Chapter 5: **Recruitment limitation of woody species in a herbivore-dominated novel ecosystem**

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**Abstract**

Current rapid changes in land use, climate and ecosystem management increasingly lead to novel ecosystems, i.e., configurations of species, abiotic factors and processes without any clear historical equivalent, but with key conservation values. There is an urgent need to improve our understanding of the ecological processes that affect the diversity, functioning and services in such newly created environments. We investigated woody species recruitment in the Oostvaardersplassen (OVP), a Dutch nature reserve that was reclaimed from the freshwater lake IJsselmeer in 1968 and in part shortly used for agriculture. The free-ranging large herbivore populations (red deer, Konik horses and Heck cattle) that occur in the area are regulated in this system by winter survival, as no large predators are present, nor any form of human interference. The resulting very high large herbivore densities (2.4 ha\(^{-1}\)) in combination with underlying large-scale hydrological and soil heterogeneity current have led to three main vegetation structures: tall reed beds in the wettest, undrained part, tall rough vegetation in the higher areas of the drained part and short grazing lawns in the lower areas of the initially drained part. We investigated how larger herbivores affect woody species recruitment in this system, and thus ultimately determine the diversity of the vegetation structure on smaller scales. We transplanted saplings of six woody species (two pioneers, two spiny shrubs, and two forest species) in the two dominant vegetation types of the drained part of the ecosystem, i.e. tall roughs and short lawns. Plots contained three levels of accessibility to large herbivores: full access (no exclosure), limited access (1m high exclosure, mimicking a grazing refuge), and no access (2m high exclosure, mimicking temporal herbivore absence). We tested how tree sapling performance and survival of the six woody species was affected by herbivore accessibility, surrounding vegetation type (tall roughs or short lawns) and soil-tillage (mimicking wild boar rooting, presently not yet present in OVP). After two years, no single sapling survived where large herbivores had full access, while overall survival in the partial and full exclosures was 28 and 27.5%, respectively. Sapling survival in the exclosures strongly depended on the combination of vegetation type and soil tillage. Survival was much higher in initially short lawns than in tall roughs, most likely due to reduced light competition, suggesting that intense grazing followed by (simulated) sudden large herbivore disappearance can promote tree establishment. Soil tillage positively influenced the pioneer tree species. We conclude that tree recruitment in the OVP is currently strongly limited by the large herbivore populations, while at the same time future fluctuations in herbivore density (e.g., due to harsh winters
or local inaccessibility of areas due to flooding) are expected to lead to strong tree recruitment events. We discuss the different relationships between spatial heterogeneity at different scales, free-roaming large herbivore population dynamics without large predators, and woody species recruitment in this novel ecosystem.

5.1 Introduction

Many ecosystems are now increasingly and irreversibly changed to a point at which they have no historical equivalent, or arise under mostly new environmental conditions (Jackson and Hobbs 2009; Hobbs, Higgs and Harris 2009). These so-called “novel ecosystems” especially arise from strong land use changes where new conditions are created over large spatial extents. Examples include new habitats formed after abandonment of cropland or pastures (Cramer et al. 2008), through land reclamation in coastal estuaries or peatlands (Verhoeven and Setter 2010) or through combinations of those. Simultaneously, climate change can contribute to the establishment of ecological conditions without clear recent equivalents (Jackson and Hobbs 2009). And, some invasive species from other continents can so strongly modify local key ecosystem features (as fire regimes) that they lead to ecosystems without any obvious historical analog in the region of invasion (Jackson and Hobbs 2009). Increasingly, such ecosystems can also play an important role to preserve many species of plant and animals and associated ecological processes in a relatively new “ecological setting”. Better understanding of the main aspects of the functioning of these novel ecosystems is needed to better plan for, or protect their conservation values and ecosystem services (Seastedt et al. 2008).

A clear example of a novel ecosystem is the Oostvaardersplassen area (OVP) in the Netherlands. The OVP belongs to the province Flevoland, a large area of land (polder) that was reclaimed from the freshwater lake IJsselmeer in 1968, which in turn originated from the closing off the brackish Zuiderzee estuary from the North Sea by the Afsluitdijk (a 32 km long dike through the mouth of the IJssel estuary) in 1930. The area now has a very fertile clay soil (Vulink 1991; Vulink 2001), and is situated at 2 to 5 m below sea level. The present nature conservation area consists of a drained area and an undrained area, separated by a low level or dike (Fig. 5.1). The wetter part is elevated up to 2 meters above the drier part, due to soil inclination in the drained part. The whole area was originally designated for agricultural use and industrial development, and partly shortly used for agriculture, before it was re-designated as a nature reserve in the mid 1970’s due to surprising bird breeding bird occurrences after the reclamation of which several were extinct from the country at that moment. Greylag Geese (Anser anser) were one of the species that started molting and breeding in the wet, undrained part of the area and their grazing activities in the reed beds were thought to promote the occurrence of other endangered species, such as Bearded Reedling (Panurus biarmicus), Bluethroat (Luscinia svecica) and Spoonbill (Platalea leucorodia). The Greylag Geese were therefore considered to be an important species for the key ecosystem processes in the area as they kept the developing reed beds open in the wet, undrained part, thus facilitating several rare bird species that are characteristic of young reed beds. To preserve the goose population and their associated ecosystem functions, a grassland part briefly used for agriculture was added to the conservation area. Furthermore, to keep this grassland open and short (and thus suitable for the geese) two large grazer species were introduced in 1983 and 1984: Heck cattle (Bos
The Oostvaardersplassen consists of an undrained and a drained area, separated by a low levee (or dike). The drained area has a lower elevation as a result of soil subsidence/compaction. A small part of the drained area has been used as a soil deposit (as the result of ditch making in the region) and is elevated above the drained area. The undrained area contains open water with reed beds. The drained area consists mostly of short grassland, while the soil deposit area and other elevated parts of the drained area (near the edges of the reserves) are dominated by tall reed swards. Image from Bing Maps, © 2013 Microsoft Cooperation and Digital Elevation Model (DEM) from the AHN-1 (Algemene Hoogtekaart Nederland: Current Elevation Map of the Netherlands, Topografische Dienst).

Fig. 5.1
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primigenius taurus) and Konik horse (Equus ferus caballus) respectively. In 1992 red deer (Cervus elaphus) were introduced to this herbivore assembly, that since then consisted of a wide range of functional ungulate types, namely a ruminant (cattle) and a hindgut grazer (horses) as well as an intermediate feeder (red deer), while a typical ‘soil disturber’ as wild boar (Sus scrofa) may be introduced in the future (Vera 2008). The three large herbivores started mostly using the drained, drier part of the ecosystem, while only the deer now irregularly use the wet reed beds.

An important novelty in the management regime of the OVP has been that instead of regulating fixed stocking rates, or regular removal or culling to enforce top-down control over the large herbivore populations, a hands-off policy was chosen since the start of their introduction. Also, none of the large herbivores are predated on at any life stage (red fox is the largest predator in the ecosystem consuming only smaller prey), consequently the densities of large herbivores in the OVP are regulated by food availability and winter conditions (ICMO 2010). In 1983, 32 Heck cattle were introduced in the area followed by 20 Konik horses in 1984 and 42 red deer in 1992. At fall 2011 their populations had grown to 360 heads of cattle (0.18 ha⁻¹), 1,150 horses (0.58 ha⁻¹) and 3,300 red deer (1.7 ha⁻¹), resulting in a total number of large herbivores to 4,810 (2.4 ha⁻¹, taking only the drier part into account) (ICMO 2010) and associated metabolic biomass (body mass⁰.⁷³) of 135 kg ha⁻¹. These high densities of large herbivores in combination with underlying large-scale hydrological and soil heterogeneity has currently led to three main vegetation structures: tall reed beds in the wettest, undrained part, tall rough vegetation in the higher areas of the drained part and short grazing lawns in the lower areas of the drained part that resulted from soil settlement after drainage (Fig. 5.1). Researchers monitoring bird populations have expressed concern that the current high herbivore densities impair the current and future biodiversity values of the drained area of the ecosystem, due to the current lack of smaller-scale spatial heterogeneity in the vegetation. (Bijlsma 2007). On the other hand, there is no clear reference how this area “should look like” in terms of ecosystem dynamics and species it “should have”, as the most important ecological developments in the area mostly happened unanticipated, without obvious historical analogues. This 40 year-old ecosystem is still very young relevant to ecological time scales for substantial heterogeneity to arise. In comparison, the 1000 year old New Forest National Park in southern England famous for its grazer-mediated vegetation mosaics has hosted a variety of large herbivore populations since it was set aside as a Royal Hunting Forest 11th century.

One class of ecosystem processes that strongly affects ecosystem diversity, functioning and services are herbivore-tree-grass interactions (Turner 1989; Turner, Gardner and Dale 1989; Olff et al. 1999; Hargrove et al. 2000; Scheffer et al. 2001; Koniak et al. 2010). In grazed ecosystems, the ratio grassland to woodland and the spatial distribution of grassland and woodland at different scales is strongly determined by factors that affect tree sapling survival (Rao et al. 2003; Bakker et al. 2004; Smit, Den Ouden and Müller-Schärer 2006; Moe et al. 2009). The now-mature shrub and tree species that had established before the herbivore introductions in the 1983/4 (mainly the softwood, poorly defended pioneers Salix alba and Sambucus nigra) are currently dying due to old age and debarking, and recruitment of hardwood, herbivore-defended woody species appears inhibited. In combination with the grass being cropped short due to the currently high number of herbivores, the landscape within the drained part of the ecosystem has increasingly become open. In this study we explore the factors that affect tree sapling survival in the novel ecosystem OVP,
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with its large herds of (semi) wild herbivores roaming the fertile clay soils of the former sea floor.

Several factors are known to affect sapling survival (Clark et al. 1999). First of all, several studies have shown that browsing and trampling by large herbivores limit sapling survival, especially when herbivore densities are high (Côté et al. 2004). Secondly, light competition between tree saplings and herbaceous plants has been shown to limit sapling survival, particularly in more productive ecosystems (Smit and Olff 1998; Vandenberghe 2006; Vandenberghe et al. 2008). Thirdly, soil properties such as low nutrients, high moisture and limited oxygenation can limit tree sapling survival (Bezkorowajnyj et al. 1993; Kozlowski 1999; Kuijper et al. 2010). The strength of these three limiting factors for sapling survival (herbivory, competition and poor soil conditions) is expected to vary between tree species with different traits, such as shade tolerance, browsing tolerance, avoidance and resistance (Vandenberghe et al. 2008; Vandenberghe et al. 2009), and ability to cope with waterlogging. For instance, spiny or thorny shrubs have been shown to be less limited by large herbivores than pioneer and forest species, while forest species are less limited by light competition than pioneer and shrub species, and pioneers are better at establishing in disturbed soils (Finegan 1984). Furthermore, the strength of the limiting factors for these different functional groups may also interact with the surrounding vegetation type. For instance, tall vegetation (e.g. tall roughs) has been shown to attract fewer herbivores than short vegetation (e.g. grazing lawns) due to the relatively low nutritional quality of the former (Augustine and McNaughton 1998), and thus may indirectly reduce the negative impact of herbivory (Vandenberghe et al. 2006; Van Uytvanck et al. 2008; Smit and Ruifrok 2011). On the other hand, tall vegetation will lead to increased competition for light experienced by seedlings and saplings. Lastly, temporary absence of or low accessibility to herbivores may alter the dominance and strength of the limiting factors for the different functional groups, e.g., a shift from browsing to light competition as the limiting factor (Smit and Olff 1998).

Landscape-scale tree recruitment in grazing ecosystems can occur through windows of opportunity for regeneration. For example, temporal absence of herbivores due to animal movements and preference shifts, avoidance of local areas with high predation risk, or larger-scale population crashes due to diseases or harsh winters. In addition, local (patch-scale) recruitment opportunities for trees may arise through natural barriers such as coarse woody debris, dense spiny thickets, or variation in topography causing islands to be (temporarily) surrounded by water. However, such patch-scale recruitment opportunities arising from natural causes are generally rare or even absent in many of these novel ecosystems that were once designed and used as agricultural land, as they are characterized by spatially, rather uniform starting conditions (initially created that way), especially at smaller scales.

To study the relevant determinants of tree species recruitment, the potential of local windows of opportunity, and associated small-scale vegetation heterogeneity in the OVP we performed an exclosure study in the drained part of the area. We transplanted a large number of tree saplings of 6 different species (n = 7100) and simulated temporal absence and low accessibility of large herbivores via full (2 m tall fence) and partial enclosures (1 m tall fence, where the deer could jump over but the Heck cattle and Konik horses not), respectively. We tested how tree sapling survival of different functional groups (2
pioneers, 2 defended shrubs, 2 forest species) was affected by accessibility, surrounding vegetation type (either tall roughs or short lawns) and soil-disturbance (undisturbed and tillaged soil, mimicking wild boar). We expected that sapling survival outside the exclosures might be higher in rough vegetation and higher for spiny shrubs. We also expected that sapling survival would be higher inside full exclosures than in partial exclosures, with higher survival in short lawns and for the forest species. Lastly, we expected that soil tillage would particularly favor pioneer species, which is relevant for the potential introduction of wild boar in the future.

5.2 Methods

5.2.1 Study area
The nature reserve the Oostvaardersplassen or OVP (52° 26’ N, 5°19’E) measures 5600 ha. The OVP belongs to the province Flevoland, a large area of reclaimed land (polder) from a freshwater lake that was declared dry in 1968 (Vera 2008) with a very fertile soil (Vulink 1991; Vulink 2001). Average yearly temperatures vary between 9.6 °C and 9.9 °C and average annual rainfall is between 825 mm and 875 mm (averages over 1981-2010, data from www.knmi.nl). The area consists of two distinct parts separated by an undrained wetland (3600 ha) and a relatively dry drained area (2000 ha). As a result of soil subsidence due to soil compaction upon drainage, the drained part is up to 1.5 m lower than on the undrained, wet part, yielding a reversed wet/dry profile with topography (Fig. 5.1). Within the drained part, an area of approximately 350 ha is somewhat (30-50 cm) elevated as it was used as a soil deposit in the 1960s when ditches and canals in the area were dug. The undrained part consists of open water and reed roughs with the original soil profile of wet clay of several meter thick, that remained after the embankment of the area. This clay layer is several meters thick, and rests on a Pleistocene sandy base layer. The drained part consists mostly of short grassland (~65%), dominated by short palatable grasses (mainly Poa trivialis and Lolium perenne), and tall reed roughs (~35%) (dominated by Phragmites australis and Carduus crispus). Most of this reed rough is located on the slightly elevated soil deposit.

The largest carnivores that occur in the area, and spontaneously arrived, are the red fox (Vulpes vulpes) and the white-tailed eagle (Haliaeetus albicilla) that only catch smaller prey. Hence cattle, horses and red deer are not utilized by these predators at any life stage, except as carrion. Herbivore populations are also not human-regulated, apart from a ‘mercy culling’ practice in late winter to minimize animal suffering (ICMO 2010), where animals are shot that are unlikely to make it through the winter based on their condition in combination with the weather forecast. Consequently, herbivore densities are (indirectly) bottom-up regulated with recorded annual mortality rates up to 30% and higher in harsh winters, with similar rates of recruitment during the favorable growing season (Vulink 2001, Vera 2008, ICMO 2010). Although the area is topographically uniform, two dominant vegetation types can be identified in the drained part of the OVP: lawns and roughs. Lawns cover ca. 60% of the grasslands of the OVP and are dominated by short palatable grasses (mainly Poa trivialis and Lolium perenne,) that are intensively grazed during the growing season (May-October) by all large herbivores as well as by large numbers of geese in winter and early spring (predominantly Branta leucopsis, ca. 20.000). Tall reed roughs (dominated by Phragmites australis and Carduus crispus) cover ca. 40 % of drained part of the OVP and are intensively grazed after the growing season when the grazing lawns are mostly depleted (starting around November up to March).
5.2.2 Experimental set-up
The experiment started at April 16th 2010, at the beginning of the growing season, and was situated in the drained part of the OVP (Fig. 5.1). The experiment consisted of 10 plots, each of which measured 35 m × 12 m. Five plots were located in tall Rough vegetation (average 3.75 m below sea level) and five plots in short Lawn vegetation (average 4.0 m below sea level) (Fig. 5.2). Vegetation height of both types was equally short at this period (< 4 cm). Within each vegetation type, plots were spread over a distance of 500m, while the distance between plots of different vegetation types ranged from 140m to 280m (Fig. 5.2). The Lawn plots were each situated at an elevation of about 25 cm lower than the tall vegetation, and the resulting differences in soil factors (e.g. moisture and texture) in combination with the grazers are probably responsible for the differences in vegetation structure.

Each plot contained three compartments (subplots). One compartment was fully accessible to all herbivores (grazed control), while two compartments had a different type of exclosure: a partial exclosure of 1m high fence (mesh width of 20 cm × 20 cm) allow-
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ing reduced access to red deer but not to cattle and horses, and a full-exclosure of 2 m high excluding access to red deer, cattle and horses. The full-exclosure (13 m × 12 m) shared one of its sides with the partial exclosure (8 m × 12 m). The open access compartment (8 m × 12 m) was separated from the partial exclosure by a 6 m buffer (Fig. 5.2) to avoid edge effects (e.g. herbivores may be attracted to the exclosures). The full-exclosure had a larger surface area than the partial exclosure or control, because part will be used in a follow-up experiment (monitoring long-term vegetation dynamics and soil-soil fauna feedbacks). To achieve soil tillage, we used a tractor to plough the soil 20-30 cm deep over an area of 4 m × 12 m in the two exclosure types and in the control. With this treatment we intended to mimic wild boar uprooting, a process that may be important for tree recruitment via alteration of soil properties (e.g. Barrios-Garcia and Ballari 2012), but currently does not occur as there are no wild boars in the area. A third of each plot was not planted with tree saplings as it was used to monitor vegetation dynamics (species composition, abundance, and height) in permanent plots of 2 m × 2 m. We transplanted in total 7100 one-year-old saplings (origin: Staatsbosbeheer Zaad en Plantsen, Driebergen, all autochthonous plant material), 2119 saplings in the control, 1787 saplings in the partial exclosure and 3194 saplings in the full-exclosure. We used six species: two non-defended, palatable pioneer shrub species, Salix alba (n = 1055, initial height after planting = 36 cm ± 9 (mean ± SD)) and Sambucus nigra (n = 1258, height = 12 cm ± 5), two herbivore-defended shrub species, Rosa canina (n = 1101, height = 33 cm ± 11) and Crataegus monogyna (n = 1239, height = 34 cm ± 9), and two forest canopy species, Quercus robur (n = 1191, height = 34 cm ± 9) and Fraxinus excelsior (n = 1256, height = 23 cm ± 6). All these species occur as seed sources in or nearby the study area. Saplings were planted in rows using a tractor over the length of the plot. First a slit of 15 cm deep was cut in the soil after which saplings were planted by hand. To avoid that the saplings would be easily pulled out by the herbivores prior to establishment, the tractor drove along both sides of the slit to close it firmly.

To summarize, each plot consisted out of 12 rows in total, with ca. 70 cm between rows, and each row contained one species. In the first six rows all six species were present in a random order for each plot, and the next 6 rows were also randomly ordered, but we made sure that rows 6 and 7 did not contain the same species. Within each row distance between saplings was 50 ± 10 cm (Mean ± SD (minimum distance 31 cm).

5.2.3 Measurements and analyses

We scored the number of living saplings the first week after transplantation (t = 0) and repeated this measurement after 50, 388 (ca. 1 year) and 753 days (ca. 2 years). These observations were done in spring when saplings were best visible; in summer and fall the vegetation in the exclosures was too tall and dense (locally up to 180 cm) to relocate saplings without severely damaging the surrounding vegetation. Saplings without leaves and without living stem (brownish color under bark), as well as saplings that had been removed by herbivores were considered dead. We calculated the number of dead saplings by subtracting the number alive from the number transplanted at day 0. As sapling survival in the controls (fully accessible to all herbivores) was already very low after 50 days (6% in the control vs. 73% inside full and partial exclosures) and virtually zero after 1 year, we decided not to perform any further statistical analyses on the control data.

To examine how sapling survival was affected by vegetation type and soil tillage in the partial and full exclosures, we used a generalized linear model (GLZ) for each species separately, for year 1 and 2. We used GLZs with a binomial error distribution and logit
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link function, with sapling survival (alive/dead) as the dependent variable and vegetation type, soil tillage presence, exclosure type (full vs. partial) and plot as independent variables. We nested plot ID within vegetation types to correct for possible random variation between the plots (Quinn and Keough 2002). Some exclosures had been visited shortly by cattle and horses due to a break-through event in early spring 2011. To control for this we used break through as an independent factor in the survival analyses of those exclosures. Besides survival of the saplings, we measured the height of three randomly selected living individuals per row per treatment combination, from ground to the highest green part. If less than three saplings were alive, we recorded all saplings. If no saplings were alive, we did not take height into account for that specific record. We compared sapling height between full and partial exclosure using ANOVA, with the absolute height as dependent variable and exclosure type (full vs. partial) as independent variable for each species separately.

In addition, we measured vegetation height and plant species composition and abundance in each plot for each treatment combination. We measured vegetation height by dropping a Styrofoam disc of 24 cm diameter and 65 g from a fixed height on the vegetation at the beginning (May) and peak of the growing season (August). We took vegetation relevées in June at year 0 and 1, using 1 m² permanent quadrats (pq) (Fig. 5.2), where we identified all species present and estimated species cover using the Braun-Blanquet scale. We converted the cover score to median percentage and determined the three most abundant plant species per treatment combination. At the end of the first growing season of year 1 we measured light availability using a AccuPAR model LP-80 PAR/LAI Ceptometer at 0, 30 and 100 cm height in a random subset of the plots (Lawn: 1, 4, and 5, Rough: 8, 9 and 10). At the same time we measured changes in oxygenation of the soil at 10 cm depth using a random subset of the plots (Lawn: 1, 2, and 3, Rough: 6, 7 and 9). For these measurements we used five electrodes with a platinum tip and one Ag/AgCl calomel reference electrode (Cole-Palmer®) that were connected to a Graphtec GL200 Datalogger (Graphtec GB Ltd). After one year in spring we measured soil compactability using a penetrometer (dropping an 8 kg rod with a diameter of 25 mm from 75 cm and measured penetration depth). Light and soil measurements (redox potential and soil compaction) were analyzed with full factorial ANOVAs using vegetation type, exclosure type and soil tillage as independent variables for sapling survival. To verify whether the partial exclosures were indeed visited by herbivores, we regularly checked for the presence of dung pellets, snow tracks and for signs of browsing on the saplings.

5.3 Results

5.3.1 Survival outside exclosures (controls)
After 2 years we found that none of the 2119 saplings survived outside the exclosures (Table 5.1). Sapling survival was already extremely low at day 50 outside the exclosures (6%) compared to the partial and full exclosures (66 and 62%, respectively) (Table 5.1), indicating that herbivory is an important limiting factor outside the exclosures. Furthermore, we found a strong effect of woody species at day 50 and after 1 year: after 50 days Cra- taea and Rosa had a much higher survival compared to other species, but only in Lawn and more so in undisturbed soil. Also after 50 days, in undisturbed Lawn, Crateae and Rosa had a 10 and 12 times higher survival compared to the other species in undisturbed
Lawn (Table 5.1). After 1 year only nine individuals were still alive outside the exclosure of which six *Crataegus*, two *Rosa*, and one *Quercus*. Except for one *Crataegus*, all these saplings were found in Lawn, with the majority situated in undisturbed soil (Table 5.1).

**5.3.2 Survival inside exclosures**

Overall tree sapling survival in the exclosures (partial and full exclosures combined) declined from 64%, to 40% and 28% after 50 days, 1 year and 2 years, respectively (Table 5.1 and 5.2). However, there were large differences between species: at year 1 *Sambucus* survival was only 5%, while the survival of all other species was above 34% (Table 5.1). After 2 years *Sambucus* survival was even lower (4%), and *Fraxinus* survival was only 11%, while all other species had an average survival above 25% (Table 5.1). Survival was highest for *Crataegus* (65% and 48% at year 1 and 2 respectively, Table 5.1).

Inside the exclosures sapling survival was always higher in Lawn than in the tall reed Rough for all species, except for *Fraxinus* after 50 days (Table 5.1), and in most cases this effect was significant (Table 5.2). Average survival for all species was 1.5, 1.7 and 2.2 times higher in Lawn compared to Rough after 50 days, 1 year and 2 years, respectively. After 2 years, the survival of *Rosa* and *Crataegus* was 3.0 and 2.6 times higher in Lawn than in Rough, respectively (Table 5.1).

Soil tillage benefited all species after 50 days; survival was on average 1.6 times higher in disturbed soil and this effect was significant for all species (Table 5.2). However, Soil tillage eventually only benefited the pioneer species, *Sambucus* and *Salix*, after 1 year and 2 years (Table 5.2). Interestingly, after 2 years we found a negative effect of Soil tillage on survival of *Quercus* and *Crataegus*, but this was only significant for *Crataegus* and occurred especially in Lawn (Table 5.2). There also was a significant interaction between vegetation type and Soil tillage for *Sambucus*, *Salix* and *Crataegus* after 1 year, and for *Quercus* after 2 years. For *Sambucus* and *Salix* this is because the positive effect of soil tillage was larger in Lawn than in Rough; e.g. after 2 years survival was 6.9 and 2.5 times higher in disturbed Lawn compared to undisturbed Lawn (for *Sambucus* and *Salix* respectively), while their survival was only 1.5 and 1.9 times higher in disturbed Rough compared to undisturbed Rough (Table 5.1). The significant interaction between vegetation type and Soil tillage for *Crataegus* after 1 and 2 years, and for *Quercus* after 2 years reflects a negative impact of Soil tillage in Lawn and a positive impact in Rough; survival after 2 years 2 was 0.7 and 0.6 times lower in disturbed Lawn than in undisturbed Lawn (for *Crataegus* and *Quercus* respectively), while their survival was for both species 1.4 times higher in disturbed than in undisturbed Rough (Table 5.2). In addition, the interaction between vegetation type and disturbance was significant for *Salix* and *Rosa* after 50 days, but these differences were very small (Table 5.1).

Exclosure type affected sapling survival after 50 days (Table 5.2): interestingly, survival was higher in the partial exclosure, but these effects are very small, except for *Fraxinus* (Table 5.1 and 5.2). In contrast, after 1 year all species had a higher survival in the full exclosure, except for the shrub species *Crataegus* and *Rosa* (Table 5.1 and 5.2). This effect is only significant for *Quercus*, with 1.6 higher survival in the full exclosure compared to the partial exclosure, and this tendency continued for *Quercus* after 2 years (Table 5.1 and 5.2). We found the opposite trend for *Crataegus* after 2 years with a lower survival in the full exclosure than in the partial exclosure (41% and 56%, respectively, Table 5.1).
Herbivore-mediated structural diversity of vegetation and 5.2). The interaction between vegetation type and exclosure type was significant for Quercus after 1 year and 2 years, with a stronger impact of exclosure type in Lawn than in Rough (Table 5.1). In Lawn, Quercus survival in the full exclosure was 1.7 times higher than in the partial exclosure after 1 and 2 years. In Rough, Quercus survival was 1.3 and 1.2 higher after 1 year and 2 years, respectively (Table 5.1 and 5.2).

5.3.3 Sapling height
Sapling height outside exclosures was not considered here due to the extremely low number of survivors and immediate height reduction by browsing. For all species (except Sambucus on which we lacked most height data) saplings were tallest in the full exclosure in the disturbed Lawn, and lowest in the partial exclosures in the undisturbed soil (both for Lawn and Rough), both after 1 year and 2 years (Table 5.3). For most species, there was a significant effect of exclosure type and Soil tillage (which promoted height growth), and for some species vegetation type was significant (Table 5.4). The significant effect of exclosure type probably reflects the effects of the red deer visiting the partial exclosures. After 2 years the differences in height between exclosure types became stronger. Salix was the tallest species, while Quercus remained the shortest (Table 5.3).

5.3.4 Changes in vegetation and soil
Within four months (August 2010), the average vegetation height for the Lawn and Rough plots in the undisturbed controls was 10 ± 3 and 30 ± 14 cm, respectively (means ± SD). In the full and partial exclosure this was 39 cm ± 9 and 41 cm ± 10 respectively for Lawn and 80 cm ± 32 and 82 cm ± 27 for Rough. The tillaged soil remained bare for the first two months but vegetation recovered after four months (August 2010), with 11 ± 12 cm (Lawn) and 13 ± 14 cm (Rough) outside the exclosures and 66 ± 29 cm (Lawn) and 86 ± 34 cm (Rough) in the full exclosure. Light measurements show that after 6 months, the light conditions in the canopy for tree saplings were more favorable in Lawn than in Rough in both the full and partial exclosure (Fig. 5.3). At the start of the growing season in 2011 (after 1 year), vegetation outside the exclosures was still very short (average lower than

![Fig. 5.3](image-url) Light intensity at 30 cm height in lawn vegetation (white bars) and rough vegetation (grey bars) in the different exclosure types (grazed control, partial exclosure and full exclosure) with significant effects of vegetation type ($F_{(1,91)} = 10.4^*$), exclosure type ($F_{(2,91)} = 11.5^{***}$) and the interaction between vegetation and exclosure type ($F_{(2,91)} = 3.3^*$). * P < 0.005, ** P < 0.01, *** P < 0.001.
### Table 5.1

Herbivore-mediated structural diversity of vegetation

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<th>Species</th>
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<th>Res.DF V</th>
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<th>D</th>
<th>V×E</th>
<th>E×D</th>
<th>V×E×D</th>
<th>ID (V)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sambucus nigra</td>
<td>259</td>
<td>78</td>
<td></td>
<td></td>
<td>5**</td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Salix alba</td>
<td>252</td>
<td>79</td>
<td>1</td>
<td></td>
<td>1**</td>
<td>5*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rosa canina</td>
<td>211</td>
<td>79</td>
<td>1</td>
<td></td>
<td>5**</td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Crataegus monogyna</td>
<td>223</td>
<td>79</td>
<td>1</td>
<td></td>
<td>5**</td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Quercus robur</td>
<td>288</td>
<td>79</td>
<td>1</td>
<td></td>
<td>5**</td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Fraxinus excelsior</td>
<td>312</td>
<td>79</td>
<td>0</td>
<td></td>
<td>8**</td>
<td></td>
<td></td>
<td>1</td>
</tr>
</tbody>
</table>

### Table 5.2

Results from the generalized linear mixed model analysis (GLZ) on effects of Vegetation type (V), Exclosure type (E), Soil tillage (D), plot number (ID), breakthrough event (B) and their interactions on sapling survival of the different woody species after 1 and 2 years.

<table>
<thead>
<tr>
<th>Species</th>
<th>Res. Dev.</th>
<th>Res.DF V</th>
<th>E</th>
<th>D</th>
<th>V×E</th>
<th>E×D</th>
<th>V×E×D</th>
<th>ID (V)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sambucus nigra</td>
<td>133</td>
<td>79</td>
<td>2</td>
<td>4</td>
<td>1</td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Salix alba</td>
<td>303</td>
<td>79</td>
<td>1</td>
<td>4</td>
<td>1</td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Rosa canina</td>
<td>406</td>
<td>79</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Crataegus monogyna</td>
<td>444</td>
<td>79</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Quercus robur</td>
<td>271</td>
<td>79</td>
<td>2</td>
<td>3</td>
<td>1</td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Fraxinus excelsior</td>
<td>174</td>
<td>79</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td></td>
<td></td>
<td>1</td>
</tr>
</tbody>
</table>
Table 5.3 Mean sapling height ± SE (cm) year 1 and year 2 for the five woody species. Darker grey indicates a larger height.

<table>
<thead>
<tr>
<th>Vegetation:</th>
<th>Lawn</th>
<th>Rough</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil tillage:</td>
<td>Partial</td>
<td>Full</td>
</tr>
<tr>
<td>Salix alba</td>
<td>43 ± 4</td>
<td>46 ± 4</td>
</tr>
<tr>
<td>Rosa canina</td>
<td>29 ± 3</td>
<td>57 ± 5</td>
</tr>
<tr>
<td>Crataegus monogyna</td>
<td>34 ± 2</td>
<td>51 ± 3</td>
</tr>
<tr>
<td>Quercus robur</td>
<td>23 ± 2</td>
<td>32 ± 3</td>
</tr>
<tr>
<td>Fraxinus excelsior</td>
<td>20 ± 3</td>
<td>30 ± 2</td>
</tr>
<tr>
<td>Mean:</td>
<td>38</td>
<td>59</td>
</tr>
</tbody>
</table>

Table 5.4 Results of ANOVA tests on effects of Vegetation type (V), Exclosure type (E), Soil tillage (D), plot number (ID), and their interactions on sapling height of the different woody species after 1 and 2 years. Indicated are the F values, with darker grey indicating higher values. * P < 0.005, ** P < 0.01, *** P < 0.001.

<table>
<thead>
<tr>
<th>Vegetation:</th>
<th>Lawn</th>
<th>Rough</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil tillage:</td>
<td>Partial</td>
<td>Full</td>
</tr>
<tr>
<td>Salix alba</td>
<td>141 ± 20</td>
<td>175 ± 14</td>
</tr>
<tr>
<td>Rosa canina</td>
<td>71 ± 6</td>
<td>107 ± 8</td>
</tr>
<tr>
<td>Crataegus monogyna</td>
<td>70 ± 4</td>
<td>91 ± 5</td>
</tr>
<tr>
<td>Quercus robur</td>
<td>40 ± 5</td>
<td>60 ± 5</td>
</tr>
<tr>
<td>Fraxinus excelsior</td>
<td>50 ± 9</td>
<td>74 ± 11</td>
</tr>
<tr>
<td>Mean:</td>
<td>88</td>
<td>108</td>
</tr>
</tbody>
</table>

Table 5.5 Soil penetration depths in mm (means ± SE) in lawn and rough vegetation, with and without Soil tillage, and in the three exclosure types (control, partial and full exclosure), 1 and 2 years after initiation of the experiment.
Herbivore-mediated structural diversity of vegetation

3 cm in both Lawn and Rough in disturbed and undisturbed soil). Inside the exclosures vegetation was also lowered (26 ± 18 cm and 38 ± 24 cm, Lawn and Rough respectively), because during winter vegetation fell over. In tillaged soil the vegetation remained taller (54 ± 26 cm and 51 ± 38 cm, Lawn and Rough respectively). During the summer of 2011 vegetation reached similar levels as the summer of 2010.

At the beginning of our experiment Lawn plots were dominated by *Lolium perrenne* (26%), *Plantago major* (20%) and *Poa trivialis* (15%). After one year, species dominance had not changed outside the exclosures, but had changed in the full exclosures; *Dactylis glomerata* (24%), *Carduus crispus* (13%) and *Lolium perrenne* (8%) dominated. Rough was initially dominated by *Poa trivialis* (53%), *Carduus crispus* (19%) and *Stellaria media* (7%) and this did not change after one year in the control but had changed in the exclosure; *Phragmites australis* (19%), *Urtica dioica* (19%) and *Stellaria media* (11%) became the dominant species. In disturbed Lawn outside the exclosure at year 1 *Lolium perrenne* (21%), *Polygonum aviculare* (20%) and *Sisymbrium officinale* (4%) dominated. In Rough the same species dominated: *Lolium perrenne* (22%), *Polygonum aviculare* (9%) and *Sisymbrium officinale* (6%). In the full exclosure in disturbed Lawn *Carduus crispus* (57%), *Dactylis glomerata* (8%) and *Urtica dioica* (6%) dominated, while in Rough *Carduus crispus* (60%), *Urtica dioica* (13%) and *Cerastium arvense* (8%) dominated. There were no strong differences in vegetation composition between the full and partial exclosure.

Table 5.6 Results of ANOVA tests on the effects of Vegetation type (V), Soil tillage (D), Exclosure type (E), plot number (ID), and their interactions on penetration depth of the soil (soil compatibility) for year 1 and 2. * P < 0.005, ** P < 0.01, *** P < 0.001, n.s. = non-significant

<table>
<thead>
<tr>
<th></th>
<th>Year 1</th>
<th></th>
<th>Year 2</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DF</td>
<td>MS</td>
<td>F</td>
<td>MS</td>
</tr>
<tr>
<td>Vegetation</td>
<td>1</td>
<td>922</td>
<td>4 *</td>
<td>3910</td>
</tr>
<tr>
<td>Soil tillage</td>
<td>1</td>
<td>12211</td>
<td>56 ***</td>
<td>65623</td>
</tr>
<tr>
<td>Exclosure</td>
<td>2</td>
<td>11818</td>
<td>55 ***</td>
<td>1277</td>
</tr>
<tr>
<td>ID(V)</td>
<td>2</td>
<td>281</td>
<td>1 n.s.</td>
<td>512</td>
</tr>
<tr>
<td>V × E</td>
<td>2</td>
<td>283</td>
<td>1 n.s.</td>
<td>983</td>
</tr>
<tr>
<td>E × D</td>
<td>2</td>
<td>2737</td>
<td>13 ***</td>
<td>143</td>
</tr>
<tr>
<td>V × D</td>
<td>1</td>
<td>2605</td>
<td>12 **</td>
<td>148</td>
</tr>
<tr>
<td>V × E × D</td>
<td>2</td>
<td>1130</td>
<td>5 **</td>
<td>122</td>
</tr>
<tr>
<td>Residuals</td>
<td>286</td>
<td>216</td>
<td></td>
<td>216</td>
</tr>
</tbody>
</table>

Outside the exclosures, penetration depth (reflecting degree of soil compaction) was not different between Lawn and Rough or between disturbed and undisturbed soils in year 1 and 2 (Table 5.5). However, penetration depth differed significantly and considerably inside and outside exclosures, and between the partial and full exclosures (Table 5.6). Inside the exclosures at year 1, tillaged soil was much more compact than undisturbed soil, particularly in Lawn, but these differences were less pronounced at year 2 (Table 5.5). In addition we found that inside the exclosure soil oxygenation/aeration was higher (208 mV ± 52 inside full exclosure vs. 51 mV ± 107 in the control) (F (1,10) =12, P < 0.01). Hence, there is a strong indication that soils in the exclosures (both full and partial) are less compacted and more oxygenated than in the grazed controls, especially where soil is disturbed.
5.4 Discussion

We studied woody sapling survival in a novel ecosystem on fertile clay soils where an assemblage of three large herbivore species are bottom-up regulated, resulting in very high animal abundances. We tested how tree sapling survival of different functional groups (two pioneers, two defended shrubs, two forest species) was affected by accessibility, surrounding vegetation type (either tall roughs or short lawns) and soil-disturbance (undisturbed and tillaged soil, mimicking wild boar). Firstly, we found that the high large herbivore density at the time of the study was significantly limiting tree sapling survival outside the exclosures; none of the > 2000 saplings survived outside the exclosures after two years. Secondly, we found strong effects of initial vegetation type in both the full and partial exclosure, with a higher survival in Lawn than in Rough. Because lawns are formed under high grazing intensity, the higher sapling survival in Lawn may indicate an indirect positive effect of large herbivores on tree recruitment, but only when periods of high herbivore densities are followed by periods of low densities - or absence - of large herbivores. In such situations, establishing tree seedlings may experience less light competition in previously heavily grazed areas. Thirdly, we found that sapling survival in the partial exclosure was almost as high as in the full exclosure, despite some visiting red deer in the former. This suggests that landscape structures that similarly reduce but not prevent the accessibility to large herbivores, such as woody debris, shrub tickets or water barriers may play an important role for tree recruitment in such herbivore-dominated temperate ecosystems. Lastly, we found a temporal effect of Soil tillage for sapling survival that was species dependent; especially pioneer species seemed to benefit from Soil tillage, which may point at a positive potential role for wild boar in facilitating tree recruitment in this area, once introduced.

The lack of any saplings surviving outside the exclosures is likely due to the very high herbivore abundances in combination with very uniform initial conditions and the young age of the ecosystem. For comparison, a study of Van Uytvanck et al. (2008) on former agricultural lands in Flanders (ca. 250 km from OVP) with human top-down regulated herbivores (metabolic biomass ca. 58 kg ha\(^{-1}\) compared to 135 kg ha\(^{-1}\) in OVP) found much higher sapling survival after two years of grazing (between 20-60% survival for \textit{Quercus} and \textit{Fraxinus}). They further found that sapling survival was higher in tall roughs (dominated by \textit{Carex} sp. and \textit{Juncus} sp.) than in lawns, suggesting facilitative effects of the former against herbivore grazing. We expected similar protective effects of roughs for sapling survival in our study, but we did not find any difference between tall roughs and lawns as no saplings survived. Current herbivore densities in combination with the uniform starting conditions in the OVP are probably too high for saplings to profit from potential facilitative effects from surrounding vegetation, or to get feedbacks started where unpalatable vegetation reduces herbivory, leading to further decline of palatability, e.g. through facilitation of thorny species. These findings are in line with Smit et al. (2007) who show that under high grazing pressure facilitative effects of nurse plants for associated species decline as these nurse plants themselves get damaged at high grazing pressure.

The limiting effects of herbivores are likely mainly due to browsing and trampling, as most saplings outside the exclosure were fully browsed or trampled after 50 days, while those that were still present (6%) were all severely damaged. However, we cannot exclude that there are additional indirect negative effects of herbivore trampling via compaction of the soil. Already after 7 months, the soil in the exclosures was less dense and more oxygen-
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ated than in the grazed controls, indicating that large herbivores also have strong effects on soil properties, but that these effects are also quickly reversible by soil biota, most likely earthworms in this case, which were observed in high densities in the exclosures. Several studies have shown that low oxygenation and high soil density negatively affects tree recruitment (Bezkorowajnyj, Gordon and McBride 1993; Kozlowski 1999). This indicates that uprooting in the grazing lawns (e.g. for remaining Phragmites rhizomes by wild boar) may have indirect positive effects on tree recruitment in ecosystems that are trampled on by large herbivores (Barrios-Garcia and Ballari 2012), but it appears that such potential positive effects would currently be overruled by the direct negative effects of high density of large herbivores in the OVP.

Overall sapling survival was significantly higher inside the exclosures (partial and full) than outside exclosures. In the exclosures we found a strong effect of vegetation type, with a higher survival in Lawn than in Rough. We mainly attribute this effect to differences in light conditions in Rough versus Lawn. Within a few months the vegetation in Rough was already twice as tall as compared to Lawn, and light intensity was significantly lower in rouges than in Lawn. Light competition with herbaceous plants has strong effects on tree sapling survival (Vandenberghe 2006; Vandenberghe et al. 2008), especially in fertile ecosystems when large herbivores are temporary excluded (Smit and Olff 1999). Because lawns are often the result of intensive grazing (Augustine and McNaughton 1998; Díaz et al. 2007), we argue that the high herbivore density in the OVP has an indirect positive effect on tree sapling survival (window of opportunity), but only when it is followed by a period of low herbivore density or temporal absence, as has been proposed by other studies (Bakker et al 2004, Smit et al. 2010).

Sapling height differed between the full and partial exclosure, where all species were shorter in the partial exclosure in both years. These differences are most likely attributable to herbivore visits to the partial exclosures, particularly by red deer. We frequently observed red deer pellets in these partial exclosures, and most saplings showed browsing damage by red deer, especially in Lawn. Also deer tracks were regularly seen in the snow during suitable winter conditions. Clear indications of visits by Heck cattle and Konik horses (dung, browsing damage) in the partial exclosures were not detected. These results indicate that our partial exclosures effectively realized low accessibility to the plots, similar to natural physical structures such as due to coarse woody debris, rocky outcrops and crevices, that would (temporary) reduce access to saplings, or only allow particular species to enter (at low densities, in this case red deer). The importance of these structures as refuges for grazing sensitive plant species, such as tree saplings, has been shown for several ecosystems (Milchunas and Noy-Meir 2002). Here, we found evidence that such mimicked refuges (more difficult to access places) may be very important in grassland ecosystems with high densities of large herbivores. Interestingly, the well-defended Crataegus performed better in the partial exclosure than in the full exclosure. This is an indication that this spiny species benefited from the occasional red deer visits, possibly because of the removal of the surrounding vegetation, while browsing only a little on Crataegus due to its defences. The lack of any herbivory in the full exclosures probably increased the competition for light of other plant species and the saplings.

The impact of soil tillage on sapling performance was only temporal and effective for a few woody species. Therefore, this treatment mostly likely resulted in an initial nutri-
Herbivore-mediated structural diversity of vegetation

ent pulse, causing faster initial growth, but without lasting effects. After 50 days we found
in both the full and partial exclosure a positive effect of soil tillage for all species. After
one and two years this positive effect only remained for the two pioneer species Sambucus
and Salix. For Crataegus and Quercus there was actually a negative effect of disturbance
in Lawn, but a positive effect in Rough. This trend was also present for Rosa and Fraxinus,
but not significant. It is possible that this is because Soil tillage in addition to nutrients
reduces soil anoxia as well as light competition (the vegetation composition was initially
quite different). Moreover, the effect on light competition changed from positive to nega-
tive over time in this treatment; in the first months there is no surrounding vegetation due
to tillage, but after four months the vegetation was already taller in the tillaged soils than
in the undisturbed soils probably due to the nutrient flux that resulted from the treatment.
The (initially fast growing) pioneer species Sambucus and Salix benefitted most from the
initially improved soil conditions, (see also Finegan 1984) in contrast to the other woody
species. This implies that, if wild boar were introduced into the OVP, rooting by wild boar
will particularly favor these or other pioneer species, especially in combination with local
grazing refuges.

In this research we focused on the sapling phase as this is often the limiting phase
for tree recruitment in grazed ecosystems (Rao et al. 2003; Bakker et al. 2004; Smit, Den
Ouden, and Müller-Schärer 2006; Moe et al. 2009). However, seed dispersal and germina-
tion may also be limiting for successful tree recruitment (Clark et al. 1999). In the OVP
we did find natural seedlings, especially under roost trees used by birds (such as starlings).
Under one adult Crataegus more than 200 Crataegus seedlings were found and several
Quercus seedlings (unpublished data), indicating that seed dispersal does take place and
that germination is possible for at least these two species. Additional experiments with
cached acorns (Quercus seeds) revealed that also seed removal by rodents (mostly wood
mouse Apodemus sylvatica) may play a significant role for recruitment in the OVP (unpub-
lished data). On the other hand, several studies show that seed removal by rodents not nec-
essarily leads to seed mortality and may in fact be an important mechanism to redistribute
seeds to refuges, when available (Smit and Verwijmeren 2010).

It should be noted that while the large herbivores in the drained part of OVP most-
ly prevented the establishment of small-scale vegetation heterogeneity, they are the driver
of major large-scale vegetation heterogeneity in the OVP area. The main vegetation types
of short grazing lawns, tall roughs and the reedbeds clearly result from the differential
habitat preferences by the grazers, in interaction with heterogeneity in hydrology and soil
conditions. The current high densities suppress small-scale heterogeneity in vegetation
structure, but promote landscape-level heterogeneity in vegetation structure, as without
them the whole are would likely be covered with tall reedbeds with scattered pioneer trees
(Willows), as small nearby ungrazed areas show.

5.4.1 Synthesis and applications
Our results suggest that the current high herbivore densities are limiting tree recruitment in
the drained part of the ecosystem, which has impact on the small-scale structural diversity
of the vegetation and characteristics of the landscape. With the densities present during
the study, in combination with the uniform starting conditions, the drained part of the
landscape of the OVP is likely to continue to keep its current open vegetation structure for
a while. However, our results also show the potential of simple one-time interferences that
Herbivore-mediated structural diversity of vegetation may enhance possibilities for tree recruitment, while maintaining the current hands-off management on the large herbivore assemblage. If the stimulation of local tree recruitment would be seen as very important in the short run (next to 5-10 years, rather than wait for it to form spontaneously in the long run), then one possibility could be to establish grazing refuges, e.g. via deposition of large woody debris. Another measure would be to stimulate between-year fluctuations in local herbivores densities. This could be done by: i) connecting adjacent woodlands (Hollandse Hout) to the conservation area, which would significantly draw away the grazers from the grassland areas, especially during winter and early spring when they are food limited or in very warm summers when they are looking for shade. Also, with relatively simple measures (digging a limited set of small canals), some parts of the area could be made inaccessible for the herbivores during wet years, while allowing access during drier years, potentially creating local windows of opportunity for tree regeneration. Finally, harsh long upcoming winters in combination with the current high density and scarce food stocks at the onset of winter may cause population crashes that may result in tree recruitment events. Due to such fluctuations, large herbivores will promote short lawn vegetation during periods of high density, that have a positive effect on tree recruitment at subsequent periods of low herbivore density, positively affecting the development of structural diverse landscapes. However, such interferences should be carefully balanced against maintaining the benefits of this unique setting where unaffected populations of multiple large herbivores can free interact, and we can still learn a lot form the resulting natural processes. We still know very little about the resulting community dynamics and its consequences for long-term ecosystem development under the conditions now prevailing in the OVP.

Our findings are not only relevant for the OVP, but are also applicable to transform many novel ecosystems into ecological and or social-economical valuable ecosystems. This applies particularly to ecosystems that are designated to support high densities of large herbivores, such as game reserves, rangelands or wild parks. Future novel ecosystems with a nature designation can be more carefully optimized with respect to initial conditions of landscape heterogeneity and herbivore density regimes to maximize returns with respect to biodiversity values, development of natural processes and ecosystem functioning. Our study shows an important point for novel ecosystems where large grazers are introduced and develop unregulated populations: small-scale vegetation heterogeneity driven by biotic processes (grass-shrub-tree dynamics) does not arise easily within the first decades when starting from a uniform state. Patience is likely required here: an ecosystem of 40 years is quite in its infancy. Nevertheless our results suggest that more attention should be given to the initial conditions of such novel ecosystems. Creation of more small-scale initial abiotic heterogeneity (in hydrology and topography in this case) is likely for the subsequent processes of biotically created small-scale heterogeneity through herbivore-vegetation interactions.

Acknowledgements

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