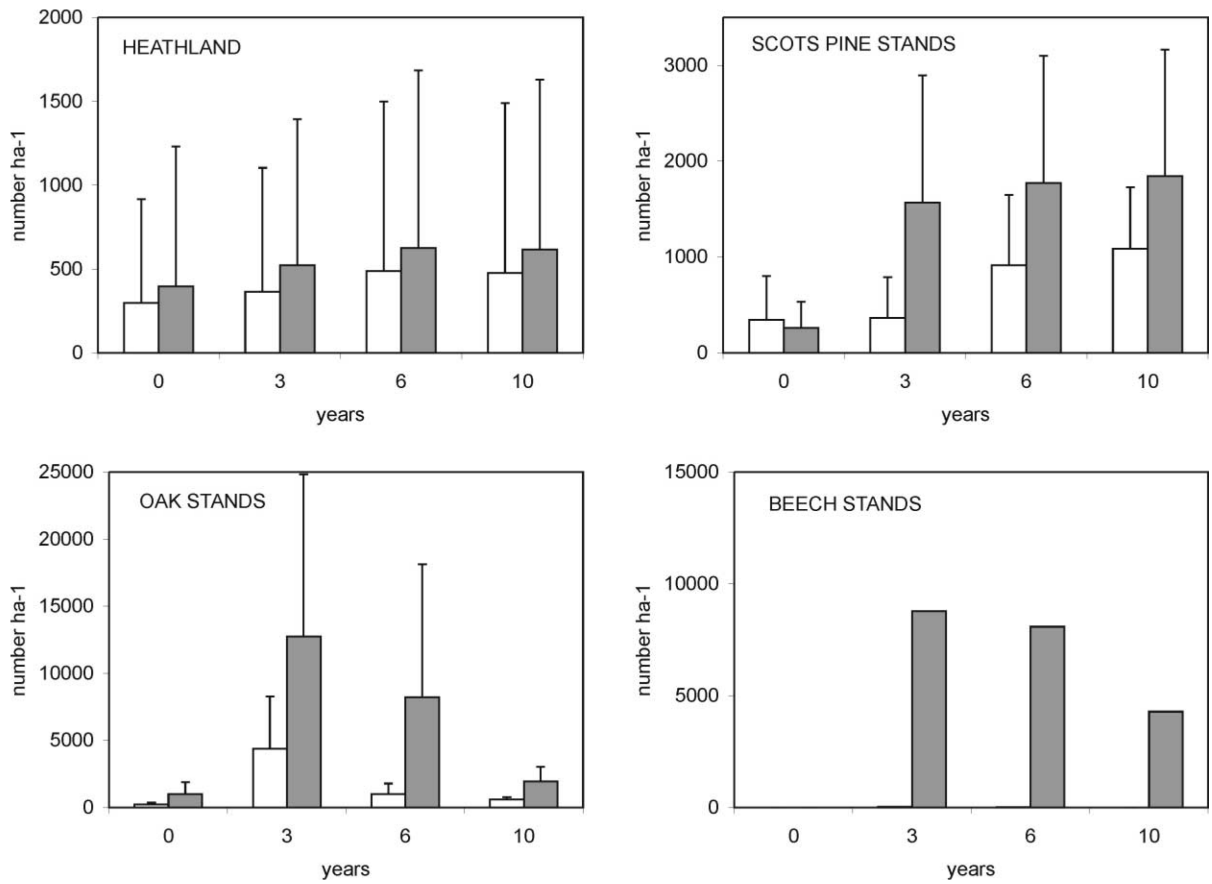

Fig. 2. Changes in the number of seedlings and saplings in the unfenced (open columns) and fenced plots (filled columns) in the different vegetation types during the 10-year research period. Lines show standard errors.

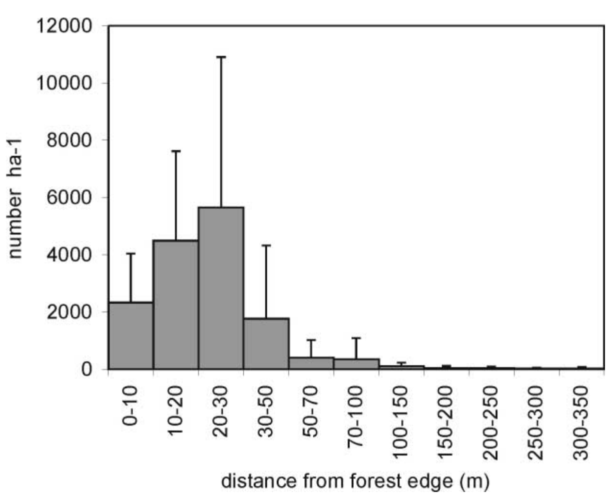

Fig. 3. Relationship between the regeneration of Scots pine on heathland and the distance to the nearest forest edge. With standard error bars.

(*Sorbus aucuparia*), birch (*B. pendula* and *B. pubescens*) and pedunculate oak (Fig. 4).

The exclusion of ungulates had no significant effect on young tree density (Fig. 2) nor on height growth (Fig. 5). Annual height increment of Scots pine was 19 cm, under both browsed and unbrowsed conditions (Fig. 6).

3.2. Regeneration in Scots pine stands

Tree regeneration in the Scots pine stands was initially low (Fig. 2). Most individuals were smaller than 100 cm and pedunculate oak was the most numerous species (Fig. 4). In the years following the reduction of ungulate densities, regeneration strongly increased in number ($F_{3,32}=6.65$, $P=0.001$). This increase was highest in the fenced plots, although with the exception of birch and rowan, the differences with unfenced plots were not statistically significant (Fig. 4).

The largest effects of browsing were observed on the height growth of saplings. Mean height of the regeneration in the unfenced plots did not change significantly following the reduction of ungulate densities (Fig. 5), but strongly increased in the exclosures ($F_{3,32}=8.99$, $P<0.001$). Annual height increment under unbrowsed conditions varied between 18 and 38 cm, dependent on the tree species (Fig. 6). Silver birch was the fastest growing species.

3.3. Regeneration in oak stands

During the first 3 years, tree regeneration in the oak stands strongly increased, especially in the exclosures

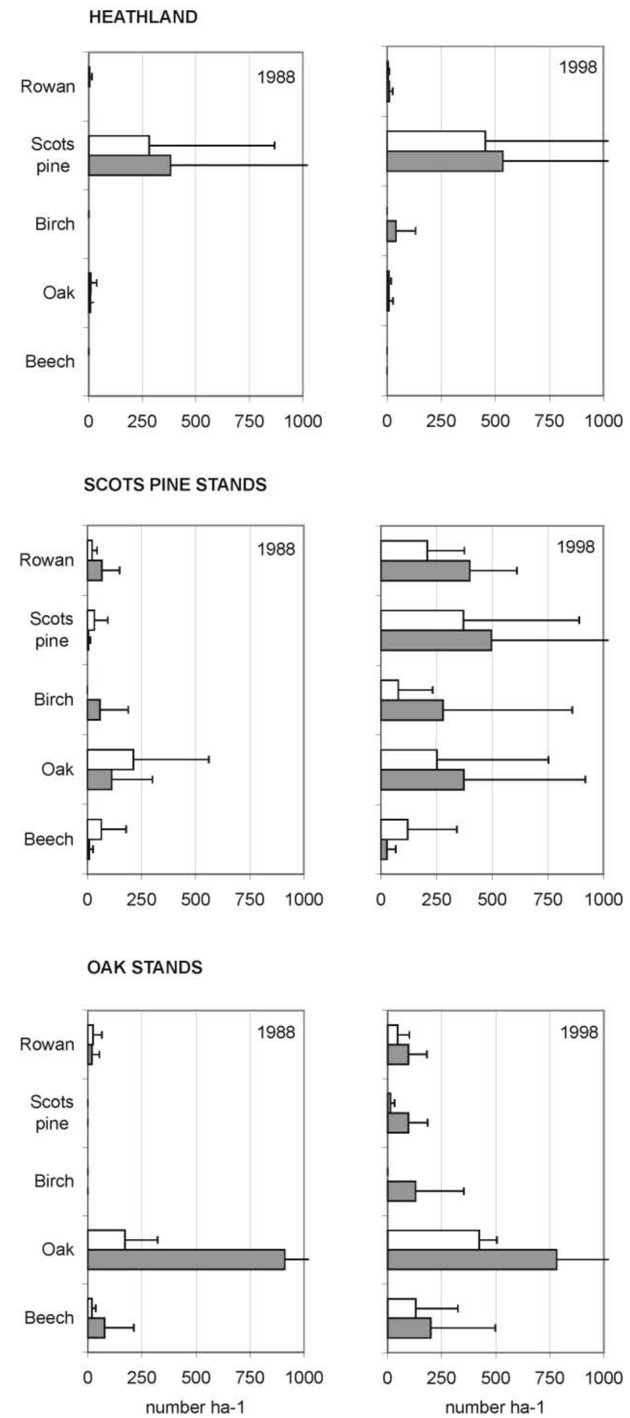

Fig. 4. Changes in the regeneration of woody species in the unfenced (open column) and fenced (filled column) plots between 1988 and 1998 in the different vegetation types. With standard error bars.

(Fig. 2). However, the mortality rate of seedlings was high, and numbers decreased again in the subsequent years. Tree numbers in the fenced plots were significantly higher over the whole period compared to the unfenced plots ($F_{1,16} = 11.31$, $P < 0.01$). Initially, the regeneration in the oak stands was dominated by seedlings of pedunculate oak (Fig. 4). Reduction of ungulate numbers resulted in an increase in regeneration in the unfenced plots for all species except birch. A complete exclusion of ungulates (fenced plots) further increased the regeneration of most species.

Mean height increased significantly only in the fenced plots ($F_{3,16} = 5.43$, $P < 0.01$; Fig. 5). Rowan, silver birch and beech showed the highest annual height increment of 25–30 cm (Fig. 6). Under browsed conditions mean height of tree seedlings initially decreased, due to the emergence of a large number of seedlings, and only slightly increased during the subsequent years. After 10 years the mean height of seedlings did not reach beyond the height of the herb layer of 50 cm and annual height increment was < 5 cm. Only beech showed a significant height increment (Fig. 6).

3.4. Regeneration in beech stands

In the beech stands, regeneration was initially totally absent (Fig. 2). The major reduction in ungulate numbers did not result in the establishment of any seedlings during the 10-year period.

In the fenced plot, seedlings became established in high numbers (Fig. 2). This cohort consisted predominantly of beech with $< 0.5\%$ of sessile oak. Height growth was rather small and mean tree height after 10 years was still < 1.0 m (Fig. 5). Annual height increment of the beech seedlings in the fenced plots reached 12 cm. Seedlings of sessile oak did not show any significant height growth.

3.5. Dynamics of bramble

The exclusion of ungulates resulted in an explosive increase of bramble (*Rubus* spp.) in some plots ($P < 0.05$), especially in those with an open canopy such as most Scots pine stands and to some extent the oak stands (Table 2). In the unfenced plots, bramble occurred only in very low numbers, a situation that did not change during subsequent years.

3.6. Selective impact of ungulate browsing on regeneration

The selective effect of browsing on the species composition of the regeneration layer was revealed by comparing the relative species composition of the height classes 5 and 6 (saplings > 1.5 m) between unfenced and fenced plots for the different vegetation types (Fig. 7). Saplings in these height classes escaped from the high mortality risks during germination and early establishment and were growing into the shrub-layer.

The results suggested that under ungulate browsing pressure, mainly beech and Scots pine were able to regenerate successfully in most vegetation types. Beech dominated the regeneration in the Scots pine and oak

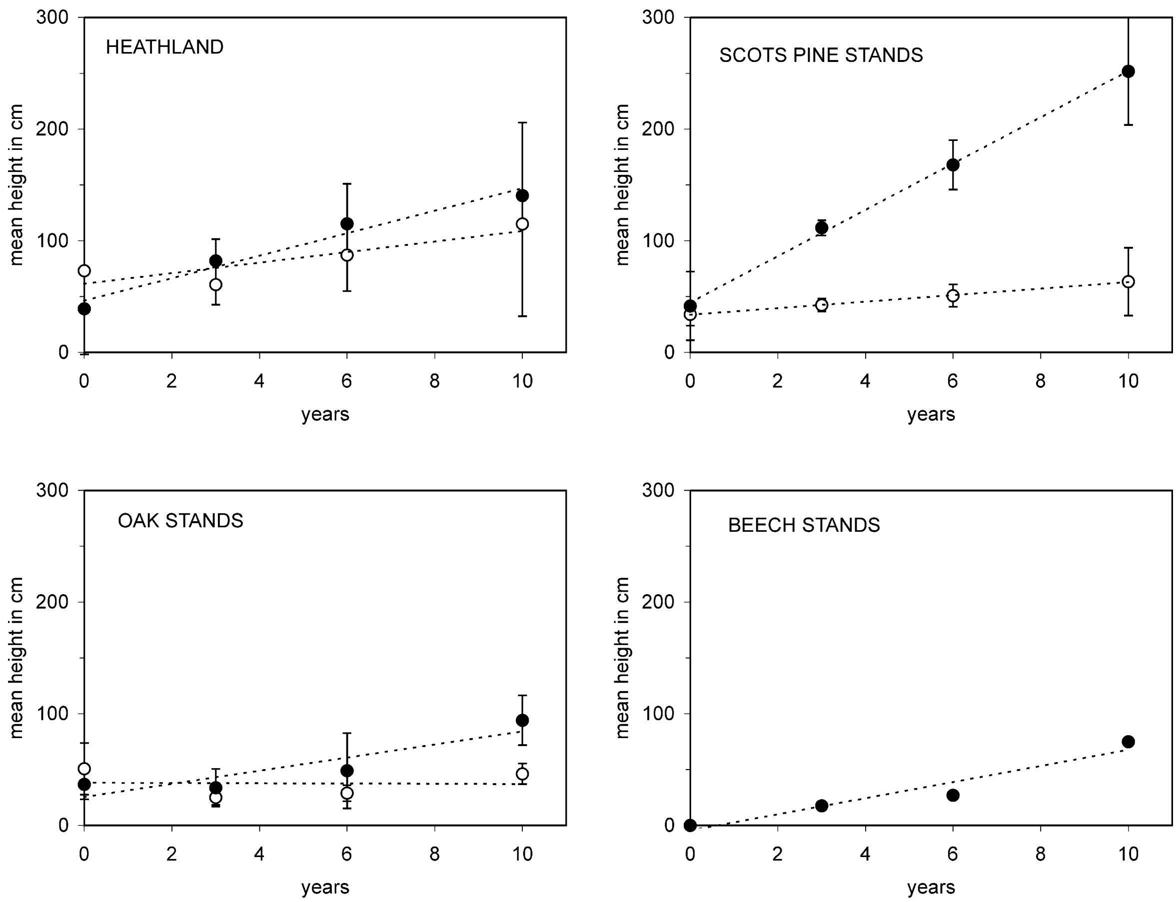

Fig. 5. Changes in the mean height of saplings in the unfenced (open symbol) and fenced plots (filled symbol) in the different vegetation types during the 10-year research period.

stands, whereas Scots pine dominated the regeneration on heathland.

Complete exclusion of the ungulates resulted in the regeneration of a variety of tree species in the Scots pine and oak stands including Scots pine, beech, birch, oak and rowan. On heathland and in the beech stands, the species composition of the regeneration was not affected by fencing, and consisted predominantly of Scots pine and beech, respectively.

4. Discussion

4.1. Forest succession and the impact of reduced ungulate densities

Our results clearly show that without mowing or burning, heathland was rapidly invaded by Scots pine, especially in plots close to the forest edge. It is a well known phenomenon that, after cessation of management, heathland succession accelerates towards woodland (Bullock and Pakeman, 1997). Deer browsing had no impact on this process. Bokdam and Gleichman (2000) observed the same for cattle for another heathland on the Veluwe. The rate of Scots pine invasion was highly variable between plots, but was partly related to the distance from the forest edge. Fencing increased the regeneration of birch species and some other palatable species like rowan, but not of pedunculate oak.

According to the forest succession scheme for sandy soils of Fanta (1986), the establishment of birch and oak species characterises the early succession of Scots pine forest to deciduous forest communities, i.e. birch–oak and oak–beech forest, which are both indigenous forest types in the study area. This succession pattern was only observed in the absence of ungulates. With red deer, roe deer and wild boar present in a total density of ca. 14 animals km^{-2}, both oak species and to some extent silver birch were too severely browsed to show any successful regeneration under an open canopy of Scots pine. Among the broadleaved species, only beech was successfully regenerating (Fig. 7). This agrees with earlier findings, that beech is less severely browsed and has a larger browsing tolerance (Van Hees et al., 1996). Therefore, it is likely that Scots pine and beech will become the next dominant species under the canopy of Scots pine and oak stands. Beech regeneration was prevented by browsing only under its own canopy, where

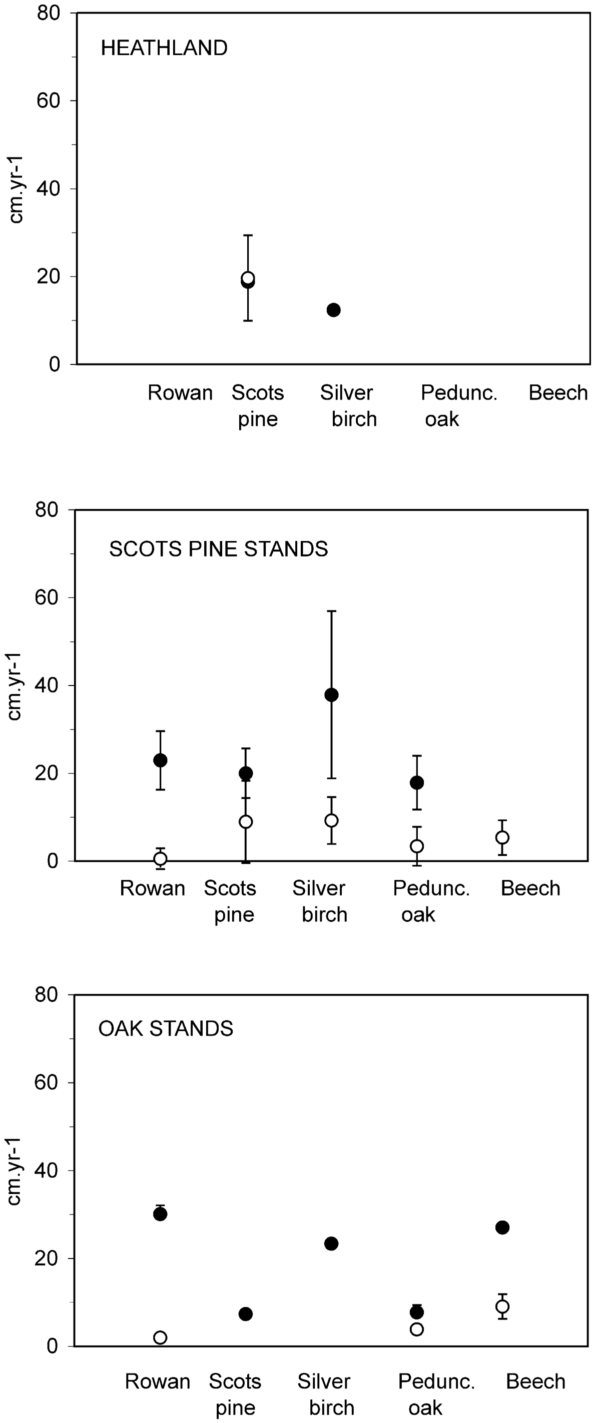

Fig. 6. Annual height increment (cm) of the regeneration in the unfenced (open symbol) and fenced plots (filled symbol) in the different vegetation types.

due to the absence of any other forage, the browsing pressure on beech and oak seedlings was very high.

Mean annual consumption by the ungulates was estimated as 4–5 g m^{-2} dry weight per year (2.5% of live herbivore biomass; Van Soest 1982). The annual net primary production in this forest-heathland amounts to 200–300 g m^{-2} dry weight per year (Diemont, 1996;

Table 2
Changes in the density of bramble (*Rubus* spp.) shrubs (number ha^{-1} and standard deviation within parentheses) in the unfenced and fenced plots in the different vegetation types during the 10-year period

Vegetation type	Unfenced				Fenced			
	1988	1991	1994	1998	1988	1991	1994	1998
Heathland	–	–	–	–	–	–	–	76
								(239)
Scots pine forest	258	99	120	60	434	1,237	2,595	4,085
	(558)	(166)	(230)	(107)	(950)	(1,693)	(3,438)	(4,281)
Oak forest	–	6	6	6	6	297	530	718
	–	(10)	(10)	(10)	(11)	(370)	(601)	(353)
Beech forest	–	–	–	–	–	–	–	–

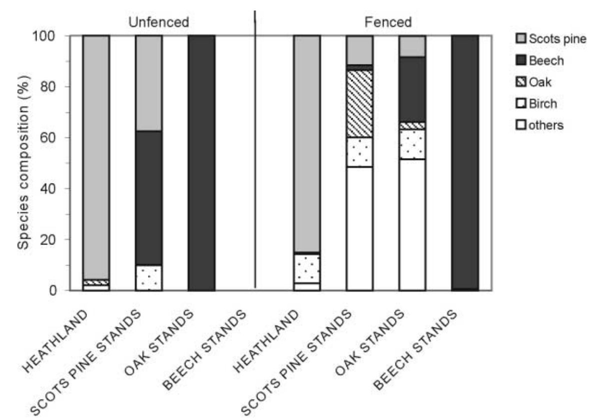

Fig. 7. Relative species composition of the regeneration cohort >1.5 m (height classes 5 and 6) in the unfenced and fenced plots in the different vegetation types after ten years (1998). In the unfenced beech plots, regeneration was absent (Birch = *B. pendula* and *B. pubescens*; Oak = *Q. robur and Q. petraea*).

Nabuurs, 1996). Therefore, present-day browsing pressure is equivalent to 1.5–2.5% of the annual net primary production. Although this is a light browsing intensity, according to the criteria of Milchunas and Lauenroth (1993), it shows how large the impact of browsing ungulates can be to forest regeneration on poor soils with a relatively low quality of available forage. This was also confirmed by a modelling study (Jorritsma et al., 1999). An earlier field study in the same area demonstrated a small effect on tree regeneration by rooting and browsing of wild boar (Groot Bruinderink et al., 1996).

The results clearly indicate that under the present-day browsing intensity neither of the oak species (*Q. robur* and *Q. petraea*) will become dominant in the forest canopy but will be out-competed, mainly by beech. A similar trend was observed in the central hardwoods region of the United States, where oaks were lost from the forest ecosystem as a result of continuously high deer numbers (Anderson and Katz, 1993).

4.2. Conversion management and spatial scale

It can be questioned how ungulate populations should best be managed to promote the regeneration of the broadleaved species of natural birch–oak and oak–beech forest communities, typical of these sandy and loamy-sand soils. The regeneration of the shade-intolerant oak is generally only successful in large gaps and clearings, on grassland and on heathland (Jones, 1959; Pigott, 1983; Worell and Nixon, 1991; Vera, 2000). The mechanism whereby thorny shrubs like holly (*Ilex aquifolium*) or bramble (*Rubus* spp.) protect saplings of highly palatable species from being grazed (Morgan, 1991; Worrell and Nixon, 1991), the so-called associational resistance (Olff et al., 1999), is not likely to operate with selective intermediate feeders and browsers, like roe deer or sheep (Pigott, 1983) present in these stands. Indeed, dense bramble invasion only occurred when protected from grazing (especially under pine). Similar results were shown by Linhart and Whelan (1980) after fencing an oak-woodland from sheep and cattle grazing.

A further temporary reduction of ungulate pressure is a management option. It will allow the regeneration of a more varied assemblage of broadleaved species, including oak, as observed in the fenced plots. However, in this case, it is expected that all vegetation types will rapidly develop into closed pine or broadleaved woodland, as indicated by the fenced plots, with open patches of grass or shrub vegetation almost absent.

A mosaic of grassland, heathland and woodland rather than continuous forest is thought to be a more natural state with higher conservation values (Rackham, 1998; Vera, 2000). Therefore, large herbivores are indispensable, as other large-scale disturbance regimes such as fire are not very likely in this climate zone. Only windthrow may create conditions suitable for tree regeneration, but this acts only at a small scale and occurs on average only every 20–30 years (Pontailler et al., 1997).

What is a desirable level of browsing? A wide range of studies indicates that herbivore density and grazing impact is not linearly related (Putman, 1996; Hester et al., 2000). Marked increases in tree regeneration might occur if herbivore densities fell below certain threshold levels, as was demonstrated for oak in the New Forest (Peterken and Tubbs, 1965). In our view, the regeneration of highly palatable broadleaved species like pedunculate and sessile oak, will only become successful if temporal or spatial fluctuations in ungulate pressure are allowed to occur. Historical research in woodlands suggest that regeneration under natural conditions is an episodic process, with often long periods lacking any regeneration alternating with periods of successful establishment of a new woodland generation (Rackham, 1998). For the forest-heathland of this study, it means that enlargement of the available range of the ungulates is a desirable option. This will result in a browsing regime which is more variable in space and time. It is hypothesised that this would allow the regeneration even of the most susceptible woody species, like both oak species. It is a challenge for the management of the area to maintain a half-open landscape without too much human interference, while supporting a high species diversity.

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