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Original article

The role of rodents in the seed fate of a thorny shrub in an ancient wood pasture

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ABSTRACT

Thorny shrubs play a crucial role for the diversity and dynamics in wood pastures: they protect non-defended plants from large herbivores and thus facilitate tree establishment in the landscape through associational resistance. How thorny shrubs themselves establish in wood pastures – the main bottleneck for a dynamic shifting of grassland – shrub – woodland mosaics – is an essential unanswered question. We studied post-primary dispersal seed fate – i.e. removal, predation, secondary dispersal and survival of seeds after primary dispersal – of the thorny shrub blackthorn (*Prunus spinosa*) in an ancient wood pasture in the Netherlands. Blackthorn seeds are primarily dispersed by frugivorous birds and may secondarily be dispersed by scatter-hoarding rodents.

We performed two cafeteria-style experiments with blackthorn seeds placed on dishes in the dominant vegetation types. In the first we monitored seed removal in grassland, swards or blackthorn shrubs and determined rodent species abundance by live-trapping. In the second we followed tagged blackthorn seeds under shrubs and in swards to determine seed removal, predation, survival and secondary dispersal patterns. Tagged seeds were retrieved using a metal detector and by visual means. We recorded dispersal direction and distance, vegetation type, seed handling (burial, consumption) and rodent species responsible via bite marks.

Seed removal and number of live-trapped rodents differed between vegetation types, with higher removal and rodent captures under shrubs than in swards and grassland. All retrieved seeds were depredated, predominantly by the wood mouse (*Apodemus sylvaticus*). Disproportionally high seed numbers were retrieved in the vegetation type where originally placed (shrubs or swards).

Our study suggests that rodents play an important role for blackthorn in wood pastures, predominantly as seed predators rather than secondary seed dispersers. Predation is particularly high under blackthorn shrubs, suggesting that primary seed dispersal by birds away from shrubs into grassland or swards is a prerequisite for blackthorn recruitment in wood pastures.

1. Introduction

Wood pastures are grazed (semi-) natural savanna-like landscapes that consist of mosaics of short grasslands, tall swards, shrub thickets and patches of (isolated) trees, supporting high levels of floral and faunal diversity (Kollmann and Schneider, 1999; Peterken and Francis, 1999; Ewald, 2000). Wood pastures have developed in NW Europe under the influence of traditional livestock farming practices since Neolithic times (Pott and Hüppe, 1991) or may even have been formed naturally in earlier times by now extinct wild large herbivores (the aurochs *Bos primigenius* and the tarpan *Equus ferus*) (Vera, 2000), particularly in riverine floodplains (Svenning, 2002). Yet, these once-abundant wood pastures have declined drastically during the last decades in Europe, mainly due to changed and intensified land use (Gillet and Gallandat, 1996; Pywell et al., 2002). Presently, there is increased interest in the few remaining ancient wood pastures and active natural processes therein, as they serve as models for the various 'nature development' or 're-wilding' projects (described in Maris, 2009) in Europe. Hence, there is an urgent need for an improved understanding of the main ecological processes for the sustainable management of both the ancient and newly created wood pastures.

One of the hypothesized key processes operating in wood pastures is facilitation through associational resistance – i.e. reduced

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herbivore damage due to an unpalatable, protective neighbouring plant (Tavahnainen and Root, 1972; Atsatt and O'Dowd, 1976; Hay, 1986; Hjältén et al., 1993; see also review by Barbosa et al., 2009). This facilitation process has been suggested to lead to a cyclic shifting of grassland – shrub – tree mosaics over space and time (cyclic shifting mosaics theory (Olff et al., 1999)): unpalatable plants in grassland facilitate other unattractive forbs and shrubs, which protect attractive tree seedlings that eventually will outcompete their facilitators. Grassland should reappear after the death of these trees due to a combination of high grazing pressure and resource competition. Various descriptive and experimental studies have now indeed shown that toxic, spiny or thorny plants facilitate the survival of tree seedlings in the presence of large grazers (Kuiters and Slim, 2003; Bakker et al., 2004; Smit et al., 2005, 2006, 2007; Van Uytvanck et al., 2008). But while their importance is presently recognized, very little is known about the factors that drive the dynamics of these keystone nurse plants (Smit et al., 2009). The establishment phase of new nurse plants in grazed landscapes is seen as the crucial bottleneck for the further development of cyclic shifting mosaics in wood pastures (Olff et al., 1999) but appears to be a rare process in nature and has received no attention thus far. Here, we considered establishment limitation of blackthorn (*Prunus spinosa*) – a thorny shrub species that is particularly important for the establishment of trees in wood pastures in NW Europe (Pott and Hüppe, 1991; Olff et al., 1999; Vera, 2000; Bakker et al., 2004) – and investigated the fate of blackthorn seeds after primary dispersal in an ancient wood pasture.

Blackthorn seeds are primarily dispersed in wood pastures by frugivorous birds, particularly by common blackbird (*Turdus merula*), song thrush (*Turdus philomelos*), mistle thrush (*Turdus viscivorus*), redwing (*Turdus iliacus*) and fieldfare (*Turdus pilaris*) (Sorensen, 1981; Snow and Snow, 1988). Birds foraging on the stone fruits of blackthorn defecate or regurgitate the seeds while foraging or perching, resulting in seed deposition under and close to shrubs and the formation of steep seed shadows (Kollmann, 1995). Birds mainly transport seeds between shrubs and less to short grassland (Martínez et al., 2008), but excretion of blackthorn seeds by birds in short grassland has been observed as well (Sorensen, 1981). However, the fate of these seeds after primary dispersal remains unknown: various studies on animal-dispersed fleshy fruits show that these patterns of primary seed dispersal do not accurately reflect the final observed recruitment patterns, resulting in spatial discordance (Jordano and Herrera, 1995; García and Ortiz-Pulido, 2004). Seed predation and secondary seed dispersal (any significant movement of seeds after initial dispersal from plants) are important reasons for this discordance.

While some studies regard rodents only as seed predators – using seed removal as indicator for seed predation (Hulme, 1997; Kollmann et al., 1998; Manson and Stiles, 1998; Fedriani and Manzaneda, 2005), other studies show that rodents can play a crucial role as secondary seed dispersers, particularly via scatter-hoarding behaviour (Jensen and Nielsen, 1986; Vander Wall, 1993, 2003; Kollmann and Schill, 1996). Scatter-hoarding, i.e. the burial of single or a few seeds in many shallow caches, often results in incomplete seed recovery and reduced seedling competition (Hollander and Vander Wall, 2004). In contrast, larder-hoarding, i.e. the burial of many seeds at a single deep cache (e.g. in burrows), makes complete recovery more probable and prevents successful germination (Hulme and Kollmann, 2005).

As blackthorn seeds are preferred forage for granivorous rodents (Kollmann et al., 1998), secondary seed dispersal and predation by rodents are expected to play a crucial role for blackthorn in wood pastures. In addition, vegetation type has been shown to affect rodent activity in terms of seed removal (Kollmann, 1995; Kollmann and Schill, 1996; Hulme, 1997; Manson and Stiles, 1998; Smit et al., 2008) and seed dispersal (Den Ouden et al., 2005; Lu and Zhang, 2004), with higher rodent activity in dense vegetation types with high cover. This may have important consequences for survival chances and establishment patterns of blackthorn in wood pastures. As of now, secondary dispersal and predation of blackthorn seeds have not been documented in these heterogeneous landscapes, so the seed fate after primary dispersal in the various vegetation types remains unclear.

In this study we investigated post-primary dispersal seed fate of a thorny nurse shrub in an ancient wood pasture. In two cafeteria-style experiments we studied post-dispersal seed removal, seed predation and secondary seed dispersal patterns of blackthorn in the main vegetation types: short grassland, tall sward patches and shrub thickets. We expected to find differences between vegetation types in post-dispersal seed removal, seed predation and secondary dispersal patterns with (1) highest seed removal in shrub thickets, (2) secondary seed dispersal directed towards 'safe' vegetation types (e.g. shrub thickets and tall swards) and (3) highest seeds predation in shrub thickets.

2. Materials and methods

2.1. Study site

The study was conducted in the Junner Koeland (100 ha) along the river Overijsselse Vecht in the Netherlands (52°32′N; 6°29′E), managed as a nature reserve by the State Forestry Service since 1967. The Junner Koeland is one of the very few remnant ancient wood pastures in Western Europe that has been grazed by livestock for centuries, probably since medieval times (Bakker et al., 2004). The area consists of a mosaic of short grazed grasslands dominated by red fescue (*Festuca rubra*) and common bent (*Agrostis capillaris*) (further referred to as 'grassland'), tall unpalatable swards dominated by soft rush (*Juncus effusus*) (referred to as 'swards'), thorny shrub thickets dominated by blackthorn (referred to as 'shrubs') and woodland with predominantly pedunculate oak (*Quercus robur*), and has a very rich flora and fauna. During our study (January 2007–March 2009) the area was grazed year-round by ca. 15 horses and varying numbers of cattle, ranging from ca. 20 individuals in January to ca. 60 in July. Other vertebrate herbivores that occur in the study site are roe deer (*Capreolus capreolus*), brown hare (*Lepus europaeus*), European rabbit (*Oryctolagus cuniculus*), common vole (*Microtus arvalis*), bank vole (*Clethrionomys glareolus*) and wood mouse (*Apodemus sylvaticus*).

2.2. Study 1: seed removal and rodent abundance

We collected fruits directly from blackthorn shrubs at the study site in November 2006 and stored them at 5 °C until further handling. In January 2007 fruit pulp was removed (to mimic primary dispersal by birds) and fruit stones were air-dried at room temperature (20 °C) during one night. Blackthorn seeds are enclosed by a hardened endocarp, together forming the fruit stone (mean length × width × thickness = 8.8 mm × 6.1 mm × 8.0 mm (Depypere et al., 2007)). Unless stated otherwise, we use the term "seed" to refer to a seed and its enclosing endocarp.

Shortly after, we randomly selected 21 plots in each of the three main vegetation types: grassland, swards and shrubs. All 63 plots were widely spaced over the study site. In each plot we placed 9 blackthorn seeds on a small plastic dish (diameter 5.5 cm, height 1 cm) with fine mesh at the bottom to allow water drainage. The selected seed number per dish is within the range of observed number of seeds of fleshy fruits in birds faeces (1–11) (Jordano and Schupp, 2000; Martínez et al., 2008). We recorded seed removal 1, 3, 8, 18, 22, 43 and 72 days after placing the seeds.

In early April, after the last recordings of seed removal, we determined rodent species and abundance in 30 of the total of 63