

# Large herbivores as a driving force of woodland-grassland cycles

The mutual interactions between the population dynamics of large herbivores and vegetation development in a eutrophic wetland



Perry Cornelissen

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This research was conducted under the auspices of the graduate school for Production Ecology and Resource Conservation (PE&RC).

# Large herbivores as a driving force of woodland-grassland cycles

The mutual interactions between the population dynamics of large herbivores and vegetation development in a eutrophic wetland

**Perry Cornelissen**

## **Thesis**

submitted in fulfilment of the requirements for the degree of doctor  
at Wageningen University

by the authority of the Rector Magnificus

Prof. Dr. A.P.J. Mol

in the presence of the

Thesis Committee appointed by the Academic board

to be defended in public

on Tuesday 10 January 2017

at 4 p.m. in the Aula

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Large herbivores as a driving force of woodland-grassland cycles: The mutual interactions between the population dynamics of large herbivores and vegetation development in a eutrophic wetland  
151 pages.

PhD thesis, Wageningen University, Wageningen, NL (2017)  
With references, with summary in English

ISBN 978-94-6343-015-9  
DOI 10.18174/396698

To Floortje and Wouter

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# CHAPTER 1

## GENERAL INTRODUCTION

### Scope of this study

Conservation and restoration of biodiversity are major objectives for managers of nature reserves and in many cases large herbivores are considered to be 'keystone' species to achieve these goals (e.g. Wallis De Vries et al. 1998; Zabel and Anthony 2003; Danell et al. 2006; Rotherham 2013). Large herbivores are major drivers of changes in the structure and functioning of terrestrial ecosystems, because they modify nutrient cycles, soil properties, net primary production, patterns in vegetation structure and composition, and fire regimes (Gordon 2006). Through their impact on plant community structure (openness and height) (e.g. Bakker 1998; Hester et al. 2006; Thompson Hobbs 2006; Smit and Putman 2011), large herbivores affect most other plant and animal species in these communities (e.g. Root 1973; Cody 1975; Olff and Ritchie 1998; Van Wieren 1998; Olff et al. 1999, Adler et al. 2001; Suominen and Danell 2006).

To restore and maintain species diversity, controlled grazing with large wild and domestic herbivores at low stocking rates has developed towards a major strategy for conservation management in Europe (e.g. Wells 1965; Thalen 1984; Gordon et al. 1990; Bakker and Londo 1998; Hodder and Bullock 2009). In this context, traditional livestock farming landscapes (e.g. man-made wood pastures, heathland, chalk grasslands) serve as a reference (Pott and Hüppe 1991; Signal et al. 1994; Piek 1998). The strategy of controlled grazing has been challenged by a more 'natural' grazing strategy, which is inspired by present natural or near-natural grazing systems in Africa and North America, but also by grazed ecosystems in the remote past, which were present during different Pleistocene and Holocene periods (e.g. Van de Veen 1975; Vera 1997; Soulé and Noss 1998; Donlan et al. 2006). Often, such strategies are part of the so-called 'Rewilding' concept (e.g. Hodder and Bullock 2009; Pereira and Navarro 2015), which suggests the (re-)introduction of large, wild herbivores and carnivores, or domestic cattle and horses, as substitutes for their extinct wild ancestors, in areas where these species have gone extinct. Ideally, such (re-)introduced large herbivores should not be managed as livestock but as wild, self-regulating herbivores without population control. They should be viewed as an integral part of new wilderness ecosystems in which food, predators and parasites affect population dynamics, habitat use and evolutionary development of the large herbivores. During the past decade, this strategy and its consequences for landscape development has received much attention, especially concerning the effects of large herbivores on the landscape (e.g. Birks 2005; Mitchell 2005; Svenning 2002; Vera et al. 2006; Hodder and Bullock 2009).

The *wood-pasture theory* of Vera (1997) assumes that in north-western Europe and in the absence of human influence, large herbivores are the primary factor responsible for the development of park-like landscapes with natural regeneration of shrubs and trees in the grazed grasslands. This theory suggests that high numbers of wild herbivores may assist the degeneration of woodlands and their transition to grassland by browsing and bark stripping which cause mortality of shrubs and trees (Crawley 1997; Gill 2006), and maintain short grazed grasslands which therefore provide opportunities for the re-establishment of shrubs

and trees in these natural 'pastures'. These transitions require not only the mortality of trees and shrubs but also their regeneration. Many doubt whether spontaneous grazing is sufficient to create gaps in forests, stop wood encroachment and create and maintain open landscapes. Pott (1998) argues that in north-western Europe, human intervention is needed to create openness and to allow the characteristic high grazing pressure required to maintain the wood-pasture-mosaic landscape. Svenning (2002) concluded from his palaeoecological studies that closed forests predominated in the pre-agricultural Holocene, but that these forests included localized longer-lasting openings (e.g. around ponds and probably also grassy glades in the uplands). For the floodplains he concluded that the dominant vegetation would be a mixture of open marshes, meadows, dry grassland, scrub and forest. Svenning assumes that large herbivores and fire have been the most likely key factors responsible for the replacement of woodlands by grassland vegetation in north-western Europe. Mitchell (2005) agrees that large herbivores (wild and domestic) can have significant impacts on contemporary forest structure and composition, but believes that fires and wind-throw were the principle drivers that created gaps. The large herbivores were assumed to maintain these gaps, but they were not believed to be able to create them.

Large herbivores can be responsible for creating openings, if they are able to damage shrubs and trees causing mortality. However, woody plants are not defenceless against the attacks of large herbivores. They may deter large herbivores chemically with secondary metabolites, which may be toxic or reduce digestibility (Palo and Robbins 1991), or physically by producing defence structures such as thorns, spines, hairs or thick cuticles (Hester et al. 2006). Plants may also physically avoid large herbivores through their location: for example, by growing near unpalatable plants – a strategy known as *associational resistance* (e.g. Hester et al. 2006; Barbosa et al. 2009).

The establishment of trees and shrubs in the created grasslands, as suggested by the *wood-pasture theory*, requires the arrival and survival of their seeds in safe sites, germination, survival and the development towards reproducing plants. Large herbivores may accelerate these processes by creating gaps for germination by trampling, or by reducing competition for light by grazing and browsing of tall grasses, herbs or shrubs (e.g. Crawley 1997; Gill 2006; Hester et al. 2006). Vera (1997) and Olff et al. (1999) mention that a prerequisite for the (re-)establishment of woody species in the created grasslands is a temporary reduction of the large herbivore populations.

Whether self-regulating large herbivores do indeed play the key role in wood-pasture cycles, as hypothesised by Vera (1997), is still heavily debated and remains an unanswered question (e.g. Svenning 2002; Bradshaw et al. 2003; Kirby 2004; Birks 2005; Hodder and Bullock 2009; Szabo 2009; Whitehouse and Smith 2010; Sandom et al. 2014). It is not the question whether large herbivores do affect the development of shrubs and trees, as many studies have shown such impacts (e.g. Crawley 1997; Gill 2006; Hester et al. 2006), but rather whether these impacts are sufficiently strong enough to convert closed forest into open grassland when the populations of grazers are left entirely unmanaged (Hodder and Bullock 2009).

In the 'Rewilding' concept with the goal of restoring natural ecosystem processes and reducing human control of landscapes (see Pereira and Navarro 2015), large herbivores play a key-role in the large scale dynamics of landscapes. Allowing unmanaged population dynamics of herbivores aims at self-sustaining ecosystems (i.e. ecosystems able to maintain their structure, function and resilience over time; Cerqueira et al. 2015) which provide ample

opportunities for the former, native biodiversity. Such developments would stimulate ecotourism and the regional economy in parts of Europe where the countryside has been abandoned by a multitude of people. In such 'rewilded' landscapes the large herbivores are assumed to be free ranging (in unfenced areas), while their habitat use and population dynamics are determined by other natural processes such as competition, facilitation, predation, vegetation succession, flooding, changing weather conditions, etc. Ideally, wild large herbivores and also carnivores colonize these areas spontaneously through migration or dispersion. However, if areas are isolated, locally extinct wild large herbivores are often reintroduced. Within the framework of the European Rewilding concept, horses and cattle are often introduced as relatives of recently extinct large herbivores such as wild horses and Aurochs (Pereira and Navarro 2015). The 'Rewilding' concept has only just started to be implemented (e.g. Helmer et al. 2015), so that much can be learned about the mutual interactions between the population dynamics of the large herbivores and vegetation development. Another crucial question is whether the concept of rewilding can be used as an effective and feasible tool in the conservation of biodiversity in the fragmented European landscape. Is this concept also applicable to smaller isolated and therefore less heterogeneous areas? Do such areas provide sufficient opportunities for viable populations of different large herbivore and carnivore species? Starting from the metapopulation theory (Hanski and Gilpin 1997), many studies have shown the effect of small areas on local extinction of species (see Lindenmayer and Fischer 2006). Sufficient area and connectivity of isolated habitats, ecosystems or landscapes provide the opportunities for viable populations of many plant and animal species (Lindenmayer and Fischer 2006). But the question remains if this will lead to a self-sustaining ecosystem as suggest in the 'Rewilding concept' (Pereira and Navarro 2015; Cerqueira et al. 2015).

The Oostvaardersplassen, a man-made wetland nature reserve in the Netherlands, is often referred to as one of the first areas where the rewilding concept has been applied to (e.g. Lorimer and Driessen 2013; Jørgensen 2015). In this eutrophic wetland, vegetation has developed spontaneously in large parts of the area since 1968 (reclamation of the polder Zuidelijk Flevoland), while the area was grazed by cattle, horses and red deer, introduced in 1983, 1984 and 1992 respectively. The aim of these introductions was to create large scale open grasslands for wetland birds. The population numbers of the large herbivores are not controlled, large predators are not present and the area is fenced. The population sizes of the large herbivore species are bottom-up regulated by plant biomass production and the conditions during the winters. Interactions between different herbivore species, both facilitation and competition among large herbivores and between large and small herbivores (geese), have crucial impacts on large herbivore population dynamics. This setting provides an ideal opportunity to study plant-herbivore interactions and their impacts on landscape development.

### **Aim of this study**

The aim of the present study is to gain more insight into the mutual interactions between the population dynamics of large herbivores and vegetation development in eutrophic wetlands. For this purpose we studied:

- The impacts of free ranging large herbivores on vegetation development, and especially on the wood-pasture cycle, in an isolated, fenced eutrophic wetland;
- Habitat use and population dynamics of free ranging large herbivores, when they are only limited by primary biomass production;
- The mutual interactions between long-term vegetation development and herbivore population dynamics in an isolated, fenced eutrophic wetland

The study was mainly conducted at the Oostvaardersplassen nature reserve in the Netherlands (Chapters 2, 3, 5, 6, 7; Fig 1). As no thorny shrubs were present at the Oostvaardersplassen, the effect of large herbivores on thorny shrubs (Ch. 4) was conducted at the 'Afferdense en Deestse waard', a floodplain area along the river Waal in the Netherlands. Chapter 5 is based on data from the Oostvaardersplassen and Zoutkamperplaat, a polder in the Lauwersmeer in the Netherlands.



Fig. 1. Map of the Netherlands and locations of the study areas

### Thesis outline

This thesis is divided into three parts. Part 1 (Chapters 2, 3 and 4) focuses on the effects of free ranging large herbivores on the development of shrubs and trees and different vegetation types such as grassland, tall herbs and reed. **Chapter 2** describes the effects of a bottom-up regulated population of cattle, horses and red deer on the development of woody vegetation in the Oostvaardersplassen. Using aerial photographs from 1980 to 2011, we

analysed the development of shrubs and trees before and after introduction of the large herbivores in 1983, at grazed and ungrazed sites and at sites dominated with reed or tall herb vegetation. **Chapter 3** describes how large herbivores have changed the vegetation of the Oostvaardersplassen from woodland to grassland. This will be accomplished by recording the 1996, 2002 and 2012 vegetation cover, density of woody species and intensity of browsing and bark loss of woody species in grazed and ungrazed sites. **Chapter 4** describes an enclosure experiment in the Afferdense and Deestse Waard, a floodplain along the river Waal. In many European countries, measures (e.g. excavating) have been taken in the floodplains to enhance safety against flooding and for the rehabilitation of the endangered natural river habitats such as floodplain forests. However, wood encroachment decreases the flow capacity of the floodplain. In many floodplains, large herbivores are used to control vegetation development. We investigated the effects of excavating and grazing by cattle and horses on wood encroachment throughout a period of twelve years (1996-2007). The thorny shrub *Crataegus monogyna* was of particular importance in this study as it provides the highest hydraulic resistance, and as it plays a key role in wood-pasture cycles.

Part 2 (Chapters 5 and 6) deals with the factors that determine habitat use and population dynamics of large herbivores such as food availability and competition. **Chapter 5** examines the effect of animal density and sward height on diet composition, diet quality and body condition of cattle and horses at the Oostvaardersplassen and the Zoutkamperplaat. **Chapter 6** explores the role of food limitation and interspecific competition in regulating the dynamics of large herbivores and how this affects vegetation development. The large herbivore assemblage of the Oostvaardersplassen consists of cattle, horses and red deer and the area is visited by tens of thousands of geese.

Part 3 explores in **Chapter 7** the long-term (110 years) effects of weather and small herbivores (geese) on the population dynamics of large herbivores and the establishment of woody species. A simulation model was used to study if variability in weather conditions would be of sufficient magnitude to maintain long-term coexistence of large herbivores, and to provide windows of opportunity for the establishment of thorny shrubs in grazed grasslands and create vegetation heterogeneity.

**Chapter 8** presents the synthesis of the results and discusses management implications and future perspectives.

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## CHAPTER 2

### EFFECTS OF LARGE HERBIVORES ON WOOD PASTURE DYNAMICS IN A EUROPEAN WETLAND SYSTEM

Perry Cornelissen, Jan Bokdam, Karlè Sýkora, Frank Berendse

*Basic and Applied Ecology* 2014, 15, 396-406

#### Abstract

Whether self-regulating large herbivores play a key role in the development of wood-pasture landscapes remains a crucial unanswered question for both ecological theory and nature conservation. We describe and analyse how a 'partly self-regulating' population of cattle, horses and red deer affected the development of the woody vegetation in the Oostvaardersplassen nature reserve (Netherlands). Using aerial photographs from 1980 to 2011, we analysed the development of shrubs and trees. Before the large herbivores were introduced in the Oostvaardersplassen in 1983, the woody vegetation increased and vegetation type significantly affected the number of establishments. Cover of woody species increased further from 1983 to 1996, not only by canopy expansion but also by new establishments. After 1996, cover of the woody vegetation decreased from 30% to <1% in 2011 and no new establishments were seen on the photographs. Survival of *Sambucus nigra* and *Salix* spp. increased with increasing distance to grassland, which is the preferred foraging habitat of the herbivores. These results support the hypothesis of Associational Palatability. In addition, our results show that the relative decline in cover of *Sambucus nigra* and *Salix* spp. over a certain period was negatively correlated with the cover of *Sambucus nigra* in the beginning of this period, presenting some evidence for the Associational Resistance and Aggregational Resistance hypothesis. Our research shows aspects necessary for the woodland-grassland cycle, such as a strong decline of woody vegetation at high numbers of large herbivores and regeneration of shrubs and trees at low densities. Thorny shrubs, which are important for the cycle, have not yet established in the grasslands. It seems that a temporary decline in herbivore numbers is necessary to create a window of opportunity for the establishment of these woody species.

#### Introduction

Controlled grazing by large wild and domestic ungulates has become a major strategy for conservation management in Europe (e.g. Wells 1965; Thalen 1984; Gordon et al. 1990; WallisDeVries et al. 1998). Traditional livestock farming landscapes, e.g. man-made wood-pasture, often serve as reference (Pott and Hüppe 1991; Bignal et al. 1994; WallisDeVries et al. 1998). This approach has been challenged by Van de Veen (1975) and Vera (1997). Inspired by natural grazing systems, these authors have suggested reintroducing wild large herbivores and carnivores, and also domestic cattle and horses in Northwest Europe, as substitutes for their wild, extinct ancestors. Ideally, reintroduced ungulates should be managed not as livestock but as wild self-regulating herbivores, and considered to be an integral part of ecosystems. The Wood-Pasture theory of Vera (1997) attributes a key role to

large wild herbivores under natural conditions. High numbers of wild herbivores may assist the transition of woodland to grassland by browsing and bark stripping which causes mortality of shrubs and trees (Crawley 1997; Gill 2006), and maintain short grazed grasslands and therefore provide opportunities for the re-establishment of shrubs and trees in these natural 'pastures'.

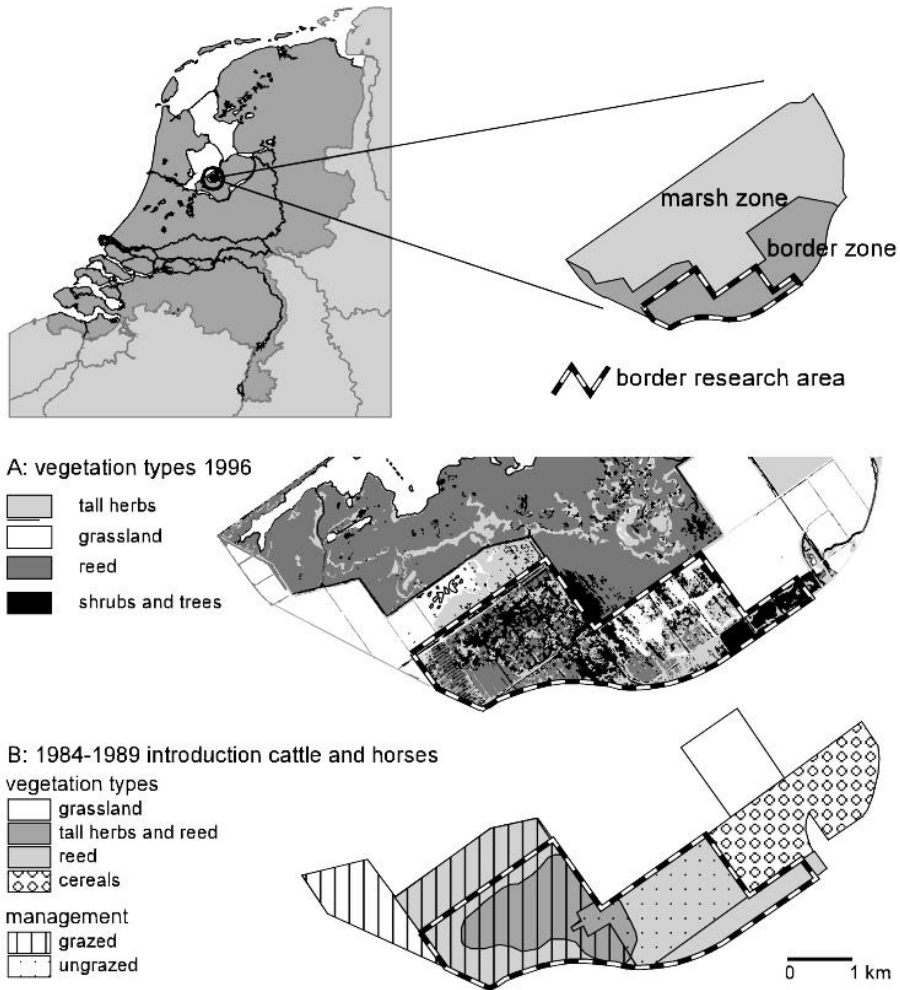
Woody plants are not defenceless victims of large herbivores. They may deter large herbivores chemically with secondary metabolites, which may be toxic or reduce digestibility (Palo and Robbins 1991). Plants may also physically avoid large herbivores through their location: for example, by growing near unpalatable plants – a strategy known as Associational Resistance (see e.g. Hester et al. 2006; Barbosa et al. 2009). It is also possible that the risk of a plant being eaten is enhanced when an individual of this plant is surrounded by palatable species – also known as Associational Palatability (Olf et al. 1999). A hypothesis logically derived from Associational Resistance and Associational Palatability is that the aggregation of individuals of an unpalatable plant will decrease herbivory losses of this plant in a palatable neighbourhood (Aggregational Resistance hypothesis).

The establishment of trees and shrubs in the natural 'pastures' requires the arrival and survival of seeds, their germination, seedling and sapling survival and growth. Large herbivores may accelerate these processes by trampling (creating gaps for germination) or by grazing or browsing of tall grasses, herbs, shrubs or trees (reduction of competition for light) (see e.g. Crawley 1997; Gill, 2006; Hester et al. 2006). Vera (1997) and Olf et al. (1999) also mention that a prerequisite for the (re-)establishment of thorny shrubs in the created grasslands is a temporary reduction of the large herbivore populations. Whether self-regulating large herbivores do indeed play a key role in wood-pasture landscapes, however, remains an unanswered question (Vera 1997; Olf et al. 1999; Van Uytvanck 2009).

The Oostvaardersplassen, a wetland reserve in the Zuidelijk Flevoland polder in the Netherlands, which was reclaimed from lake IJsselmeer in 1968 (Fig. 1), provides a unique opportunity to test plant-herbivore theories. Spontaneous vegetation succession has occurred since 1968 in much of the area, while the Oostvaardersplassen has been grazed by introduced herbivores from 1983. Vegetation surveys in the late 1990s and early years of this century found that the woody vegetation was dominated by *Sambucus nigra* (Jans and Drost 1995; Cornelissen et al. 2006). *Sambucus* produces *cyanogenic glycosides* (Atkinson and Atkinson 2002) which can be toxic to or lethal in birds and mammals (Griess et al. 1998; Majak and Hale, 2001). Ungulate herbivores can counteract the effects of toxic compounds with varying success. Many ruminants can detoxify toxic compounds better than hindgut fermenters (Van Soest 1994). Vulink (2001) showed that horses, in contrast to cattle, did not eat *Sambucus*.

Field observations by the managers of the Oostvaardersplassen at the end of the 1980s, suggested that the large herbivores increased the invasion of *Sambucus nigra* and were not able to assist the development of open grasslands. In an effort to halt the spread of *Sambucus nigra*, red deer were introduced in 1992. By the end of the 1990s, it was clear that the cover of *Sambucus nigra* as well as *Salix* spp. was decreasing (Cornelissen et al. 2006) and that the decrease seemed to be faster near the grasslands preferred by the large herbivores. This effect of distance was also found by Clarke et al. (1995) and Hester and Baillie (1998), who showed that defoliation of a less preferred shrub by sheep and red deer was higher near the edge of preferred grass patches than further away. Other authors also observed that as herbivores focus their grazing on the preferred vegetation, the use of the less preferred

vegetation will be concentrated in those areas where the preferred vegetation is abundant (Oom et al. 2002).



**Fig. 1.** Location of Oostvaardersplassen, research area, sites and treatments.

The abovementioned factors play a role in the interactions between large herbivores and the woodland-grassland cycle and are subject to our research. Based on these, we hypothesised that: (1) New establishments of *Sambucus nigra* occur more frequently in extensively grazed areas than in ungrazed areas due to the positive effects of herbivores on establishment of woody species such as creating gaps by trampling; (2) Woody vegetation dominated by an unpalatable shrub can be strongly diminished by a more or less ‘partly self-regulating’ multi-species large herbivore population; (3) The relative decline of *Salix* spp. and the less palatable species *Sambucus nigra* is negatively correlated with the distance to the

palatable grasslands preferred by the large herbivores; (4) The relative decline of *Sambucus nigra* and *Salix* spp. is negatively correlated with the cover of the unpalatable shrub *Sambucus nigra*; (5) Woody species do not regenerate in grasslands under high grazing pressure.

To test these hypotheses we analysed the vegetation development using aerial photographs.

## Material and methods

### Research Area

The Oostvaardersplassen (5600 ha) is a man-made, eutrophic wetland in Zuidelijk Flevoland polder in the Netherlands, reclaimed from lake IJsselmeer in 1968 (see Vulink and Van Eerden 1998). Originally the Oostvaardersplassen was planned as an industrial and agricultural area. At the end of the 1970s, part of the area had already been prepared for agricultural use. In an area of about 750 ha (the research area, see Fig. 1), only ditches had been dug and a road provided. The original vegetation had been left to develop spontaneously (Jans & Drost, 1995). This area (Fig. 1A) was used to monitor the development of woody species.

Three habitat types can be distinguished in the research area: grasslands (*Poa trivialis* L., *Lolium perenne* L., *Trifolium repens* L.), reed vegetation (*Phragmites australis* (Cav.) Steud.) and a semi-open mosaic vegetation of reed, tall herbs (*Urtica dioica* L., *Cirsium* spp. Mill.), *Sambucus nigra* and *Salix* spp. The distinction in these types was made on the basis of subsequent vegetation maps (Jans and Drost 1995; Cornelissen et al., 2006). Most of the *Salix* spp., mainly *Salix alba* L., established on the bare soil in 1968, immediately after the water was pumped out of the polder and the surface area became dry. *Sambucus nigra* established some years later.

In the area with spontaneous vegetation succession, shrubs and trees were not evenly distributed (Fig. 1A). The cover of *Sambucus nigra* was greater at locations with a mosaic vegetation of tall herbs (e.g. *Urtica dioica*, *Cirsium* spp.) and reed (*Phragmites australis*) than in areas with a 100% reed vegetation (Jans & Drost, 1995). This dense reed vegetation had thick litter layers (up to 25 cm; personal observation by Cornelissen) which can have major impact on seedling establishment and subsequent performance (Crawley 1997). The thick litter layers were absent in the tall herb vegetation. Such differences in litter layer could have been responsible for the differences in establishment and cover of woody species between the two vegetation types.

Most of the large herbivores of the Oostvaardersplassen were introduced. Only Roe deer (*Capreolus capreolus* L.) spontaneously colonised the area in the early 1970s, but decreased strongly after 1992 and had gone after 2005. Cattle, horses and red deer were introduced into the Oostvaardersplassen: 32 Heck cattle (*Bos taurus* L.) in 1983, 18 Konik horses (*Equus caballus* L.) in 1984, and 52 red deer (*Cervus elaphus* L.) in 1992. The introduced animals were restricted to small areas during the first period after introduction to get used to the new environment. Thereafter, they were introduced to larger areas. Cattle and horses were introduced into the research area in 1984 and 1986 respectively. Between 1992 and 1996 the area grazed by cattle and horses was enlarged several times. In 1996 cattle and horses could use the entire Oostvaardersplassen. Red deer were introduced in March 1992 and were kept in a small enclosure for about 4 months. After this period, the red deer were released and could use the entire Oostvaardersplassen as well. In January 2013, 300 cattle,

1150 horses and 3200 red deer were present. Currently, individuals considered to have no chance of survival are shot at the end of winter, in order to prevent unnecessary suffering. There are no large predators in the area and the large herbivores do not get supplementary feeding. A survey in the early 1990s revealed that small mammal herbivores (rabbit or hare) were rare (Lange and Margry 1992; unpublished data).

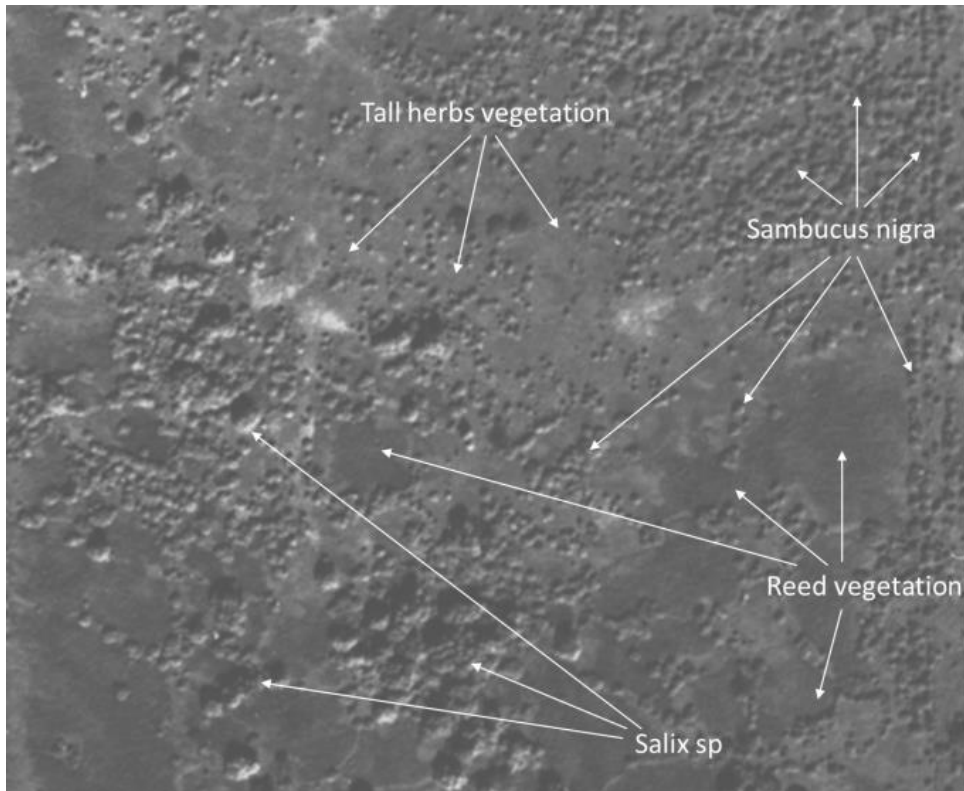
### Aerial photographs and measurements

We used near infrared aerial photographs from 8 different years over the period 1980 to 2011, to measure the development of *Sambucus nigra* and *Salix* spp. (Table 1). We digitised and geo-referenced the photographs (using Erdas Imagine 8.4 and ArcMap) to analyse the development of *Sambucus nigra* in GIS (using ArcView). For 2005, 2009 and 2011 we used existing and already digitised and geo-referenced true colour aerial photographs (obtained from the Ministry of Infrastructure and the Environment).

On the photographs, the vegetation types and *Sambucus* and *Salix* spp. were distinguished by shape, texture, colour, and shadow (indication of height) (Fig. 2). The smallest distinguishable *Sambucus nigra* shrubs have a crown diameter of about 1 m. We determined age, crown diameter and internal crown cover of *Sambucus nigra* to ascertain at what age the species has a crown diameter of about 1 m, in order to date the establishment of *Sambucus nigra* plants. For this purpose, we sampled un-browsed shrubs in reed and tall herb vegetation near the Oostvaardersplassen with similar abiotic conditions. Roe deer were present, but in low densities (pers. comm. State Forestry Service). We determined age by cutting the shrub to the ground and counting the annual rings. Internal canopy cover was estimated visually as a percentage of the area of ground occupied by the crown. At an age of 3 years, most *Sambucus nigra* shrubs had a canopy diameter of 1 m and a crown cover >50% (Fig. 3). We assumed that from this age on, *Sambucus nigra* is visible on aerial photographs. On photographs taken in 1985, for example, specimens established during 1982-1985 cannot be identified. Only new establishments from before 1982 are identifiable (Table 1).

**Table 1.** Year when aerial photograph was taken, new establishments of *Sambucus nigra* visible on photo and management during that period.

Year photo	Period of new establishments on the image	Management during new establishments
1980	1969-1977	Ungrazed
1985	1978-1982	Ungrazed
1988	1983-1985	Introduction cattle in part of the research area in 1984
1992	1986-1989	Grazed by cattle and introduction horses in part of the area in 1986
1996	1990-1993	Grazed by cattle and horses and introduction red deer in 1992
2005	1994-2002	Grazed by cattle, horses and red deer
2009	2003-2006	Grazed by cattle, horses and red deer
2011	2007-2008	Grazed by cattle, horses and red deer



**Fig. 2.** Example of an aerial photograph. For the analysis, near infrared and true colour images were used. On the black and white photograph, the vegetation types (reed, tall herbs) and *Sambucus nigra* and *Salix* spp. can be distinguished by shape, texture, and shadow (indication of height).

For *Salix* spp. we used a different method. In order to distinguish young *Salix* spp. from *Sambucus* on the aerial photographs of 1980, 1985 and 1988, we first analysed the aerial photographs from 1996. At that time all *Salix alba* and some other *Salix* spp. were full grown, as most had established in 1969 (Jans and Drost, 1995). These mature *Salix* trees and shrubs had a much larger canopy diameter than full grown *Sambucus* shrubs (10-20 m versus up to 4 m). Their shadows in summer were also longer (6-12 m versus 2-3 m). Based on the 1996 analysis we could distinguish *Salix* spp. from *Sambucus nigra* on photographs of earlier and later years.

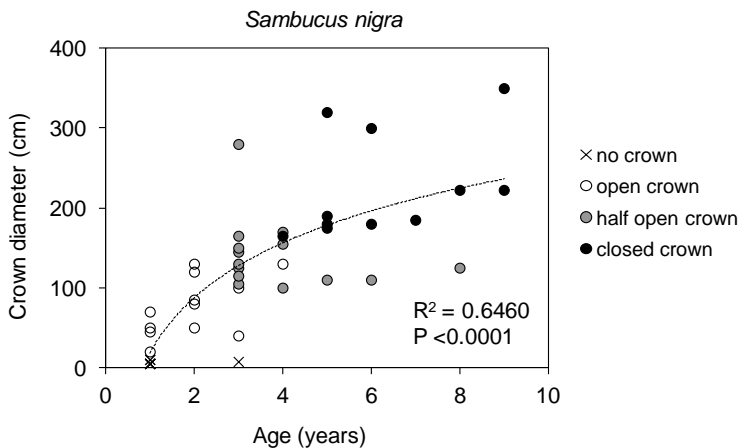
From the aerial photographs, it was not always possible to distinguish between living and dead standing shrubs. Thus the cover of *Sambucus nigra* or other woody species reported in the results includes both living and dead standing individuals.

We studied the effects of the introduction of cattle and horses on new establishments of *Sambucus* in the period 1978-1985. From 1978-1982, before introduction of cattle and horses in 1984, *Sambucus* establishment was examined in the research area to assess if there were already differences between the areas that were grazed and ungrazed in the following period 1982-1985 (Fig 1B). In this following period, new establishments were examined in the grazed and ungrazed research area. Furthermore, we distinguished between dense reed

vegetation and a mosaic vegetation of tall herbs and reed (Fig. 1B). We excluded plots at locations with human impact (roads, ditches, car tracks). The effects of large herbivores and vegetation type on newly established *Salix* spp. were not analysed, as almost all *Salix* spp. were already established in 1969 (Jans and Drost 1995).

In the part of the research area that was grazed since 1984, we also determined new establishments of *Sambucus* in the different vegetation types after 1985 to examine at what herbivore density regeneration stops.

After 1996, when *Sambucus nigra* and *Salix* spp. declined, the whole border zone was grazed year-round. For the analyses of the decline in relation to distance to nearest grassland or to cover of *Sambucus nigra*, we used all plots in the research area.



**Fig. 3.** Logarithmic relation between age and crown diameter for different crown covers. No crown = 0-25% cover; open crown = 26-50% cover; half-open crown = 51-75% cover; closed crown = 76-100% cover.

### Sampling

For measurements on the photographs we selected 166 plots, using a grid of 200 m throughout the whole research area. Areas in the eastern part of the research area where part of the original vegetation was removed in 1990 and immediately sown with grasses (Fig. 1A), were excluded. The plots measured 50x100 m and the longest side of the plots was oriented east-west. Within the plots, the cover of *Sambucus nigra* and *Salix* spp. was determined using a GIS (ArcView). For each year for which photographs were available, we determined total cover of *Sambucus nigra* and *Salix* spp. and cover of new establishments that had survived from previous years. New establishments were shrubs and trees that were not visible on a previous photograph. Outgrowth from previously recorded shrubs was not considered to be new establishments.

We determined distances from all plots to the nearest grasslands (Fig. 1), to analyse the correlation between distance to palatable grasslands and the relative decrease of *Sambucus nigra* and *Salix* spp. between successive years. The distances were measured in ArcView from the centre of the plot to the nearest grassland, taking into account barriers such as ditches. To analyse the correlation between the cover of *Sambucus nigra* and the relative decrease

of *Sambucus nigra* and *Salix* spp., we used the cover of *Sambucus* at the beginning of a period. For example, the relative decrease of *Sambucus* or *Salix* over the period 1996-2005 was correlated with the cover of *Sambucus* in 1996.

### Statistical analysis

Data were tested for normality using the One-Sample Kolmogorov-Smirnov test (Sokal and Rohlf 1981). To meet the assumptions of the statistical tests, data in percentages were arcsine transformed (Sokal & Rohlf, 1981).

To test if the increase or decrease of total cover of *Sambucus* or *Salix* spp. between successive years (Fig. 4) was significant, we used General Linear Model Repeated Measures (GLM-RP) Contrasts.

GLM-RP was used to test the effects of management (grazed or ungrazed by cattle and horses after 1984) and vegetation type (tall herbs or reed) on new establishments of *Sambucus nigra* (Fig. 5, Table 2). Both main effects, management and vegetation type, and their interaction are in the model. New establishments per period were expressed as the annual increase of cover of new establishments per plot.

We used GLM-RP to test the effect of period (1983-1985 to 2007-2008) and vegetation type (tall herbs or reed) on new establishments of *Sambucus nigra* in the grazed situation (Fig. 6). Both main effects, period and vegetation type, and their interaction are in the model. New establishments per period were expressed as the annual increase of cover of new establishments per plot.

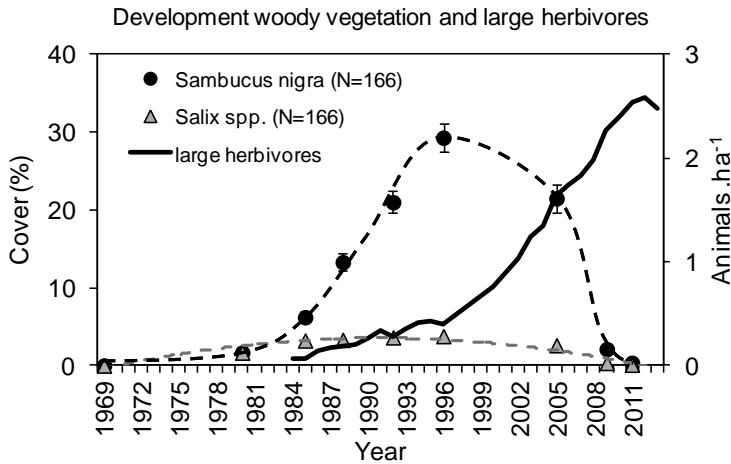
We used linear and non-linear regression to test neighbour effects on the decline of *Sambucus nigra* and *Salix* spp. (Fig. 7 and 8). The dependent values were transformed to meet the assumptions for linear regression (Sokal and Rohlf 1981). We have chosen the type of association with the highest determination coefficient (R-square) and lowest significance level (P-value).

All data were analysed using SPSS version 20 (Norusius 2006).

### Results

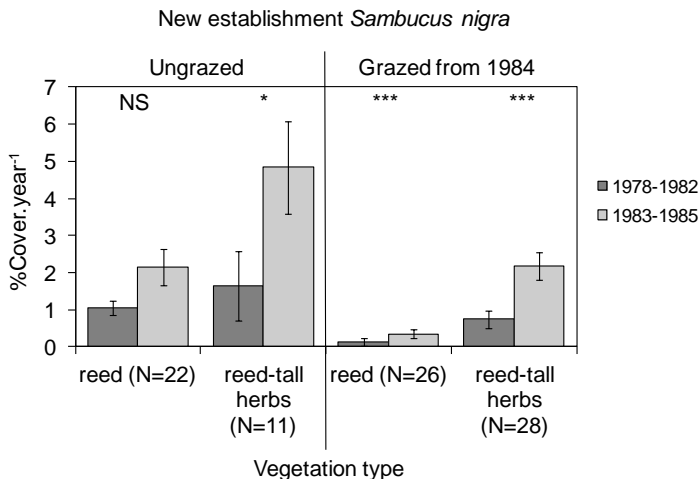
After reclamation of the polder in 1968, *Sambucus nigra* and *Salix* spp. cover increased significantly till 1996 and then decreased significantly (both species and both periods  $P < 0.0001$ ) (Fig. 4). The change from increase to decrease coincided with a total herbivore density of about 0.5 animals per ha.





**Fig. 4.** Development of *Sambucus nigra* and *Salix* spp. cover and densities (January 1) of introduced large herbivore population (Heck cattle, Konik horses, red deer). Error bars represent standard errors of the mean.

Before the introduction of cattle and horses into the research area, the numbers of establishments differed between the areas destined to be grazed or not, with significantly lower establishment in the area to be grazed after 1983 (Fig. 5; Table 2). New establishments of *Sambucus* increased in 1983-1985 compared to 1978-1982, irrespective of grazing regime. Also, new establishments increased in both vegetation types, however in tall herbs vegetation, the increase was higher than in reed vegetation (Fig. 5; Table 2).

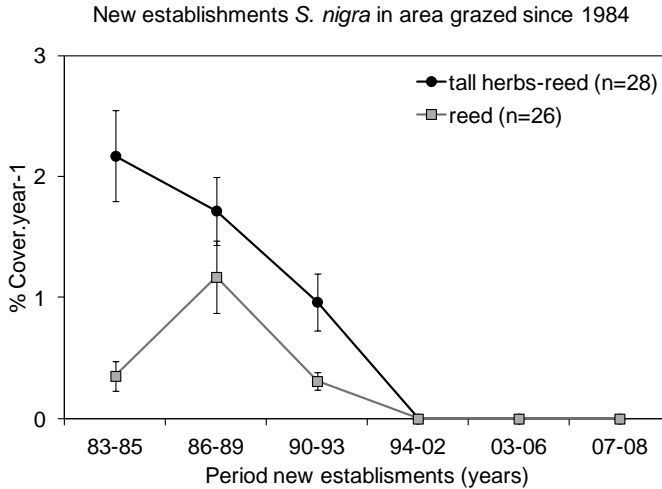


**Fig. 5.** New establishments of *S. nigra* per year for different periods, vegetation types and management. NS, \*\*\*\* gives the results of GLM-RP contrasts for testing differences between successive periods. NS = not significant; \* P < 0.05; \*\* P < 0.01; \*\*\* P < 0.001; \*\*\*\* P < 0.0001. Error bars represent standard errors of the mean.

**Table 2.** Results of GLM repeated measures on new establishments before and after introduction of cattle and horses in the western part of the research area. V = vegetation type (tall herbs or reed); M = management: grazed by cattle and horses after 1984 (yes or no).

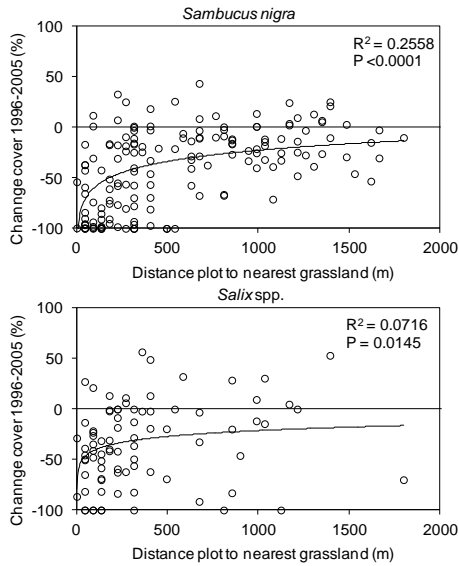
Source	df	1978-1982 (before introduction)			1983-1985 (after introduction)		
		MS	F	Sig.	MS	F	Sig.
Corr. model	3	0.029	9.241	<0.0001	0.082	15.154	<0.0001
Intercept	1	0.343	109.108	<0.0001	1.155	214.703	<0.0001
V	1	0.016	4.997	<b>0.0281</b>	0.149	27.784	<0.0001
M	1	0.058	18.365	<0.0001	0.113	20.973	<0.0001
VxM	1	0.006	2.027	0.1583	0.000	0.045	0.8318
Error	83	0.003			0.005		
Total	87						
Corr. total	86						

In the grazed area, new establishments were declining during the period 1983-1993 to zero after 1996 (Fig. 6). These new establishments were significantly affected by the interaction of the main effects period and vegetation type ( $P = 0.0486$ ).

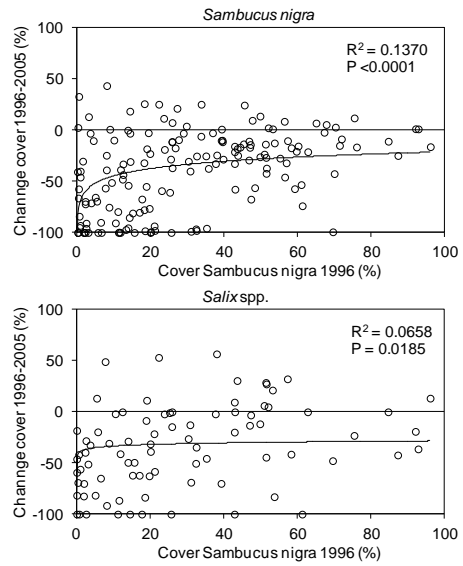


**Fig. 6.** New establishments of *S. nigra* per year for different periods and vegetation types in the research area grazed by large herbivores since 1984. Error bars represent standard errors of the mean. N = number of plots.

The relative change in *Sambucus* and *Salix* cover between 1996 and 2005 was significantly correlated to the distance to the nearest grassland (Fig. 7) and to the cover of *Sambucus* in 1996 (Fig. 8). Cover of *Sambucus nigra* in 1996 was not correlated with the distance to the nearest grassland ( $R^2 = 0.0214$ ;  $P = 0.0607$ ), so there is no collinearity. Relative changes in cover of *Sambucus* or *Salix* in other periods, showed weak correlations with distance to nearest grassland or cover of *Sambucus* (low R-square values; Table 3 and 4).



**Fig. 7.** Logarithmic relations between distance to nearest grassland and relative change in cover of *Sambucus nigra* (above) and *Salix* spp. (below) between 1996 and 2005.



**Fig. 8.** Logarithmic relations between cover of *Sambucus nigra* in 1996 and relative change in cover of *Sambucus nigra* (above) and *Salix* spp. (below) between 1996 and 2005.

**Table 3.** Logarithmic correlations between distance to nearest grassland and relative change in cover.  $R^2$  = coefficient of determination;  $P$  = P-value;  $N$  = #plots.

Period of change in cover	<i>Sambucus nigra</i>		N	<i>Salix</i> spp.		
	$R^2$	P		$R^2$	P	N
1996-2009	0.1382	<b>&lt;0.0001</b>	159	0.0260	0.1456	83
1996-2011	0.0364	<b>0.0160</b>	159	0.0102	0.3644	83
2005-2009	0.0478	<b>0.0078</b>	147	0.0191	0.2406	74
2005-2011	0.0312	<b>0.0323</b>	147	0.0068	0.4953	74
2009-2011	0.0018	0.6464	122	0.0068	0.4838	33

**Table 4.** Logarithmic correlations between *Sambucus nigra* cover and relative change of cover of *Sambucus nigra* or *Salix* spp. R<sup>2</sup> = coefficient of determination; P = P-value; N = #plots.

Year of cover of <i>Sambucus nigra</i>	Period of change in cover	Change in cover of					
		<i>Sambucus nigra</i>			<i>Salix</i> spp.		
		R <sup>2</sup>	P	N	R <sup>2</sup>	P	N
1996	1996-2009	0.0269	<b>0.0387</b>	159	0.0547	<b>0.0333</b>	83
	1996-2011	0.0228	0.0574	159	0.0330	0.1004	83
2005	2005-2009	0.0350	<b>0.0233</b>	147	0.0311	0.1327	74
	2005-2011	0.0042	0.4364	147	0.0184	0.2491	74
2009	2009-2011	0.0012	0.7095	122	0.0014	0.8379	33

## Discussion

Large herbivores can have a positive effect on establishment by zoochory (dispersal of seeds), by trampling (creating germination gaps), and by grazing and browsing tall herbs and grasses (reduction of light competition) (Crawley 1997; Mouissie 2004; Hester et al. 2006). Our results did not show differences in new establishments of *Sambucus* between grazed and ungrazed areas in reed or tall herb vegetation. An explanation could be that during 1983-1985, the animal numbers were too low and the animals may not have used the entire area available to them. Positive effects could have occurred but at a very local scale and as a result of this, new establishments may not have occurred in our plots. Although we could not demonstrate positive effects of large herbivores on new establishments, our results show that new establishments were seen in the grazed area, but only when herbivore densities were low (<0.5 N/ha).

Our results showed that during the period of new establishments of *Sambucus*, vegetation type had important effects on these establishments in both grazed and ungrazed areas. This effect coincided with the great differences in thickness of the litter layer between the two vegetation types. Plant litter can greatly affect seedling establishment and subsequent performance (Crawley 1997; Xiong and Nilsson 1999). Within the dense reed vegetation a 10-20 cm litter layer of leaves and stems was present during the 1980s and 1990s, but litter was sparse or absent below the tall herb vegetation (personal observations by Cornelissen). Hefting et al. (2005) showed that herbaceous litter decomposes about 1.9 times faster than reed litter, which is why reed litter accumulated in the reed vegetation. Because of this difference, more opportunities for species such as *Sambucus nigra* to germinate were present within the mosaic vegetation.

After 1996, at >0.5 animals per ha, cover of *Sambucus* and *Salix* strongly decreased from 30% to less than 1% in 2011. Field studies (Cornelissen et al. 2014; Chapter 3) showed that browsing and bark stripping by large herbivores turned the woody vegetation into grassland. Although *Sambucus* contains toxic *cyanogenic glycosides* and horses at the Oostvaardersplassen do not eat *Sambucus* (Vulink 2001), the toxicity of the secondary compounds were apparently not strong enough to deter cattle and red deer. We conclude that the assemblage of introduced large herbivores was very well able to reduce the woody vegetation of the Oostvaardersplassen, even though this woody vegetation is dominated by an unpalatable shrub, such as *Sambucus nigra*.

Our results agree with the concepts of both Associational Resistance and Associational Palatability (see Barbosa et al. 2009). The correlation between distance to nearest grassland,

the preferred habitat type of the large herbivores, and the decline of *Sambucus* and *Salix* agrees with findings of Clarke et al. (1995) and Hester and Baillie (1998), who showed a similar correlation between defoliation of a less preferred shrub and the distance to the preferred grass patches. Oom et al. (2002) observed that the use of the less preferred vegetation was concentrated in those areas where the preferred vegetation is abundant. This observation supports the Associational Palatability hypothesis which states that the risk of a plant being eaten is enhanced when an individual of this plant is surrounded by palatable species. In our research it is not the surrounding by palatable species but the closeness to palatable species which seems to be decisive. The correlation between cover of the unpalatable *Sambucus* and the relative decline of *Salix* suggests Associational Resistance for the palatable *Salix* and agrees with results from other studies which showed the protection of palatable species surrounded by other unpalatable species (e.g. White and Whitham 2000; Callaway et al. 2000; Bossuyt et al. 2005; Baraza et al. 2006). Our results also suggest Aggregational Resistance as a third mechanism. This is depicted by the relative decline of the unpalatable *Sambucus* which was less when it was surrounded by more individuals of its own kind.

So far, it is still unknown at what distances neighbour interactions operate (Barbosa et al. 2009). Our results suggest that they operated at different scale levels: Associational Palatability seems to operate at a landscape level (distance to nearest grassland up to 2 km) and Associational Resistance and Aggregational Resistance at much smaller scales (the within-plot cover of *Sambucus nigra* from a few metres to tens of metres).

Regeneration of woody species occurred at low herbivore densities (<0.5 N/ha). After 1996, when the densities of large herbivores increased, no new establishments were visible on the aerial photographs. This was confirmed by two vegetation maps of the Oostvaardersplassen (Jans and Drost 1995, Cornelissen et al. 2006) and a detailed field study (Cornelissen et al. 2014; Chapter 3). During this field study, no seedlings were found in the grazed Oostvaardersplassen, whereas seedlings of various woody species were found in an ungrazed control site. We conclude that in the Oostvaardersplassen, large herbivores may have positive effects (dispersal of seeds by zoochory, creating gaps by trampling and reducing competition for light by grazing tall herbs and grasses) and certainly have negative effects (browsing and bark loss) on the establishment of woody species. Both mechanisms (positive and negative) may occur simultaneously, but at low densities of herbivores, seedling browsing plays a minor role, while at high densities browsing leads to seedling eradication with huge impacts on forest regeneration.

The wood-pasture theory of Vera (1997), further elaborated by Olff et al. (1999), attributes a key role to large wild herbivores and their substitutes as a causal factor for creating a park-like landscape and complete forest regeneration cycles. Our research revealed important conditions to be satisfied for the woodland-grassland cycle, such as the opportunities for regeneration of shrubs and trees at low herbivore densities and the strong decline of woody vegetation at high densities. However, to date there has been no regeneration of thorny shrubs in the created and already existing grasslands (Cornelissen et al. 2014) as the wood-pasture theory predicts. Seedlings of the thorny shrub *Crataegus monogyna* and of the tree *Quercus robur* were observed (by Cornelissen) in the grazed area in 2010-2013, but none survived the winter, when grazing is intense because of the high numbers of large herbivores. Vera (1997) and Olff et al. (1999) mention that establishment of thorny shrubs needs a temporary decrease in large herbivore numbers. Without

management, population numbers can fluctuate greatly as a result of disease, severe winters, or food or water shortages (Young 1994; Clutton-Brock and Coulson 2002). Low density periods create windows of opportunity for thorny shrubs and other pioneer woody plants to establish.

The Oostvaardersplassen is a very young nature reserve with highly productive grasslands. Total herbivore numbers appear to have reached maximum numbers of the area in 2011. Despite a decrease of total herbivore numbers of 20-30% during the last two years (unpublished data), the densities are still relatively high. Since maximum numbers have apparently been reached, severe winters and food shortages will have stronger impacts on the populations. A combination of a wet spring and dry summer (low net primary production) followed by a severe winter may reduce herbivore numbers in the Oostvaardersplassen to such low levels that forest patches may regenerate.

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## CHAPTER 3

### TRANSITION OF A *SAMBUCUS NIGRA* L. DOMINATED WOODY VEGETATION INTO GRASSLAND BY A MULTI-SPECIES HERBIVORE ASSEMBLAGE.

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*Journal for Nature Conservation*, 2014, 22, 84-92

#### Abstract

We describe and analyse how large herbivores strongly diminished a woody vegetation, dominated by the unpalatable shrub *Sambucus nigra* L. and changed it into grassland. Density of woody species and cover of vegetation were measured in 1996, 2002 and 2012 in the grazed Oostvaardersplassen. In 2002 and 2012 we also measured density and cover in an ungrazed control site. In 2002 we measured intensity of browsing and bark loss of *Sambucus* shrubs in the grazed and control sites. In the grazed site the density of *Sambucus* and *Salix* spp. declined significantly between 1996 and 2012, and large areas changed into grassland. In the control site the density of *Sambucus* increased significantly during this period, the density of *Salix* spp. did not change, and the vegetation consisted of a mixture of woody species and a field layer dominated by tall herbs. In 2002 and 2012 the percentages of dead *Sambucus* shrubs were significantly higher in the grazed site than in the control site. In 2002 the percentages of twigs browsed and ring barked stems of *Sambucus* shrubs were significantly higher in the grazed site than in the control site. Our results show that debarking caused mature *Sambucus* shrubs to die, but that heavy browsing may have helped this process. Our results also point to a significant neighbour effect on the break down of *Sambucus*, suggesting that Aggregational Resistance and Associational Palatability were both active. Essential conditions for the break down of this woody vegetation were the presence of large herbivores, the low ratio between the areas of summer and winter feeding habitats and the competition amongst herbivores. Browsing may have been responsible for seedling death, as seedlings were found only in the control site and not on the old and newly established grasslands in the grazed site.

#### Introduction

Controlled grazing by large wild and domestic ungulates has become a major strategy for conservation management in the Netherlands and elsewhere in Europe (e.g. Wells 1965; Bülow-Olsen 1980; Buttenschön and Buttenschön 1982; Thalen 1984; Gordon et al. 1990; Welch 1997; Bakker and Londo 1998; WallisDeVries et al. 1998; Gerken and Görner 2001). Herbivore species, breeds, densities, seasons and scales of the grazed area are usually adjusted to the desired openness and biodiversity criteria. Man-made wood-pasture, heathland, chalk grassland and other traditional livestock farming landscapes have served as reference levels (Pott and Hüppe 1991; Signal et al. 1994; Piek 1998). This approach has, however, been challenged by a new, more 'naturalistic' grazing (or 'new wilderness') paradigm (Van de Veen 1975; Vera 1997, 2000). Inspired by near-natural African and North American grazing systems, these authors have suggested reintroducing wild large herbivores

and carnivores and also domestic cattle and horses in Northwest Europe, as substitutes for their wild ancestors lost since the Atlantic Period (7000-5000 BP). Ideally, such re-introduced ungulates should be managed not as livestock but as wild self-regulating herbivores, and viewed as an integral part of new wilderness ecosystems without population control. The debate between the supporters of both management strategies is focussing on whether and under which conditions large herbivores might create and maintain openness in woodland and on the consequences of such grazing conditions for biodiversity. The question of whether large herbivores can create and maintain open grasslands in woodland landscapes also remains a crucial issue for ecological theory (Vera 1997, 2000; Olff et al. 1999; Van Uytvanck 2009). The Wood-Pasture theory of Vera (1997, 2000) attributes, under natural conditions, a key role to large wild herbivores as a causal factor for creating a park-like landscape with forest regeneration in grasslands. High numbers of wild herbivores may contribute to the transition of woodland to grassland, maintain short grazed grasslands and therefore opportunities for the re-establishment of shrubs and trees in these natural 'pastures'. The transition of woodland to grassland and the maintenance of open grasslands require mortality of trees and shrubs. Trees and shrubs may be killed as a result of ageing, storm, fire, insects or diseases, but they may also die because of large herbivores (especially by debarking and pulling down) (Braun 1963; Crawley 1997; Gill 2006). The (re-)establishment of trees and shrubs requires the arrival and survival of tree seeds, their germination, seedling and sapling survival and growth. Large herbivores may delay or accelerate these processes in various ways. Crawley (1997), Gill (2006) and Hester et al. (2006) give an overview of some of these ways for example dispersion of seeds through coats or faeces (see also Mouissie 2004); creation of gaps for germination in closed vegetation by trampling, which creates bare soil; reduction of competition for light by grazing and browsing of tall grasses, herbs, shrubs and or trees. Vera (1997, 2000) and Olff et al. (1999) mention that (re-)establishment of thorny shrubs in these grasslands also needs a temporary reduction of the large herbivore populations to create a 'Window of opportunity' for the thorny shrubs.

Many doubt the effectiveness of naturalistic grazing to create gaps in forests, stop wood encroachment and create and maintain openness. Pott (1998) argues that human intervention is needed to create openness and to allow the characteristic high grazing pressure required to maintain the wood-pasture landscape. Mitchell (2005) agrees that large herbivores (natural and domestic) can have a significant impact on contemporary forest structure and composition, but believes that the forest canopies were maintained and fires and wind throw were probably the principle drivers who created gaps that herbivores maintained but which they could not create.

Woody plants are not defenceless victims of large herbivores as evidenced by the many grazed areas with unwanted wood encroachment. Trees and shrubs may tolerate or avoid being destroyed by large herbivores (see Milchunas and Noy Meir 2002; Hester et al. 2006). The relative importance of each strategy depending on across plant species, plant developmental stages, plant neighbours, habitats, seasons, and herbivore species. Plants may deter large herbivores chemically with secondary metabolites (Rhoades 1979; Palo and Robbins 1991), which may be toxic (alkaloids and *cyanogenic glycosides*) or reduce digestibility (tannins and lignins) (e.g. Coley et al. 1985; Robbins et al. 1987; Bryant et al. 1991). Ungulate herbivores can counteract the effects of toxic compounds with varying success. Many ruminants can detoxify toxic compounds better than hindgut fermenters, and within the ruminants, browsers are better able to cope with plant secondary metabolites

than typical grazers (Hofmann 1989; Van Soest 1994). *Sambucus nigra* L. is one of the plant species that produce *cyanogenic glycosides* (Conn 1973; Atkinson and Atkinson 2002), which can be toxic to or lethal in birds and mammals (see Griess et al. 1998; see Majak and Hale, 2001). *Salix* spp. do not produce *cyanogenic glycosides* (Palo and Robbins 1991). They have only a low chemical defence against herbivory, based on *phenolic glycosides* (Palo and Robbins 1991).

Plants may also physically avoid large herbivores through location, such as growing near unpalatable plants – a strategy known as Associational Plant Refuge or Associational Resistance (see Pfister and Hay 1988; Hester et al. 2006). It is also possible that the risk of a plant being eaten is enhanced when an individual of this plant is surrounded by palatable species (known as Associational Palatability; Olff et al. 1999). A hypothesis logically derived from Associational Resistance and Associational Palatability is ‘Aggregational Resistance’: that aggregation of individuals of an unpalatable plant will decrease herbivory losses of this plant in a palatable neighbourhood.

A unique opportunity to test plant-herbivore theories and the ability of large herbivores to maintain openness is provided by the Oostvaardersplassen, a wetland reserve in the Zuidelijk Flevoland polder in the Netherlands, where there is a more or less self-regulating multi-species large herbivore population. In the relatively young Oostvaardersplassen the woody vegetation consists almost solely of *S. nigra* and *Salix* spp., with *Sambucus* as the dominant species (Jans and Drost 1995; Cornelissen et al. 2006).

In this paper we describe and analyse how a woody vegetation, dominated by the unpalatable shrub *S. nigra* is being strongly diminished and transformed into open grassland by a thriving multi-species large herbivore population in the Oostvaardersplassen, how the strong decline is correlated with neighbouring plant species, and if, in accordance with the Vera hypothesis (Vera 1997, 2000), regeneration of woody species in the open grasslands takes place. During the study period 1996-2012, the total herbivore density increased from 0.4 to 2.6 ha<sup>-1</sup>. We hypothesized that: (1) Woody vegetation, dominated by an unpalatable shrub, can be broken down by a more or less uncontrolled multi-species large herbivore population and changed into grassland; (2) The effect of the large herbivores (browsing and debarking) on the unpalatable shrub will be negatively correlated with the degree of aggregation (cover) of the unpalatable shrub; (3) Regeneration of woody species in newly created grasslands does not take place under these high grazing pressures.

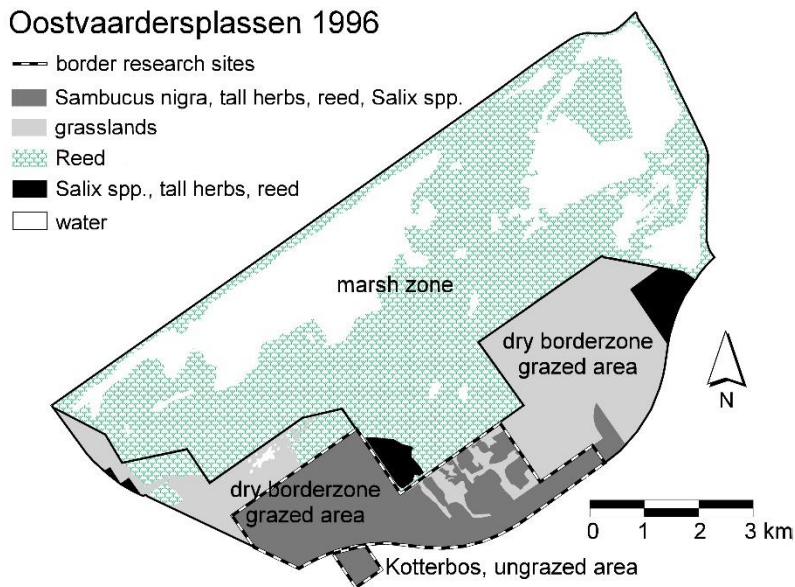
## Material and methods

### *Study Area*

The Oostvaardersplassen is a man-made wetland in Zuidelijk Flevoland polder in the Netherlands. It became established in the lowest part of the polder when the polder was endiked in 1968. In 1974-1975, the marsh (3600 ha) was embanked to stop it drying out as the ground of the drained surrounding land settled. In 1975 a pump and outlet were also constructed to regulate the water level in the marsh. In 1982 a dry border zone (2000 ha; some of it cultivated) was added to the wet marsh in order to extend the array of habitats in a hydrological gradient from wet to dry (see Vulink and Van Eerden 1998).

The study was conducted in the southwest part (750 ha) of the grazed dry border zone of the Oostvaardersplassen where most of the woody species established, and in the ungrazed control site Kotterbos (30 ha; Fig. 1). In both sites different habitat types can be

distinguished: grasslands (*Poa trivialis* L., *Lolium perenne* L., *Trifolium repens* L.), dry reed vegetation (*Phragmites australis* (Cav.) Steud.) and a semi-open mosaic vegetation of reed, tall herbs (*Urtica dioica* L., *Cirsium* spp. Mill.), *S.nigra* and *Salix* spp. (Jans and Drost 1995; Jans et al. 1998; Cornelissen et al. 2006). Most of the *Salix* spp., mainly *Salix alba* L., established on the bare soil immediately after the water was pumped out of the polder and the surface area became dry in 1968. *Sambucus nigra* established some years later in the Oostvaardersplassen mostly in the southwest part of the dry border zone, but throughout the Kotterbos control site. The Kotterbos site was part of the Oostvaardersplassen until 1983, when a railway cut it off. It has the same age, soil type, and hydrology as the rest of the Oostvaardersplassen, and it had an identical spontaneous vegetation development until 1983, the first year in which large herbivores were introduced into the Oostvaardersplassen.



**Fig.1.** Oostvaardersplassen study area, showing vegetation types of 1996, and the locations of the grazed and ungrazed control sites.

Roe deer from the mainland were already naturally colonizing the area in the early 1970s. In 1983 32 Heck cattle (*Bos taurus* L.) were introduced into the Oostvaardersplassen and in 1984 18 Konik horses (*Equus caballus* L.) were introduced. By 1992, *Sambucus* covered large parts of the border zone and its cover was still increasing by canopy expansion, and new establishment (Jans and Drost 1995; Jans et al. 1998). In 1992/1993 52 red deer (*Cervus elaphus* L.) were introduced to stop ongoing encroachment by *Sambucus* which was reducing the opportunities for waterfowl (Cornelissen and Vulink 2001). The manager decided to monitor the ongoing *Sambucus* expansion to see if red deer were able to halt it and measurements were carried out in 1996 (Baartmans 1996) and repeated in 2002 and 2012.

The density of Heck cattle in the Oostvaardersplassen increased from 0.18 ha<sup>-1</sup> in 1996 to 0.32 ha<sup>-1</sup> in 2002 but by 2012 had fallen back to 0.18 ha<sup>-1</sup>. In the same period, the density of Konik horses increased from 0.12 ha<sup>-1</sup> in 1996 to 0.61 ha<sup>-1</sup> and the density of red deer

increased from 0.10 in 1996 to 1.79 ha<sup>-1</sup> in 2012. Roe deer density decreased from 0.03 ha<sup>-1</sup> in 1996 to 0.005 ha<sup>-1</sup> in 2002, to 0 in 2012. The Kotterbos site was ungrazed by cattle, horses and red deer, but here roe deer densities varied between 0.02 ha<sup>-1</sup> and 0.04 ha<sup>-1</sup> (pers. comm. State Forestry Service). Small mammal herbivores, such as rabbit (*Oryctolagus cuniculus* L.) or hare (*Lepus europaeus* Pallas.), which can also browse and debark were rare in the Oostvaardersplassen during the research period. In 1987 there was a field inventory of small mammals (Lange and Margry 1992), and from 1996 to 2012 small herbivores (birds and mammals) were included in the habitat use counts of the large herbivores in the Oostvaardersplassen (unpublished data). In total, only 3 hares and no rabbits were counted. Large carnivores, such as the wolf, are not present at the Oostvaardersplassen.

#### *Plots, patches and sites*

In 1996, 75 plots of 20x5 m were laid out randomly in the southwest part of the grazed dry border zone where most of the *Sambucus* shrubs established (Fig. 1), using grid lines (spaced at 50 m) and GPS coordinates. In order to describe the development of the woody vegetation, especially of the unpalatable *Sambucus* population, and to test interannual differences, both in 2002 and 2012, we again laid out 75 different plots of the same size, located randomly in the same wooded part of the grazed site.

In 2002 and 2012 we also investigated the woody vegetation in the Kotterbos control site (30 ha) by using 30 randomly selected plots of the same size as those in the grazed site.

To investigate Aggregational Resistance, the cover of *Sambucus* scrub in 1996 was taken as the benchmark for the period 1996 to 2002 over which the effects were examined, and the cover of 2002 was assumed to be the result of the grazing during that research period. We tested neighbour effects by examining the correlation between the cover (as aggregation parameter) of *Sambucus* in 1996 and the percentage of browsed shrubs per plot, the percentage of twigs browsed per shrub, the percentage of shrubs with ring barked stems per plot and the percentage of ring barked living stems per shrub in 2002. In order to measure *Sambucus* cover in 1996 for the plots of 2002, we plotted the coordinates of the plots of 2002 on the aerial photographs of 1996 used to make the vegetation map of 1996 (Jans et al. 1998). The plots demarcated in the field in 2002 could not be plotted accurately on the aerial photographs because the GPS apparatus had an inaccuracy of ca. 10 m. Therefore, on the aerial photographs, for each plot we marked out a patch of 50x50 m, which ensured that the plot would be included.

#### *Measurements*

The living and dead standing individuals of all woody species in each plot were counted in 1996, 2002 and 2012 in the grazed area and in 2002 and 2012 in the control site. It was not possible to count the number of dead fallen shrubs or trees because of their disintegration. In 2002 and 2012 the numbers of seedlings of all woody species were counted for each plot in both sites.

In 2002 we examined herbivore activity in more detail in both sites. Per *Sambucus* shrub we counted the number of twigs available up to 2 m height (Van der Hoek et al. 2002) and the total number of twigs browsed. We also estimated bark loss per living or dead stem (>3 cm diameter) per *Sambucus* shrub. We distinguished three classes of bark loss: 1) 100% bark loss (ring barked); 2) 11-99% bark loss (heavy debarking); 3) 0-10% bark loss (light debarking). For both twig browsing and bark loss assessments, 10 *Sambucus* shrubs (living or dead) were

selected at random per plot. This was done along a 20 m transect within the plot, making the selection at 2 m intervals (thus a total of 10 selection points). The shrub nearest to a point was selected for measurements. If there were fewer than 10 individuals per plot, all individuals were selected. We did not repeat these measurements in 2012, as then in the plots in the grazed area there were only 4 living *Sambucus* shrubs and no living *Salix* spp.

In 1996, 2002 and 2012 we described the vegetation in the plots by estimating the cover (estimated vertical projection on the ground) of two different structural layers (Table 1). We distinguished: 1) herbaceous plants (with the classes: grassland; tall herbs and reed; a fourth class was bare soil); 2) woody plants (with the classes shrubs and trees).

For determining the cover of *Sambucus* in the patches in 1996 we used digitized Near Infrared aerial photographs taken in July 1996, scale 1:10,000 and a GIS (ArcView).

### *Statistical analysis*

Statistical analyses were carried out to test differences among years or between sites, and relationships between cover of *Sambucus* and twig browsing or bark loss. For each year we calculated the mean densities of living+dead individuals, of living individuals and of dead individuals. The average shrub mortality (expressed as the percentage of dead individuals per site) was calculated as average of the mortality values per plot. The averages of twigs browsed or ring barked stems per site are based on the averages per individual per plot.

Data were tested for normality using the One-sample Kolmogorov-Smirnov test (Sokal and Rohlf 1981). To meet the conditions of the statistical tests, data on density and number of twigs were log-transformed and data of cover or percentages twig browsing and bark loss were arcsine transformed (Sokal and Rohlf 1981).

Differences in cover of vegetation or densities of shrubs and trees among years per site (1996, 2002 and 2012) were tested using a One-Way Anova, since the plots in all years were randomly chosen and the values of the plots of all years can be considered as independent from each other. Differences in mortality of individuals, percentages of twigs browsed or bark loss between years per site (2002 and 2012) were tested using an independent t-test.

Over the period 2002-2012, GLM procedures were used to test if year and site affected cover of vegetation, densities or mortality of *S. nigra* or *Salix* spp.

Differences in total twigs available, percentage of twigs browsed, and percentage of living or dead stems ring barked between sites in 2002, were tested using an independent t-test.

To test neighbour effects on twig browsing and ring barking we correlated the cover of *Sambucus* in each patch in 1996 with the percentage of browsed shrubs per plot, the percentage of browsed twigs per shrub, the percentage of shrubs with ring barked living stems per plot, and the percentage of ring barked living stems per shrub in 2002, using linear and non-linear regression (Norusius 2006).

All data were analysed using SPSS for Windows version 14.0 (Norusius 2006). All error bars in graphs represent Standard Errors of Mean (SEM).

The used nomenclature for plant species was according to Van der Meijden (2005).

**Table 1** Characteristics of the grazed and ungrazed control sites. Cover of vegetation types is based on the estimated cover of vegetation types in plots in 1996, 2002 and 2012 (see methods). The ungrazed control site was not measured in 1996. The cover of vegetation types was estimated for two structural layers: 1) herbaceous vegetation with the classes: bare soil; grassland; tall herbs; *Phragmites australis*; 2) woody vegetation with the classes: shrubs and trees. The cover is given as a percentage of the area; within parentheses SEM are given. Column A gives the results of the One-Way Anova to test an effect of year on vegetation cover of the different classes for each study site. \*:P<0.05; \*\*: P<0.01; \*\*\*: P<0,001; \*\*\*\*: P<0.0001.

Vegetation	Grazed (750 ha; 75 plots)				Ungrazed (30 ha; 30 plots)			
	1996	2002	2012	A	1996	2002	2012	A
Bare soil	13 (1.8)	4 (1.2)	0 (0.0)	****	-	23 (5.5)	16 (5.8)	NS
Grassland	17 (3.1)	43 (4.2)	92 (2.9)	****	-	5 (2.0)	0 (0.0)	**
Tall herbs	47 (3.4)	40 (3.7)	<1 (0.1)	****	-	61 (5.8)	83 (5.8)	***
Reed	23 (4.1)	13 (3.1)	7 (2.9)	***	-	11 (3.8)	<1 (0.2)	***
Shrubs	14 (2.4)	12 (2.6)	<1 (0.3)	****	-	37 (5.5)	63 (4.9)	**
Trees	5 (1.5)	0 (0.0)	0 (0.0)	***	-	14 (4.8)	33 (5.9)	*

**Table 2** Species composition of living woody species in the grazed and ungrazed study sites. The table shows the percentages based on the total number of living shrubs and trees found in the plots. The ungrazed control site was not measured in 1996.

	Grazed			Ungrazed		
	1996	2002	2012	1996	2002	2012
<b>Shrubs</b>						
<i>Sambucus nigra</i>	96	100	100	-	67	66
<i>Salix pentandra</i> L.	1			-		
<i>Salix viminalis</i> L.	<1			-		
<i>Salix dacyclados</i> Wimm.	<1			-		
<i>Salix aurita</i> L.	<1			-		
<i>Salix caprea</i> L.	<1			-	<1	<1
<i>Salix triandra</i> L.	<1			-		<1
<i>Salix cinerea</i> L.				-		<1
<i>Sambucus racemosa</i>				-		<1
<i>Ribes rubrum</i>				-		<1
<b>Trees</b>						
<i>Salix alba</i>	<1			-	30	32
<i>Quercus rubra</i>				-	1	1
<i>Betula pendula</i>				-	<1	
Total shrubs and trees	374	222	4	-	413	709

## Results

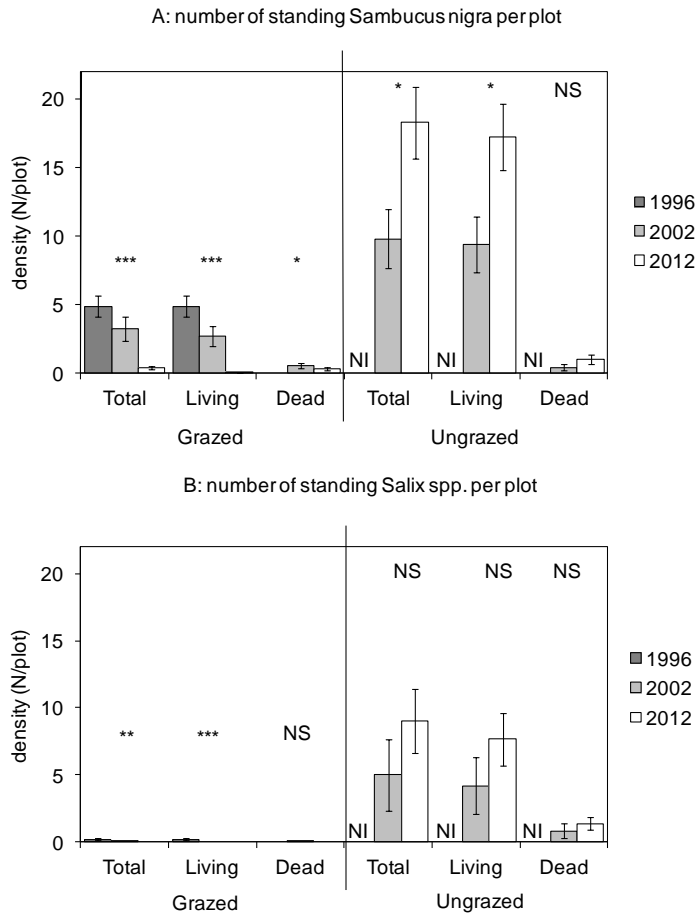
In the area grazed by cattle, horses and red deer, the vegetation changed significantly from one dominated by tall herbs and reed in 1996 to one dominated by grassland in 2012, and shrubs and trees disappeared (Table 1). In the control site, the vegetation was dominated by tall herbs in 2002 and 2012, grassland and reed disappeared, and shrubs and trees increased significantly (Table 1). During the period 2002-2012, the cover of all structural classes except for reed and bare soil was significantly affected by the interaction effect of year and site (all P-values <0.0001). Reed was significantly affected by only the main effect year ( $P = 0.0012$ ) and bare soil was significantly affected by both main effects year ( $P = 0.0002$ ) and site ( $P < 0.0001$ ).

The dominant shrub species in the grazed and control sites was *S. nigra* (Table 2). Other shrub species were mainly *Salix* spp. In the plots in the grazed site, *Salix* shrubs were present only in 1996. The only tree species present in the grazed area was *Salix alba* and it was found only in 1996. In the control site *S. alba* was dominant and also *Quercus rubra* L. and *Betula pendula* Roth were found.

In the grazed area, densities of living+dead *Sambucus* shrubs and of living shrubs decreased significantly and the density of dead shrubs increased significantly from 1996 to 2012 (Fig. 2; photographs 1 to 5). In the control site the densities of living+dead *Sambucus* shrubs and living shrubs increased significantly from 2002 to 2012 (Fig. 2). The density of dead *Sambucus* shrubs did not change significantly. Over the period 2002-2012, the densities of living+dead *Sambucus* shrubs and of living shrubs were significantly affected by the interaction effect of year and site (both P values <0.0001). During this period the density of dead *Sambucus* shrubs was not affected by year or site.

In the grazed site, the densities of living+dead *Salix* spp. and of living *Salix* spp. decreased significantly from 1996 to 2012 (Fig. 2). In the control site, *Salix* spp. densities did not change. Over the period 2002-2012, the densities of *Salix* spp. (living+dead, living or dead ) were significantly affected only by site (all P values <0.0001) and not by year or the interaction effect of year and site.





**Fig. 2.** Density of *Sambucus nigra* (A) and *Salix* spp. (B) per plot in the grazed site and the ungrazed control site for living+dead, living, and dead shrubs or trees only. Differences among years were tested using One Way Anova: NS = not significant; \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ . NI = Not investigated in 1996.

**Photo 1.** Grazed site 1996



**Photo 2.** Grazed site 2002



**Photo 3.** Ungrazed site 2002



**Photo 4.** Grazed site 2012

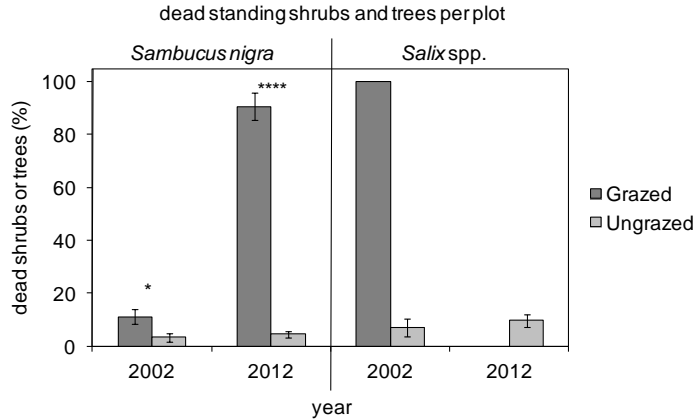


**Photo 5.** Ungrazed site 2012

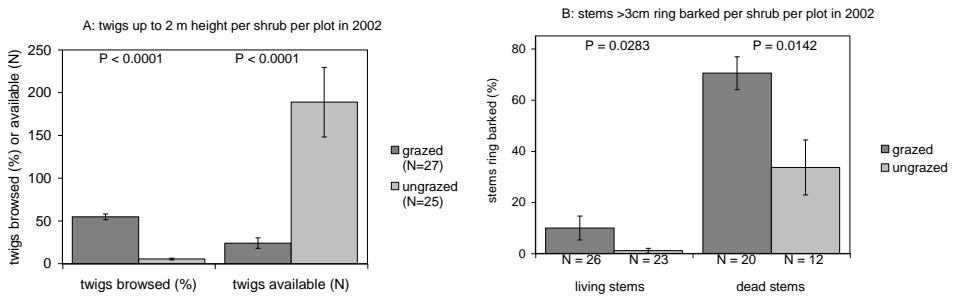


The percentage of dead *Sambucus* shrubs was significantly affected by the interaction effect of year and site ( $P < 0.0001$ ) (Fig. 3). The percentage of dead *Salix* spp. was significantly affected only by site ( $P < 0.0001$ ) and not by year or the interaction effect of year and site.

In 2002, twig-browsing intensity and debarking of *Sambucus* shrubs was significantly affected by the large herbivores (Fig. 4A and B). The total number of twigs up to 2 m height, i.e. available to the herbivores, also correlated with the intensity of twig browsing during the previous years.



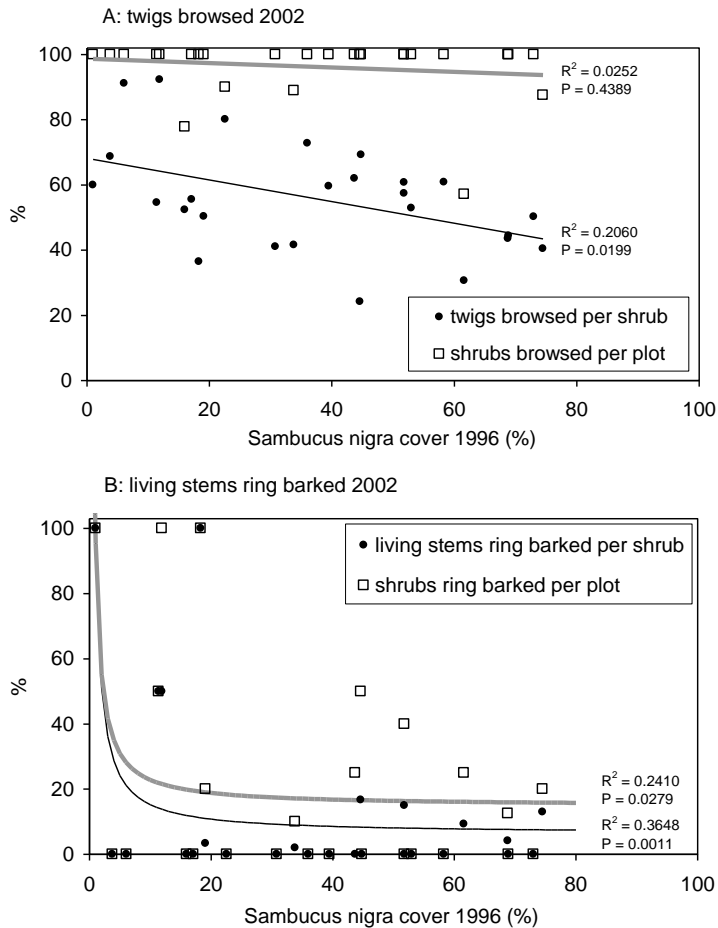
**Fig. 3.** Mortality of *Sambucus nigra* and *Salix* spp., presented as the percentage of dead individuals per plot. Differences between the grazed and ungrazed control site were tested using independent t-tests: \* =  $P < 0.05$ ; \*\*\*\* =  $P < 0.0001$ . No tests were performed for *Salix* spp. because in 2002 *Salix* was present in only one plot and in 2012 *Salix* was absent in the grazed site.



**Fig. 4.** Percentages of twigs browsed and number of twigs up to 2 m height per individual per plot (A) and percentages of living or dead stems (>3 cm diameter) ringbarked per individual per plot (B) in 2002 for the grazed and ungrazed sites. The P-values show the results of the t-tests for differences between sites. In brackets the number of plots in which *Sambucus* was present (used to calculate the averages and SEM).

To test neighbour effects, we examined the correlation between twig browsing and bark loss of *Sambucus* shrubs in 2002 and the cover of *S. nigra* in 1996. The percentage of shrubs with browsed twigs per plot was not correlated with the cover of *Sambucus* in 1996, because almost all shrubs were browsed (Fig. 5A). The other parameters declined significantly with the cover of *Sambucus* (Fig. 5A and B).

In 2002 and 2012, seedlings were found only in the control site. In 2002, they were all *Sambucus* seedlings: 0.4 seedlings per plot (SEM = 0.25, N = 30). In 2012, the seedlings found were not only *Sambucus* (1.3/plot; SEM = 5.0; N=30) but also *Q. robur* (0.4/plot; SEM = 1.3; N = 30) and *Crataegus monogyna* Jacq. (0.03/plot; SEM = 0.1; N = 30). There was no significant difference in *Sambucus* seedling numbers between 2002 and 2012 ( $P = 0.2659$ ).



**Fig. 5.** Relation between cover of *Sambucus nigra* per 'patch' in 1996 and the percentage of shrubs with browsed twigs per plot and the percentage of twigs browsed per shrub per plot in 2002 (A) and between cover of *Sambucus nigra* per 'patch' in 1996 and the percentage of shrubs with living stems ringbarked per plot and the percentage of living stems ringbarked per shrub per plot in 2002 (B). Based on *Sambucus nigra* shrubs within the grazed site.

## Discussion

The most appropriate approach to investigate the effects of the herbivores on woody vegetation is a replicated enclosure experiment. Unfortunately, the unique character of the Oostvaardersplassen made this impossible. Nevertheless, a grazing impact study needs to include a comparison with a suitable control site. Our control site was once contiguous with the Oostvaardersplassen. Its age, soil and weather conditions are the same and its vegetation has also developed spontaneously. At the start of the study period, differences in vegetation composition between the control site and the Oostvaardersplassen were negligible. Our results show that this is no longer the case in terms of the quantities of twigs browsed or of

stems ring barked. Although bark loss can also be caused by other factors such as diseases or insects, most of the bark loss can be attributed to browsing by cattle, horses or red deer, as teeth marks were clearly visible on the stems from which bark has been stripped. Furthermore, there were many sightings of herbivores debarking *Sambucus* and *Salix* spp. Twig browsing or debarking can also be caused by small mammal herbivores, such as hares or rabbits, but as these small herbivores were not present at the Oostvaardersplassen (see study area), this possibility can be ruled out.

*Sambucus* had been eradicated in 2012. This process must have started at some point in time between 1996 and 2002, given the increase of *Sambucus* cover between 1974 and 1996 (Jans and Drost 1995; Jans et al. 1998), the significant decline of shrub density between 1996 and 2002 (Fig. 2) and the occurrence of dead individuals in 2002 (Fig. 2). Based on our data it can be inferred that the decline of mature *Sambucus* shrubs within the Oostvaardersplassen was caused by mortality due to grazing, as other potential mortality factors such as insects, fungi or fire could not be detected. Ageing was rejected as major mortality factor. In 2002 the *Sambucus* population was younger than the potential lifespan of at least 25 years for this species (Atkinson and Atkinson 2002). Self-thinning is an improbable explanation for mortality, because of the shade tolerance of *Sambucus* (Atkinson and Atkinson 2002). It is known that ring barking kills woody plants by interrupting phloem transport (Braun 1963; Crawley 1997; Gill 2006). We conclude that debarking led to the mortality of mature *Sambucus* shrubs, but that heavy browsing may have helped this process by making the stems more vulnerable to debarking. Although large herbivores are known for their negative effects on woody species which can cause mortality (e.g. Gill 1992, 2006; Kuiters et al. 1996; Putman 1996; Crawley 1997; Pott 1998; Cornelissen and Vulink 2001; Skarpe and Hester 2008; Reimoser and Putman 2011) and perhaps the strong decline of the woody vegetation under the high density of large herbivores was more or less predictable, our study shows for the first time these negative effects of a more or less self-regulating multi-species assemblage of cattle, horses and red deer on a woody vegetation and its transition into grassland in a temperate north-western European nature reserve.

Browsing on its own may have led to the mortality of seedlings of woody species in the grazed site as they are generally more susceptible to browsing than older (and taller) individuals (Hester et al. 2006). Seed predation, inhibited germination and seedling mortality may all play a role too, but from our data we conclude that the absence of regeneration is largely attributable to browsing by large herbivores. Our results agree with many other studies who showed the negative browsing effects of grazing on regeneration of woody species (e.g. Prins and Van de Jeugd 1993; Kuiters et al. 1996; Rousset and Lepart 2000; Russel and Fowler 2004; Smit et al. 2006; Vandenberghe et al. 2009).

Specific plant associations may decrease or increase the likelihood of detection and/or vulnerability to herbivores (Barbosa et al. 2009). Our results point to two different neighbour effects on the strong decline of *Sambucus*. Between 1996 and 2002 the results suggest Aggregational Resistance: the unpalatable species is grazed less when it has a larger biomass (Olf et al. 1999). After 2002, the remaining shrubs and trees became more and more surrounded by palatable plant species. So the results also emphasize the risk of palatable lawns as neighbour (Associational Palatability) even for unpalatable woody plants. We suggest that in the Oostvaardersplassen they were both in operation. During the early stage (1996-2002) when herbivore densities were low, Aggregational Resistance may have played a major role. But as the densities of herbivores increased and the vegetation surrounding the

remaining shrubs and trees changed into grassland, the mechanism of Associational Palatability may have become dominant.

In the Oostvaardersplassen, herbivores' foraging behaviour and habitat use is determined by their preference for short grasses (De Jong et al. 1997; Cornelissen and Vulink 2001), which have high nutritional value and grow in the extensive open grasslands. As long as these grasslands provide the amount of food needed, the herbivores will graze on these grasslands and their impact on other vegetation types will be low. During winter, when net primary production and food quality are low, the amount of grass available per animal will decrease. Then the use of other food plants will increase and so will the impact on other vegetation types (see Cornelissen and Vulink 2001). This mechanism does not differ from plant-herbivore interactions in natural systems (see e.g. Jarman and Sinclair 1979; Owen-Smith 2008). Two other conditions in addition to the presence of a large herbivore assemblage of species with a high browsing and debarking capability (De Jong et al. 1997; Vulink et al. 2000) could have been essential for the observed break down. Firstly, the area of summer feeding habitats (short grasslands) was almost the same size as the area of winter feeding habitats (tall herbs, reed and shrubs) (Cornelissen 2006), although the food in the winter feeding habitats during winter was of much lower quantity and quality than the food in the summer feeding habitats during summer. As a result of the fertile clayey soil (former seabed) of the Oostvaardersplassen, these highly productive summer feeding grasslands (on average during this period 800-1200 g dry matter.m<sup>-2</sup>.year<sup>-1</sup>; Cornelissen 2006) could support high numbers of large herbivores during summer (May-October). During winter (November-April), the summer feeding grasslands could no longer support these high numbers, so the herbivores had to deal with the much lower food quantity and quality of the winter feeding habitats and had a large impact on these habitats. Secondly, competition could have been an important condition, as all three herbivore species prefer the short grasses of the extensive open grasslands. Overlap in a fundamental niche indicates potential for competition where resources become limiting (Putman 1996) as occurs during winter when the Oostvaardersplassen grassland are much less productive and there is insufficient standing crop for sufficient intake. Given that total herbivore numbers at the beginning of each year in the Oostvaardersplassen increased almost sixfold between 1996 and 2012, it is plausible that more intensive competition during winter between 1996 and 2012 was important in excluding animals from these grasslands and forcing them to turn to other vegetation types for their food.

Our research demonstrates that cattle, horses and red deer can strongly diminish palatable woody species, such as *Salix* spp., and unpalatable shrubs, such as *S. nigra*, and that they can prevent these and other woody species from regeneration in the newly created grasslands. Previous studies involving repeated vegetation mapping (Jans and Drost 1995; Cornelissen et al. 2006), have shown that woodland has never encroached in the extensive open grasslands in the Oostvaardersplassen that were already present from 1983 on. In this phase of the vegetation development of the relatively young Oostvaardersplassen, the more or less self-regulating large herbivore populations are preventing such encroachment, strongly diminish the existing woody vegetation, and thereby creating and maintaining an open landscape. One reason for this is that these large herbivore populations are able to survive at high densities at the Oostvaardersplassen. It remains to be seen whether other woody species will invade the area. Resource-mediated Successional Grazing Cycle theory (Bokdam 2003) suggests that the prevailing conditions in the Oostvaardersplassen make this

unlikely, because a high grazing lawn productivity will allow a high ungulate density and bring a high risk of mortality for seedlings of woody species. However, as food supply is not the same every year, but varies among years as a result of variation in weather condition and also other factors determine animal numbers, it is likely that animal numbers will fluctuate. Young (1994) has shown these fluctuations for many different herbivore species. As at the Oostvaardersplassen different factors that can affect herbivore numbers are present, for example annual variation in net primary production and severity of winter, and increasing competition with several thousands of geese during winter en spring, it is likely that large herbivores numbers at the Oostvaardersplassen will fluctuate in future, creating 'windows of opportunity' for thorny shrubs and thus opportunities for regeneration of trees.

Although *Sambucus* and *Salix* spp. were strongly diminished, our research does not demonstrate that these large herbivores are also able to break down all woody vegetation or prevent regeneration of woody plants in general. Other woody species with other plant defence mechanisms, (e.g. thorny shrubs *C.monogyna*, *Rosa canina* L. or *Prunus spinosa* L.) which are known to be well protected against large herbivores (Linnart and Whelan 1980; Good et al. 1990; Baraza et al. 2006) are very scarce in the Oostvaardersplassen and were not recorded in the plots. There are various reports about the ability of these shrubs to facilitate the establishment of other, more palatable woody species such as *Quercus*, *Fraxinus* or *Acer* in grazed areas (e.g. Herrera 1984; Olf et al. 1999; Baraza et al. 2006). Although mature shrubs of *C.monogyna* and *P.spinosa* can protect themselves and other woody species to a certain extent, establishment can be a problem, especially in areas with high numbers of herbivores (Good et al. 1990), since when young, their thorns are not yet developed. We do not yet know why *Crataegus*, *Rosa* or *Prunus* were not present in our plots during the research period, or whether they are likely to establish in future. As mentioned above, the high numbers of animals could prevent the establishment. But in future, as it is likely that numbers of large herbivores will fluctuate, establishment can be possible. In the coming years we intend to investigate which factors (soil, vegetation, herbivore densities) determine their occurrence in the Oostvaardersplassen.

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## CHAPTER 4

# EFFECTS OF FLOODPLAIN RESTORATION AND GRAZING ON WOOD ENCROACHMENT ALONG A LOWLAND RIVER IN NW-EUROPE

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### Abstract

In many countries worldwide, measures have been taken in floodplains for flood prevention and to rehabilitate river habitats. In the Netherlands, floodplains were lowered by excavating to enlarge the discharge capacity and to create opportunities for development of river habitats such as forest. As forest can obstruct the water flow through the floodplain, their development has to be controlled in some cases. In many floodplains, vegetation development is controlled by cattle and horses. We carried out an enclosure experiment over a twelve year period in a partly excavated and year-round grazed floodplain along a lowland river in the Netherlands. We focussed on the thorny shrub hawthorn (*Crataegus monogyna* Jacq.) as it plays an important role in the obstruction of the water flow and in the wood-pasture cycle. Most hawthorn shrubs established on the excavated part of the floodplain with low cover of tall herbs. The total number of established hawthorn was negatively related to inundation on the lower parts of the excavated sites and positively related to inundation on the higher parts of the excavated sites. The herbivores negatively affected establishment and growth of hawthorn. Although lowering the floodplain by excavation will increase discharge capacity of the floodplain in the short term, it will decrease in the long term as excavation also increases opportunities for floodplain forest. If flood prevention and nature rehabilitation are both goals to be achieved in a floodplain, hawthorn encroachment can be controlled by a clever design of the measures and grazing management.

### Introduction

Natural large rivers are important for nature conservation because of their high biodiversity and their corridor function (e.g. Dynesius and Nilsson 1994; Naiman and Décamps 1997; Hughes et al. 2001; Tockner and Stanford 2002). Large rivers and their floodplains also have high economic value as they are used for shipping, agriculture, industrial activities, urbanization and recreation (e.g. De Waal et al. 1995; Naiman et al. 2002; Tockner and Stanford 2002). In the past few centuries, the large natural rivers and floodplains have dramatically changed through embankments, canalizations, dams, weirs, groynes, and reclamation of the floodplain for agriculture (e.g. Dynesius and Nilsson 1994; Rosenberg et al. 2000; Tockner and Stanford 2002; Bunting et al. 2013). As a consequence, natural floodplains have become endangered landscapes, and many riverine habitat types such as floodplain forest have become rare (e.g. Dynesius and Nilsson 1994; Brown et al. 1997; Olson and Dinerstein 1998; Tockner and Stanford 2002; Bunting et al. 2013). Restoration and conservation of these floodplain forests have become an important goal in river management (e.g. Brown et al. 1997; Leyer et al. 2012; Bunting et al. 2013).

However, floodplain forest can seriously obstruct water flow and reduce the discharge capacity of rivers, resulting in high water levels and associated safety risks (Makaske et al. 2011; Leyer et al. 2012). In order to achieve the safety goals, control of establishment and growth of woody species is sometimes needed. Especially of thorny shrubs such as hawthorn (*Crataegus monogyna* Jacq.), as they have the highest hydraulic roughness of different floodplain vegetation types (Van Velzen et al. 2003).

In many conservation areas in the Dutch floodplains, year-round grazing with low numbers of cattle and horses (<0.4 per ha; Kuiters et al. 2003) is used as a management tool to control vegetation development. Some shrub and tree species such as *Salix* spp. or *Populus* spp. can easily be suppressed by large herbivores (Van Splunder 1998; Baraza et al. 2006; Cornelissen et al. 2014a, b), but others, like hawthorn, have found to be relatively resistant to grazing because of its thorns (Gill 2006; Hester et al. 2006). Because of this physical defence mechanism, hawthorn and other thorny shrubs also play an important role in the woodland-grassland cycle of the wood-pasture hypothesis of Vera (2000). Once established in grazed areas, hawthorn can serve as refugium, protecting other, more palatable tree species (Baraza et al. 2006; Gill 2006) and initiate forest development.

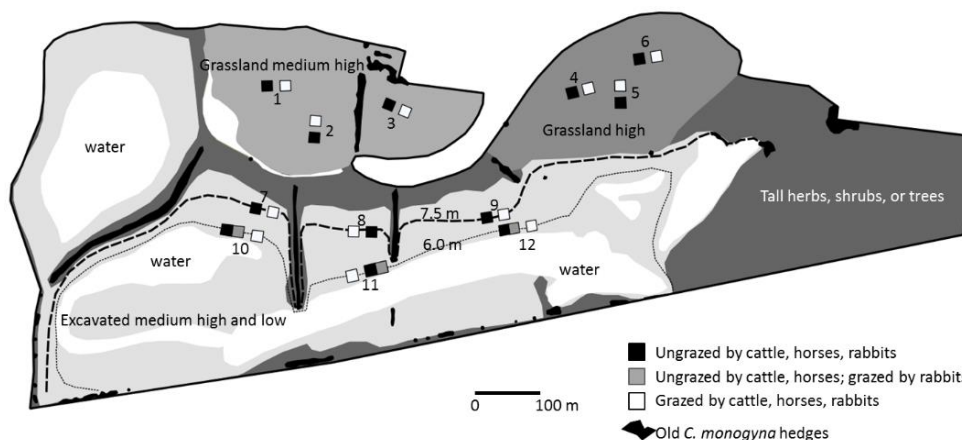
In order to optimize both safety and ecological values, it is important to monitor wood encroachment after restoration measures for safety and ecology are taken and grazing management has started. In general, establishment and growth of shrubs and trees in floodplains largely depend on flooding, substrate, light and root competition with grasses and tall herbs, and herbivores, especially during the early life stages of the woody species (Jones et al. 1989; Streng et al. 1989; Siebel, 1998; Van Splunder 1998; Hughes et al. 2001; Vreugdenhil et al. 2006).

To understand the impact of grazing, inundation and vegetation on wood encroachment, we carried out an enclosure experiment over a twelve year period in a restored and year-round grazed floodplain along the river Waal in the Netherlands. We focused on the thorny shrub hawthorn because of its high flow resistance and its role in the wood-pasture hypothesis. This shrub is less flood tolerant than softwood species (Vreugdenhil *et al.* 2006). Hawthorn germinates on bare soil and in grazed grasslands, and survival of seedlings is low in shaded environments (Watt 1934). Hawthorn can resist grazing pressure better than non-thorny softwood species, (Good et al., 1990; Baraza et al. 2006). We expected that: (1) in the excavated areas with bare sandy soils and low cover of tall herbs, more hawthorn establish than in the non-excavated, vegetated areas with high cover of tall herbs; (2) establishment of hawthorn is negatively related to inundation; (3) cattle and horses affect the establishment and growth of hawthorn; (4) in the grazed grasslands more hawthorn establish than in the ungrazed grasslands.

## Material and methods

### *Study area*

The study was conducted in the floodplain of the Afferdense and Deestse Waarden (51°53'44" N; 5°37'40" E) along the river Waal in the Netherlands. The study area was approximately 46 ha. In 1996, 23 ha of this area, originally covered with grasslands, was excavated and the first section of a new side channel was dug out within the lowered floodplain to enlarge the discharge capacity and create opportunities for nature development (Fig. 1).



**Fig. 1.** Location of the strata grassland high, grassland medium high, excavated medium high, excavated low, and blocks (nr 1-12) in the study area. The blocks consist of grazed and ungrazed plots indicated by the black, grey and white squares. The dashed lines in the excavated part of the floodplain indicate the elevation levels of 6.0 m (low) and 7.5 m (medium high) + NAP.

The unexcavated parts of the study area consisted of nutrient rich clayey soils and the excavated parts of nutrient poor sandy soils (Table 1). Water levels of the river Waal at the study area varied within and among years (see appendix). High levels were reached during winter and low levels during summer. Average water levels were higher during 1999-2003 and lower during 1996-1998 and 2003-2007.

On the nutrient rich soils the vegetation consisted mainly of short grasslands (e.g. *Lolium perenne* L., *Poa trivialis* L., *Festuca rubra* L., *Trifolium repens* L., *Potentilla reptans* L., *Taraxacum* spp., *Cirsium arvense* (L.) Scop., *Urtica dioica* L.; 12 ha), and a mosaic of tall herbs, tall grasses, and willows (e.g. *C. arvense*, *U. dioica*, *Symphytum officinale* L., *Phalaris arundinacea*, *Glyceria maxima* (Hartm.) Holmb., *Salix* spp.; 11 ha). On the excavated areas, vegetation was almost absent during the first year. In the second year, pioneer species (e.g. *Chenopodium album* L., *Erigeron canadensis* (L.) Cronq., *Matricaria maritima* (L.) W.D.J.Koch, *Rumex maritimus* L.) colonized the area. Within the study area, some old hawthorn shrubs and hedges were present. These were remnants of the former agricultural landscape.

Before 1996, the study area was grazed by high numbers (1-2 animals/ha) of dairy cattle, and parts of the grasslands that were invaded by tall herbs such as *C. arvense* or *U. dioica*, were mown. After 1996, the study area was grazed during summer (April-November) by privately owned cattle (c.15 cows) and horses (c. 20 mares). During winter (November-March), the owner moved the cattle to the farm for supplementary feeding and shelter, but the horses remained in the area. The horses did not get supplementary feeding and the grasslands were not mown anymore.

**Table 1** Characteristics strata study area. Inundation characteristics are averages and standard errors of mean (within parentheses) over the period 1996-2007. NAP is the Dutch reference level for elevation, which is about sea level.

		Strata			
		Not excavated		Excavated	
		high	medium high	medium high	low
-Vegetation 1996		Grassland	Grassland	Bare soil	Bare soil
-Soil (% lutum (<2µm))		26	25	4	3
-Elevation (m +NAP)		9.0	7.5	7.5	6.0
-Total inundation (days)	January-December	7 (2)	27 (6)	27 (6)	83 (13)
	March-October	3 (1)	12 (4)	12 (4)	42 (10)
-Inundation frequency (N)	January-December	1 (<1)	3 (1)	3 (1)	7 (1)
	March-October	1 (<1)	1 (<1)	1 (<1)	4 (1)
-Average length inundation event (days)	January-December	5 (1)	8 (1)	8 (1)	14 (2)
	March-October	3 (1)	5 (1)	5 (1)	12 (3)
-Average water depth during inundation (cm)	January-December	16 (6)	93 (11)	93 (11)	115 (9)
	March-October	5 (4)	65 (15)	65 (15)	88 (12)

#### *Exclosure experiment*

We carried out an exclosure experiment to describe the effects of herbivores, vegetation and inundation on establishment and growth of woody species. The experiment consisted of 12 blocks (i.e. experimental unit; Hurlbert 1984) to test the effect of herbivores. Each block consisted of an ungrazed (exclosure) and a grazed plot (both 15x15 m). The grazed plot was randomly placed at a distance of 10 m from the exclosure. All exclosures were made to exclude not only cattle, horses but also small herbivores such as rabbits and hares.

Based on elevation and excavation, we distinguished four different strata: (1) excavated low; (2) excavated medium high; (3) grassland medium high; (4) grassland high (Fig. 1, Table 1). The strata grassland low and excavated high were not present in the study area. Although the strata are not replicated, as replication was not possible on this scale, we used these strata in our experiment to describe the effects of inundation and vegetation, next to herbivores, on establishment and growth of woody species in this floodplain. To describe the effect of vegetation and grazing by all herbivores on vegetation and hawthorn, we compared the stratum grassland medium high with excavated medium high. To describe the effect of inundation and grazing by all herbivores on vegetation and hawthorn, we compared the stratum excavated medium high with excavated low. The stratum grassland high was not used in these tests as no hawthorn established in this stratum. To analyse these effects, in each stratum 3 blocks were randomly placed after the excavation in the summer of 1996.

In the stratum 'excavated low' we expected high numbers of established *Salix* spp. and a rapid increase in cover and height of these species immediately after excavation (Van Splunder 1998). To investigate the effect of small herbivores on these fast colonizing, palatable softwood species, we added an extra exclosure to the blocks in this stratum, excluding only cattle and horses.



### *Inundation*

River water level data were obtained from the Ministry of Infrastructure and the Environment. We determined total number of days with inundation, number of inundation events (frequency), average length of inundation events and average water depth during inundation as they explained most of the variation in establishment and growth in the other studies (e.g. Siebel 1998; Van Splunder 1998; Vreugdenhil et al. 2006). We also distinguished two periods for the inundation parameters: January-December and March-October (growing season).

### *Herbivore numbers and daily energy expenditure*

The number of cattle and horses stayed the same over the years from 1996 to 2007 (see section study area). We counted the numbers of hares and rabbits during evenings in winter (December-January) using a light. In 1997, 1999 and 2007, eight counts per winter were carried out along a fixed route throughout the whole study area. Within the floodplain, no roe deer (*Capreolus capreolus* L.) or beaver (*Castor fiber* L.) were present (pers. comm. State Forestry Service).

To compare the impact of grazing by large and small herbivores and to compare our results with others (e.g. Bakker *et al.* 2004), we transformed herbivore densities into daily energy expenditure (DEE). According to Bakker *et al.* (2004), the amount of energy an average animal spends daily is two times basal metabolic rate (BMR):  $DEE = 2 \times 2930 \times W^{0.75}$  kJ per day. For cows and mares of different ages (1-15 years old) we assumed an average weight of 350 kg based on Cornelissen *et al.* (1995), for rabbits we used an average weight of 1.5 kg (Wallage-Drees 1988) and for hares 4 kg (Lange *et al.* 1994).

### *Vegetation surveys*

In August 1997, 1999, 2001 and 2007, we assessed vegetation cover and height of two structural layers: (1) low grasses and low herbs; (2) tall herbs. We established four permanent quadrats of 2x2m within the ungrazed plot at 2 m distance from the fence of the enclosure, and in the same way within the grazed plot. Cover was estimated (vertical projection on the ground in percentages) and height was measured with a ruler and a polystyrene disk (radius 50 cm, weight 320 g) which was lowered over the ruler on to the sward. When the disk could not be lowered on to the sward, the height was measured with the ruler. Average cover and height were calculated for each ungrazed and grazed plot. These averages were used to calculate averages and standard errors of cover and height of grazed and ungrazed vegetation for each stratum.

In August 2007, cover and height of all woody species were assessed in the total area (15x15 m) of the ungrazed and grazed plot. Cover was estimated visually as a percentage of the area of ground occupied. Heights of woody plants were measured with a ruler. The measurements per ungrazed and grazed plot were used to calculate averages and standard errors of cover and height of woody species in grazed and ungrazed plots per stratum.

In November 2007, all hawthorn plants present in the ungrazed and grazed plots were harvested for age determination to investigate the effect of inundation, vegetation and grazing on establishment and growth. Height, crown diameter (mean of maximum and minimum diameter), stem circumference and total number of twigs (up to 2 m height) were measured before the destructive harvest. Circumference was later transformed into an

average stem diameter, as it is an important parameter for determining the hydraulic roughness of the shrub.

The used nomenclature for plant species was according to Van der Meijden (2005).

#### *Age determinations of hawthorn*

Age determination of hawthorn was based on growth rings and was carried out as described by Decuyper et al. (2014).

#### *Statistical analysis*

We used Generalized Linear Models with a poisson distribution and a log-link function to test the effects of elevation (medium high or low), excavation (yes or no) and herbivores (yes or no) on total number established hawthorn in 2007; the test showed that there was no overdispersion. We also nested block within excavation or elevation to correct for possible random variation among blocks.

To test the effect of grazing by rabbits on the total number of established hawthorn in 2007, we compared the ungrazed and grazed plots in the stratum excavated low. We used Generalized Linear Models with a negative binomial distribution and a log-link function to test these effects because of overdispersion. Grazing (yes or no) was used as predictor. Block was also incorporated to correct for possible random variation among blocks.

General Linear Model Repeated Measures was used to test the effects of excavation or elevation and herbivores (between-subjects factors) and year (within-subjects factor) on the dependent variables cover and height of low grasses and herbs and tall herbs. We nested block within excavation or elevation to correct for possible random variation among blocks. To meet the assumptions of the statistical test, data in percentages were arcsine transformed (Sokal and Rohlf 1981).

General Linear Model Univariate procedure was used to test differences between slopes or intercepts of the different relations between inundation and established hawthorn or hawthorn growth. Non-linear relations were transformed to get linear relationships before testing differences between slopes or intercepts.

All data were analysed using SPSS for Windows version 23 (Norusis 1996). All error bars in graphs represent Standard Errors of Mean (SEM).

## **Results**

#### *Herbivore numbers and DEE*

Horses grazed the area year-round in the same numbers every year: 20 mares. Cattle grazed the area from April till November in the same numbers every year: 15 cows. During the winters of 1997/1998, 1999/2000 and 2007/2008, average rabbit numbers within the study area were respectively 35, 25 and 90. Hares were almost not present (average <1).

During summer, DEE per day of the 35 large herbivores was about 1650 MJ for the whole study area, and during winter DEE was about 950 MJ. DEE of rabbits varied between 20 and 70 MJ for the whole study area. During winter, total DEE of mares was about 15-50 times higher than that of rabbits. As DEE of the large herbivores almost doubled during summer, the difference between large and small herbivores probably will have been even greater during that period.

*Established woody species*

The results of the survey in 2007 (Table 2) reflect the net effect of establishment and mortality and the net effect of growth and losses over 12 years. In general, less woody species established on the grasslands than on the excavated strata. Within the grasslands, no woody species established at all on grassland high. On the excavated substrates, thorny shrubs established more on the medium high level and *Salix* spp. more on the low level. Heights of woody species varied among strata and between grazed and ungrazed.

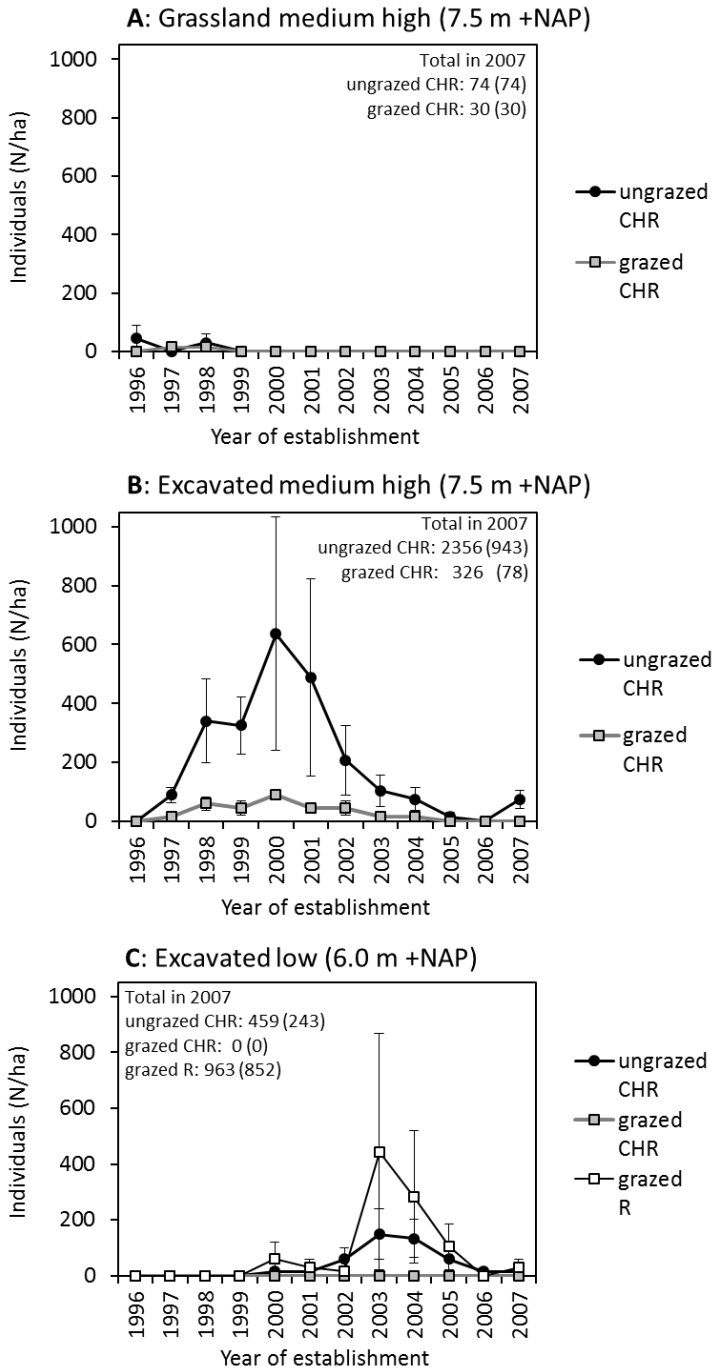
**Table 2** Average cover and height of woody species in 2007. SEM is given in parentheses. C = cattle; H = horses; R = rabbits.

Habitat Elevation Grazed/ungrazed Herbivores	Strata								
	Grassland High		Grassland Medium high		Excavated Medium high		Excavated High		
	Ungr.	Gr CHR	Ungr	Gr CHR	Ungr	Gr CHR	Ungr	Gr CHR	Gr R
	<b>Cover (%)</b>								
<i>Crataegus monogyna</i>	0	0	5 (5)	2 (1)	15 (6)	2 (1)	3 (2)	0	3 (2)
<i>Rosa canina</i>	0	0	0	0	9 (6)	7 (3)	1 (<1)	0	1 (<1)
<i>Rubus ceasius</i>	0	0	19 (18)	0	7 (3)	1 (1)	4 (<1)	0	3 (1)
<i>Cornus sanguinea</i>	0	0	0	0	<1 (<1)	0	0	0	0
<i>Sorbus aucuparia</i>	0	0	0	0	0	0	<1 (<1)	0	0
<i>Fraxinus excelsior</i>	0	0	0	0	0	0	0	0	<1 (<1)
<i>Populus nigra</i>	0	0	0	0	0	0	<1 (<1)	0	1 (1)
<i>Salix</i> spp.	0	0	0	0	10 (5)	0	40 (15)	3 (1)	32 (9)
<b>Total woody cover</b>	<b>0</b>	<b>0</b>	<b>21</b> (20)	<b>2</b> (2)	<b>28</b> (9)	<b>9</b> (3)	<b>43</b> (16)	<b>3</b> (1)	<b>34</b> (11)
	<b>Height (cm)</b>								
<i>Crataegus monogyna</i>			450 (-)	412 (-)	120 (20)	78 (26)	47 (125)		77 (27)
<i>Rosa canina</i>					150 (29)	147 (29)	83 (13)		105 (18)
<i>Rubus ceasius</i>			85 (5)		37 (13)	20 (-)	53 (12)		53 (12)
<i>Cornus sanguinea</i>					65 (-)				
<i>Sorbus aucuparia</i>							60 (-)		
<i>Fraxinus excelsior</i>									20 (-)
<i>Populus nigra</i>							390 (-)		275 (-)
<i>Salix</i> spp.					300 (50)		483 (17)	12 (2)	427 (18)

**Table 3** P-values Generalized Linear Model with Poisson distribution and log-link for total number of established hawthorn in 2007. G = grazing (yes or no); E = elevation (7.5 m or 6.0 m) or excavation (yes or no); GxE = interaction effect; Block was nested within the factor Elevation or Excavation to correct for possible random variation among blocks. The bold p-values highlight that the effects are significant.

	G	Elevation	E Excavation	G x E	Block (E)
Grassland 7.5 m vs Excavated 7.5 m	<b>0.0006</b>		<b>&lt;0.0001</b>	0.2344	<b>&lt;0.0001</b>
Excavated 7.5 m vs Excavated 6.0 m	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>		a	<b>&lt;0.0001</b>

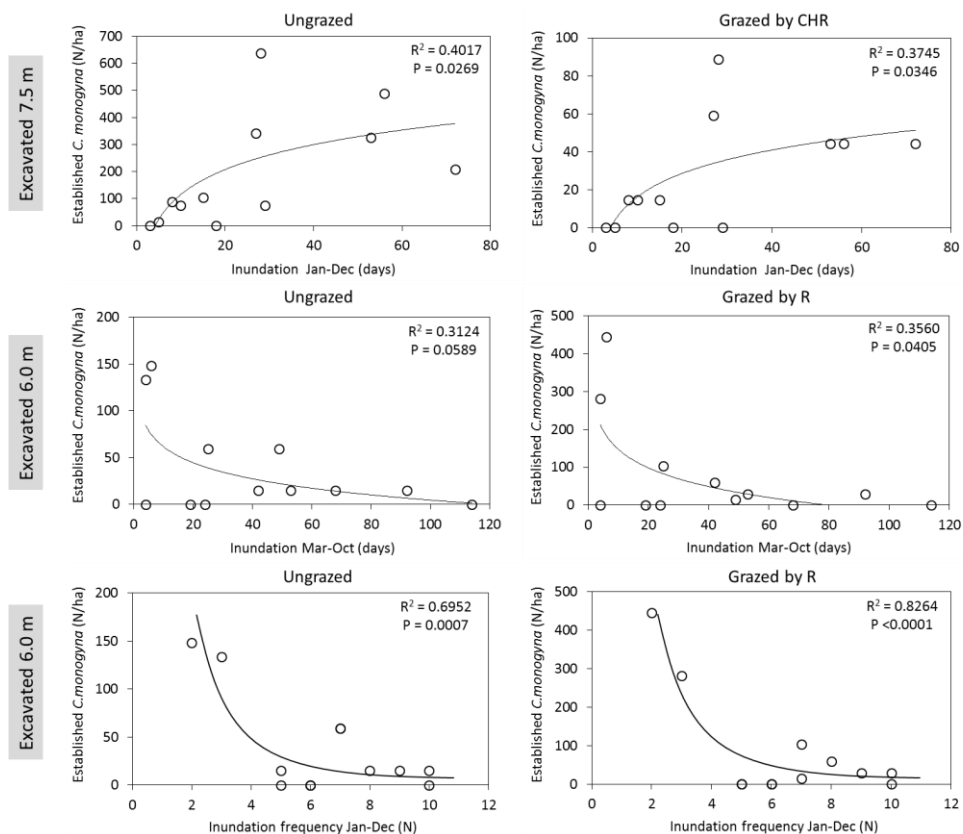
a) Unable to compute due to absence of hawthorn in grazed excavated 6.0 m



**Fig. 2.** Established hawthorn in different strata and for different years of establishment. C=cattle, H=horses, R=rabbits. In the corner of the graphs the average total number of hawthorn, established over the period 1996-2007, is given; SEM within parentheses.

### Effects of rabbits

Total number of established hawthorn in 2007 in the plots grazed by rabbits (Fig. 2) was not different from the ungrazed plots ( $P = 0.9882$ ). Growth parameters of hawthorn in the plots grazed by rabbits were not different from the ungrazed plots (see appendix). Cover and height of low grasses and herbs and of tall herbs in plots grazed by rabbits (Fig. 4) were not different from the ungrazed plots (Table 4).



**Fig 3.** Relations between inundation and established hawthorn (top and middle) and between inundation frequency and established hawthorn (bottom) in ungrazed and grazed strata. Establishment of hawthorn during the period 1996-2007. C=cattle, H=horses, R=rabbits. Note differences Y- and X-axes.

### Effects of excavation, inundation and large herbivore grazing

The total number of established hawthorn over the period 1996-2007 was affected by herbivores and elevation or excavation and was highest on the ungrazed excavated medium high stratum and absent on grassland high and on the grazed excavated low stratum (Fig. 2, Table 3). The years in which hawthorn established differed among strata (Fig. 2). On grassland

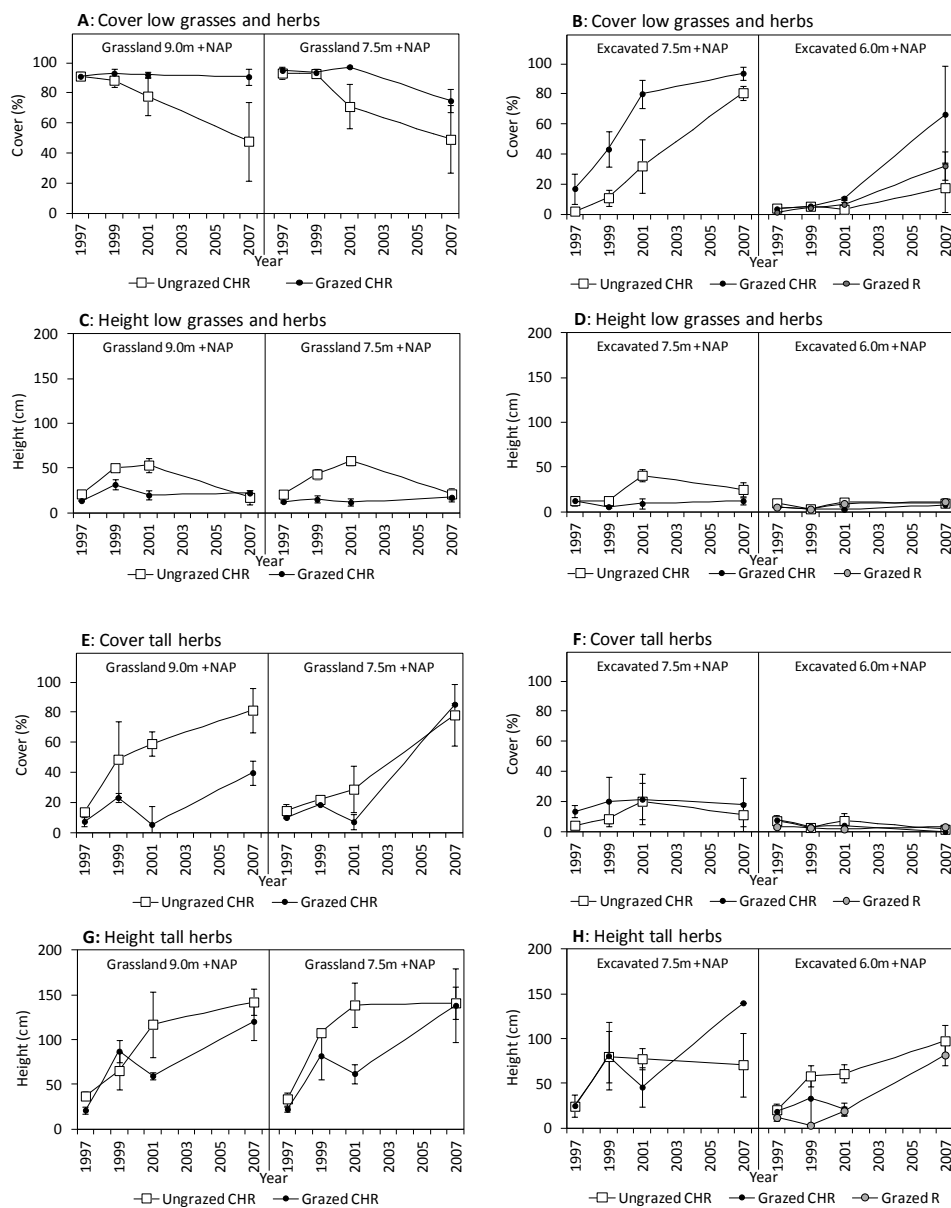
medium high, hawthorn only established during the first three years. On excavated medium high, they established almost during the whole period, but the highest numbers established between 1998-2002. On excavated low, most of the hawthorns established between 2002-2005.

Establishment on the excavated strata was related to water level dynamics. In general, more hawthorn established on the less inundated excavated medium high stratum than on the more inundated excavated low stratum, indicating a negative relation to inundation (Fig. 2, Table 3). However, if we look in detail, establishment on excavated medium high was positively related to inundation whereas on excavated low it was negatively related (Fig. 3). In the grazed excavated strata, relationships were the same as in the ungrazed strata.

Of the growth parameters only height was affected (see appendix). In the ungrazed sites, shrubs were 50-100 cm lower on excavated medium high than on excavated low. On excavated medium high, shrubs were 25-50 cm higher in the ungrazed than in the sites grazed by all herbivores.

Cover and height of the grass and herb layers differed between strata, years and between grazed and ungrazed sites (Fig. 4; Table 4). The cover of low grasses and herbs decreased in the grasslands and increased on the excavated strata. On the grasslands, the decrease of cover was greater in the ungrazed than in the grazed sites. On the excavated strata, the increase of cover was lower in the ungrazed than in the grazed sites. The height of the low grasses and herbs was greater in the grasslands than in the excavated strata and height was also greater in ungrazed than in grazed sites.

The cover and height of tall herbs increased strongly on the grasslands. On the excavated strata, cover was stable, but height increased.



**Fig. 4.** Development of cover and height of the structural layers ‘low grasses and herbs’ and ‘tall herbs’ for different strata and in grazed and ungrazed situations. C=cattle, H=horses, R=rabbits.



**Table 4** P-values General Linear Model Repeated Measures for the effects of grazing and elevation or excavation on cover and height of low grasses and herbs and tall herbs. **A, B** and **C** show the results of the comparisons between different strata. Grazing = grazed or ungrazed by cattle, horses and rabbits. Elevation = 9.0 m vs 7.5 m or 7.5 m vs 6.0 m. Excavation = yes or no. Year = 1997, 1999, 2001, 2007. **D** shows the results of the comparison between plots grazed by rabbits and ungrazed plots on the stratum excavated low.

	Grasses and herbs		Tall Herbs	
	Cover	Height	Cover	Height
<b>A. Grassland 9.0 m vs Grassland 7.5 m</b>				
<i>Test of Between-Subjects Effects</i>				
Grazing	0.4770	<b>0.0005</b>	<b>0.0170</b>	<b>0.0225</b>
Elevation	0.9207	0.4264	0.7119	0.2218
Grazing x Elevation	0.8899	0.2662	<b>0.0267</b>	0.4567
Block (within Elevation)	0.7144	0.9951	0.2132	0.3905
<i>Test of Within-Subjects Effect</i>				
Year	<b>0.0016</b>	<b>&lt;0.0001</b>	<b>0.0001</b>	<b>&lt;0.0001</b>
Year x Grazing	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	0.3875	<b>0.0105</b>
Year x Elevation	0.9627	0.3046	0.0900	0.7185
Year x Grazing x Elevation	0.8761	0.9555	0.6587	0.2826
<b>B. Grassland 7.5 m vs Excavated 7.5 m</b>				
<i>Test of Between-Subjects Effects</i>				
Grazing	<b>0.0495</b>	<b>0.0083</b>	0.8015	<b>0.0233</b>
Excavation	<b>0.0065</b>	<b>0.0436</b>	<b>0.0262</b>	<b>0.0489</b>
Grazing x Excavation	0.1543	<b>0.0318</b>	0.5611	0.1062
Block (within Excavation)	0.8496	0.9300	0.3488	0.4961
<i>Test of Within-Subjects Effect</i>				
Year	<b>&lt;0.0001</b>	0.1676	<b>0.0060</b>	<b>0.0001</b>
Year x Grazing	<b>0.0003</b>	<b>0.0241</b>	0.7302	<b>0.0324</b>
Year x Excavation	<b>0.0002</b>	0.0602	<b>0.0023</b>	0.1371
Year x Grazing x Excavation	<b>0.0022</b>	<b>0.0336</b>	0.7909	0.6087
<b>C. Excavated 7.5 m vs Excavated 6.0 m</b>				
<i>Test of Between-Subjects Effects</i>				
Grazing	<b>0.0174</b>	0.3408	0.9297	<b>0.0103</b>
Elevation	<b>0.0087</b>	<b>0.0404</b>	0.2063	<b>0.0387</b>
Grazing x Elevation	0.4235	0.5569	0.3179	0.0577
Block (within Elevation)	0.5449	0.9099	0.3378	0.4482
<i>Test of Within-Subjects Effect</i>				
Year	<b>&lt;0.0001</b>	0.7767	0.1837	<b>0.0086</b>
Year x Grazing	0.1613	0.1971	0.4845	0.0734
Year x Elevation	<b>0.0057</b>	0.8392	0.3483	0.2544
Year x Grazing x Elevation	0.1359	0.4527	0.4091	0.0634
<b>D. Excavated 6.0 m: Grazed by Rabbits vs Ungrazed</b>				
<i>Test of Between-Subjects Effects</i>				
Grazing	0.3669	0.6077	0.4586	0.0657
Block	0.3889	0.9157	0.6732	0.0626
<i>Test of Within-Subjects Effects</i>				
Year	0.1503	0.0832	0.2286	0.1475
Year x Grazing	0.3470	0.4698	0.1414	0.4078

## Discussion

### *Effects of excavation*

Our study showed that in the excavated areas of the floodplain more hawthorn established than in the non-excavated areas, supporting our first expectation. Other woody species were also more present on the excavated areas than on the grasslands. After excavation, bare substrate was exposed over large areas for a few years, while the fertile soil layer was removed. The development of tall herb vegetation was much less than on the non-excavated grasslands, providing more opportunities for hawthorn and other woody species to establish. Similar effects of vegetation cover on establishment of woody species have been described in other studies (e.g. Siebel 1998; Bokdam and Gleichman 2000; Niinemets and Valladares 2006). In the non-excavated areas, the woody seedlings have to compete with tall herbs such as *C.arvense* and *U. dioica* for light and nutrients. These fast growing tall herbs are stronger competitors in a highly productive environment, such as the grasslands on the clayey soils, than the seedlings of woody species. We may conclude that the tall herb vegetation played an important role in the establishment of hawthorn and the other woody species.

Our detail study of hawthorn showed that more shrubs established on the medium high excavated sites than on the low excavated sites. This supports our second expectation that establishment is negatively affected by inundation. However, when looking in more detail to this relationship, the negative relation was true for the excavated low sites, but not for the medium high excavated sites, where the relation was positive. We assume that on excavated low sites and during periods with high water levels, inundation was sufficiently frequent, to prevent seeds to germinate and establish as more inundation causes mortality of seedlings due to drowning or oxygen deprivation in the soil (Niinemets and Valladares 2006; Vreugdenhil et al. 2006). Only during periods with relatively low water levels (2003-2007), hawthorn established on the low excavated sites and survived afterwards. The less frequent inundation on excavated medium high probably caused the higher survival of hawthorn than on the excavated low sites, but this does not explain the positive relation between inundation and establishment. A potential explanation for this positive relation could be seed dispersal by water. During field observations (pers. obs. P. Cornelissen), fruits were found in drift line material. As fruits of hawthorn can also be dispersed by water, lower water levels can lead to less or no seed deposition by water on the higher grounds. Although hawthorn seeds can also be dispersed by wind (very short distances), birds and mammals (short and long distances; Good et al. 1990; Martinez et al. 2008), only water can disperse large amounts of seeds at once over longer distances.

On grassland medium high, a similar positive relation between inundation and seed deposition exists. The effect, however, is different from that on excavated medium high. The difference may be explained by the greater increase of cover and height of tall herbs on the grasslands than on the excavated sites.

Inundation also affected the height of hawthorn. Our results showed that height was greater on the excavated low than on the excavated medium high sites. This could be explained by shoot elongation to overcome flooding events. This was demonstrated by Siebel (1998), where partially submerged seedlings of *Q. robur* and *Fraxinus excelsior* L. showed a significantly larger increase in stem length than unflooded ones. Probably, hawthorn uses the same mechanism to overcome inundation.

### *Effects of grazing*

On the excavated low sites, rabbits did not affect the establishment and growth of hawthorn, and the cover and height of grasses and herbs. Therefore, we conclude that the described herbivore effects on establishment and growth of hawthorn were caused by cattle and horses, supporting the third expectation. Bakker et al. (2004) showed negative effects of rabbits on woody species that equalled those of cattle. However, in their study area DEE of rabbits equalled that of cattle, whereas in our study area DEE of rabbits was >15 times lower than that of cattle and horses during winter. Kuiters and Slim (2003) reported significant effects of rabbits on tree regeneration only at very high densities of 50 rabbits per ha, which is about 25 times higher than in our study area.

On the grasslands, too few hawthorn established to test our fourth expectation. According to the wood-pasture theory (Vera 2000), large herbivores play a key role as a causal factor for the development of park-like landscapes with shrub and tree regeneration in grazed grasslands. Vera (2000) and Olff et al. (1999) also mention that the intensively grazed grasslands in the woodland-grassland cycle need a temporary reduction of the large herbivore densities to create a 'window of opportunity' for the (re-) establishment of shrubs and trees. In our study area, the change in grazing management in 1996 from intensively to extensively grazed, could have been the reason for hawthorn to establish on grassland medium high during the first three years of the research period, when cover and height of tall herbs were still low. In the ungrazed plots after 1998, the cover of tall herbs had already increased up to more than 20% and heights exceeding 1 m. Apparently, this was enough to prevent hawthorn or other woody shrubs and trees to establish. In the grazed plots, the cover and height of tall herbs decreased again in 2001, but this did not lead to new establishments of hawthorn, or other woody species, in the grazed plots. This could be explained by the fact that within these grazed sites, locations with dominance of tall herbs prevented survival of seedlings through competition for light, while on the locations with dominance of low grasses and herbs, grazing pressure was too high, indicated by the low height of the low grasses and herbs, for seedling survival. The fact that no woody species established on grassland high was probably caused by a faster increase of cover and height of the tall herb layer and absence of input of large numbers of seeds by water (for example hawthorn) during the first years compared with grassland medium high.

### *Implications for management*

Our study confirmed that excavation, which increases the discharge capacity of the floodplain, also increased opportunities for shrub and tree regeneration and floodplain forest development. For safety purposes, control of the woody species is necessary as shrubs and trees can seriously obstruct water flow and reduce the discharge capacity of the river. Our research showed that large herbivores can control wood encroachment, but much depends on the grazing management regime. Although there was a strong negative effect on establishment of hawthorn, the numbers of cattle and horses were not sufficiently high to permanently stop the development or reduce growth of this shrub. To suppress hawthorn, more animals and herbivore types (grazers, intermediate feeders and browsers; large and small herbivores) are needed (e.g. Good et al. 1990; Williams et al. 2010; Cornelissen et al. 2014a).

To resolve the wood encroachment problem in floodplains with a safety goal, several solutions are available, aiming at minimizing establishment and growth. First of all, it is

possible to reduce the areas with the elevation that give the highest opportunities for establishment of shrubs and trees. Another possible measure is to replace the clayey top layers, that were initially removed, back onto the excavated area. This will enhance a rapid recovery of the grass and herb layer, diminishing the opportunities for establishment and growth of woody species. A third option is periodically lowering large areas of the floodplain or digging side channels to increase the flow capacity of the floodplain so that a larger area with forest development is acceptable. This measure is also known as the “cyclic floodplain rejuvenation” (Baptist et al. 2004). Finally, grazing regimes can be introduced with a higher capacity to control woody plants. A herbivore assemblage with higher numbers of cattle and horses (>1 animal per ha), more intermediate feeders (e.g. red deer), browsers (e.g. roe deer) and small herbivores (beavers, rabbits and hares) will stimulate browsing. Preferentially, these grazing regimes should start immediately after excavation to control establishment for several years, at least until vegetation cover has developed to a sufficient level.

For rehabilitation of the natural floodplain forests, lowering the floodplain and digging side channels are ideal measures for shrub and tree regeneration in grazed systems. Our research showed that hawthorn, a key species of the wood-pasture hypothesis (Vera 2000), can establish in high numbers, creating opportunities for the establishment of palatable and less protected hardwood tree species (Barbosa et al. 2009) and initiate floodplain forest development in these grazed areas.

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Appendix 1

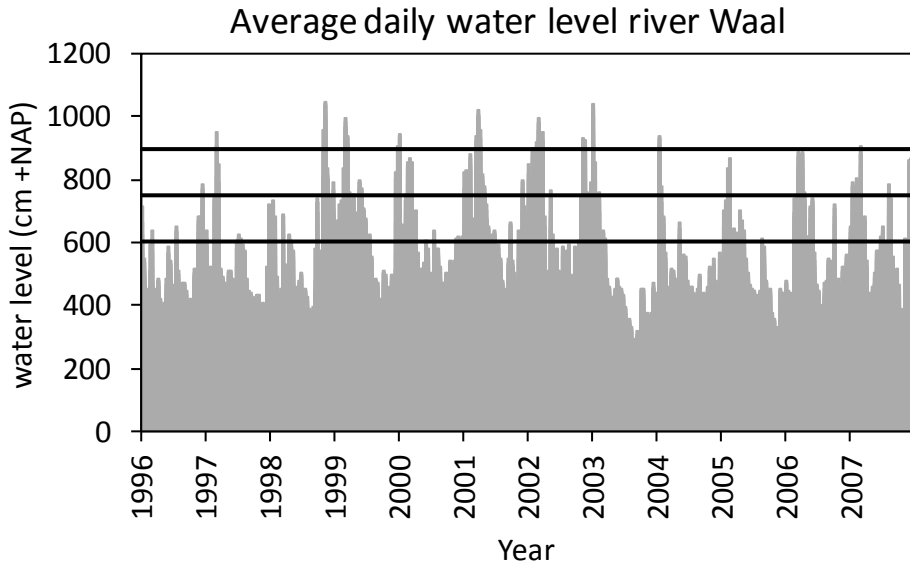
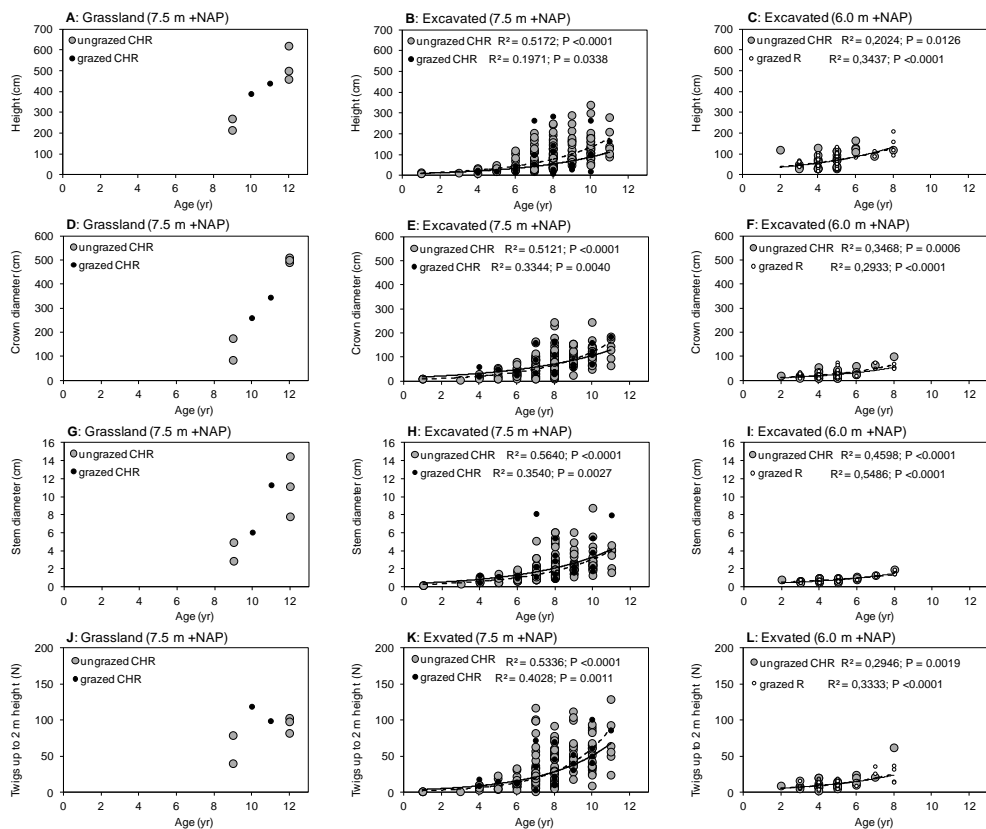


Fig. A. Average daily water level of the river Waal at the Afferdense and Deestse Waarden. The horizontal lines show the surface levels of the different strata at 6.0, 7.5 and 9.0 m +NAP.



**Fig. B.** Height (A-C), crown diameter (D-F), stem diameter (G-I) and twigs (J-L) of hawthorn in relation to age for different strata and in grazed and ungrazed situations. C=cattle, H=horses, R=rabbits. Within the graphs  $R^2$  and P-values are given for the relations. See table A (below) for results testing differences between relations.

**Table A** P-values General Linear Model Univariate for testing differences in slopes and intercepts of regression lines between strata and between grazed and ungrazed (see Fig. B above). CHR = cattle, horses and rabbits. R = rabbits The bold P-values highlight that the differences are significant.

	Excavated medium high vs excavated low for ungrazed CHR		Ungrazed CHR vs Grazed CHR on excavated medium high		Ungrazed CHR vs Grazed R on excavated low	
	Slopes	Intercepts	Slopes	Intercepts	Slopes	Intercepts
Height	0.4633	<b>&lt;0.0001</b>	0.5355	<b>0.0159</b>	0.8290	0.9007
Crown	0.7795	0.7965	0.1495	0.4985	0.8167	0.2819
Stem	0.1001	0.5687	0.4353	0.1097	0.2806	0.3595
Twigs	0.6137	0.0771	0.2380	0.8725	0.7902	0.9641



## CHAPTER 5

### DENSITY-DEPENDENT DIET SELECTION AND BODY CONDITION OF CATTLE AND HORSES IN HETEROGENEOUS LANDSCAPES

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*Applied Animal Behaviour Science*, 2015, 163, 28-38

#### **Abstract**

For some decades, grazing by cattle and horses is used as a management tool to achieve different nature management goals. For managers there are still questions to be answered about the effects of herbivore densities on their performance, vegetation development and biodiversity. This study examines the effect of density on diet composition, diet quality and body condition of cattle and horses. We expressed density as the ratio between consumption and net primary production of the preferred grasslands. Over a period of one year, we studied sward height and diet composition, diet quality and body condition of free ranging cattle and horses in two different study areas with different ratios between consumption and production. Our results showed that the amount of preferred high quality grasses in the diet of cattle and horses was lower when herbivore density was higher. As a result diet quality was lower and as a result of that body condition was affected. In October body condition of cows was lower and in March body of cows and mares was lower in the high density area. A striking difference between cattle and horses was that during the growing season and at high densities, the amount of preferred grasses in the diet of cattle decreased whereas that of horses increased. This was most likely caused by sward height which became probably too low for cattle. As cattle prefer grass heights of 9-16 cm, grass heights lower than those make it difficult for cattle to achieve a sufficient instantaneous intake rate. This means that in homogeneous areas and at high herbivore densities, horses can outcompete cattle. In this paper the effects of density dependent diet selection on vegetation development and conservation management are discussed.

#### **Introduction**

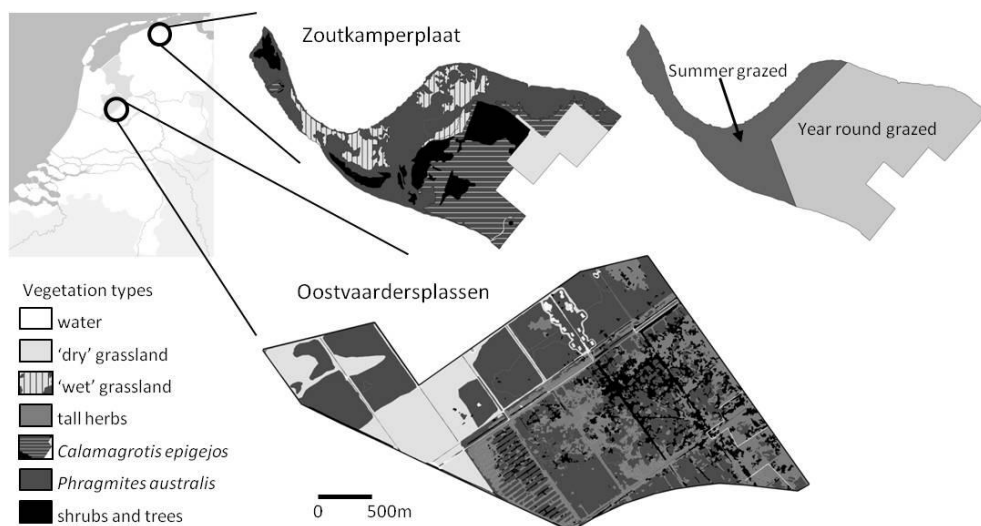
In many European countries, controlled grazing by large herbivores in conservation areas is practised to achieve nature management goals (e.g. Bülow-Olsen 1980; Thalen 1984; Welch 1997; WallisDeVries et al. 1998; Gerken and Görner 2001). Recently, year-round grazing with self-regulating populations of large herbivores as a goal in itself, has received much attention (e.g. Vera 1997; Olff et al. 1999; Kirby 2004; Hodder and Bullock 2009; Rotherham 2013). Although both management options are practiced, we still know little about the effects of herbivore species, assemblages and densities on vegetation development, biodiversity and performance of the herbivores; especially the long term effects (Hodder and Bullock 2009).

Foraging behaviour of large herbivores is an important determinant in the selection of habitats (Bailey and Provenza 2008) and determines growth, survival and reproduction of the animal (Prins and Van Langevelde 2008a). There are several foraging behaviour theories

(Charnov, 1976; Stephens and Krebs, 1986; Provenza, 1995; 1996) that explain how animals assemble a varied diet in order to maximize their fitness (Prins and Van Langevelde 2008b). In general, herbivores will select food that is rich in energy and proteins and low in toxins (Bailey and Provenza 2008). They will select low quality food as the quality or quantity of the preferred high quality food decreases and the low quality food becomes more profitable to achieve optimal fitness.

Cattle and horses are grazers specialized in diets with high cell wall contents (Hofmann 1989; Duncan 1992). They show a high preference for grasses (Duncan 1983; Putman 1996; Gordon 1989a; Van Wieren 1996). Although herbivores do not instantaneously respond to the availability per capita, the distribution and availability of these grasses per capita will affect diet composition and quality. Diet quality affects body condition (Klein 1970; Kie 1988; Prins 1996; WallisDeVries 1996; Stewart et al. 2005), which determines foraging activity, growth and reproduction (Kie et al. 2003, Roche et al. 2009). The effect of quantity of preferred food per capita on diet composition is well known for herbivores in the Northern hemisphere (e.g. Putman, 1996; Kie et al., 2003). For example the amount of grasses or forbs in the diet decreases during winter when the quantity of these forages decrease (Kie et al., 2003). Likewise, an increase in herbivore numbers leading to a decrease in forage availability per capita, will relate to a similar shift in diet composition. When the supply of grasses in grassland is abundant in relation to the number of herbivores, there will be little need for the herbivores to use less preferred vegetation types. But when the supply of grasses is low, herbivores will have to move to other less preferred vegetation types in order to meet their energy and nutrient demands. As horses are able to feed faster and therefore achieve a higher intake on short grassland swards than cattle (Menard et al. 2002), there could be an effect of sward height on diet selection. Gordon (1989b) showed that cattle left short grazed grasslands during winter and moved to grasslands with higher swards, while ponies remained on the short grazed grasslands. Menard et al. (2002) showed that horses preferred grasses shorter than 5 cm and cattle preferred grasses 9-16 cm in height. As sward heights on the preferred grasslands decrease, due to increased densities of large herbivores, sward height can become a constraint for cattle in an earlier stage than for horses.

In this study we examine the influence of herbivore density on diet selection, diet quality and body condition in free ranging cattle and horses in heterogeneous landscapes. We expected that the percentage of grasses in the diet, diet quality and body condition are lower in areas with high herbivore densities, and that on short swards horses will have higher amounts of grasses in the diet than cattle. We will discuss the effects of density dependent diet selection on vegetation development and conservation management.



**Fig. 1.** Location study areas and vegetation types May 1991 – April 1992. For Zoutkamperplaat grazing management is given in the right figure. During winter, part of the area (summer grazed area) was fenced off to prevent the animals escaping the area across the ice.

**Table 1** Vegetation types and plant species at the Zoutkamperplaat (ZKP) and Oostvaardersplassen (OVP). During winter (November-March), part of the Zoutkamperplaat was fenced off to prevent the animals escaping the area across the ice (see Fig. 1).

Vegetation type and species	ZKP (1991-1992)		OVP
	Apr-Oct	Nov-Mar	1991
<b>'Dry' grassland</b>	ha (%)	ha (%)	ha (%)
<i>Lolium perenne</i> , <i>Dactylus glomerata</i> , <i>Festuca rubra</i> , <i>F. arundiancea</i> , <i>Poa trivialis</i> , <i>Trifolium repens</i>	40(13)	40 (19)	135(21)
<b>'Wet' grassland</b>	40(13)	10(5)	
<i>Agrostis stolonifera</i> , <i>Juncus gerardi</i>			
<b>Reed</b>	120(37)	50(24)	195(30)
<i>Phragmites australis</i>			
<b>Bush grass</b>	120(37)	110(52)	
<i>Calamagrostis epigejos</i>			
<b>Mosaic vegetation</b>	<10(<1)	<10(<1)	320(49)
<i>Salix</i> spp., <i>Sambucus nigra</i> , <i>Hippophae rhamnoides</i> (ZKP only), <i>Cirsium</i> spp., <i>Urtica dioica</i> , <i>P. australis</i> , <i>P. trivialis</i>			
<b>Total area</b>	320(100)	210(100)	650(100)

## Materials and methods

### Study areas

The study was conducted in two managed wetlands in the Netherlands (Fig. 1), Zoutkamperplaat (53°20'N, 6°10'E), and Oostvaardersplassen (52°26'N, 5°26'N). Zoutkamperplaat (about 320 ha) is located on the borders of Lake Lauwersmeer. This lake was a former estuary, which was separated from the Waddensea in 1969. A few years after the lake was separated from the sea, salinity levels dropped to those of fresh water. Scottish Highland

cattle and Konik horses were introduced in 1989 and now graze year-round in the study area. In the months November-March, part of the area (approximately 110 ha; Fig. 1) was fenced off to prevent the animals escaping the area across the ice. Five vegetation types were distinguished in this study area: 'dry' grassland, 'wet' grassland, bush grass, reed and a mosaic of tall herbs, reed, shrubs and trees (Table 1). The difference between 'dry' and 'wet' grassland is that 'wet' grasslands are flooded during winter and the 'dry' grasslands are not. At the Zoutkamperplaat, part of the reed vegetation, located in the area that is fenced off during winter, is also flooded during winter. During summer, the depth to the ground water table was approximately 1.0 m. Soil fertility was relatively low and clay content varied between 5-8% for areas covered with the vegetation types 'wet' grassland and Reed (*Phragmites australis*) and between 8-15 % for areas covered with 'dry' grassland and Bush grass (*Calamagrostis epigejos*).

The Oostvaardersplassen nature reserve was established in 1968, when the polder "Zuidelijk Flevoland" was reclaimed from the freshwater Lake IJsselmeer. In 1983, year-round grazing with Heck cattle and Konik horses started in the dry border zone. The total area grazed by cattle and horses was approximately 650 ha. Three vegetation types were distinguished: 'dry' grassland; reed; and a mosaic of tall herbs, reed, shrubs and trees (Table 1). The depth to the ground water table was about 1.0 m during summer and 0.3 m during winter. The soil fertility was higher than that of the Zoutkamperplaat with clay contents that vary between 30 and 40%.

At the Zoutkamperplaat, stocking rate of cattle and horses was about 1.3 animals per ha on the preferred vegetation type 'dry' grassland (Table 2). At the Oostvaardersplassen, stocking rate was about 1.6 animals per ha. At the Zoutkamperplaat, animal numbers were controlled by the manager. At the Oostvaardersplassen, animal numbers were not controlled by the manager; the populations of Heck cattle and Konik horses were self-regulating. In both areas no large predators were present.

Body weight of mature Scottish Highland bulls was about 750 kg and of cows about 475 kg (Cornelissen et al. 1995). Body weight of Heck cattle was similar to that of Scottish Highland cattle (unpublished data). Both areas were used by Konik horses (a Polish horse breed). Body weight of mature stallions was about 450 kg and of mares about 425 kg (Cornelissen et al. 1995). Earlier research (Vulink 2001) showed that Heck cattle, Scottish Highland cattle and Konik horses had a strong preference for grasses of 'dry' grassland and a low preference or no preference for species such as *Juncus gerardii*, *Phragmites australis*, *Calamagrostis epigejos* or *Cirsium* spp. Scottish Highland cattle, Heck cattle and Konik horses are also used in other nature reserves and have shown to be tough breeds that can easily live outdoors throughout the year and need very little to no care from man.

**Table 2** Animal numbers and densities at, and total size of the Zoutkamperplaat (ZKP) and Oostvaardersplassen (OVP) from May 1991 until April 1992. During winter (November-March), part of the Zoutkamperplaat was fenced off to prevent the animals escaping the area across the ice (see Fig. 1).

Area	Season	Animals (N)		Size (ha)	Animals per ha			'Dry' grassland		
		Cattle	Horses		Total Area	Cattle	Horses	Total	Cattle	Horses
ZKP	Apr-Oct	30	21	320	0.09	0.07	0.16	0.73	0.53	1.26
	Nov-Mar	25	23	210	0.12	0.11	0.23	0.73	0.53	1.26
OVP	Jan-Dec	130	70	650	0.20	0.11	0.31	1.00	0.57	1.57

### *Net primary production of the preferred 'dry' grasslands*

Net primary production (NPP) was measured in both study areas. In each study area one sampling site was used of about 50 x 50 m. Within this sampling site, 3 sampling units of 4 x 1.25 m, as similar as possible in botanical composition and cover of grasses, were protected from grazing by cages for about four weeks. Before the cages were placed, the vegetation was cut with a portable power scythe at a height of 2 cm. At the end of this period, forage within the cages was cut with a portable power scythe at a height of about 2 cm. Per sampling unit, all cut fresh material was weighed in the field and a sub sample was taken to the laboratory to determine dry weight (Mannetje 1978). The sub samples were oven-dried at 70° C for 15 h, followed by 1 h at 105° C. After sampling, the cages were moved a few meters to 3 new sampling units within the sampling site. Before placing the cages on the new sampling units, the vegetation of these new units was cut at a height of about 2 cm. The amount of dry matter per sampling unit per month was used to calculate the average amount of the sampling site, and the averages per month of the sampling site were added up to a total per growing season or year. The amounts of dry matter per sampling unit were transformed into g dry matter per m<sup>2</sup>.

At the Oostvaardersplassen NPP was measured monthly during the growing season from May 1991 to October 1991. In both areas NPP was measured monthly from July 1994 to October 1994 and once every 2 months (because of low production) from November 1994 to May 1995. NPP during May-October at the Zoutkamperplaat in 1991 was estimated, based on NPP measurements from Zoutkamperplaat and Oostvaardersplassen over the period July 1994 to May 1995.

### *Sward height of the preferred 'dry' grasslands*

Sward height of the preferred short grazed 'dry' grasslands was measured along transects, using a polystyrene disc (radius 50 cm, weight 320 gram), with a small hole in the centre, which slides over a measuring staff. The disc was gently lowered on to the sward, and the height of the vegetation was read off on the staff. At the Oostvaardersplassen sward heights were measured along 4 transects, varying from 150 to 300 m. Every 5-10 m heights were measured. Measurements were taken monthly from April 1991 until April 1992. At the Zoutkamperplaat sward heights were measured along 3 transects of 300 m. Every 10 m heights were measured. Measurements were taken monthly from April 1991 until April 1992. The average heights per transect were used to calculate the average sward height and standard error of mean of 'dry' grassland per area. We also used the averages of the standard deviations per transect to indicate the heterogeneity of the sward structure.

### *Stocking rate expressed as the ratio between consumption and production (C:P)*

Usually densities of herbivores are expressed as the number of herbivores per ha of the total area. However, these densities, based on total area, are of no use when studying the effect of density on diet composition or habitat use in different heterogeneous habitats, and to compare these results, as it does not give any information about the amount of the preferred vegetation type per animal. In our research the preferred vegetation type of cattle and horses is 'dry' grassland. For our purpose, the number of cattle and horses per ha 'dry' grassland, their key-resource, is a better parameter to predict the effects of density on diet, habitat use and body condition. However, this is also not a meaningful parameter in the context of this study (Kie et al. 2003), because of the variation in soil fertility and net primary

production between areas. A given number of animals per ha in an area with a low net primary production will have different effects on the herbivores and on the vegetation, than in an area with a high net primary production. In order to include functional differences between densities of cattle and horses, we used the ratio of the theoretical maximum consumption of cattle and horses to net primary production of 'dry' grassland over the period May-October. In this study we will refer to this ratio as C:P.

The theoretical consumption of cattle and horses was calculated as follows:

$$C = N_h \times \text{DMI}_h \times T + N_c \times \text{DMI}_c \times T$$

where:

C sum of the maximum dry matter intake (kg) of all cattle and horses

$N_h$  number of horses of  $\geq 1$  year old

$N_c$  number of cattle of  $\geq 1$  year old

$\text{DMI}_h$  daily dry matter intake (kg) for horses

$\text{DMI}_c$  daily dry matter intake (kg) for cattle

T the number of days in the period 15 May to 16 October (the same period as the net primary production was measured).

For cattle we used a maximum DM intake per day of 2.5% of their body mass (Cordova et al. 1978; Van Soest 1994). Average body mass of Scottish Highland cattle  $>1$  yr old at the Zoutkamperplaat was about 400 kg (Cornelissen et al. 1995). The same body mass was used for Heck cattle at the Oostvaardersplassen. For horses a DM intake per day of 3% of their body mass (Duncan 1992) was used. Average body mass of Konik horses  $>1$  year old at the Zoutkamperplaat was about 300 kg (Cornelissen et al. 1995). The same body mass was used for Konik horses at the Oostvaardersplassen.

We used the same C:P for both periods May-October and November-March. We assumed that the stocking rate at year  $i$  would also be of influence on the parameters in the winter period following year  $i$ .

#### *Diet composition and quality*

Diet composition was determined once every three to four weeks from May 1991 until April 1992. Observations were done during daylight. The composition of the diet was based on the distribution of the animals over the vegetation types and on a number of bite-count protocols during grazing in these different vegetation types (see also Fig. 1 for the location of the vegetation types). The distribution over the vegetation types was recorded every hour from one hour before sunrise to one hour after sunset. During observations the location and activity (grazing, walking, standing, lying, others) of all visible animals was recorded and the vegetation types they were seen in. No distinction was made between male and female animals. Observations of cattle and horses in the Oostvaardersplassen were performed by car along a regular route, and in the Zoutkamperplaat on foot. The reason for these different observations methods was determined by area and herd size. At the Zoutkamperplaat, the total herd of cattle and horses consisted of relatively small numbers of animals (about 30 cattle and 20 horses), and in most cases the individuals of the herd used the same areas at the same time. At the Oostvaardersplassen, the total herd consisted of relatively large numbers of animals (130 cattle and 70 horses), and the herd of cattle was always split up in

several smaller groups, which were scattered over a large area. On average >90% of the animals were counted during observations.

Bite-counts were done during 10 minutes. During this time interval all bites taken of different food plants within a vegetation type were counted (Hobbs et al. 1983). During an observation day, bite-counts were done for 3 to 5 individuals (male or female) of 2 years and older in each of the vegetation types they were seen on during the recordings of the distribution of the animals over the vegetation types. To take account of diurnal patterns, we carried out bite counts in vegetation types at the same time of the day they were seen on during the recordings of the distribution. To compensate for the differences in bite size which is for example dependent on plant height (Edouard et al., 2009) or biomass (Chirat et al., 2014), the observers simulated the bites taken by cattle and horses in the different vegetation types by clipping and hand plucking. They collected the material in order to calculate dry matter weight per bite. For describing diet composition, we grouped the food plant species into six forage classes: (1) grasses of 'dry' grassland (*Lolium perenne* L., *Dactylus glomerata* L., *F. rubra* L., *F. arundinacea* Schreb., and *Poa trivialis* L.); (2) grasses and graminoids of 'wet' grassland (*Agrostis stolonifera* L. and *Juncus gerardi* Loisel); (3) *Phragmites australis* (Cav.) Steud., (4) *Calamagrostis epigejos* (L.) Roth, (5) browse (*Salix* spp. L., *Sambucus nigra* L., and *Hippophae rhamnoides* L.); and (6) other species (mostly herbs such as *Cirsium arvense* (L.) Scop., *Urtica dioica* L., and *Trifolium repens* L.). Forage classes are different from vegetation types. Vegetation types are separate areas within the reserves (Fig. 1), and they are dominated by certain plant species (Table 1). However, within a vegetation type patches can occur with other plant species from other vegetation types. For example, the vegetation type 'dry' grassland is dominated by short grazed grasses and herbs, but in some patches within this grassland reed, thistles or a small shrub can dominate the vegetation. During bite count protocols, animals can also eat these other plants. Therefore we used forage classes in which we grouped the different plant species as mentioned above. The number of bites per food plant during the bite counts was multiplied by the simulated bite size. For each bite count protocol in a given vegetation type, the food plants were grouped into the forage classes and within each forage class the dry weights of the food plants were added up. The total dry matter weight of the forage classes per bite count protocol per vegetation type were then multiplied by the relative distribution of the animals over the vegetation types (indication for time spent on each vegetation type). Based on these weighted dry matter weights per forage class, the relative diet composition was calculated.

The forage samples taken for determining dry matter weight per bite were also taken to determine the quality of the diet based on digestible organic matter (DOM), crude protein (CP), and neutral detergent fibre (NDF). For determination of forage quality, forage samples were oven-dried at 70°C for 15 h, followed by 1 h at 105°C, and milled with a 1-mm screen. For cattle, *in vitro* DOM was determined according to Tilley and Terry (1963), using rumen fluid of sheep. Horses have a lower digestive efficiency than cattle (Hintz 1969; Udén and Van Soest 1982). We converted measured *in vitro* DOM contents for cattle into *in vitro* DOM contents for horses, according to Smolders et al. (1990). CP was calculated by multiplying total Kjeldahl nitrogen by 6.25 according to Mould and Robbins (1981). NDF was determined according to Van Soest (1994). The results for DOM, CP, and NDF content are expressed as percentages of the amount of DM.

In both study areas, all observations, bite-counts and forage samples were taken by the same observers.

#### *Sample size and body condition*

Body condition was scored visually, and in some cases manual palpation was possible. The body condition score system was derived from other systems that are based on an evaluation of fat deposits in relation to skeletal features (e.g. Henneke et al. 1983; Edmonson et al. 1989). We assigned scores from 1 (poor; emaciated and carrying virtually no fat) to 9 (very fat). Body condition was assessed twice a year: once at the end of summer in October and once at the end of winter in March. At the Zoutkamperplaat cattle and horses were driven into a corral in October and March for medical examination. This made it possible to score body condition also by manual palpation. This enabled a better assessment of body condition in the longhaired Scottish Highland cattle. The animals of the Oostvaardersplassen were not driven into a coral twice a year, but the animals were approachable in the field up to 1 meter. All the examined horses could even be physically examined in the field. In both areas body conditions of males and females were scored. At Zoutkamperplaat about 10 males and 10 females of 2 years and older were scored each time. At Oostvaardersplassen 30 cows, 30 bulls, 20 mares and 20 stallions of 2 years and older were scored each time. Assessments were performed by the same observer in both areas.

#### *Statistical analysis*

The results of the observations for diet composition and quality were used to calculate monthly values. When two observations were made in one month, the average of the two observations was used. The monthly values (N=12) were used to test differences between areas or between species.

For each study area Analysis of Variance (ANOVA) was used to test if DOM, CP or NDF contents differed among vegetation types. When DOM, CP or NDF contents differed significantly among vegetation types, Tukey's post-hoc tests were performed to test which vegetation types differed from the others. For the vegetation types 'dry' grassland and reed ANOVA was used to test if DOM, CP or NDF differed between the two study areas. We used General Linear Model Univariate (GLMU) to test the effect of study area and herbivore species (both fixed factors) on the percentage of the forage class 'dry' grassland in the diet, and on the DOM, CP and NDF contents of the diet.

Mann-Whitney tests were performed to test effects of area, month or sex on body condition scores of cattle and horses. To meet the assumptions of the statistical tests, data in percentages were arcsine transformed (Sokal and Rohlf 1981) (the figures show the untransformed data). SPSS (Norušis 2005) was used for all statistical analyses.

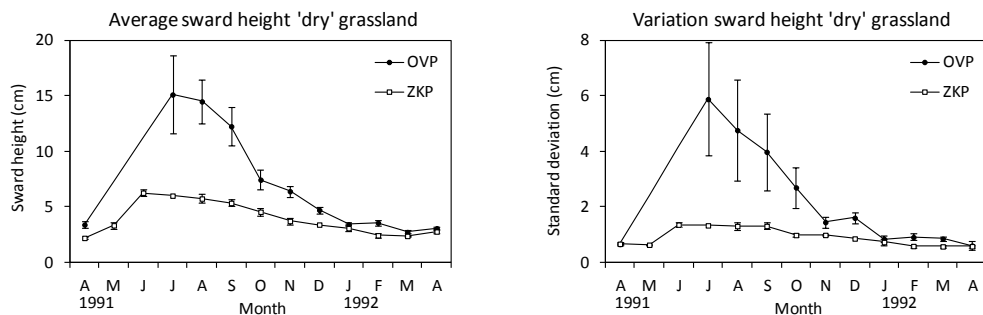
## **Results**

In 1991 the NPP of 'dry' grassland at the Oostvaardersplassen over the period May-October was 830 g DM.m<sup>-2</sup>. During 1994-1995, the annual NPP of 'dry' grassland at the Oostvaardersplassen and Zoutkamperplaat was respectively 1200 and 470 g DM.m<sup>-2</sup>. Based on this difference, we estimated NPP at Zoutkamperplaat in 1991 at 325 g DM.m<sup>-2</sup>. Based on these amounts of NPP in 1991 and the theoretical consumption of cattle and horses in 1991, the C:P ratios for Oostvaardersplassen and Zoutkamperplaat were respectively 0.28 and 0.55. Based



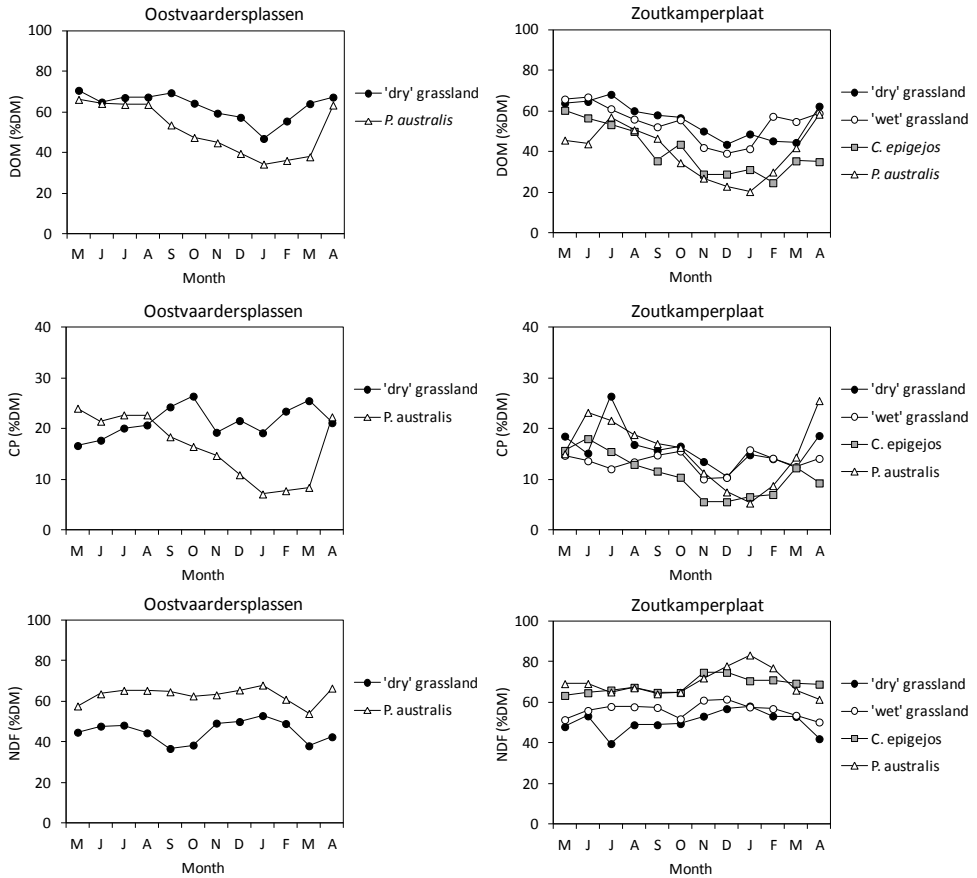
on these C:P ratios, Oostvaardersplassen can be regarded as the area with low herbivore densities and Zoutkamperplaat as the area with high herbivore densities.

Sward heights and standard deviations of the preferred 'dry' grasslands were higher at the Oostvaardersplassen than at the Zoutkamperplaat ( Fig. 2). Differences were greater during summer than during winter. Only in March-April, sward heights were similar in the two areas.



**Fig. 2.** Sward height (left) and variation of sward height (right) of 'dry' grassland at the Oostvaardersplassen (OVP) and Zoutkamperplaat (ZKP). The variation is expressed as the mean of the standard deviation per transect. Error bars represent standard errors of mean. C:P for Oostvaardersplassen is 0.28 and for Zoutkamperplaat 0.55.

On average, DOM, CP and NDF content differed significantly among vegetation types in both areas (both areas and all parameters  $P < 0.05$ ; Fig. 3). DOM content of 'dry' grassland was higher and NDF content of 'dry' grassland was lower than that of reed and bush grass vegetation types (both areas  $P < 0.05$ ). At Zoutkamperplaat CP content of 'dry' grassland was higher than that of bush grass ( $P < 0.05$ ) and at Oostvaardersplassen CP of 'dry' grassland was higher than that of reed ( $P < 0.05$ ). At the Oostvaardersplassen, DOM and CP contents of 'dry' grassland were higher and NDF content was lower than at the Zoutkamperplaat (all  $P < 0.05$ ). For Reed, DOM content was higher and NDF content lower at the Oostvaardersplassen than at Zoutkamperplaat (both  $P < 0.05$ ). CP of reed did not differ between the areas.



**Fig. 3.** Digestible Organic Matter (DOM), Crude protein (CP) and Neutral Detergent Fibre (NDF) of the main forage classes of the study areas; averaged per month over a period of two years (April 1991-April 1993). C:P for Oostvaardersplassen is 0.28 and for Zoutkamperplaat 0.55.

Diet composition differed between study areas and periods (Fig. 4). In general, the average percentage of 'dry' grassland grasses and herbs in the diet of cattle and horses was higher at the Oostvaardersplassen than at the Zoutkamperplaat ( $P < 0.0001$ ). Herbivore species had no effect ( $P = 0.2200$ ) and there was no interaction effect between study area and herbivore species. Although there was no significant effect of herbivore species on the amount of 'dry' grassland grasses in the diet because of the temporal variation, there are some clear differences between cattle and horses. At the Oostvaardersplassen and during the growing season (May-October), the diet of cattle and horses showed more resemblance than during the winter season (December-March). During winter, the horses had less 'dry' grassland grasses and herbs and more reed and the forage class 'others' in the diet than cattle, who assembled a diet consisting of almost only 'dry' grassland grasses and herbs. At the Zoutkamperplaat, diet composition of cattle differed from horses during both periods. During the growing season, the amount of 'dry' grassland grasses in the diet of cattle decreased whereas the amount of this forage class in the diet of horses increased. During winter, a more or less same difference

between cattle and horses was visible as at the Oostvaardersplassen with more 'dry' grassland grasses and less other forage classes in the diet of cattle than in the diet of horses.

DOM, CP and NDF content of the diet differed between study areas and herbivore species (in all cases  $P < 0.05$ ; Fig. 5), and there were no interaction effects between study area and herbivore species. In general DOM and CP contents were higher in the diet of cattle than that of horses, and was higher at the Oostvaardersplassen than at the Zoutkamperplaat. In general, the NDF contents in the diet were higher for horses and were higher at the Zoutkamperplaat.

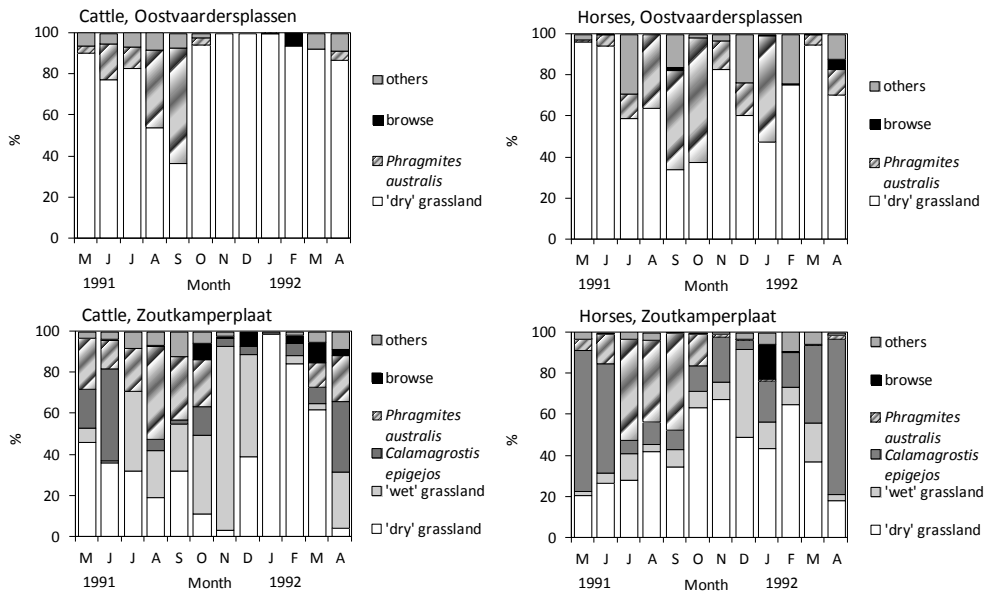
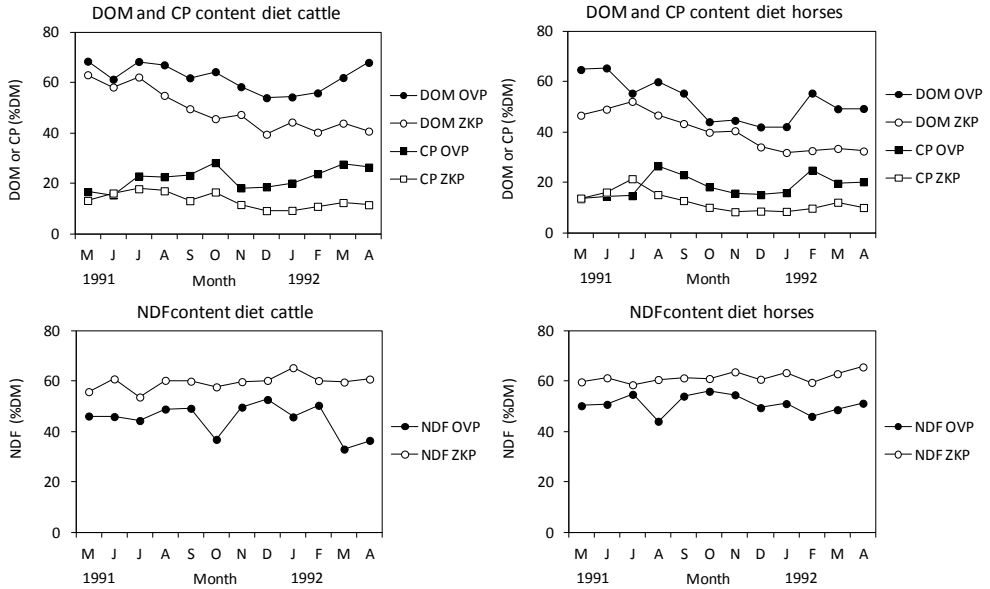
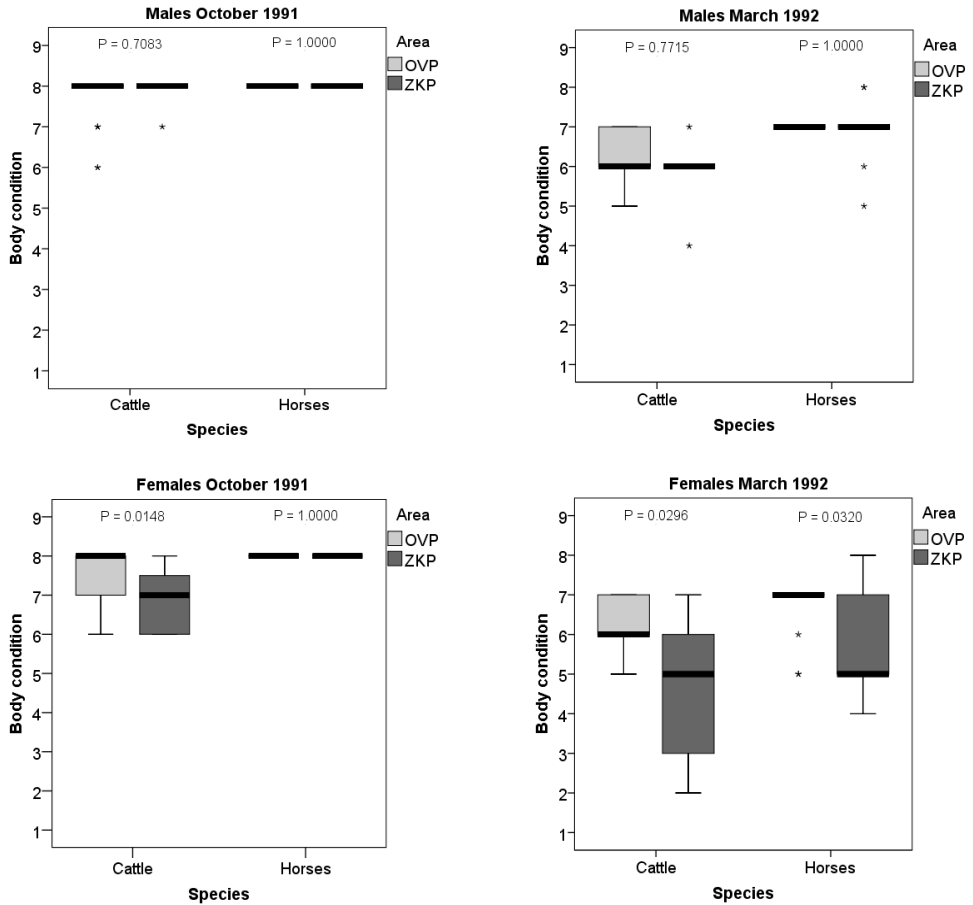


Fig. 4. Diet composition of cattle and horses at the Oostvaardersplassen and Zoutkamperplaat. C:P for Oostvaardersplassen is 0.28 and for Zoutkamperplaat 0.55.



**Fig. 5.** Diet quality of cattle and horses at the Oostvaardersplassen (OVP) and Zoutkamperplaat (ZKP). DOM = digestible organic matter; CP = Crude protein; NDF = Neutral Detergent Fibre. C:P for Oostvaardersplassen is 0.28 and for Zoutkamperplaat 0.55.

In October and March, body condition of male cattle and horses did not differ between Oostvaardersplassen and Zoutkamperplaat (Fig. 6). Female body condition of cattle differed between Oostvaardersplassen and Zoutkamperplaat in October and March. For female horses there was only a difference between the two study areas in March. In both areas, body condition of male and female cattle and horses differed between October and March (all  $P < 0.05$ ).



**Fig. 6.** Box plots of body condition scores of male and female cattle and horses of 2 years and older in October and March at the Oostvaardersplassen (OVP) and Zoutkamperplaat (ZKP). Horizontal lines are medians, the lower and upper boxes the 1<sup>st</sup> and 3<sup>rd</sup> quartile, the lower and upper whiskers the minimum and maximum value, the asterisks the extremes. P-values above bars give significance levels of Mann-Whitney U-test for differences between OVP and ZKP. C:P for Oostvaardersplassen is 0.28 and for Zoutkamperplaat 0.55.

## Discussion

### *Diet composition*

The observed diet compositions agree with many other studies of cattle and horses that show a preference for grasses (e.g. Duncan 1983; Gordon 1989a; Putman 1996; Van Wieren 1996; Menard et al. 2002). The lower amounts of 'dry' grassland grasses in the diets of cattle and horses at the Zoutkamperplaat compared with Oostvaardersplassen are similar with Pinchak et al. (1990). They showed that the amount of alternative forage in the diet was inversely related to the supply of high quality food plants.

During the growing season (May-October), composition of the diet of cattle and horses was rather similar at the Oostvaardersplassen whereas at the Zoutkamperplaat the diet differed markedly. In the diet of cattle, the amount of 'dry' grassland grasses decreased from May to October and in the diet of horses the amount increased. This could be due to the fact that horses are able to forage on shorter grass swards than cattle (Gordon 1989b; Menard et al. 2002). In general, when herbivore densities are high more plant tissue will be eaten from the preferred food plants, leading to lower swards. Cattle and horses prefer shorter swards, as the quality of short grazed swards is higher than taller mature swards. However, there is a difference between cattle and horses in the way they can utilize short swards. Horses can reach a higher instantaneous intake on short swards than cattle and can maintain this difference for daily intake by their longer feeding times (Menard et al. 2002). Menard et al. (2002) showed that cattle were unable to graze on short grasslands and preferred heights of 9-16 cm, whereas horses preferred grass heights of less than 8 cm. During May-October, sward heights of 'dry' grassland at the Zoutkamperplaat were decreasing and below the preferred heights of 9-16 cm for cattle as mentioned by Menard et al. (2002). It shows that horses can profit more and longer from these high quality swards at high C:P than cattle. This gives horses a competitive advantage over cattle at high densities. During this period, cattle of the Zoutkamperplaat increased their intake of 'wet' grassland grasses. Their quality is just a little bit lower than that of 'dry' grassland grasses but the sward height of this vegetation type was a few centimetres greater than that of 'dry' grassland (Cornelissen et al. 1995) as it was less grazed during the first two months of the growing season.

During winter, the amounts of 'dry' grassland grasses in the diet of cattle and horses were higher than expected based on the availability of these forage plants. Apparently, 'dry' grassland grasses, even with a lower quality and availability (low sward heights) than during the growing season, were the best option during that period as the quality of the other vegetation types was even lower and little or no live material was present (e.g. reed or bush grass). It also means that the total intake, especially for cattle, was much lower during winter than during the growing season. Another difference during winter were the higher amounts of 'dry' grassland grasses in the diet of cattle than of horses. As horses can deal with plants with higher cell wall contents by accelerating excretion of fibre (e.g. Iason and Van Wieren 1991), they can compensate for the lower digestibility of these plants by increasing their intake. This enables them to achieve a higher intake than cattle (Vulink 2001).

#### *Diet quality and body condition*

Although there was an effect of difference in quality of the forage plants between Oostvaardersplassen and Zoutkamperplaat (Fig. 2), which will lead to a lower diet quality at Zoutkamperplaat, the amount of 'dry' grassland grasses in the diet and on diet quality will also have contributed to the diet quality. At a higher C:P, the amounts of 'dry' grassland grasses in the diet are lower, which will lead to a lower quality of the diet. The difference between DOM contents of the diets of cattle and horses was not only caused by difference in diet composition but also by the lower digestive efficiency of horses compared to cattle (Hintz 1969; Udén and Van Soest 1982).

We did not find the expected effect of C:P on body condition in all situations. Male body condition was not affected at all. Although the energy and nutrient requirements of males are lower than for females (pregnancy and lactation; Prins and Van Langevelde 2008a), a lower body condition for males can be expected at high C:P. The C:P difference between the

two areas was apparently too small to detect effects. In cows, body condition was more affected by C:P than in mares. This difference is most likely a result of differences in digestive physiology as cattle are ruminants and horses hindgut fermenters. Duncan et al. (1990) and Illius and Gordon (1992) showed that, compared to similarly sized ruminants, hindgut fermenters have higher rates of food and energy intake which compensate the lower digestion. As a consequence, equids extract more nutrients from food than bovids, not only from low quality food but also from medium and high quality food. According to Illius and Gordon (1992), the advantage of equids only holds when food supply is abundant. When resources are limited and food intake is restricted, the more efficient digestion by ruminants would give them advantage over equids, since they require less food to meet their energy requirements. However, when the preferred resources are limited, as shown in this study, cattle cannot take the advantage over horses because their intake is restricted by the low sward height (Menard et al. 2002) resulting in lower body condition.

#### *Implications for management*

This study indirectly shows how C:P will affect vegetation development and biodiversity. When animal densities are low, cattle and horses will meet most of their requirements by taking up grasses of 'dry' grassland. Their impact on this vegetation type will be restricted to the area exploited. This explains the high average standard deviations of the sward height at the Oostvaardersplassen (low C:P), indicating high heterogeneity of the sward structure. At low stocking rates, grazing impact on other vegetation types will be limited. At increasing stocking rates, the food supply of 'dry' grassland is no longer sufficient and the herbivores will switch to less preferred vegetation types. They will fully exploit the grasslands, resulting in short, homogeneous swards (i.e. low standard deviations of the sward height). The impact on the less preferred vegetation types will increase and growth of coarse grasses (*P. australis*), tall herbs (*C. arvensis*, *U. dioica*), shrubs or trees can be suppressed (Cornelissen et al. 2014a, b). Subsequently, plant species composition and vegetation structure of these other vegetation types can change (Crawley 1997), attracting other plant and animal species (Vulink 2001; Kie et al. 2003; Van Wieren 1998; Van Wieren and Bakker 2008).

One of the conservation aims for many wetlands and floodplains is maintaining large areas of short grazed vegetation, which can function as foraging area for herbivorous water birds such as geese (Cornelissen and Vulink 2001a, b; Vulink and Van Eerden 1998). In these areas, vegetation types with *P. australis*, *C. epigejos*, tall herbs, shrubs and trees are less desired. To decrease undesirable vegetation types, high densities of herbivores will be necessary. However, from our results we can deduce that competition occurs between cattle and horses on the short grazed, high quality 'dry' grasslands at higher animal densities (i.e. high C:P). Since horses have the advantage over cattle on the short grazed 'dry' grasslands at high densities (Menard et al. 2002), as well as on the lower quality vegetation types (Duncan et al. 1990; Illius and Gordon 1992), horses will outcompete cattle at higher densities in restricted areas without predation (cf. Menard et al. 2002). In restricted areas with controlled animal numbers, managers should be aware of this. In order to achieve the high densities necessary for the conservation aims, several options are possible such as, using fewer horses than cattle, varying densities of large herbivores between summer and winter by expanding the area in winter, or supplementary feeding during winter. In restricted areas with self-regulating populations of cattle and horses at high densities, competition between cattle and horses will take place. In a heterogeneous area with abundant forage alternatives, this could

lead to resource partitioning (Putman 1996) so that the two species can co-exist. However, in a homogeneous area dominated by the preferred grassland and without abundant alternatives, competition may lead to a lower body condition and fitness of cattle than of horses. This will lead to a decrease of the cattle population and increase of the horse population. Ultimately, under severe competition this may lead to the extinction of cattle in the restricted, homogeneous area. In providing opportunities for cattle and horses to coexist, spatial heterogeneity appears to be a key factor (Putman 1996) as mentioned above. Connecting the homogeneous grazed area to other areas with different soil types, ground water levels, vegetation types or other variables, will increase heterogeneity. Disturbance could also affect coexistence (Putman 1996). If the disturbance could disrupt population growth of the dominant competitor or of both, they could coexist because the preferred forage would not be depleted for cattle. Climatic fluctuations are disturbances that disrupt population growth (Young 1994). The question is if climatic fluctuations in Western Europe are strong enough to disrupt population growth of cattle and horses to let them coexist in a restricted, homogenous area.

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## CHAPTER 6

### REWILDING EUROPE: EARLY DYNAMICS OF A MULTISPECIES GRAZING ECOSYSTEM

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#### **Abstract**

In Europe there is a growing interest in re-establishing ecosystems with a dominant role of natural processes. We examined a unique 30-year study on the interplay between vegetation development and the dynamics of barnacle geese, greylag geese, red deer, horse and cattle populations in the newly created Oostvaardersplassen wetland ecosystem. This area is without human regulation or natural predation on the largest herbivores species. With the growth of the total herbivore biomass, we found that the largest herbivore was being outcompeted by smaller species. We explain this phenomenon by associated changes in vegetation structure, food availability and overall population densities. Our findings illustrate the importance of sufficient size and heterogeneity of protected areas for the long-term coexistence of different-sized herbivores in grazed landscapes without human or large predator interference.

#### **Introduction**

Ecosystems dominated by large herbivores, such as those found in Western North America, Northern Asia and throughout Africa, have unique ecological features with regard to trophic structure, natural ecosystem processes and spatial heterogeneity (Frank et al. 1998; Olf et al. 2002; Harris et al. 2009; Hopcraft et al. 2010). These ecosystems are nowadays very rare or absent in Western Europe, Eastern and Southern North America, and Eastern and Southern Asia. Land use in these more densely populated regions is dominated by agricultural, industrial and urban activities. This results in small and fragmented natural areas for nature conservation that may not be capable of sustaining wildlife and natural processes (Bokdam and WallisDeVries 1992; Lindenmayer and Fischer 2006). Consequently, the potentials and benefits of restoring large herbivore-dominated ecosystems in these regions are heavily debated (Benayas et al. 2009; Caro and Sherman 2009; Jackson and Hobbs 2009; Davis et al. 2011; Huynh 2011; Seddon et al. 2014).

In Europe, conservation managers traditionally maintain or restore grazing ecosystems by maintaining relatively low and fixed stocking rates (Bakker 1989; Olf and Ritchie 1998; WallisDeVries et al. 1998; Olf et al. 1999; Hodder and Bullock 2009). Novel conservation strategies where large herbivore populations are re-introduced without population regulation by culling or hunting (i.e. rewilding) are increasingly debated (Hodder and Bullock 2009; Jørgensen 2015; Nogués-Bravo et al. 2016) and promoted (Pereira and Navarro 2015). Some of the key drivers of these novel rewilding strategies (e.g. Svenning 2002; Birks 2005; Sandom et al. 2014; Jørgensen 2015; Pereira and Navarro 2015) are:

- growing public interest in wilderness;
- objections against culling or hunting wild animals;
- increased appreciation for ecosystems with a dominant role of natural processes;
- the unique species assemblages that can develop in these ecosystems;
- the notion that the traditionally managed, pre-industrial landscapes, such as man-made wood-pastures, heathland or chalk grasslands, cannot accommodate many of the species that went extinct in earlier days.

One key issue is the inclusion or exclusion of top predators, such as wolves in protected areas that are embedded in cultural landscapes. Top predators are generally not introduced in such unmanaged grazing ecosystems due to their large area requirements for viable populations (>100 km<sup>2</sup>; Okarma et al. 1998, Mech and Boitani 2003), sensitivity to poor landscape connectivity and low societal tolerance for larger predatory wildlife (Treves and Bruskotter 2014). However, ecosystems where the largest herbivores are not regulated by predation are not necessarily unnatural. In tropical savannas without human interference and large populations of predators, mega herbivores, such as rhinos and elephants, or other large herbivores > 100 kg in size such as buffalo or migratory wildebeest may be only weakly affected by predation and can dominate the herbivore guild, with important consequences for ecosystem structure and functioning (McNaughton 1985; Owen-Smith 1988; Fritz et al. 2002; Sinclair et al. 2003; Hopcraft et al. 2010).

In the absence of predators, key questions in rewilding are which factors control herbivore populations and whether multiple large herbivore species can coexist as largely “closed” populations in isolated reserves. In our temperate climate, animal numbers of unregulated predator-free single-species large herbivore populations, such as red deer and Soay sheep on abandoned islands (Coulson et al. 2001; Bonenfant et al. 2009), generally are regulated by intraspecific competition for food combined with severe winter conditions generally regulates animal numbers (Coulson et al. 2001). However, little is known about the unregulated dynamics of multi-species herbivore assemblages in these ecosystems where the large species (such as cervids, equids and bovids) are predation-free while the smaller herbivores (such as rabbits, hares or geese) are not.

In our study, we explored the role of food limitation and interspecific competition in regulating the dynamics of a unique multispecies grazing ecosystem: the Oostvaardersplassen in the Netherlands. This 56 km<sup>2</sup> grazing ecosystem developed from a reclaimed former lake bed, and represents one of the first European ‘large herbivore rewilding’ projects whose long-term multi-species dynamics of a large herbivore assemblage with hardly any population regulation by humans, can now be evaluated. The large herbivore assemblage consists of cattle, horses and red deer and the area is visited by tens of thousands of geese.

Geese, red deer, horses and cattle all prefer high quality grass swards when available (Clutton-Brock et al. 1982; Duncan 1983; Pratt et al. 1986; Gordon 1989; Van Wieren 1996; Vulink 2001). However, the height of the sward drives its utility for different species with cattle requiring taller swards than horses or deer, and geese capable of using the shortest swards, based on their body size and muzzle width (Illius and Gordon 1987; Murray and Illius 1996; Arsenault and Owen Smith 2002; Kleynhans et al. 2011). It is known that the preferred grass height for cattle is above 9 cm, whereas horses, red deer and geese prefer to graze on swards below 9 cm (Clutton-Brock et al. 1982; Illius and Gordon 1987; Vickery and Gill 1999; Vulink

2001; Menard et al. 2002; Bos et al. 2005). The consequences for population dynamics of this in a multispecies context has so far remained unclear.

With increased populations of all herbivore species, competitive exclusion is expected to become more important where the species with the lowest  $R^*$  is expected to win (Tilman 1982; Ritchie and Tilman 1993). As a result, the species with lowest resource availability at population equilibrium (birth and death rates balance) excludes all others. In the Oostvaardersplassen ecosystem, sward height can be considered to be an analogue for the resource concentration  $R$  in Tilman's model. Different heights that correspond to the balance between birth and death rates equivalence can be interpreted as an equivalent of  $R^*$ . This is supported by Illius and Gordon (1987) and Murray and Illius (1996) who showed that larger herbivores are more constrained by sward height than smaller ones, resulting in higher  $R^*$ . We therefore expect that smaller herbivores will outcompete the larger ones when the herbivore populations are not regulated by predators. The plant–herbivore theory (Huisman and Olff 1998; Bagchi and Ritchie 2012) suggests that even if larger herbivores preferentially use coarser vegetation types lower in nutritional quality, they can be outcompeted by smaller herbivores and the greater the disparity in size the stronger the competitive effect.

### Study area

The Oostvaardersplassen was established in 1968, when the polder Zuidelijk-Flevoland was reclaimed from the freshwater lake IJsselmeer. As a result, the area features highly fertile uniform marine silt-clay deposits. Endangered and characteristic wetland bird species immediately colonized the area after it fell dry, leading to the establishment of a protected marshland of approximately 36 km<sup>2</sup>, which was embanked in 1975 to maintain a high water level. In the marsh, moulting greylag geese play a key-role by creating a mosaic of shallow water and different reed vegetation types needed by many of the visiting marshland birds (Vulink and Van Eerden 1998; Beemster et al. 2010). To create a more fully functional wetland ecosystem, hosting various endangered bird species, a drained border zone of about 20 km<sup>2</sup> was added to this marshland in 1982. In the drained zone, groundwater tables are regulated between 0 and -100 cm below ground level. The fertile marine deposits, resulted in highly productive grasslands in the drained zone with aboveground net primary productivity approaching 1200 g DM/m<sup>2</sup> per year (Vulink 2001). To maintain short grazed grasslands for herbivorous wetland birds and small open water bodies for fish eating birds in this drained zone, Heck cattle (*Bos taurus*; 32 individuals in 1983), Konik horses (*Equus caballus*; 18 individuals in 1984) and red deer (*Cervus elaphus*; 52 individuals in 1992) were introduced. Roe deer (*Capreolus capreolus*), a typical browser, colonized the area spontaneously during the 1970's and left the area during the 1990's as the populations of cattle, horses and red deer increased. The grazed grasslands and small open water bodies became used by large numbers of greylag (*Anser anser*) and barnacle geese (*Branta leucopsis*; Vera 2009), and by spoonbills, egrets, herons and waders (Voslamber and Vulink 2010).

The introduced Heck cattle, Konik horses and red deer populate a fenced area of 56 km<sup>2</sup> without internal barriers. There are no large predators and the large herbivores are allowed to grow in numbers without culling or hunting. The rapid growth of large herbivores numbers and resulting increase in winter mortality, led to societal concerns about animal welfare. In response, a policy of early reactive management was adopted, where animals in poor condition in late winter are shot before they die naturally. This was done to avoid unnecessary suffering without significant impacts on population dynamics of the species involved (ICMO2 2010).

## Methods

Population numbers of Heck cattle, Konik horses and red deer on 1 May of each year were based on weekly countings by car along a fixed route for determining habitat use of large and small herbivores. During observations, the location and activity of all visible animals were recorded. During spring and summer, when plant biomass is in ample supply, both large and small herbivores prefer the drained grasslands, providing good opportunities to estimate population sizes of all herbivores. The average number of geese per observation per year were also based on these weekly countings.

Mortality of the large herbivores is recorded on a daily basis. The rangers patrol the whole area daily to execute the policy of early reactive management (ICMO2 2010). Births are recorded on a weekly basis for cattle and horses and once a year in August-September for red deer. For cattle and horses the rangers patrol the total drained zone by car and count the total number of calves and foals. Red deer calves are counted once in August-September when the calves are taken to the grasslands by the hinds. Four groups of two rangers each count the calves by car in four different areas that cover the entire drained zone.

To account for different per unit body mass energy use of small and large herbivores, we expressed herbivore numbers as the daily energy expenditure (DEE) per unit area of the different populations. For large herbivores we expressed daily energy expenditure (DEE) at twice the basal metabolic rate (BMR):  $DEE = 2 \times 70 \times (\text{live body weight})^{0.75} \text{ kcal day}^{-1}$  (Demment and Van Soest 1985; Sinclair et al. 2007). For geese we expressed daily energy expenditure at  $2.55 \times BMR$ :  $DEE = 2.55 \times 1.22 W^{0.6052} \text{ kcal/day}$  (Mooij 1992). For cattle we used an average live body weight of 420 kg, for horses 375 kg, red deer 120 kg, greylag geese 3.2 kg, and barnacle geese 1.8 kg.

Based on aerial photographs (1996, 2008, 2012) and satellite images (2000, 2004), vegetation maps were made once every four years of the important vegetation structure types (see appendix).

Sward height of the grasslands was measured along 6 transects (0.6 to 1.2 km in length). Every 50 m along a transect, height was determined using a disk which was lowered over a measure stick onto the sward. When the disk could not be lowered on to the sward, height was measured with the measure stick.

To quantify differences in  $R^*$  among the mammalian species, we related per capita birth and mortality rates per species to the available food (i.e. sward height). For the geese this was not possible as they mainly reproduce outside the area.

## Results

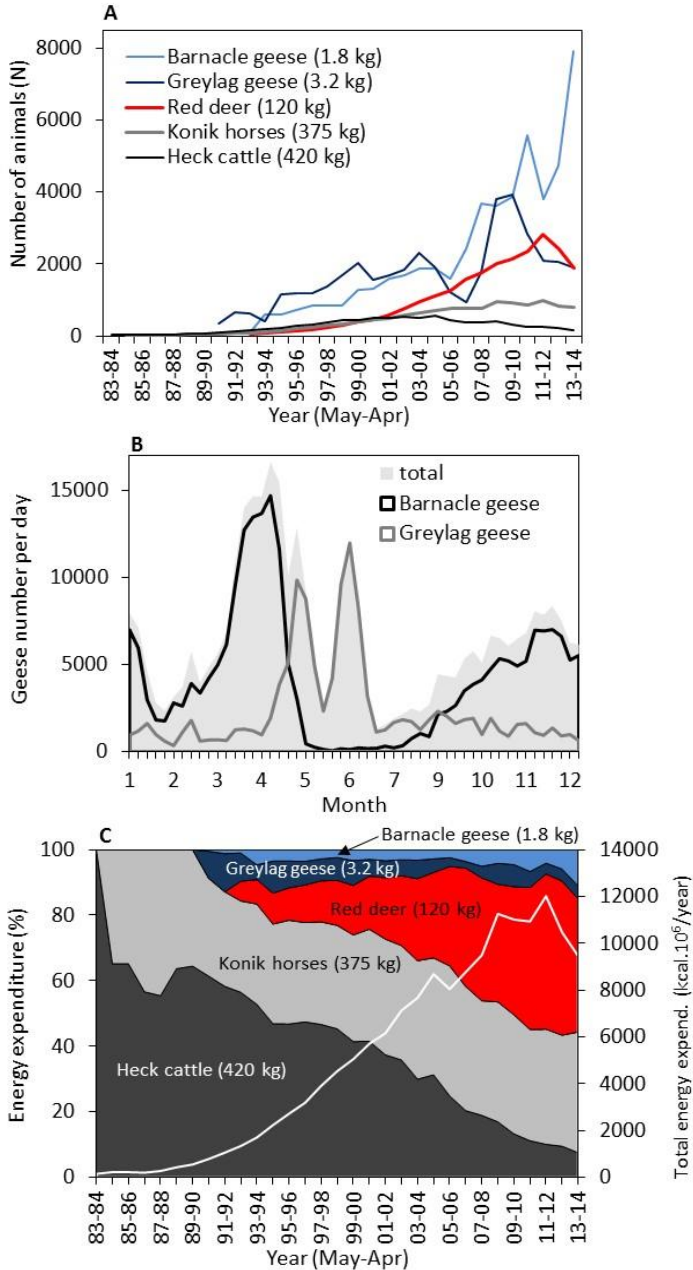
The introduced large herbivore populations initially increased exponentially after which different species reached maximum numbers in different years (Fig. 1A). The population of cattle peaked around the year 2000, and gradually declined afterwards. After 2000, the populations of horses and red deer continued to increase, and in 2009 horses reached maximum numbers and in 2011 red deer peaked. Roe deer (not included in Fig. 1A) achieved maximum numbers at the beginning of the 1990s of up to 100 animals. During the 1990s, their numbers rapidly decreased to less than 10 animals in 2000, and after 2005, roe deer was not present anymore in the area grazed by cattle, horses and red deer.

During the research period, the numbers of barnacle geese increased, while greylag geese declined after 2010 (Fig. 1A). The increase of barnacle geese at the Oostvaardersplassen was in

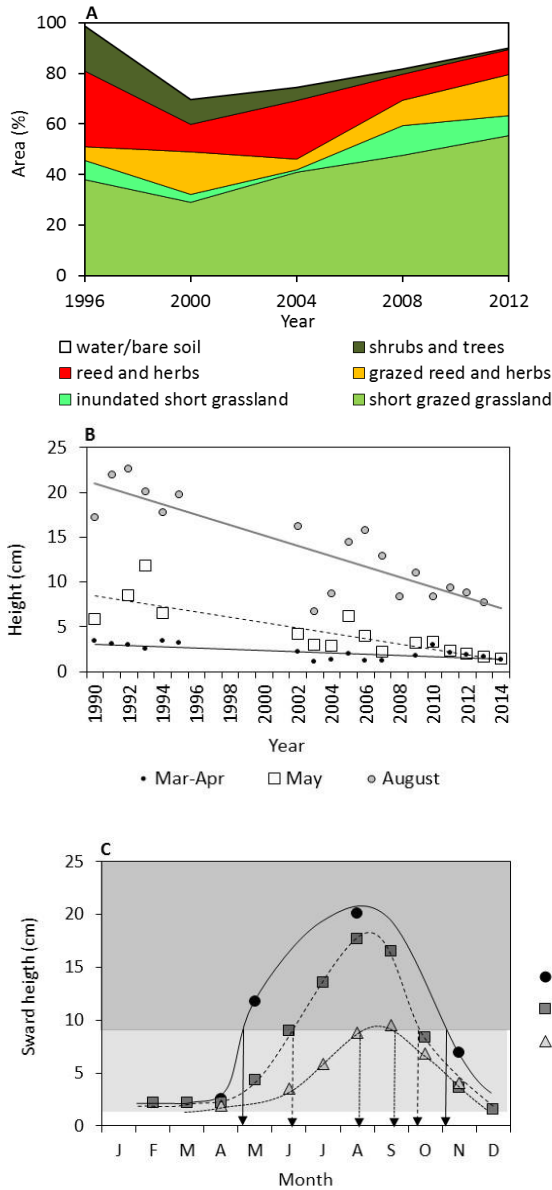


line with their regional populations in the Netherlands, whereas population development of greylag geese was not (see appendix). At the Oostvaardersplassen, both geese species are present year-round but they differ in timing of their peak abundances (Fig. 1B). This is predominantly so at the end of winter and during spring (start of the growing season and main period of food limitation of the large herbivores) when high numbers of barnacle geese visit the Oostvaarderplassen grasslands. When this species leaves for their arctic breeding grounds at the end of May, they are followed up by moulting greylag geese (Fig. 1B).

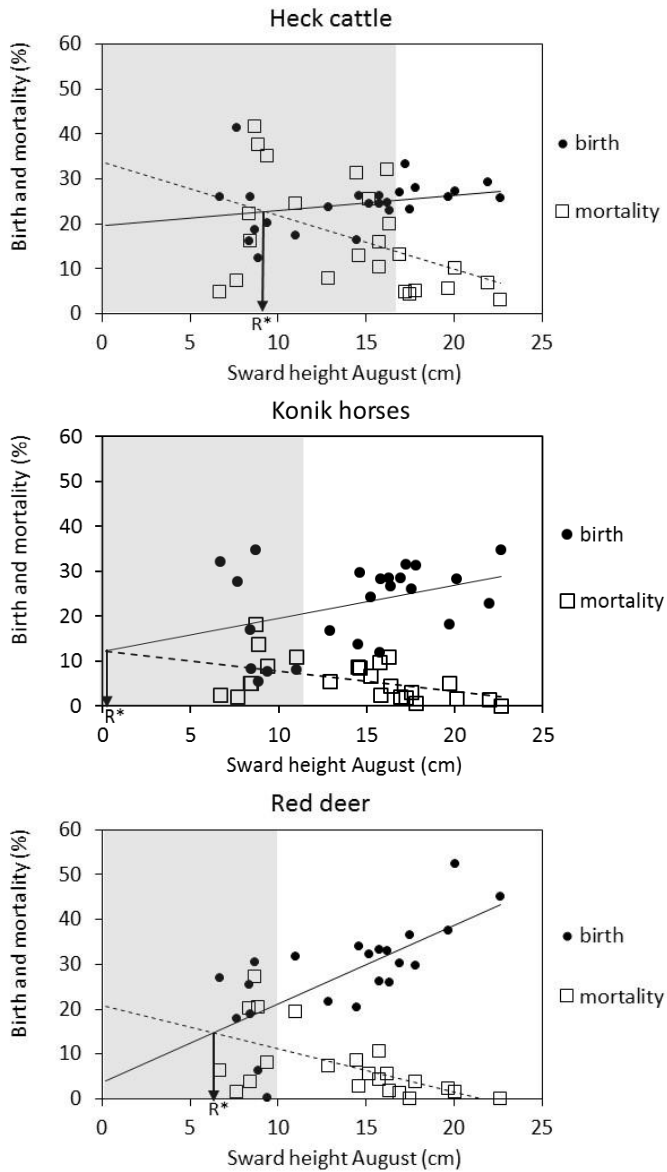
The summed daily energy expenditure per unit area (DEE) of the whole herbivore assemblage increased until 2008, after which it levelled off (Fig. 1C). The change in the relative energy expenditure of the different herbivore populations followed a body size gradient (Fig. 1C). Initially, Heck cattle dominated the overall herbivore guild energy expenditure (and thus consumption) and their relative energy expenditure declined gradually over a period of thirty years from 95% to 5%. Horses became then next species of importance. Their relative energy expenditure was approximately 40% and stayed remarkably constant over the whole period (Fig. 1C) despite the drastic changes in the numbers of all other species (Fig. 1A). The decline in relative importance of Heck cattle was associated with an increase in energy use by red deer and geese. At the end of the study, red deer were responsible for half of the energy expenditure of the mammalian herbivores, while both geese species together became responsible for about 15% of the total energy expenditure.



**Fig. 1** Population development of large and small herbivores. **A:** population numbers of large herbivores on May 1 of each year and the average number of geese per observation per year. **B:** the average numbers of geese per day visiting the short grazed grasslands during the year (averaged over the period 2006-2014). **C:** Energy expenditure of large and small herbivores. The white line gives the total energy expenditure of all herbivores together.



**Fig. 2.** Vegetation development. **A:** development of the major vegetation structure types, presented as a percentage of the border zone (c. 20 km<sup>2</sup>). In 2000 water bodies were created in the short grazed grasslands. **B:** average sward height of the preferred grasslands for different months over the years. Sward heights were significantly correlated with year. March-April:  $R^2 = 0.7346$ ;  $P < 0.0001$ ; May:  $R^2 = 0.6847$ ;  $P = 0.0001$ ; August:  $R^2 = 0.3049$ ;  $P = 0.0175$ . **C:** course of the average sward height of the preferred grasslands during the year for 1992 (low herbivore numbers), 2002 (medium) and 2012 (high). The dark shaded area indicates the preferred grass heights for cattle; the light shaded area the preferred grass height for the other herbivores. Below 2 cm, grass height becomes a constraint for all herbivores. The area between the vertical arrows indicate the period over which cattle are not constraint by sward height.



**Fig. 3.** Birth and mortality in relation to sward height of the short grazed grasslands in August. Birth is presented as the net birth given as a percentage of the total population in May and mortality is presented as the mortality of animals of 1 year and older given as a percentage of the total population in May. The vertical arrows indicate the sward height at which an equilibrium  $R^*$  (mortality = net birth) is reached. The shaded area indicates the range of the sward height in which mortality exceeded net birth several times. Within the un-shaded area, mortality never exceeded net birth. For missing data of sward height in August between 1996 and 2001 we estimated sward height based on the linear regression in fig. 2B.

Concurrent with these changes in animal numbers and DEE (Fig. 1A, C), grasslands increased at the expense of reed and tall herbs, while the elder thickets and willow woodlands disappeared. The area became dominated by short grazed vegetation (Fig. 2A). Within the grasslands, sward height decreased as herbivore numbers increased over time (Fig. 2B). Over the study period, the seasonal differences in sward height were substantially reduced. Initially, biomass strongly accumulated throughout the growing season from March to August, while in the last years this increase was much smaller (Fig. 2C). Standing biomass in the short grazed grasslands has apparently declined over the study period due to the significantly increased grazing pressure (Fig. 1A, C).

Analysis of the changes in sward height throughout the year shows that the period in which the demands for cattle (in terms of sward height) are met, has become shorter over the years (Fig. 2C). For the other herbivores, their height demands are still met most of the year; even at high herbivore numbers. In addition, vegetation heights at the start of the growing season, an important period of food limitation for the larger herbivores, are increasingly shorter (<3 cm) due to the increase in geese numbers (Fig. 1A).

For all large herbivore species, net birth rates were positively and mortality negatively correlated with sward height. The estimated 'vegetation height'  $R^*$  was highest for cattle (c. 9 cm), intermediate for red deer (c. 6 cm) and lowest for horses (almost 0 cm).

## Discussion

The results of this study show that the interplay among the lawn-grazing herbivores is dependent on interspecific differences in body size, minimum sward heights that can still be exploited, and additional resources such as leaves and bark of woody species, or roots of nettle and reed. As expected, cattle had a higher 'vegetation height'  $R^*$  than red deer. This illustrates that when red deer reduce sward heights to less than 9 cm, winter mortality of cattle increases due to food shortage, while we found their per capita birth rates to be more stable. Interestingly, the estimated  $R^*$  for the Konik horses was close to zero cm sward height. This surprising result is very likely to be explained by the additional resources, such as nettle and reed rhizomes that the horses can exploit. These additional resources are probably also responsible for the approximately constant contribution to the assemblage energy use (Fig. 1C). At the Oostvaardersplassen, horses, unlike cattle and red deer, dig up and eat nettle and reed rhizomes during winter when food resources above the ground are strongly limiting. This is supported by the lower slope of the sward height-dependence of the per capita (winter) mortality of the horses compared to the cattle (Fig. 3A,B).

Without large herbivores, this highly productive ecosystem would be dominated by tall grasses and herbs, such as 2 m tall reeds, thistles and stinging nettle, with increasing invasion of shrubs and trees, as is shown in neighbouring ungrazed areas (Cornelissen et al. 2014). When total large herbivore abundances increased over time, the grazers created short grazed grasslands and by doing so, facilitated geese. The results suggest that, as visiting geese numbers increased over the years, strong competition between the smallest and the largest herbivores (cattle) developed, especially during winter and spring. And so the geese, in turn, gradually outcompeted their earlier facilitators on the grasslands. This led the larger herbivores increasing their exploitation of the nutritionally poorer vegetation types, such as reed, tall herbs, shrubs and trees, which were turned into grasslands. As a result, the area

became increasingly dominated by short grazed grasslands maintained at a lower biomass than required to support the largest herbivore's population. This hypothesis is supported by the nearly 60% decline in cattle numbers since 2000 associated with further increases in goose numbers (Fig. 1A).

These results call into question whether different-sized large herbivores can coexist long-term in such isolated, highly productive, and relatively homogeneous areas without large predators. The strong competition observed may reflect that this is a very young, small and homogeneous ecosystem. Thus far spatial differentiation of habitats due to biotic feedbacks have had relatively little time yet to develop. In more heterogeneous ecosystems with abundant forage alternatives, resource partitioning may increasingly lead to coexistence as any or all of the species can change their diet and use alternative resources (De Boer and Prins 1990, Putman 1996, Stewart et al. 2002; Kleynhans et al. 2011). Further, temporal variability and catastrophes such as climatic extremes and disease outbreaks may contribute to coexistence (Young 1994; Coulson et al. 2001; Sinclair et al. 2003; Hopcraft et al. 2010), and these phenomena may have had insufficient time to manifest.

Our results suggest that long-term coexistence of large herbivores in our fragmented landscapes requires enlarging effective protected areas, e.g., by connecting existing protected areas through corridors with other large nature reserves. When protected areas are enlarged and connected, heterogeneity will increase as more different environmental conditions (including gradients in e.g. soil type, groundwater level) will become part of the grazed landscape, which will increase opportunities for resource and space partitioning.

This study illustrates that restoring and maintaining multi-species herbivore assemblages in protected areas in densely populated countries is a challenge, especially when conservation produces conditions that favour competitive exclusion.

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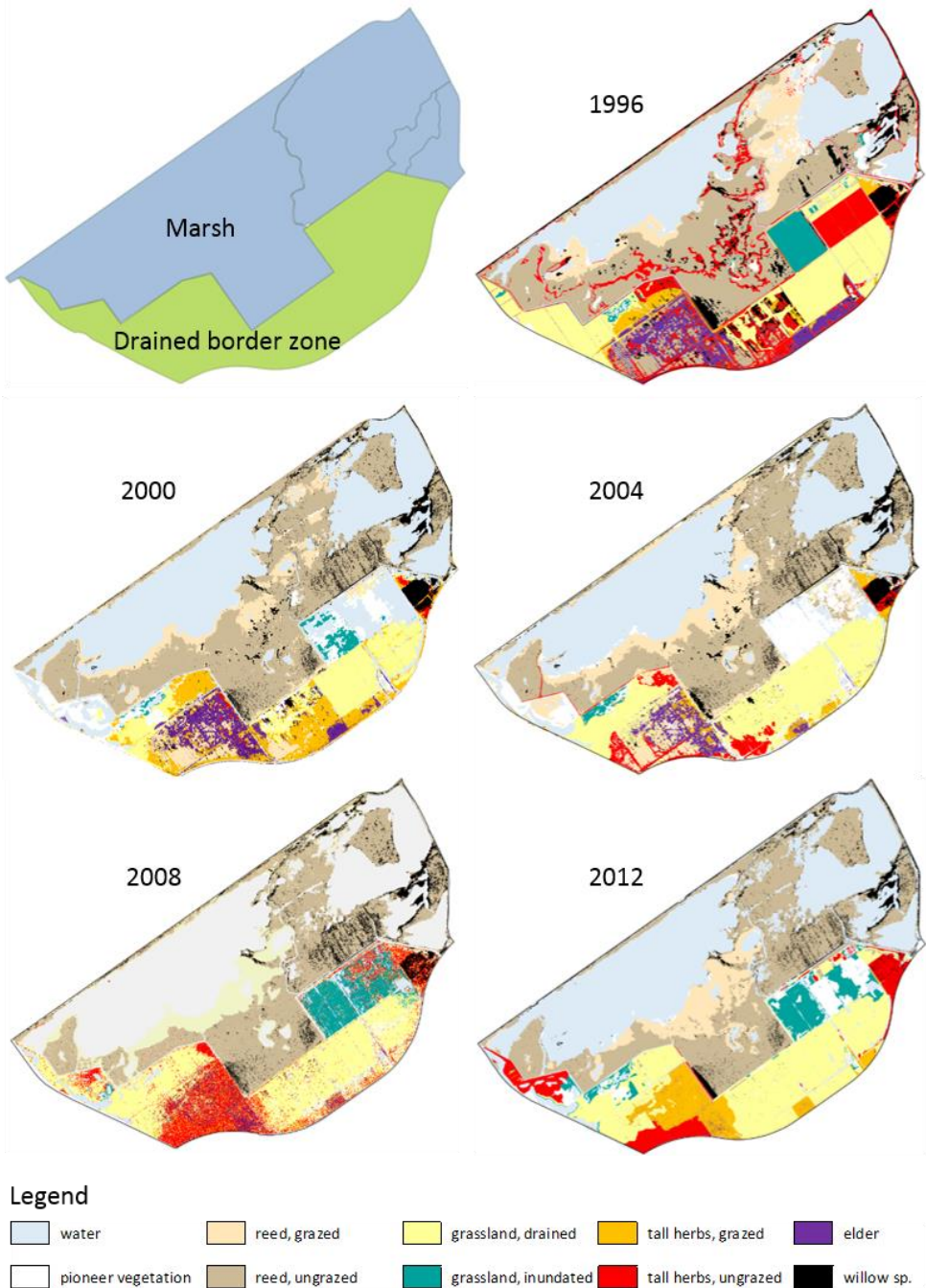
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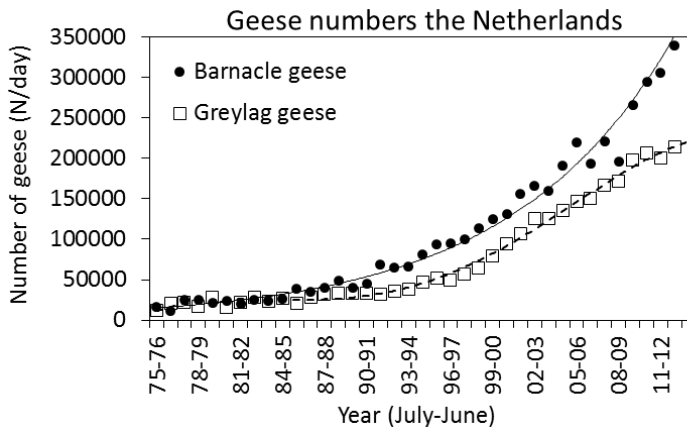
## Appendix

### 1. Vegetation maps Oostvaardersplassen



## 2. Geese numbers in the Netherlands

The most important geese in numbers in the Oostvaardersplassen are barnacle (*Branta leucopsis*) and greylag (*Anser anser*) geese. In the Netherlands more barnacle geese are present than greylag geese. The Dutch population of barnacle geese grew exponentially in the past 40 years and growth does not seem to slow down yet (Fig. 1). Greylag geese also grew exponentially, but the last few years growth seems to slow down.



**Fig 1.** Average numbers of Barnacle and Greylag geese per observation in the Netherlands. Source: Network Ecologische Monitoring, Sovon/CBS/provincies and [www.sovon.nl](http://www.sovon.nl).



## CHAPTER 7

### EFFECTS OF WEATHER VARIABILITY AND GEESE ON POPULATION DYNAMICS OF LARGE HERBIVORES CREATING OPPORTUNITIES FOR WOOD-PASTURE CYCLES.

Koen Kramer, Perry Cornelissen, Geert W.T.A. Groot Bruinderink, Loek Kuiters, Dennis Lammertsma, J. Theo Vulink, Sip E. van Wieren, Herbert H.T. Prins

#### Summary

Coexistence of large herbivores and vegetation heterogeneity is a challenge for managers of relatively small and homogeneous nature reserves in fragmented landscapes. A modelling analysis was performed to study if observed variability in weather conditions would be of sufficient magnitude to maintain long-term coexistence of large herbivore species, and to provide windows of opportunity for the establishment of thorny shrubs as predicted by the wood-pasture hypothesis. The study was applied to the Oostvaardersplassen nature reserve in the Netherlands, which has a large herbivore assemblage of Heck cattle, Konik horse and red deer. Owing to the fact that a large number of geese frequent the nature reserve, the effects of these small herbivores were taken into account in the model analyses. The results showed that weather variability increases population fluctuations and that geese reduce large herbivore numbers. The results also indicated that coexistence of the three large herbivore species is possible irrespective of weather variability and geese. However, the chances for the coexistence of cattle with the other large herbivores are reduced when weather is highly variable and geese numbers are high. If the management of large nature reserves aims at natural processes with assemblages of self-regulating large herbivore populations, our results show that weather variability and the presence of small competing herbivores may be essential factors in highly productive environments for the wood-pasture cycle creating a more heterogeneous landscape.

#### Introduction

Inspired by contemporary natural or near-natural grazing systems in Africa and North America as well as by past Pleistocene and Holocene ecosystems, (re-)introduction of wild large herbivores has recently gotten much attention (Caro and Sherman 2009; Jackson and Hobbs 2009; Huynh 2011; Navarro and Pereira 2012; Rey Benayas et al. 2009). The aim of this new management strategy is to restore historical ecosystems or increase biodiversity. In Western Europe, apart from wild herbivores, domestic cattle and horses as substitutes for their wild ancestors, are also introduced (WallisDeVries et al. 1998; Hodder and Bullock 2009). In our fragmented landscapes (Lindenmayer and Fisher 2006), these wild and domestic large herbivores are often introduced in relatively small reserves with fences to keep them inside and with large predators mostly absent. Under such conditions, the large herbivore populations are mainly regulated by food supply and winter conditions (Coulson et al. 2001). Although this management system is practiced the last 30 years in some European countries, little is known about population dynamics of the large herbivores and the effects on the environment in the

long term (McCann 2007). In this paper we describe the possible long term population dynamics of large herbivores and effects on the environment by means of a process-based model. The model was applied to one of the first areas in Europe where a multi-species assemblage of large herbivores was introduced, the Oostvaardersplassen nature reserve in the Netherlands.

In the eutrophic wetland the Oostvaardersplassen (OVP), an assemblage of cattle, horses and red deer was introduced in the 1980s. The area is fenced and animal numbers are not controlled at fixed stocking rates, but individual large herbivores considered to have no chance of survival are culled in order to prevent unnecessary suffering. The large herbivores do not get supplementary feeding. Large predators are absent and the reserve is visited every year by thousands of geese. A few years after introduction, populations of the large herbivores grew exponentially and after these first years the growth rate levelled off and numbers reached a maximum. Corresponding with the increased herbivore population, the vegetation changed from a heterogeneous mixture of grasslands, tall herbs, reed, scrub and trees to a homogeneous vegetation dominated by grasslands (Cornelissen et al. 2014a). Over the last 10 years the population of cattle has decreased, whereas the populations of horses and red deer and also the total number of geese have increased. As the vegetation becomes more dominated by short grazed grasslands, competition among the different large herbivore species becomes more severe (Putman 1996; Menard et al. 2002). It can be envisaged that this competition would lead to exclusion of the less competitive species. In this case, cattle could be outcompeted by the other large herbivores and geese because cattle cannot graze on short swards as the other herbivores can (Clutton-Brock et al. 1982; Illius and Gordon 1987; Vickery and Gill 1999; Menard et al. 2002; Bos et al. 2005).

Even in situations with potential for competition there are possible mechanisms whereby the large herbivores involved may coexist (Putman 1996). In heterogeneous areas with abundant forage alternatives, resource partitioning may lead to the coexistence of competing species (De Boer and Prins 1990; Putman 1996; Stewart et al. 2002; Kleynhans et al. 2011) as one of the species can change its diet and habitat use towards the forage alternatives in other habitats. Another mechanism is based upon disturbances which can reduce the population numbers of all herbivores or of the dominant competitor(s), such as climatic variation, predation, pests and diseases (Coulson et al. 2001; Sinclair et al. 2003; Hopcraft et al. 2010). Reduction of large herbivore numbers will lead to an increase in the amount of forage per capita for all species, enabling the competing species to coexist.

A reduction of large herbivore numbers is also an essential component of the wood-pasture hypothesis (Vera 2000), which attributes a key-role to large herbivores. High numbers of large herbivores may assist the transition of woodland to grassland by browsing and bark stripping which causes mortality of shrubs and trees (Gill 2006). Simultaneously the large herbivores maintain short-grazed grasslands and therefore provide opportunities for the re-establishment of shrubs and trees in these natural 'pastures'. However, the (re-)establishment of thorny shrubs and eventually trees in these grasslands, require a temporary reduction of the herbivore densities for a sufficient duration (Cornelissen et al. 2014a; Smit et al. 2015).

In this study we are interested in the effects of long term weather variability and geese on large herbivores and vegetation development. For this purpose we used the model FORSPACE (see Model description) and long term weather data of the past. The questions addressed in this study are: A) Is the weather variability strong enough to disrupt population numbers of large herbivores so that they can coexist? B) Can geese reduce large herbivore numbers

through competition, as they can graze the sward to even lower heights than the large herbivores? C) Does a temporary reduction in large herbivore numbers provide windows of opportunity for woody species to establish?

No analyses with respect to climate change was performed in the present study.

## Material and Methods

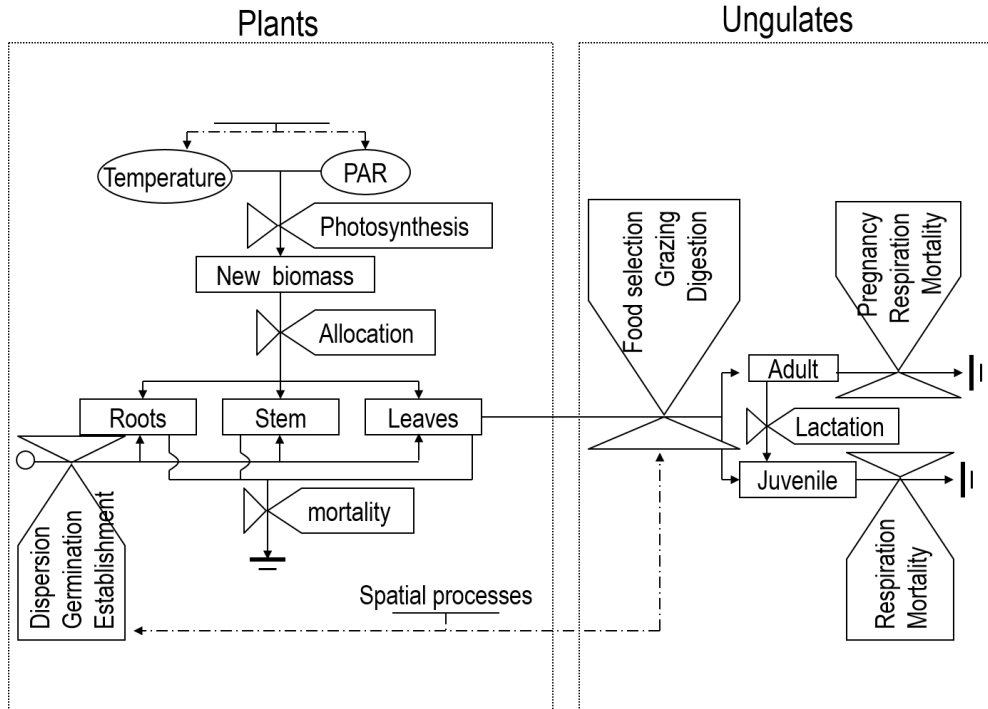
### *Research area*

The OVP-area (52°26' N, 5°19'E) is a eutrophic wetland of about 5,600 ha in Zuidelijk Flevoland polder in the Netherlands, reclaimed from lake IJsselmeer in 1968. As the area was a former lake, the bottom consists of soils with clay contents between 30-35%. Three habitat types can be distinguished in the research area: grasslands (*Poa trivialis* L., *Lolium perenne* L., *Trifolium repens* L. as dominant species), reed vegetation (*Phragmites australis* (Cav.) Steud.) and a semi-open mosaic vegetation of reed, tall herbs (*Urtica dioica* L., *Cirsium* spp. Mill.), elder (*Sambucus nigra* L.) and willow (*Salix* spp.) (Jans and Drost 1995). Most of the willow species, predominantly white willow (*Salix alba* L.), established on the bare soil primarily in 1968/1969, after the water was pumped out of the polder and the surface area became dry. Elder established some years later and establishment occurred over a longer period from the early 1970s until the early 1990s. Elder produces *cyanogenic glucosides* (Atkinson and Atkinson 2002) which can be toxic or lethal (Majak and Hale 2001). Ruminants can counteract the effects of toxic compounds better than hindgut fermenters (Van Soest 1994), which was shown by Vulink (2001) for the Oostvaardersplassen.

Cattle, horses and red deer were introduced into the OVP-area in different years: 32 Heck cattle (*Bos taurus* L.) in 1983, 18 Konik horses (*Equus caballus* L.) in 1984, and 52 red deer (*Cervus elaphus* L.) in 1992. In January 2015, about 250 cattle, 1200 horses and 3200 red deer were present. The populations of the large herbivores were counted annually. The most important geese in the OVP-area are Greylag geese (*Anser anser* L.) and Barnacle geese (*Branta leucopsis* L.). Geese were counted every week along a fixed route along the grasslands. Annual average numbers of geese per observation day increased from about 3,000 in 1996 to about 10,000 in 2014. Both species are present throughout the year with maximum numbers during winter and spring.

### *Model description*

We used the spatial-explicit and process-based model FORSPACE, which describes the feedbacks between vegetation development and herbivore density (Kramer et al. 2003; Kramer et al. 2006) (Fig. 1). In the model, plant populations are characterized by the density of plants, the weight of the different plant components, and their structural properties. These variables are calculated for each tree-, shrub-, herb- or grass species. Ungulate populations are described by the weight and number of both juvenile and adult cohorts for each ungulate species. The technical description of the model including sensitivity analyses and validation is presented Kramer (2001). The model is implemented in the dynamic GIS PC-Raster (Wesseling 1996).



**Fig. 1.** Flow diagram showing the principal processes and flow of information between plants and ungulates in the model FORSPACE.

To apply the FORSPACE model to the OVP-area, it was necessary to make adjustments with respect to a number of processes that are specific for this area. The model adjustment considers the following issues: (i) observed meteorological time series of temperature, radiation, and snow cover were used instead of statistically generated time series of these meteorological variables used in the FORSPACE model. The weather data of the weather station De Bilt of the Royal Dutch Meteorological Institute (KNMI) in the Netherlands of the past 110 years was used as data collection started in 1901. This station is situated 38 km from the OVP-area. Snow cover is defined as the fraction of the month where the vegetation is covered with snow. It is assumed that the herbivores have no access to the plants as long as there is snow cover, even though we know that this is a rather narrow assumption. (ii) Large numbers of moulting and wintering geese visit the OVP-area year-round consuming a substantial part of the annual net primary production. The intake of the vegetation is described in the same way as that of the large herbivores. However, the population dynamics of the geese are not simulated because we assume that their population dynamics are largely determined by external factors such as the food availability outside the OVP-area (Van Eerden 1998). In the model analyses we compared two geese scenarios: no geese, and high geese densities. The high geese densities are comparable to the geese numbers that visited the OVP-area during the past five years. During days with snow cover or mean daily temperature below 0°C, the number of visiting geese is set to zero as under such conditions the geese journey to warmer areas without snow cover. (iii) The parameter values of the

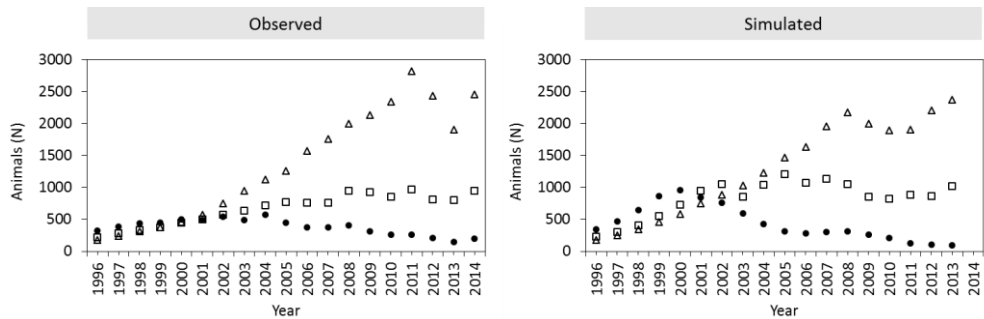


woody species willow and elder were adjusted, using measurements of growth and development on these species at the OVP-area (Cornelissen et al. 2014 a, b). (iv) The plant functional type of ‘thorny shrubs’ was added, exemplified in the area by hawthorn (*Crataegus monogyna* Jacq). All large herbivores induce mortality of hawthorn by bark peeling. Bark peeling related mortality is a specific process that cannot be described generically. Therefore, an empirical approach for this particular process and species was taken, valid for this area only. This effect is brought in the model by an increased turnover of the number of individuals of hawthorn if the total herbivore numbers exceeds 800 animals. This number is comparable to the total number of large herbivores in 1996. Before this year new establishments of woody species were seen on aerial photographs (Cornelissen et al. 2014b) and after this year no new establishments were seen on photographs and no seedlings of woody species were found in the field (Cornelissen et al. 2014a, b). We define occurrence of thorny shrubs as the presence of hawthorn and of palatable shrubs as the presence of willow and elder exceeding 1.5 m in height. It is assumed in the model that from that height onward the large herbivores do not affect the height of the thorny shrubs. However, the height of the other shrubs can be reduced, until the plant exceeds the herbivore specific maximum browsing height. This difference between thorny shrubs and non-thorny, palatable shrubs was brought into the model because hawthorn can develop a shoot in the centre of the shrub that is beyond reach of animals even though the shrub itself is below the browsing height of the animal. That process of a central leader shoot escaping browsing is not present in the willow or elder considered. (v) The effect of winter temperature on survival of the large herbivores is simulated by an increase of maintenance cost of the large herbivores if the average monthly temperature drops below 0°C. There is little information available in the literature on the magnitude of the enhancement of maintenance respiration with decreasing freezing temperatures. Therefore, the model was calibrated assuming that each herbivore species in the model survived the most severe winter in the period 1901-2013. This assumption is based on the absence of evidence in the literature that wild herbivore populations got extinct due to severe winters in any large nature reserve in Northwest Europe during this period.

### *Validation*

A model versus data comparison was performed between the observed and predicted number of herbivores over the period 1996-2013 based on the adjusted parameter values. We used 1996 as a starting point as from that year on the total area was grazed by cattle, horses and red deer. The actual number of geese and the observed weather data for this period were applied for this validation. The model results in a close match between observed and simulated numbers of the three large herbivore species, although Heck-cattle is over-estimated by the model whereas red deer is under-estimated (Fig. 2). The decrease in number of Heck cattle over time is most likely a result of competition among herbivores as the sward height of the grasslands of the OVP-area (Cornelissen et al. 2014c) decreased below minimum grazing height for cattle. In our model the minimum grazing height for cattle was set at 5 cm (Menard et al. 2002). Konik horse, red deer and geese can graze more efficiently on swards below 5 cm than cattle (Clutton-Brock et al. 1982; Illius and Gordon 1987; Vickery and Gill 1999; Menard et al. 2002; Durand et al. 2003; Bos et al. 2005; Cope et al. 2005). In the model the minimum grazing height for horses and red deer was set at 2 cm. For geese, a minimum grazing height was used of 1 cm (Durand et al. 2003; Cope et al. 2005). In the

model, it is assumed that geese, as specialist grazers (e.g. Aerts et al. 1996; Owen 1979), only graze on grasses, not on any of the other plant species in the herb layer.



**Fig. 2.** Model versus data comparison with respect to dynamics in numbers of large herbivores. Left graph shows the observed numbers of animals of 1 year and older on May 1 of each year; right graph shows the results of the model. Black circles are Heck cattle; open squares are Konik horses; open triangles are Red deer.

### *Model runs*

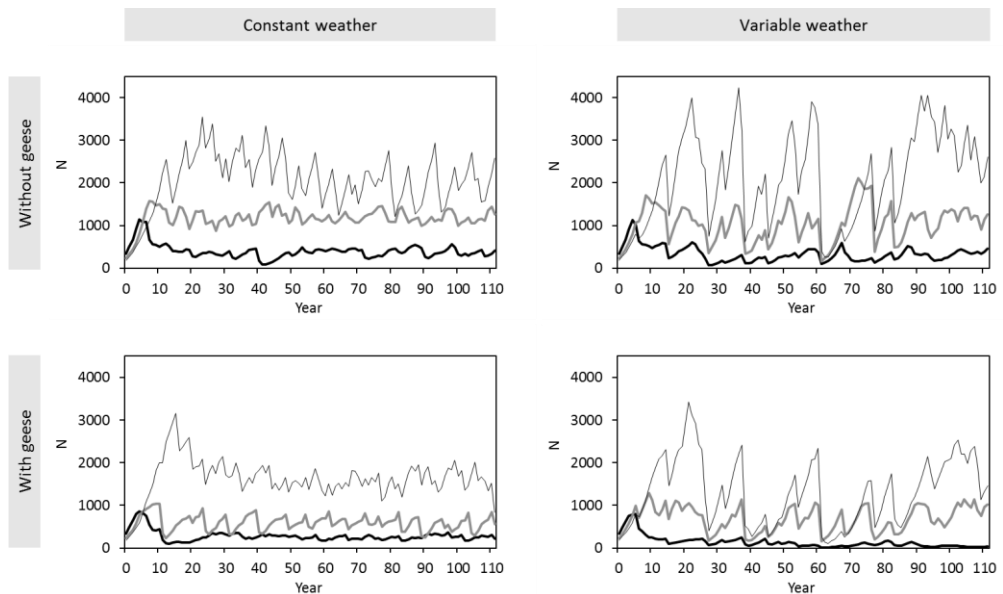
A number of scenario analyses was performed to answer the questions posed for this study. All combinations of these scenarios were evaluated with respect to: (i) Dynamics of the large herbivore populations; (ii) Effects of geese on large herbivore numbers; (iii) Opportunities for thorny or palatable shrubs to establish and grow to a size that prevents direct removal by the herbivores. These scenarios included:

- a. Variable versus constant weather, to assess the effects of weather variability. The temperature series for the scenario with variable weather were based on weather time series for the period 1901–2013. For the scenario analyses with constant weather, monthly averages over the period 1901–2013 were used for: temperature, incoming radiation, snow cover, and the duration of the growing season, based on the variable weather series.
- b. High geese density versus no geese, to assess the effects of the presence of geese. The high geese densities are comparable to the geese numbers that visited the OVP-area during the past five years.
- c. All large herbivore species versus no large herbivore species, to assess the effects of large herbivores on the opportunities for woody species to establish and grow.

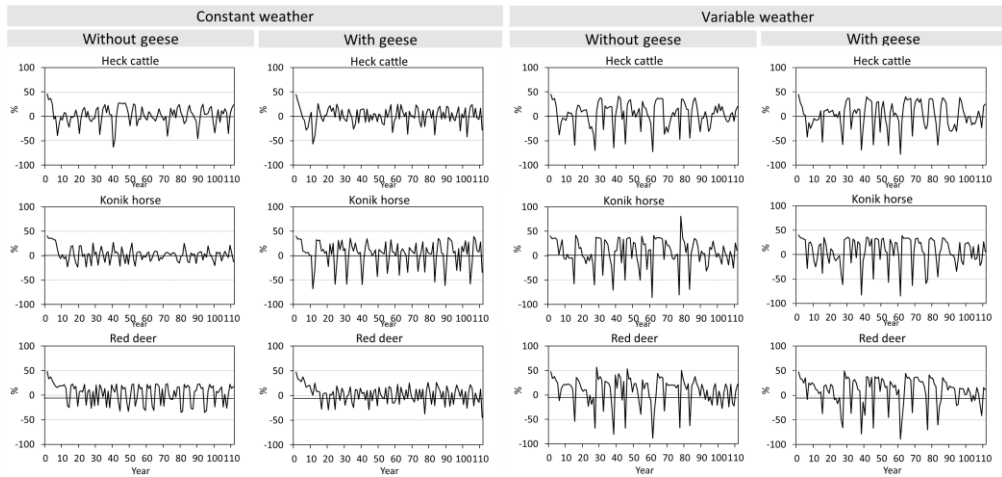
We used the animal numbers and the vegetation map of the year 1996 as a starting point for our model runs. From that year on, the whole area was grazed by the large herbivores.

## Results

Animal numbers were affected by weather and geese (Fig. 3). Weather variability led to higher maximum and lower minimum population numbers and therefore increased fluctuations in animal numbers compared to the constant weather scenarios (Fig. 3). Reductions in animal numbers were closely associated with the occurrence of severe winters. Geese were responsible for decreased numbers of the large herbivores and the absolute fluctuations. The weather and geese also affected relative fluctuations (Fig. 4). The relative increase and decrease, i.e. the change of the population number over one year given as a percentage of the population number at the beginning of that year, were much greater in the variable weather scenarios. It was also greater in the scenarios with geese, but the effect of geese was less pronounced than that of the weather. The three large herbivores species continued to coexist in all weather and geese scenarios over a period of 110 years (Fig. 3). However, the number of Heck cattle occasionally became very low in the scenario with variable weather combined with high geese densities.

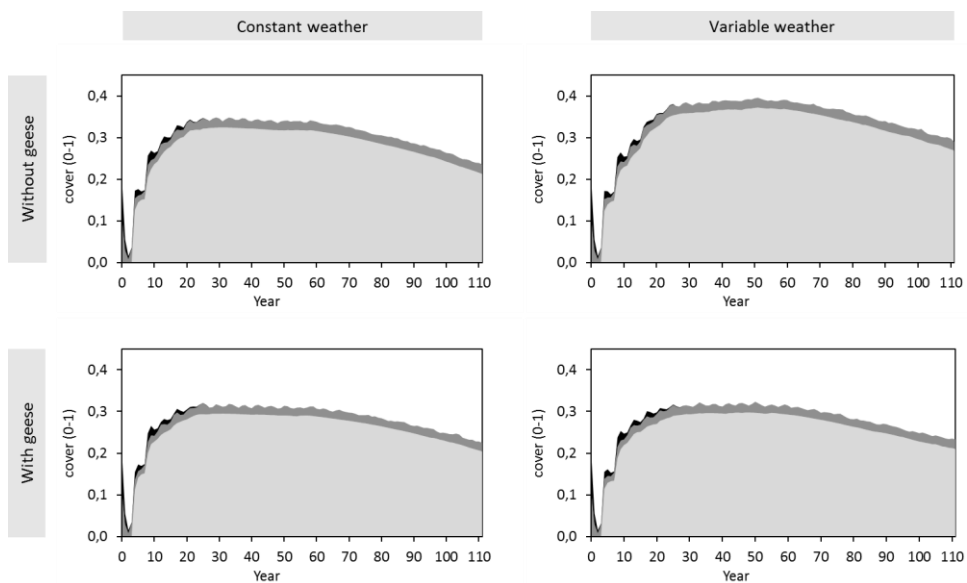


**Fig. 3.** Population dynamics in numbers of the populations of Heck cattle (thick black line), Konik horse (thick grey line) and Red deer (thin black line) in the scenarios with constant and variable weather, and without and with geese.

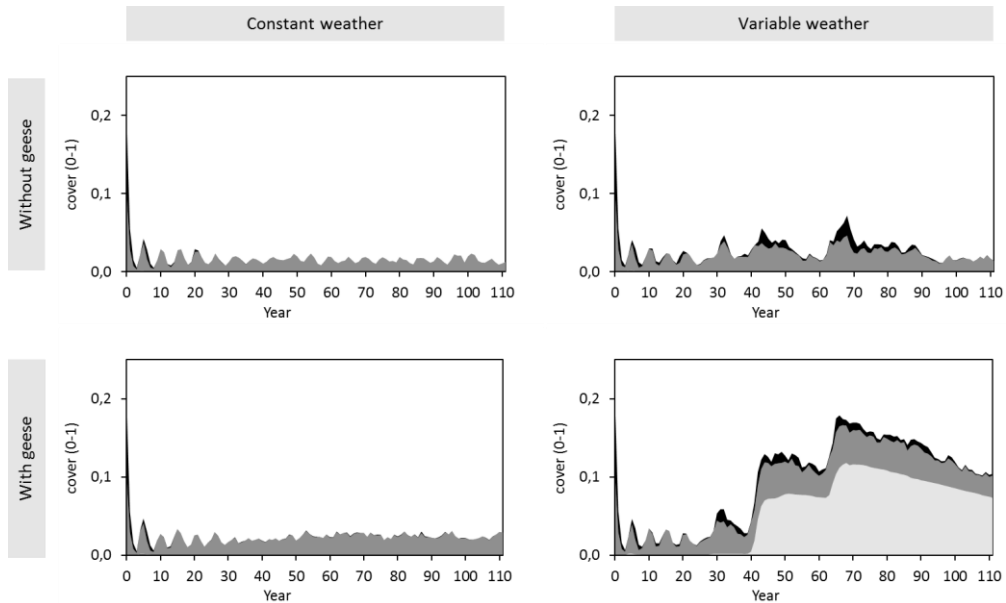


**Fig. 4.** Relative increase and decrease of the populations of Heck cattle, Konik horse and Red deer in the scenarios with constant and variable weather, and without and with geese. The increase or decrease is the change of the population number over one year given as a percentage of the population number at the beginning of that year.

Weather and geese directly and indirectly affected development of woody species (Fig. 5 and 6). The scenarios without large herbivores (Fig. 5) showed that weather variability and absence of geese led to slightly higher cover of woody species compared to scenarios with constant weather and presence of geese. In these scenarios without herbivores, the area was not covered totally by woody species. When large herbivores are absent, tall herbs and tall grasses start to dominate the vegetation, making it difficult for the woody species used in the model, to establish later on. As weather and geese affected large herbivore numbers (Fig. 3), both factors also indirectly influenced the development of woody species through the number of large herbivores. In general, the effects of the large herbivores on the development of woody species were much greater than the direct effects of weather and geese (Fig. 5 and 6). For the scenarios with all large herbivores (Fig. 6), the greatest opportunities for the establishment of woody species arose with variable weather and with geese and the smallest with constant weather and without geese. The thorny shrub hawthorn only established with variable weather and with geese, elder only with variable weather and willow established under all conditions. In the scenario with variable weather and with geese, hawthorn established twice (after two periods with the most severe winters), whereas the other two species established more frequently. But once established, hawthorn started to dominate the woody vegetation. The moments hawthorn established corresponded with a total large herbivore number of less than 800 animals which occurred for more than four years in a row (Fig. 3).



**Fig. 5.** Dynamics of hawthorn (light grey), willow (dark grey) and elder (black), exceeding 1.5m in height in the scenario without the assemblage of Heck cattle, Konik horses and Red deer, for constant and variable weather and without and with geese. Cover is presented as a proportion between 0-1.



**Fig. 6.** Dynamics of hawthorn (light grey), willow (dark grey) and elder (black), exceeding 1.5 m in height in the scenario with the assemblage of Heck cattle, Konik horses and Red deer (see fig. 2), for constant and variable weather and without and with geese. Cover is presented as a proportion between 0-1.

## Discussion

Few process-based models exist that are able to simulate the long-term dynamics of herbivore-vegetation interactions at a spatially explicit base (Bugmann 2003; Fontes et al. 2010). To understand those dynamics and how they are affected by weather variability and the presence of other herbivores such as geese, the model FORSPACE was applied for this purpose at the OVP-area (Groot Bruinderink et al. 1998). For this area a number of processes needed to be added to the general model, such as impact of geese, mortality of hawthorn due to bark peeling, and the impact of severe winters on maintenance requirements of the large herbivores. Empirical and area-specific data were taken for those processes. After adding these processes, we can conclude that the model represents the observed dynamics in herbivore numbers sufficiently well to allow model-based scenario analyses for a highly productive area as the OVP-area.

The model results showed that weather variability disrupts population numbers of large herbivores. As a result of these large decreases, food supply per capita increases. This creates opportunities for coexistence. However, coexistence was also possible in the scenarios with constant weather. In these scenarios it was expected that cattle, as the less competitive herbivore species, was not able to coexist with Konik horse, red deer and high numbers of geese. Under conditions where horses and red deer populations are not substantially reduced by severe winters, sward height of the grasslands will be too low for cattle. When the weather is constant, population numbers also fluctuate but much less than in the variable weather scenarios. The population fluctuations in the constant weather scenarios were caused by the consequences of the ever changing age distribution within the populations, which results in annual variation in mortality; and by the differences among the large herbivores with regard to years of increase and decrease of the populations, which causes differences in the strength of competition and therefore variable mortality and reproduction. Although fluctuations of animal numbers in the constant weather scenarios were much less than in the variable weather scenarios, these fluctuations might have been strong enough to create opportunities for the coexistence of the three large herbivores.

Geese substantially decreased large herbivore numbers (Fig 3). By closely harvesting the regrowth on the short grazed grasslands during winter and spring, they are strong competitors. During this period net primary production is still low and the thousands of geese can keep the sward very short (<2 cm). As cattle prefer sward heights between 9-16 cm (Menard et al. 2002) whereas horses, red deer and geese can efficiently graze on swards below 5 cm (Clutton-Brock et al. 1982; Illius and Gordon 1987; Vickery and Gill 1999; Menard et al. 2002; Durand et al. 2003; Bos et al. 2005; Cope et al. 2005), cattle will be the first species to experience the negative consequences of competition.

The model results showed that only variable weather and presence of high numbers of geese provides windows of opportunity for thorny shrubs to establish (Fig. 6). These two factors caused major decreases in large herbivore numbers needed for thorny shrub encroachment. Cornelissen et al. (2014a, b) showed that in the OVP-area the large herbivores can transform woody vegetation into grasslands, whereas woody species only established at low herbivore densities (<0.5 animals ha<sup>-1</sup>). Smit et al. (2015) conclude that large herbivores can create wood-pasture landscapes as long as grazing refuges are present. However, if the large herbivore numbers are high, the grazing refuges will not be present (Cornelissen et al. 2014b). Negative effects of high herbivore numbers on the establishment

of woody species are also reported in many other studies (see Gill 2006). Our results agree with these findings that effectively no wood-pasture cycling is possible when large herbivore species are present in high numbers without periods with very low animal densities due to fluctuations in weather conditions, diseases or other factors. However, apart from the effects of weather, high numbers of geese are also a prerequisite for the low numbers of large herbivores needed. Small herbivores also affect establishment of woody species (e.g. Kuiters and Slim 2003; Bakker et al. 2004), but these are all direct effects of the small herbivores on the woody species through browsing or debarking. In our study the effect of the geese on the establishment of woody species is not direct but indirect through competition. Geese will damage young and small seedlings in the very short grazed grasslands. However, in the highly productive OVP-area, the geese cannot keep the swards short without the large herbivores and the height of the vegetation will increase. Vulink (2001) showed that geese prefer to feed on intensively grazed, highly nutritious, short swards. As higher swards are less nutritious than shorter ones, these swards become less attractive to geese and they are eventually avoided. It is during this temporary (in our model at least 4 years) reduction of large herbivores numbers that chances increase for woody species to establish and grow. The model shows that this window of opportunity for thorny woody species only happened twice during a period of 110 years, resulting in distinct cohorts of plants as was also described by Prins and Van der Jeugd (1993) for *Acacia* in Lake Manyara National Park in Tanzania.

In our model, geese play a key role in the dry zone of the eutrophic wetland the OVP-area with regard to wood encroachment and the creation of a heterogeneous landscape. Apart from their key role in the dry zone, geese also play an important key role in the marsh zone of the OVP-area (Vulink and Van Eerden 1998). Moulting greylag geese have a great impact on the development of the reed vegetation in the marsh creating a diverse habitat, benefiting many other animal species. However, geese cannot fulfil their key role within the eutrophic wetland without the presence of two important factors. Within the marsh it is the water level dynamics that is necessary for the recovery of the grazed reed vegetation (see Vulink and Van Eerden 1998 for a detailed description). Within the dry zone it is the populations of large herbivores which facilitate the geese by creating large scale short grazed grasslands.

Although coexistence of the three large herbivores occurred in all scenarios, the chances for cattle in a highly productive homogeneous area are reduced with increasing weather variability and when geese numbers are high. A strong decrease in a small population has a greater impact on the survival of a large herbivore species than in a large population. A strong decrease in a small population can lower the numbers to such an extent that the population cannot reproduce anymore as for example all males die. In sexual dimorphic species, such as cattle and red deer, mortality of males is greater than of females (Clutton-Brock et al. 1982; Georgiadis 1985) especially when food becomes limited (Toïgo and Gaillard 2003) or winters are more severe (Clutton-Brock et al. 1982). As mortality of male cattle and red deer of the OVP-area is also higher than female mortality (unpublished data), this possibility is likely to occur when populations of cattle or red deer become small. This means that the size or the productivity of an area (i.e. the fenced nature reserve) are important factors in the survival of a population as smaller or less productive areas can contain fewer animals. In our modified landscapes with habitat sub-division, degradation and loss (Fischer and Lindenmayer 2007) resulting in small fragmented areas for nature conservation, coexistence of large (introduced) herbivores in these small, isolated and less heterogeneous areas can become difficult. Apart from temporal variation in environmental factors such as weather, resource

partitioning may also be a possible mechanism whereby the large herbivores involved may coexist (De Boer and Prins 1990; Putman 1996; Stewart et al. 2002; Kleynhans et al. 2011). Increasing heterogeneity in homogenous areas such as the OVP-area, resulting in abundant forage alternatives, may lead to resource partitioning. Increasing heterogeneity can be achieved by carrying out measures such as planting shrubs and trees, or creating wet areas with reed vegetation. Another option is to increase the area of the homogenous nature reserve using adjacent areas with other habitat types, or to create corridors to other areas with other habitat types further away (Gilbert-Norton et al. 2010). As an extension of the homogenous nature reserve may lead to an increase in total heterogeneity (and therefore resource partitioning), distribution of the large herbivores over the area may alter. This could change the chances for the establishment and survival of shrubs and trees in the original, homogenous nature reserve, benefitting the wood-pasture cycle and enhancing the overall heterogeneity. Enlarging and connecting nature reserves to create better opportunities for large herbivores and wood-pasture cycles, also benefits biodiversity to a great extent as landscape modification and habitat fragmentation are key drivers of global species loss (Hanski 2005; Fischer and Lindenmayer 2007).

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## CHAPTER 8

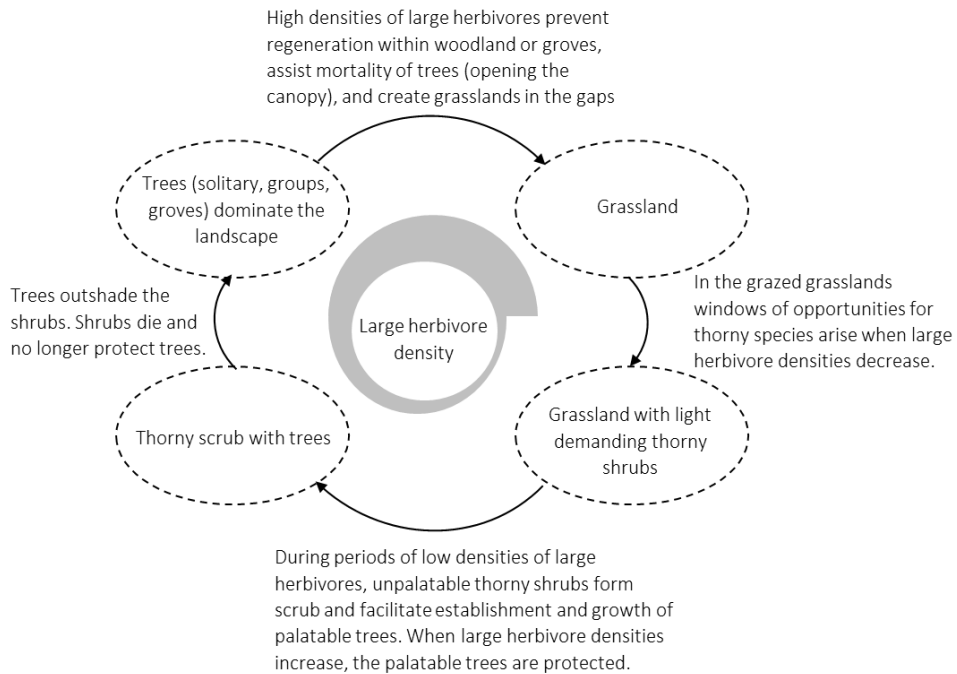
### General Discussion

Large herbivores are considered to be ‘keystone’ species to achieve conservation and restoration of biodiversity (e.g. Wallis De Vries et al 1998; Zabel and Anthony 2003; Danell et al. 2006; Rotherham 2013). Large herbivores affect plant community structure (e.g. Bakker 1998; Hester et al 2006; Thompson Hobbs 2006; Smit and Putman 2011), and by doing so, have an impact on most other plant and animal species in these communities (e.g. Root 1973; Cody 1975; Olff and Ritchie 1998; Van Wieren 1998; Olff et al 1999, Adler et al 2001; Suominen and Danell 2006). The ‘Rewilding’ concept (see Pereira and Navarro 2015) aims at restoring spontaneous ecosystem processes and reducing human control of landscapes. Unmanaged populations of large herbivores are assumed to play a key-role in the large scale dynamics of landscapes by driving cyclic wood-pasture mosaics. The question is whether these assumptions are correct in all cases. Therefore habitat use and population dynamics of large herbivores, the effects of large herbivores on vegetation development, and the mutual interactions between vegetation development and herbivore population dynamics were studied and analysed in the eutrophic wetland the Oostvaardersplassen (Chapters 2, 3, 5, 6, 7) and a fluvial floodplain (Chapter 4). The focus of the long term vegetation studies was on the wood-pasture cycles. It is still heavily debated whether self-regulating large herbivores indeed play a key role in these cycles (e.g. Svenning 2002; Bradshaw et al. 2003; Kirby 2004; Birks 2005; Hodder and Bullock 2009; Szabo 2009; Whitehouse and Smith 2010; Sandom et al. 2014). In this chapter the most important findings of these studies are discussed in the context of the wood-pasture cycle, the mutual interactions between large herbivore dynamics and vegetation development, and the management of eutrophic wetlands in our fragmented landscapes.

#### **Wood-pasture cycles in a eutrophic environment**

The “*wood-pasture theory*” or “*cyclic turnover of vegetation theory*” (Vera 1997) and the ‘shifting mosaics’ model (Olff et al. 1999) describe a landscape vegetation structure cycle, driven by large herbivores and the facilitation (associational resistance) and competition between plant species (Fig. 1). It is assumed that large herbivores are the primary factor responsible for the development of park-like landscapes with natural regeneration of shrubs and trees in the grazed grasslands. High numbers of large herbivores prevent the regeneration of woody species within woodlands and may, next along with ageing, disease and fire, contribute to the mortality of shrubs and trees by browsing and bark stripping, opening the canopy. In these open areas within the woodland, the large herbivores create and maintain short grazed grasslands. These grazed grasslands provide opportunities for the re-establishment of light demanding woody species, especially thorny shrubs, but only during periods when large herbivore numbers are low. These fluctuations in herbivore densities could be caused by seasonal differences in habitat use and by fluctuating population numbers as a result of temporary food shortages, severe winters or disease outbursts. During these periods of low herbivore numbers, established thorny shrubs can grow, protect themselves against browsing and debarking, and eventually can serve as safe sites for palatable and less protected trees. Once the trees are established within the protected

environment of thorny shrubs, they will overtop the shrubs and will out-compete the shrubs for light. When the thorny shrubs are gone, the large herbivores can return to these ‘unprotected’ wooded areas and start the cycle again. As these cycles vary in time and space, a park-like landscape develops with open grasslands, scrub, solitary trees, groups of trees and groves.



**Fig. 1.** Wood-pasture cycle showing four phases and transitions in the park-like landscape. The grey circle in the centre shows the relative large herbivore densities needed for the transitions and to maintain certain phases over longer periods. The thicker the grey line, the higher the large herbivore densities. Based on Vera (1997) and Olff et al. (1999).

Many studies have shown the impact of large herbivores on vegetation which is assumed in the wood-pasture cycle theory. These impacts include mortality of shrubs and trees through browsing and debarking, establishment of plant species by creating grazing and trampling induced gaps for germination, and dispersal of seeds in coats or faeces (e.g. Braun 1963; Crawley 1997; Mouissie 2004; Gill 2006; Hester et al. 2006; Putman et al. 2006; Rotherham 2013). Besides these direct effects, many other studies have shown the positive effects of ‘nurse’ plants and ‘safe’ sites in grazed environments on the establishment of shrubs and trees (e.g. Callaway 1992; Olff et al. 1999; Bakker et al. 2004; Smit et al. 2005; Baraza et al. 2006; Barbosa et al. 2009; Vandenberghe et al. 2009; Smit and Ruifrok 2011). Furthermore, according to Smit et al. (2015) several studies have shown that large herbivores can create and maintain a park-like landscape. However, in the above mentioned studies large herbivore densities were generally low, their numbers were top down controlled by humans, productivity in the majority of the areas was low, and in most cases effects were monitored only for a few years. So despite these studies, no study until now has shown the

effects of free ranging and bottom-up regulated large herbivore assemblages in highly productive areas over a longer period.

The study in the Oostvaardersplassen nature reserve revealed long term effects of large herbivores, that are regulated by their food supply, on vegetation development in a homogeneous eutrophic environment. The results showed that high densities of cattle, horses and red deer were able to break down the woody vegetation of the Oostvaardersplassen (Chapters 2 and 3). Even the toxic species *Sambucus nigra*, which is not eaten by horses for that reason (Vulink 2001) and less preferred by cattle than by red deer, could not stand the high grazing pressure. The breaking down of the woody vegetation, caused by browsing and debarking, started after 1996 when total large herbivore numbers exceeded 0.5 animals per ha (Chapter 2 and 3). This breaking down was greater when shrubs or trees were closer to the large scale grasslands (Chapter 2), which supports the hypothesis of associational palatability (Olf et al. 1999), but then on a landscape scale. This effect was also reported by Clarke et al. (1995), Hester and Baillie (1998) and Oom et al. (2002). The breaking down was less when a shrub or tree was surrounded by the toxic *Sambucus nigra*, presenting some evidence for associational resistance (Olf et al. 1999) and aggregational resistance. However, this is described only when herbivore numbers were low. Once densities of large herbivores increased substantially, the toxic *Sambucus nigra* was not able to give any protection as all shrubs were heavily browsed and debarked (Chapter 3). This agrees with Smit et al. (2007) who also found that facilitative effects of 'nurse' plants disappeared at high herbivore densities as the 'nurse' plants themselves got attacked.

Although the woody vegetation of the Oostvaardersplassen, which consisted mainly of *Sambucus nigra* and *Salix* spp., was broken down, the area was not suitable to study the effects of the large herbivores on woody vegetation consisting of species with other plant defence mechanisms. Woody species that are known to be well protected against large herbivores, such as thorny shrubs (Linnart and Whelan 1980; Good et al 1990; Baraza et al. 2006), are very scarce in the Oostvaardersplassen and were not recorded in the plots of the studies. Nevertheless, there is plenty of circumstantial evidence that the actual grazing pressure affects many woody species. Within the grazed area of the Oostvaardersplassen five *Crataegus monogyna* shrubs and three *Betula pendula* trees established before the introduction of the large herbivores in 1983 and are still present in the grazed area. Twigs of both species are heavily browsed up to 2 m in height. Only bark of *Crataegus monogyna* is stripped but not as heavily as with *Sambucus nigra* or *Salix* spp (pers. observ.). In 2010, as the woody vegetation in the Oostvaardersplassen disappeared, some parts of the forests adjacent to the Oostvaardersplassen were made accessible to the large herbivores to provide shelter during winter. As the original aim of these forests was forestry and recreation, they contain shrubs and trees that are not well protected against herbivory such as *Corylus avellana* or *Fraxinus excelsior* which are sometimes completely debarked up to 2 m in height. Also young trees (<15 years) of *Quercus robur* or *Acer pseudoplatanus* are not well protected as their thin bark cannot withstand herbivory yet. The stems of these young *Quercus robur* and *Acer pseudoplatanus* trees are sometimes ringbarked, whereas the older individuals show no signs of debarking (pers. observ.). Based on these experiences it can be concluded that the large herbivores of the Oostvaardersplassen can also break down other woody species, as is also demonstrated in many other studies (e.g. Braun 1963; Crawley 1997; Gill 2006), and may alongside to ageing, disease or fire, contribute to the mortality of shrubs and

trees by browsing and bark stripping and as such open up the canopy of woodland for the creation of grasslands.

During the period when the woody vegetation was broken down, the large herbivores also affected the other vegetation types, such as reed and tall herbs (Chapters 3 and 6). Over a period of 17 years (1996-2012), the mosaic vegetation of grasslands, tall herbs, reed, shrubs and trees was transformed by the increasing numbers of large herbivores into a landscape dominated by grasslands (Chapter 6). Until now, no woody species had established in these grazed grasslands (Chapter 2 and 3). Seedlings of *Crataegus monogyna* and *Quercus robur* are observed almost every year (pers. observ.), but none of them survive the winter when grazing is intense and food on the grasslands is in short supply. A recent transplanting experiment of Smit et al. (2015) in the Oostvaardersplassen showed that none of the planted saplings of thorny shrubs and palatable trees survived in grazed situations. Even in areas with tall herb vegetation (i.e. *Urtica dioica*, *Cirsium* spp.) the tall herbs did not protect the saplings, since at high herbivore densities these 'nurse' plants themselves are eaten by the herbivores. Even the toxic tall herb *Jacobaea vulgaris*, which only recently invaded parts of the grasslands, failed to protect woody seedlings (pers. observ.). Protection by spiny or toxic tall herbs ends during winter when they die and their aboveground parts are trampled down by the herbivores. Every sapling becomes visible and accessible for the herbivores. And as the saplings of the thorny shrubs have not formed spines or thorns yet, they become an easy prey for the hungry large herbivores. In the experiment of Smit et al. (2015), saplings of shrubs and trees only survived when a fence protected them; the overall survival of saplings in these exclosures was 25% after four years. Furthermore, survival in protected areas was greater when the saplings were planted in grasslands instead of in vegetation dominated by tall herbs. This was attributed to reduced light competition in the grasslands. A similar effect was found in an experimental study in a grazed floodplain (Chapter 4). In this experiment *Crataegus monogyna* established in grazed grasslands for the first two years directly following the start of the experiment. Before the start of the experiment the area was grazed with high densities of cattle during summer combined with mowing. During the experiment, the area was year-round grazed with horses, combined with cattle in summer, and overall densities were lower than before the experiment. During the first two years of the experiment, vegetation height of the grasslands was still low as a result of the former intensive management. After these first two years, vegetation height increased as tall herbs started to dominate certain areas within the highly productive grasslands because of the lower grazing intensities. Only during these first two years when vegetation was still low, *Crataegus monogyna* established in the grasslands. Also in the experiment of Smit et al. (2015) the vegetation height of the ungrazed grassland increased after the first year and the vegetation became dominated by tall herbs and resembled the ungrazed tall herb vegetation. It would be interesting to repeat the experiment of Smit et al. (2015) and plant saplings every year during the experiment to see if sapling survival decreases in time when vegetation height of the ungrazed grassland increases as tall herbs start to dominate the vegetation. If, as can be expected, the results of this experiment would be similar to the results of the experiment in the floodplain (Chapter 3), this would mean that the window of opportunity for establishment of the light demanding thorny shrubs in highly productive grasslands will be very narrow. Only for a period of one or two years after a significant reduction of large herbivore numbers, the vegetation will be low enough for the light demanding shrubs to establish because of reduced light competition.



Although in the Oostvaardersplassen no woody species have established in the grasslands in the past two decades as a result of high densities of large herbivores, we can derive from the past that during periods when densities of large herbivores were low (i.e. before 1996 at <0.5 animals per ha), shrubs of *Sambucus nigra* and *Salix* spp. established in the area grazed by cattle, horses and red deer (Chapter 2). Also in other parts of the Oostvaardersplassen with different grazing regimes in the past (see Vulink 2001), woody species established during periods of low densities of herbivores. For example, in the so called 'Driehoek' in the eastern part of the border zone, year-round grazing with low densities of Konik horses took place for several years in the early 1990s (Cornelissen and Vulink 1996). In this area, *Crataegus monogyna* was established in the grazed grasslands. After herbivore densities in the 'Driehoek' increased from the second half of the 1990s, because the red deer population had access to this area all year round and from 2010 on also Heck cattle and the large herd of Konik horses had access during winter, the once established *Crataegus monogyna* survived in these grasslands. However, browsing of these shrubs was intense and the shrubs remained very short (up to 40 cm height; pers. observ.). Furthermore, there were no new establishments of *Crataegus monogyna* in these grasslands and thorny scrub vegetation did not develop.

Based on developments so far, some important requirements for the wood-pasture cycle in the Oostvaardersplassen have not been fulfilled: (a) a temporary reduction of large herbivore number required for the establishment of light demanding thorny shrubs and the formation of thorny scrub; (b) the establishment of palatable trees within these thorny scrub; (c) the formation of dense canopies which shade out the shrubs and lead to unprotected groups of trees and groves. It is clear from the studies in the Oostvaardersplassen (Chapter 2, 3, 6; Smit et al. 2015) that a temporary reduction of large herbivore numbers is required for the establishment of woody species in the Oostvaardersplassen. Populations of large herbivores, which are regulated by food supply, can fluctuate greatly as a result of disease, severe winters, or food and water shortages (Young 1994; Coulson et al. 2001; Clutton-Brock and Coulson 2002; Sinclair et al 2003; Hopcraft et al. 2010). At the Oostvaardersplassen, the horse and red deer populations have reached maximum levels with numbers that fluctuate around these maximum levels (Chapter 6). The Heck cattle population reached maximum levels in 2000, decreased from 2000 until 2010 after which their numbers seemed to stabilize. Great fluctuations have not taken place yet as winters were on average very mild and food shortages due to bad summers have not occurred yet. In our modelling study (Chapter 7) in which weather conditions during the past 110 years were incorporated, great reductions did occur on average once every 10 years. But only twice was the total number of large herbivores low enough after a major reduction (>70%) which lasted long enough (at least 4 years) to create an opportunity for woody species to establish in the grasslands. Although the climate is changing and the average temperature and precipitation will increase (Van den Hurk et al. 2014), fluctuating weather conditions will still have a great impact on population dynamics. Periods with extreme rainfall or drought during future spring and summers can have great impacts on net primary production, leading to similar effects on mortality and recruitment as severe winters. The question is not if great population reductions will occur or not, but when and how frequently they will occur.

This frequency is also important for the formation of thorny scrubs. Establishment of thorny shrubs will not immediately lead to thorny scrubs. In the Oostvaardersplassen, the

seeds of these species are dispersed by birds, and are not dispersed in large quantities over large areas of several tens to hundreds of square meters so that they can develop scrubs. In most cases these shrubs establish as an individual in open grassland. While clonal uprooting species such as *Prunus spinosa* or some *Rubus* or *Rosa* species, can form tillers by which the thorny shrub can invade the grassland, *Crataegus monogyna* does not use this strategy (Olf et al 1999). After the first establishment of thorny shrubs in open grassland, they probably cannot provide safe sites immediately. After a reduction of large herbivore numbers, the populations will grow very fast again because of the highly productive environment (Chapter 6 and 7). The new established thorny shrubs will be browsed and stay small, and uprooting tillers have no chance to form new shrubs. It is likely that two or even more reductions in large herbivore numbers are needed to allow thorny scrub to develop. After each reduction in herbivore numbers, the earlier established thorny shrubs can expand and new thorny shrubs can establish close to the already established shrubs as birds can drop seeds close to the thorny shrub they rest on. But even then there is a possibility that the newly grown scrubs cannot provide safe sites for tree establishment. Again, if herbivore populations grow fast after a reduction, even older thorny shrubs will be browsed or used by the large herbivores to rub their coat or horns and fray their antlers. Twigs up to two meters in height will be damaged leaving shrubs and even scrubs with no protection underneath (Fig. 2 and 3).

When protective scrubs have developed, palatable trees can establish within these scrubs to form groups of trees or groves in the grazed grasslands and contribute to a park-like landscape. Although this transition has yet to be observed in the Oostvaardersplassen, many observations in other areas with controlled grazing at moderate to low densities, show that the mechanism works (e.g. Watt 1919; Tansley 1922; Burrichter et al. 1980; Pott and Hüppe 1993; Vera 1997; Olf et al. 1999; Bakker et al. 2004; Smit et al. 2005; Van Uytvanck et al. 2008). It seems likely that when scrubs have developed in the Oostvaardersplassen, this mechanism can also operate in the Oostvaardersplassen. However, as mentioned above, once the large herbivore numbers are high again soon after a low abundance interval due to the highly productive environment, the twigs of the thorny shrubs can be damaged leaving little protection for saplings of palatable trees (Fig. 2 and 3).

The establishment of thorny scrubs in river floodplains (Chapter 4) is controlled by other factors than in the Oostvaardersplassen area (see above). In river floodplains, seeds of thorny shrubs are not only dispersed by birds, but also by water during flooding events (Chapter 4). And as large amounts of seeds can be dispersed at once by water, the seeds can also be dropped off in large amounts over relatively large areas of tens to hundreds of square meters. Erosion and sedimentation, during flooding, create bare soil and thus ideal germination spots. After restoration measures in floodplains, such as excavation (mimicking erosion), the excavated area is immediately invaded by thorny shrubs and densities can go up to more than 3000 individuals per ha over a period of 12 years (Chapter 4). Due to the large numbers of seeds dropped off at once every year after a flooding, establishing shrubs are growing close together building a compact scrub within 10 years (pers. observ.). Also in highly productive grasslands close to the river, opportunities for the establishment of thorny shrubs can increase during times of high water levels when sand is deposited in these grasslands.



**Fig. 2.** Examples of heavily browsed old (background) and young (foreground) *Crataegus monogyna* in intensively grazed grasslands at the Oostvaardersplassen. The twigs of the old shrubs are browsed up to 2 m in height and the young shrub is also heavily browsed and remains short. In both cases the thorny shrubs provide no safe sites for palatable trees as long as the grazing pressure stays high.



**Fig. 3.** Example of damaged *Crataegus monogyna* scrub by large herbivores. The *Crataegus monogyna* shrubs are planted in the Oostvaardersplassen. As large herbivore numbers increase, the scrub is opened up through browsing, rubbing and walking through it. Animals use it for food (leaves, young twigs) and shelter. As access for large herbivores within the scrub increases, protection for palatable trees to establish decreases.

### Mutual interactions between large herbivores, geese and vegetation

Although much is known about the effects of large herbivores on different components of the wood-pasture cycle (see section above), little is known about the mutual interactions between large herbivore population dynamics and vegetation development in the long term and its effects on wood-pasture cycles. In addition to these interactions between large herbivores and vegetation, other processes can also play important roles, such as predation or competition with small herbivores. At the Oostvaardersplassen the presence of geese plays such a role, and was therefore incorporated in this study. The Oostvaardersplassen is visited by increasing numbers of geese ranging in the tens of thousands individuals (mainly greylag, white fronted and barnacle geese) who then forage on the grasslands. The geese are present during the whole year, but their peak abundances are during winter and spring at the start of the growing season (Chapter 6).

During the period of increasing numbers of large and small herbivores, the mosaic of grasslands, tall herbs, reed, shrubs and trees changed into a landscape almost completely dominated by grasslands (Chapters 2 and 6). Within the grasslands, the sward height and heterogeneity of vegetation structure decreased as herbivore numbers increased. These changes in vegetation were largely attributable to the increasing numbers of all herbivore species, including both large and small species. In the Oostvaardersplassen, cattle and horses' foraging behaviour and habitat use is determined by their preference for short grasses (Chapter 5), which have high nutritional value and grow in the extensive open grasslands. As long as these grasslands provide the amount of food needed, cattle and horses will graze on these grasslands and their impact on other vegetation types will be low. During winter, when net primary production and food quality are low, or when population numbers

increase the amount of grass available per animal will decrease. In this situation other food plants will be used more and more so that the impact on other vegetation types will also increase. Initially, red deer also foraged on leaves of woody species in spring and summer (De Jong et al 1996), but in autumn and winter the diet of red deer consisted almost entirely of grasses. So in autumn and winter, red deer also influenced the amount of grass available for cattle and horses. With increasing numbers of cattle, horses and red deer, the large herbivores were increasingly forced to use other food plants from vegetation dominated by tall herbs, reed, shrubs and trees. At first this foraging behaviour was only observed in winter, but eventually this behaviour continued for an increasingly longer period of time. By creating short grazed grasslands, the large herbivores facilitated high numbers of geese, which turned out to be competitors for grass. Especially during winter and spring, which are periods with limited regrowth, strong competition developed, initially among the large herbivores, and later on between the geese and the large herbivores. As geese can clip the grass very short (<2 cm), intake rate of the large herbivores on these short grasslands decreased and the large herbivores were therefore forced to forage in alternative, poorer, vegetation types. The cattle in particular experienced negative consequences from the strong competition presented by the geese as their preferred grass height is approximately 9 cm (Menard et al. 2002). Because of the very low sward height during winter and spring, intake of grasses by cattle decreased, which led to lower body condition and increased mortality and eventually to a decreasing number of cattle. Based on data of mortality and birth, the decrease (mortality > birth) of the population of cattle started when average sward height in August decreased below 9 cm (Chapter 6). These results suggest that in highly productive areas sustaining high densities of grazing large herbivores will lead to homogeneous grazing tolerant short-grazed grasslands where the largest grazers risk to be outcompeted by the smaller ones, which were facilitated by the larger ones in the beginning.

This raises the question whether an assemblage of bottom-up regulated populations of cattle, horses and red deer, or other large herbivores, can sustainably coexist in a fenced, highly productive, and homogeneous area with high numbers of geese and without large predators. Temporal variability and catastrophes, such as climatic extremes or disease outbreaks, may contribute to such coexistence (Coulson et al 2001; Hopcraft et al 2010, Sinclair et al 2003, Young 1994). In our modelling study (Chapter 7) we explored if weather variability (especially severity of the winter) could contribute to the coexistence of the large herbivores in a eutrophic environment such as the Oostvaardersplassen. Strong reductions of the whole large herbivore population as a result of severe winters could periodically provide room for the cattle population to grow. The model results showed that over a period of 110 years, cattle persisted as part of the ecosystem. However, after 110 years, the population of cattle decreased to such low numbers that the probability of coexistence in the long term becomes very small. Only when geese were absent in the system, coexistence as a result of weather variability was possible. Another possible mechanism for coexistence is resource partitioning (Putman 1996). In more heterogeneous ecosystems with abundant forage alternatives, resource partitioning may increasingly lead to coexistence as any or all of the species can change their diet and use alternative resources (De Boer and Prins 1990, Putman 1996, Stewart et al. 2002; Kleyhans et al. 2011). There is a high chance that this mechanism is currently being observed in the Oostvaardersplassen. In 2010/2011, parts of the adjacent forests were made accessible for the large herbivores to provide shelter (ICMO2

2010). From that moment on, the whole cattle population used these parts during winter for shelter but also for foraging habitat. The past three years, the cattle population did not decrease anymore and stayed more or less stable. Horses and red deer also use these forests but most of the horses and red deer stay on the grasslands within the Oostvaardersplassen. This could mean that these forests act as an alternative (i.e. a way out) during winter and spring for cattle when the sward height is too short for cattle. These results and experiences suggest that resource partitioning may be a more reliable (hence better) mechanism for long term coexistence than weather variability. This means that in the Oostvaardersplassen, the most appropriate way to provide opportunities for coexistence is to enlarge the area in order to increase the heterogeneity of the nature reserve. Making the adjacent forests accessible for the large herbivores and connect the Oostvaardersplassen with other large nature reserves such as the Horsterwold and Veluwe could achieve this.

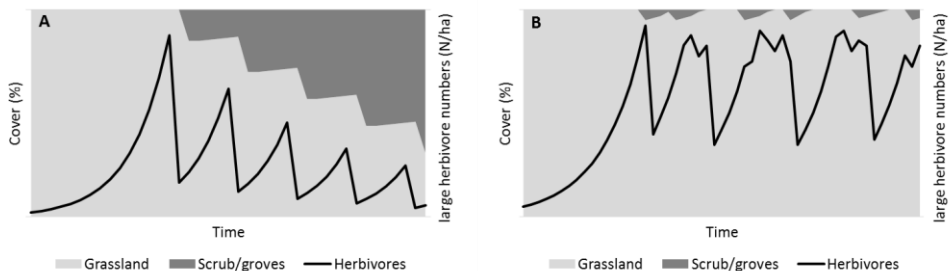
Although, according to the outcome of our model (Chapter 7), weather variability and the presence of geese provided less opportunities for the coexistence of the large herbivores in the Oostvaardersplassen in the long term, both factors contributed to the wood-pasture cycle. The results of the model show that the presence of geese is a precondition for the creation of windows of opportunity for thorny shrubs to establish. Due to the strong competition between geese and the large herbivores, the geese reduce the maximum and minimum numbers of large herbivores. Geese do not influence the degree of the variation between maximum and minimum numbers, which is primarily determined by the varying weather conditions. In the presence of geese, the minimum numbers of large herbivores after a reduction due to severe winter, are lower than without geese. The differences are small, but apparently big enough to make the wood-pasture cycle operate. A period of at least 4 years with such low population numbers is needed for thorny shrubs to survive during their first years. The results suggest that only a small impact of a small herbivore on the minimum numbers of the large herbivores can change the area from a grassland dominated system (without geese) to a wood-pasture system (with geese) (Chapter 7).

This raises another question whether a large predator, such as the wolf, could have a similar effect on this system as the geese in the model. Whether or not wolves regulate the numbers of large herbivores (i.e. top down regulation), apparently only a small impact on the minimum numbers of large herbivores is enough to increase the opportunities for the wood-pasture cycle. Apart from the impact of wolves on large herbivore numbers, wolves also have an effect on large herbivore habitat use (e.g. Ripple and Beschta 2012; Kuiper et al. 2013). By influencing the spatial distribution of large herbivores, spatial differentiation in grazing intensity occurs, giving opportunities for thorny shrubs to establish locally in less intense grazed areas. In our model, a window of opportunity for thorny shrubs occurred only twice in the presence of geese. In both cases the cover of the established thorny shrubs was relatively low: 7% cover after the first window and 5% after the second window. The impact of geese combined with a possible positive effect of wolves on wood-pasture cycles could perhaps increase the frequency of the windows of opportunity and increase the survival of established thorny shrubs.

Until now, we have seen that certain conditions for the wood-pasture cycle are fulfilled by the herbivores, but we still cannot conclude whether the large herbivores are a driving force for the whole cycle in a highly productive environment. As long as we have not experienced a full wood-pasture cycle in the Oostvaardersplassen system or another system, the future will remain unclear. For example, recently the toxic tall herb *Jacobaea vulgaris*

invaded some of the grasslands. This toxic tall herb could provide safe sites for thorny shrubs, but until now this mechanism did not operate as the tall herb loses its protective capacity in winter when parts above the ground die and are trampled down to the ground. Another way in which this toxic tall herb could influence the system is by invading more of the grasslands. By doing so the food supply for the large herbivores decreases during the summer, as they no longer graze in the grasslands where *Jacobaea vulgaris* has become abundant. This phenomenon might lead to a decrease in large herbivore numbers. And once the large herbivore densities have decreased, *Jacobaea vulgaris* can provide safe sites for scrub development as such areas will not be grazed anymore year-round.

As mentioned before, much what will happen in future will depend on the interplay between the population dynamics of the large herbivores and the vegetation. Two possible extreme outcomes are described below (Fig. 4). The first possibility (Fig. 4A) is that the reductions of the large herbivore populations are sufficient to create windows of opportunities for the establishment and growth of thorny shrubs and palatable trees. When the reductions are frequent enough, the area can be invaded by scrubs and groves, gradually converting the grassland into woodland. By doing so, the amount of the preferred food (i.e. grasses) decreases and so will the numbers of large herbivores. This will increase the opportunities for the invasion of more scrubs and groves. Then the area slowly changes into a woodland dominated landscape with low herbivore numbers and opportunities for coexistence of the large herbivores. Another possibility (Fig. 4B) is that the reductions of the large herbivore populations are not sufficient to create windows of opportunities for the establishment and growth of thorny shrubs and palatable trees. The area remains a grassland dominated system with high densities of large herbivores and the possibility that the largest herbivore species cannot coexist with the other smaller herbivores.



**Fig. 4.** Possible outcomes for the Oostvaardersplassen depending on dynamics of the large herbivore populations and vegetation. **A)** Situation in which reductions of large herbivore population are sufficient for thorny shrubs to invade the area. The shrubs are not broken down by the large herbivores and gradually the grassland is transformed into scrub and groves. When the preferred food supply decreases, population numbers decrease, increasing the opportunities for more scrub and groves. The area slowly changes into a woodland dominated system with low herbivore numbers. **B)** Situation in which reductions of large herbivore populations are not sufficient for thorny shrubs to survive. The area remains a grassland dominated system with high numbers of herbivores.

Whatever the outcome will be, the results of the study suggest that the Oostvaardersplassen-system would benefit from some adjustments such as the enlargement of the area or connecting the area to other large nature reserves. Enlargement and

connection will increase heterogeneity as more different environmental conditions will become part of the whole system. This will not only increase opportunities for resource and space partitioning and thus increase opportunities for the coexistence of the large herbivores, but also for wood-pasture cycles and biodiversity. Especially when other types of herbivores and large predators can enter the system through these corridors as they all have a specific role in the system.

### **Rewilding in a fragmented landscape**

‘Rewilding’ is a new conservation strategy for restoring some of the lost biodiversity and ecosystem functions. ‘Rewilding’ implicates restoring natural ecosystem processes and reducing human control. Unmanaged populations of large herbivores play a key-role in the large scale dynamics of landscapes where wood-pasture cycles still play a significant role and harbour high biodiversity (see Pereira and Navarro 2015). In the rewilding strategy it is essential to have large populations of free ranging and self-regulating large herbivores and predators that keep these herbivores in check (Pereira and Navarro 2015). Pereira and Navarro (2015) also mention that intervention management may be necessary at the start of the ‘rewilding’ project such as introduction of herbivore or carnivore species, or planting of woody species, but eventually the aim is to develop so called self-sustaining ecosystems.

The Oostvaardersplassen is often mentioned as one of the first ‘rewilding’ areas in Europe (e.g. Jørgensen 2015; Lorimer 2015; Smit et al. 2015). As the Oostvaardersplassen has existed for more than 45 years it begs the question of what we can learn from this area in respect to ‘rewilding’ and whether it can serve as an example for other areas. Obviously much depends on the definition one uses for ‘rewilding’, especially the degree of human control that is allowed. But if we follow Pereira and Navarro (2015), the Oostvaardersplassen is maybe not so much ‘rewilding’ as meant by Pereira and Navarro (2015). If we only consider the large herbivores, like most of the authors do who mention the Oostvaardersplassen as a rewilding area, there is indeed non-intervention, thus there is a certain amount of ‘rewilding’. The large herbivores were introduced to create large scale grasslands as feeding ground for wetland birds (Vulink and Van Eerden 1998). To achieve this objective, the large herbivore numbers were not controlled by humans but they were bottom-up controlled by the food supply. Furthermore, they were able to range the whole area freely. Simultaneously affected by other natural processes such as precipitation and evapotranspiration, water level fluctuations, competition and facilitation, population numbers of the large herbivores changed and fluctuated in a more or less spontaneous way and shaped the landscape of the area (see sections above). So far the strategy followed in the Oostvaardersplassen is close to the ‘rewilding’ concept. However, some important aspects of ‘rewilding’ are missing with regard to the spontaneous process of herbivory. The area is fenced, there are no large predators, only cattle, horses and red deer were introduced, and because it is relatively small, the abiotic conditions are rather homogeneous. If we consider the other aspects (i.e. other than herbivory) of the Oostvaardersplassen, we must conclude that it is somewhat further away from the ‘rewilding’ idea proposed by Pereira and Navarro (2015). The Oostvaardersplassen is reclaimed land from the former lake IJsselmeer, that developed after it was separated from the sea by a dyke. This makes the Oostvaardersplassen a man-made and man-managed wetland. Without management the Oostvaardersplassen would not be a wetland. If the dyke between lake Markermeer and the polder would not be maintained and the water in the polder would not be pumped out of the polder, the Oostvaardersplassen

would be a lake again. But also within the area itself management is needed. If the embankment around the marsh, that keeps the marsh wet, and the whole system of weirs to create a gradient of wet to dry habitats in the dry border zone would not be maintained, the Oostvaardersplassen would be drained and become a dry area. With the high densities of large herbivores that can be achieved on these productive soils, short grasslands probably would dominate the total area. All these conditions and management required to keep the wetland in a state to achieve for example the Natura 2000 goals, also influence the outcome of the natural process of herbivory by the large herbivores. Changing conditions and management would alter the outcome. Such interventions might involve for example, the shape of the weirs affecting water level fluctuations, or moving the weirs to other locations affecting the ratio between dry and wet areas. Such changes in abiotic conditions or natural processes such as water level fluctuations could have important effects on the total number of large herbivores, their population dynamics and habitat use and could change the influence of the large herbivores on the area.

Still the conclusion is that we have learned and can learn much from the Oostvaardersplassen with respect to 'rewilding'. We have learned a lot about bottom-up regulated populations of large herbivores in a highly productive, fenced, homogeneous area without large predators. We have seen how facilitation and competition can lead to the exclusion of the largest herbivore by the smallest herbivore. Although we have learned that a few components of the wood-pasture cycle take place in this system take place, we still do not know if the present assemblage of large herbivores under the present conditions is able to drive the whole wood-pasture cycles in homogeneous and highly productive environments. The Oostvaardersplassen provides opportunities to study many more topics of high scientific and conservation interest e.g. nutrient cycles, the role of invasive toxic species, soil dynamics in a nutrient rich and heavily grazed environment, perception of the area by visitors, decision-making on controversial issues such as allowing the natural death of large animals during severe winter.

In the near future, 'rewilding' probably will be more and more practiced in nature reserves in NW-Europe. The question is if 'rewilding' is suitable for every area. Pereira and Navarro (2015) state that it is not the question whether it should be controlled management or 'rewilding', but which management option will be more achievable and lead to sustainable results. If we look at our fragmented landscape with our relatively small and isolated nature reserves, we certainly have to ask ourselves for each reserve if 'rewilding' will be the best option.

An important issue that needs attention is the size and isolation of the reserves in the fragmented landscape. Smaller areas are more homogeneous. The Oostvaardersplassen has shown what could be the result of this with regard to the coexistence of large herbivores in the long term. We recommend enlarging the area and connecting it to other large areas. This will increase heterogeneity with more opportunities for the coexistence of large herbivores, but also most likely for wood-pasture cycles and therefore increased vegetation heterogeneity and species diversity, which benefits biodiversity. In addition to these benefits, enlargement or connection to other reserves would mean that also other large herbivore species and predators can enter the area. Making the total network of separate reserves connected through corridors, more complete enhancing the potentials for further rewilding in the future. If there are no possibilities to enlarge or connect the reserve to other areas and



only one or a few large herbivore species are introduced in the small and fenced area without large predators, rewilding might be counterproductive. In such situations, it probably will be better to look at the biodiversity goals and adjust the management. Controlled grazing may then be more suitable to achieve the goals.

The only way to find out if rewilding can work in fragmented landscapes is to start connecting areas where large herbivores are introduced or where they are already present. The Oostvaardersplassen is an area with great opportunities to study many aspects of 'rewilding' with large herbivores in fragmented landscapes. The large herbivore assemblage of the Oostvaardersplassen needs a step forward in order to enhance the opportunities for the coexistence of the herbivore species in this system. Enlargement and connecting the area with other areas, preferentially in contrasting environments, seems to be a key requirement.

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## SUMMARY

Conservation and restoration of biodiversity are major objectives for the organizations responsible for nature reserves. In many cases large herbivores are considered to be 'keystone' species to achieve these goals. They are major drivers of changes in plant community structure, which affect plant and animal species in natural ecosystems. The common strategy of controlled grazing with large wild and domestic herbivores at low stocking rates for conservation management has been challenged by a more 'natural' grazing strategy, which is part of the so-called 'rewilding' concept. The 'rewilding' concept aims at restoring spontaneous ecosystem processes and reducing human control. Unmanaged populations of large herbivores are assumed to play a key-role in the large scale dynamics of landscapes by driving cyclic wood-pasture mosaics. The question is whether these assumptions are correct in all cases. The aim of the present study is to gain more insight into the mutual interactions between the population dynamics of large herbivores and vegetation development in eutrophic wetlands. It is therefore that habitat use and population dynamics of large herbivores, the effects of large herbivores on vegetation development, and the mutual interactions between vegetation development and herbivore population dynamics were studied in the eutrophic wetland the Oostvaardersplassen and in a fluvial floodplain.

The first focus of the study was to determine whether the conditions for the wood-pasture cycle were fulfilled- in the Oostvaardersplassen. The study showed that high densities of cattle, horses and red deer were able to break down the woody vegetation in the area. The mortality of the woody species was caused by browsing and debarking and was greater closer to the large scale grasslands, which supports the hypothesis of associational palatability. Although the woody vegetation of the Oostvaardersplassen, which consisted mainly of *Sambucus nigra* and *Salix* spp., was broken down, the area was not suitable to study the effects of the large herbivores on woody vegetation consisting of species with other plant defence mechanisms. Nevertheless, there is plenty of circumstantial evidence within the grazed area of the Oostvaardersplassen that the actual grazing pressure inhibits all woody species.

During the period in which the woody vegetation was broken down, the mosaic vegetation of grasslands, tall herbs, reed, shrubs and trees was transformed by the increasing numbers of large herbivores into a landscape dominated by grasslands. Until now, no woody species have established in these grazed grasslands even though such establishments are predicted by the wood-pasture theory. Seedlings of *Crataegus monogyna* and *Quercus robur* are observed almost every year, but none survive the winter as long as herbivore densities are high. Protection by spiny or toxic tall herbs does not work as during winter these tall herbs die and their parts above the ground are trampled down by the high numbers of herbivores. The wood-pasture theory states that a reduction in herbivore numbers is needed for light demanding thorny shrubs to establish.

However, low numbers of large herbivores do not guarantee establishment of large numbers of thorny shrubs as tall herb vegetation within the grasslands can have negative effects on the establishment of thorny shrubs. In the experimental study in a grazed floodplain, *Crataegus monogyna* established in grazed grasslands only for a period of two years immediately after the start of the experiment. This was attributed to reduced light

competition in the grasslands. Before the start of the experiment the area was grazed with high densities of cattle during summer combined with mowing. During the experiment, the area was year-round grazed with low densities of cattle and horses. During the first two years of the experiment, vegetation height in the grasslands was still low as a result of the former intensive management. After these first two years, vegetation height increased as tall herbs started to dominate some of the areas within the highly productive grasslands due to the lower grazing intensities. Only during these first two years when vegetation was still low, *Crataegus monogyna* established in the grasslands. This effect of grazing on vegetation structure and reduced light competition for just one to two years was also found in the Oostvaardersplassen by other researchers. It seems that after a significant reduction of large herbivores, the window of opportunity for establishment of light demanding thorny shrubs in highly productive grasslands is very narrow (one to two years).

The results of the study show that a few important requirements for the wood-pasture cycle in the Oostvaardersplassen are not satisfied: (a) a temporary reduction of large herbivore numbers allowing the establishment of light demanding thorny shrubs and the development of thorny scrubland; (b) the establishment of palatable trees within these thorny scrubs; (c) the formation of closed canopies which shade out the shrubs and lead to unprotected groups of trees and groves. Significant reductions of the large herbivore population have not taken place yet as winters were on average very mild and food shortages due to bad summers have not occurred. In our modelling study in which the weather of the past 110 years was incorporated, significant reductions did occur on average once every 10 years. But only twice the reductions were sufficient (>70%) while low herbivore numbers lasted long enough (at least 4 years) to create an opportunity for woody species to establish in the grasslands. Even with a changing climate it probably is not the question whether great population fluctuations will occur in the future, but rather when they will occur and how frequently. This frequency is also important for the formation of thorny scrubs. Establishment of thorny shrubs will not immediately lead to thorny scrubland. After the first establishment of thorny shrubs in open grassland, they probably cannot provide safe sites for tree establishment right away. After a reduction of large herbivore numbers, the populations will grow very fast again because of the highly productive environment. The new established thorny shrubs will be browsed heavily, leaving small shrubs. Species with uprooting tillers which are poorly defended against herbivores and will have no chance to develop into new shrubs. Probably two or even more reductions in large herbivore numbers are needed to form thorny scrubs. But even then there is a possibility that the newly formed scrubs cannot provide safe sites. Again, if populations grow fast after a reduction even older thorny shrubs will be browsed or used by the large herbivores to rub their coat or horns and fray their antlers. Twigs up to two meters in height will be damaged leaving shrubs and even scrubs with no protection underneath. This will also affect establishment of palatable trees in these scrubs. Probably not only a high frequency in reductions is needed but also longer periods of low numbers of herbivores.

The second focus of our study concerns the mutual interactions between large herbivores population dynamics and vegetation development. As the Oostvaardersplassen is visited by tens of thousands of geese that forage on the grasslands, we also incorporated the geese in our study.



The transition of the mosaic vegetation into grasslands was largely attributable to the increasing numbers of all herbivore species, large and small. Cattle and horses' foraging behaviour and habitat use is determined by their preference for short grasses of the open grasslands. As long as these grasslands provide the amount of food needed, cattle and horses will graze on these grasslands and their impact on other vegetation types will be small. When population numbers increase the amount of grass available per animal will decrease which forces the animals to use other food plants in other vegetation types. This transformed the other vegetation types into grasslands. By creating more short grazed grasslands, the large herbivores facilitated high numbers of geese. As geese can clip the grass very short (<2 cm), they forced the large herbivores even more to forage in alternative vegetation types creating even more grasslands. Cattle were the first to experience the negative consequences of this strong competition as their ideal grass height is approximately 9 cm. The low sward height decreased their intake of grasses, which led to reduced body condition and increased mortality and eventually to a declining number of cattle. These results suggest that in highly productive areas the largest grazers risk to be outcompeted by the smaller herbivores, which were facilitated by the larger herbivores in the beginning. This raises the question whether an assemblage of bottom-up regulated populations of cattle, horses and red deer, or other large herbivores, can sustainably coexist in a fenced, highly productive, and relative homogeneous area with high numbers of geese and without large predators. The results of our modelling study and experiences in the field suggest that resource partitioning may be a more reliable (hence better) mechanism for long term coexistence than temporal variability due to climatic extremes or disease outbreaks. The best way to provide opportunities for resource partitioning in the Oostvaardersplassen is to enlarge the area and connect it to other reserves in order to increase the heterogeneity of the grazed system.

Although the results of our model suggest that weather variability and presence of geese gave minor opportunities for the coexistence of large herbivores, both factors were necessary for creating windows of opportunity for the establishment of thorny shrubs. Weather variability creates strong reductions of the populations of the large herbivores while geese influence the maximum and minimum numbers, which are lower when geese are present. The effects of geese on the minimum numbers are small, but apparently sufficient to make the wood-pasture cycle operate. This raises another question whether a large predator, such as the wolf, could have similar effects on these ecosystems as the geese in the model. The impact of geese combined with a possible positive effect of wolves on wood-pasture cycles could perhaps increase the frequency of the windows of opportunity and increase the survival of established thorny shrubs.

Until now, we have seen that a few conditions for the wood-pasture cycle are met by the herbivores, but we still cannot conclude if the large herbivores are a driving force for the whole cycle in a highly productive environment. As long as we have not experienced a complete wood-pasture cycle in the Oostvaardersplassen or any other area, it remains to be seen what will happen in the future. Whatever the outcome will be, the results of our study suggest that some adjustments would benefit the Oostvaardersplassen-system such as increasing heterogeneity through connecting the area with other large nature reserves. This will not only increase opportunities for resource and space partitioning and thus increase opportunities for the coexistence of the large herbivores, but also for wood-pasture cycles and increased biodiversity.

This study shows that the Oostvaardersplassen is not a 'rewilding' area in a strict sense. It is a man-made and man-managed wetland and without management the wetland would disappear. The large herbivores contribute to a certain extent to 'rewilding': they are not controlled by humans but bottom-up controlled by food supply, and they are able to range the whole area freely. However, some important aspects are missing: there is no free migration because the area is fenced; there are no large predators; only cattle, horses and red deer were introduced; and because it is relatively small, its abiotic conditions are rather homogeneous. Despite some of the imperfections, we have learned a lot with respect to certain aspects of 'rewilding': about large herbivore population dynamics, competition and facilitation and certain aspects of wood-pasture cycles in eutrophic environments. And with future development of the area, many more topics of scientific and conservation interest can be studied.

In the next future, 'rewilding' probably will be more and more practiced in nature reserves in NW-Europe. The question is if 'rewilding' is suitable for every area. An important issue that needs attention is the size and isolation of the reserves in the fragmented landscape. Smaller areas are more homogeneous and the Oostvaardersplassen has shown the effects of this on the coexistence of large herbivores in the long term. Enlarging the area or connecting it to other areas will increase heterogeneity with more opportunities for the coexistence of large herbivores, but also most likely for wood-pasture cycles, which benefits biodiversity. In addition to these benefits, enlargement or connection to other reserves would provide opportunities for other large herbivore species and predators to enter the area. Making the total network of separate reserves, more complete enhancing the potentials for further rewilding in the future. If there are no possibilities for enlargement or connection, and only one or a few large herbivore species are introduced in the small and fenced area without large predators, rewilding might be counterproductive. In such situations, controlled grazing may then be more suitable to achieve the goals.

The only way to find out if rewilding with large herbivores can work in fragmented landscapes is to start connecting areas. The Oostvaardersplassen is an area with great opportunities to study many aspects of 'rewilding' with large herbivores in fragmented landscapes. The large herbivore assemblage of the Oostvaardersplassen needs a step forward in order to enhance the opportunities for the coexistence of the herbivore species in this system. Enlargement and connecting the area with other areas, preferentially in contrasting environments, seems to be a key requirement.

## ACKNOWLEDGEMENTS

A thesis like this is never the work of just one person. Over the years that I worked on my thesis, many people have helped me who I would like to thank for their contributions.

First of all I would like to thank my promotors Frank Berendse and Karlè Sýkora and my co-promotor Jan Bokdam for their confidence in me and that they gave me the time to do the research and writing in my own pace. Thank you very much for your advices and your kind words when a manuscript was send back from the reviewers who thought differently about the contents. Special thanks to Jan, who convinced me that I could write a thesis about the research I was doing at the Oostvaardersplassen for the Ministry of Infrastructure and the Environment. Thanks to him I started this beautiful project.

When I started the PhD research, I had a full time job at the Ministry and only had time for the research during the weekends. Progress was slow during these first years. It all speeded up from 2013 onwards, when some people at the Ministry and State Forestry Service helped me by creating a so called IF-contract. Because of this I could spent more time on the research. This contract was made possible by Chris Kalden, Luitzen Bijlsma, Joost Backx, Paul Stortelder, Theo Meeuwissen, Koen van der Werff, Frans Vera, Nick de Snoo, and Jasper Kuipers whom I all would like to thank very much.

Not all data were collected by myself. I was helped by many people as well as professionals as students. Without your help, no thesis. Thanks very much for your help: Jochem Sloothaak, Kassiopeia DeVriendt, Marca Gresnigt, Roeland Vermeulen, Mathieu Decuyper, Jaap Daling, Menno Zijlstra, Moniek Bestman, Willem van der Wagen, Jan Griekspoor, Teun Koops, Peter Boelens, Bertwin Bergman, Bram Smit, Fré van der Klei, Niels Kooijman, Peter Esselink, Mieleke van Deursen, Berend Dopmeijer, Jacques Leemans, Sandra de Goei.

All chapters of my thesis are written together with many co-authors. Thank you all for your pleasant cooperation: Mark Ritchie, Marca Gresnigt, Roeland Vermeulen, Ruben Smit, Theo Vulink, Mathieu Decuyper, Frans Vera, Han Olff, Koen Kramer, Geert Groot Bruinderink, Loek Kuiters, Dennis Lammertsma, Sip van Wieren, Herbert Prins and of course Frank Berendse, Karlè Sýkora en Jan Bokdam.

Many people also helped reviewing draft versions of the chapters of the thesis. Thank you very much for your critical views on these drafts: Rory Putman, Patrick Duncan, Luc Jans, Marcel Tosserams, Jasper van Ruijven, Sip van Wieren, Michiel Wallis de Vries, Gera van Os.

And since English is not my native language, I sought assistance from some experts. Joy Burrough, Stanford Wilson, Lisa Davidson and Ben Euston thank you very much for your help. Special thanks to Stanford. You did not just correct the English but you were also very critical about the content and the scientific language.

Hans Drost and Theo Vulink thank you for supporting me as my paranymphs during the promotion ceremony. This work actually started in 1991 when you both hired me to come to work with you at Rijkswaterstaat. You learned me a lot about the large wetland systems in the Netherlands, and how to do research and analyse and report the data. And now we are standing here together again, finishing what I started with you in 1991. You were both fine colleagues on who I could trust and support not only at work but also during this ceremony.

Finally, I would like to thank my dear Gera, Floortje and Wouter who supported me during this project. Especially when the data were not appropriate to support a hypothesis or a manuscript was rejected for unclear reasons and I had to start all over again. Luckily you were there to comfort me and to change my minds. You gave me all the space to work on the thesis and forgave me my bad mood in difficult times.



## CURRICULUM VITAE

Perry Cornelissen was born on January 3 1960 in Nijmegen. After finishing the study Landscape Ecology at the Hogere Bosbouw en Cultuurtechnische School HBCS in Velp in 1988, he started his first job in 1989 at the Water Resources Consultancy WARECO in Amsterdam as a consultant soil contamination. In 1990, he accepted a temporary job for one year at the Staring Centre in Wageningen to study the effect of trees on roads. In 1991, he started his work as a researcher for Rijkswaterstaat in Lelystad, a department of the Ministry of Infrastructure and the Environment. The research was about effects of large herbivores on vegetation development and bird species in large scale wetlands in the Netherlands such as the Lauwersmeer, the Oostvaardersplassen and the Slikken van Flakkee, and in floodplains along the large rivers Waal and IJssel. Part of this research, about the effects of large herbivores on woody species, has led to this thesis. In 2005, a cautious start was made with this thesis as the Wageningen University invited him to analyse the data of the Rijkswaterstaat study and to write a PhD thesis about it. During the first years, the PhD research had to be done next to his full-time job at Rijkswaterstaat so that progress was slow. In 2013, Rijkswaterstaat and Staatsbosbeheer signed a so-called IF-contract, which made it possible for him to spend more time on his PhD research and from that moment on progress increased. Staatsbosbeheer was involved in this project because the research was carried out in areas managed by them and the results would be beneficial for them. Next to the PhD study, the work with Rijkswaterstaat consisted of giving ecological advice in nature development projects along the large rivers and lakes in the Netherlands. In 2014, he was offered a job at Staatsbosbeheer to work as a senior consultant ecology, which he accepted in February 2015.



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