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Effects of large herbivores on wood pasture dynamics in a European wetland system

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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 *S. nigra* and *Salix* spp. over a certain period was negatively correlated with the cover of *S. 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.

Zusammenfassung

Ob selbstregulierte große Herbivoren eine Schlüsselrolle für die Entwicklung von Waldweidelandschaften spielen, bleibt eine entscheidende unbeantwortete Frage, sowohl für die ökologische Theorie als auch den Naturschutz. Wir beschreiben und analysieren, wie eine teilweise selbstregulierte Population von Rindern, Pferden und Rotwild die Entwicklung der Gehölzvegetation im Naturreservat Oostvaardersplassen (Niederlande) beeinflusste. Mit Hilfe von Luftaufnahmen von 1980 bis 2011 analysierten wir die Entwicklung von Sträuchern und Bäumen. Bevor die Groß-Herbivoren 1983 nach Oostvaardersplassen eingeführt wurden, hatte die Gehölzvegetation zugenommen und der Vegetationstyp signifikant die Zahl der Neuansiedlungen

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beeinflusst. Der Deckungsgrad der Gehölzarten nahm von 1983 bis 1996 weiter zu, nicht nur durch Wachstum der Kronen, sondern auch durch neue Ansiedlungen. Nach 1996 nahm der Deckungsgrad der Gehölzvegetation von 30% auf unter 1% im Jahre 2011 ab, und keine Neuansiedlungen wurden auf den Photographien beobachtet. Die Überlebensraten von *Sambucus nigra* und *Salix* spp. nahmen mit der Entfernung zum Grasland ab, welches das bevorzugte Weidehabitat der Groß-Herbivoren darstellt. Diese Ergebnisse unterstützen die Hypothese von der Genießbarkeit durch Vergemeinschaftung. Darüber hinaus zeigen unsere Ergebnisse, dass die relative Abnahme des Deckungsgrades von *S. nigra* und *Salix* spp. über eine bestimmte Periode negativ mit dem Deckungsgrad von *S. nigra* am Anfang dieser Periode korreliert war, wodurch ein gewisser Anhaltspunkt für die Hypothesen von der gemeinschaftsbedingten Abwehr und Abwehr durch Aggregation gegeben wird. Unsere Untersuchungen zeigten Aspekte auf, die notwendig für einen Wald-Grasland-Zyklus sind: ein starker Rückgang der Gehölzvegetation bei hohen Dichten der Groß-Herbivoren und eine Regeneration der Sträucher und Bäume bei geringen Dichten. Dornentragende Sträucher, die wichtig für den Zyklus sind, haben sich bisher noch nicht auf den Grasländern angesiedelt. Es scheint, dass ein zeitweiser Rückgang der Herbivorendichten notwendig ist, um ein Gelegenheitsfenster für die Ansiedlung dieser Gehölzarten zu öffnen.

Keywords: Wood-pasture hypothesis; Woodland–grassland cycle; Aggregational resistance; Associational palatability; Oostvaardersplassen; Large herbivores

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, Duncan, Grillas, & Lecomte 1990; WallisDeVries, Bakker, & Van Wieren 1998). Traditional livestock farming landscapes, e.g. man-made wood-pasture, often serve as reference (Pott & Hüppe 1991; Bignal, McCracken, & Curtis 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 & 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, Bergman, Iason, & Moen 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 (Olff 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 Olff 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; Olff 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 & Drost 1995; Cornelissen, Roos, Den Hollander, & Van Eerden 2006). *Sambucus* produces *cyanogenic glycosides* (Atkinson & Atkinson 2002) which can be toxic to or lethal in birds and mammals (Griess, Rech, & Lernould 1998; Majak & 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*.