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Post-dispersal fate of hazel (*Corylus avellana*) nuts and consequences for the management and conservation of scrub-grassland mosaics

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ABSTRACT

Granivorous rodents and birds are both predators and dispersers of the nuts produced by many woody plants. This study examines the role of granivores as predators and dispersers of *Corylus avellana* L. and the consequences of this interaction for *Corylus* regeneration and scrub encroachment into grassland. In the Cressbrook Dale nature reserve (Derbyshire, UK), *Corylus* nuts were buried in the grassland at two distances (<15 and >70 m) from scrub vegetation (the main source of nuts, and habitat of the granivores) to estimate the rate of seed removal over 3 years, assessing also the success of dispersal and seedling establishment in the grassland. The rate of nut removal at close sites (<15 m from scrub) was consistently higher than at far sites (>70 m) over the 3 years. All sown nuts were removed over 2 years at close sites, while at the far sites around 20% of the sown nuts were still present the following spring. Grassland close to the scrub had the highest intensity of nut predation but also had the highest density of *Corylus* seedlings. *Sciurus carolinensis* was the most important disperser of hazelnuts into the grassland. This squirrel scatter-hoarded 10–12 thousand hazelnuts in 1.5 ha of grassland adjacent to scrub. In this reserve, two vertebrates – both non-native – are largely responsible for maintaining the dynamic balance between the scrub and grassland habitats. American grey squirrels disperse hazelnuts into the grassland and sheep slow the encroachment of scrub by repeated browsing.

1. Introduction

Like many nut-bearing trees and shrubs, *C. avellana* maintains a risky liaison with the animals that consume its nuts. Some animals destroy all nuts immediately and are therefore harmful to the plant (e.g. pheasants, pigeons, deer). Other animals eat as many nuts as they can during autumn, but also store large numbers for consumption during winter (e.g. mice, squirrels, jays). These nut hoarders can take a heavy toll on the annual crop, but not all hoarders are harmful to the plant. Those that occasionally fail to retrieve all cached nuts are doubtless formidable nut predators, but they are also valuable dispersers of nuts (Bossema, 1979; Price and Jenkins, 1986; Vander Wall, 1990, 2001).

Different animals select different sites to cache their harvest. Granivorous small rodents, particularly mice, are reluctant to leave the cover of woody plants because in open areas they themselves are vulnerable to predation (Price and Jenkins, 1986; Hulme, 1993; Manson and Stiles, 1998; Gómez et al., 2008). In contrast, tree squirrels and granivorous birds are quite bold and frequently hoard nuts in non-wooded areas (Vander Wall, 1990; Hulme and Kollmann, 2005). Squirrels will usually scatter-hoard nuts just a few metres away from the wood margin, mostly within 30 m (Stapanian and Smith, 1986; Gurnell, 1987; Steele et al., 2005), while birds may scatter-hoard dozens of metres away from it, frequently as far as 100 m or even further into open areas (Bossema, 1979; Kollmann and Schill, 1996; Gómez, 2003; denOuden et al., 2005; Pons and Pausas, 2007). Nuts that remain where they were produced (i.e. in woodland or scrub) are exposed to extremely intense removal and predation, whereas nuts taken out into non-wooded habitats such as grasslands have a much higher probability of going undetected by other seed eaters (Bossema, 1979; Vander Wall, 2001). Removal is further reduced if the nuts are hoarded far from wooded areas (Stapanian and Smith, 1986; Manson and Stiles, 1998; Myster and Pickett, 1993; Meiners and LoGiudice, 2003). Nuts from trees and shrubs which are hoarded in non-wooded habitats and later forgotten, promote the encroachment of woody vegetation over open habitats; hence the outcome of the interaction between nut-producing woody plants and animal nut-hoarders plays a significant role in plant succession. Even though there are plenty of studies on this interaction in temperate ecosystems (see reviews by Price and Jenkins, 1986; Vander Wall, 1990, 2001; Hulme and Kollmann, 2005), there are

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few that explore its implications for succession (Jensen and Nielsen, 1986; Stapanian and Smith, 1986; Kollmann and Schill, 1996).

Calcareous grasslands are important habitats for conservation in Western Europe; their biodiversity is high and includes a variety of rare species from different taxonomic groups (WallisDeVries et al., 2002). A major threat to the conservation of this habitat, particularly in nature reserves, is the encroachment of scrub following the reduction or abandonment of traditional grazing systems (Ward, 1990; Kollmann and Poschlod, 1997; Mortimer et al., 2000; Barbaro et al., 2001; WallisDeVries et al., 2002). Although scrub on its own is considered to be of little conservation value, when it forms part of a mosaic with calcareous grassland it becomes very important. The heterogeneity in vegetation structure intrinsic to the scrub-grassland mosaic is beneficial to a great number of species of native fauna and flora (Mortimer et al., 2000; WallisDeVries et al., 2002). The conservation of scrub-grassland mosaics is challenging and mainly depends on a grazing regime that effectively balances succession towards woody vegetation with the suppression of woody plant establishment in the grassland (Kollmann and Poschlod, 1997; Mortimer et al., 2000). A better understanding of the processes that promote and those that impede the succession of grassland to scrub is therefore essential.

This study addresses the role of vertebrate granivores as seed predators and dispersers of *Corylus*, analysing the consequences of this interaction for the regeneration of *Corylus*, and how in turn this affects scrub encroachment into the grassland. The removal rate of hazelnuts buried in calcareous grassland at two distances (<15 vs. >70 m) from scrub vegetation (the main source of nuts and habitat of the granivores) was estimated over 3 years in a nature reserve in Derbyshire, UK. Sown nuts were monitored until the following spring; the number of nuts that had escaped granivores and germinated was estimated, and the success of seedling establishment in the grassland was assessed. The relative importance of different granivores as predators and dispersers of hazelnuts at Cressbrook was also established.

2. Materials and methods

2.1. Study site

The study was carried out at Cressbrook Dale in the Peak District National Park, Derbyshire, UK (53°15–17′ Lat N, and 1°44–45′ Long W). The site is part of the Derbyshire Dales National Nature Reserve, managed by Natural England (formerly English Nature). The dale is a steep-sided valley (slope: 20–35°) roughly 2.5 km long, oriented north–south, and 0.5 km wide. Calcareous grassland covers the northern end of the dale and semi-natural ash (*Fraxinus excelsior*) woodland, its southernmost part (Balme, 1953; Merton, 1970). Scrub vegetation is also present, usually at the interface between the wood and the grassland, with *C. avellana* or *Crataegus monogyna* or both dominant in different areas (Merton, 1970). The main objective of reserve management is the preservation of the species-rich calcareous grassland and grazing by sheep is the preferred method of grassland management. Burning is no longer used and mowing is sporadic and restricted to small areas. Stocking density is kept close to four sheep per hectare for five or six months of the year. Some years Natural England also allows a few head of cattle to graze in the dale, and as a result of this research project a few Exmoor ponies have been introduced (see Discussion). Animals are brought to the reserve in mid-June, after most grassland plants have flowered and dispersed their seeds, and are taken out in mid-December. Grazing is managed so that the grassland turf has an average height of 2.5–5 cm by the end of the growing season (English Nature, 1998; PDNPA, 2001).

2.2. Seed sowing experiment

The west-facing slope close to the centre of the dale was selected for this experiment in an area well away from the main public footpaths. There, a 'scrub-grassland' edge runs in a north–south direction for over 500 m, with scrub at the bottom and grassland upslope. *Corylus* nuts were sown in the open grassland at five sites close to the scrub edge (<15 m; hereafter referred as 'close' sites) and at five sites far away from the edge (>70 m; 'far' sites; Fig. 1a). The slope at close sites was steeper (25–35°) than at far sites (10–20°). At each of the 10 sowing sites, two quadrats (1×1 m) were placed 4 m apart, perpendicular to the scrub edge (Fig. 1b). Inside each 1 m^2 quadrat, 16 sowing points were located on a 4×4 grid (separation: 20 cm). A peg buried to ground level marked the SW corner of each quadrat, and was the only device left in the field after sowing (Fig. 1c). At each sowing point a hazelnut was buried as follows: a core of soil was extracted with a commercial apple corer (19 mm diameter), the nut was placed 2–3 cm below the surface and the extracted soil core was then carefully replaced with its grassland turf in place, to minimize signs of soil disturbance. Sowing was done in autumn, shortly after most of the branches of *Corylus* were devoid of ripe hazelnuts.

The first sowing was done in 2001, then in 2002 two new quadrats were placed 4 m to the south of those sown in 2001, and this procedure was repeated in 2003 (Fig. 1b). Since nut production failed completely throughout the Peak District during 2001 (see Results), we had to buy the hazelnuts from a commercial supplier (Forestart; www.forestart.co.uk). All hazelnuts were bought in November 2001; those not sown during 2001 were kept dry inside dark plastic bags in laboratory conditions at the University of Sheffield, until sowing.

At six of the sowing sites (three far and three close sites; Fig. 1a) an extra quadrat protected by a cage was sown with hazelnuts, using the same spacing and depth of sowing as in the open quadrats (see above). The cage had a wood frame 2×2 m and 0.5 tall, completely covered (walls and roof) with chicken wire (mesh size 2.5 cm). These allowed mice and voles to enter, but kept squirrels

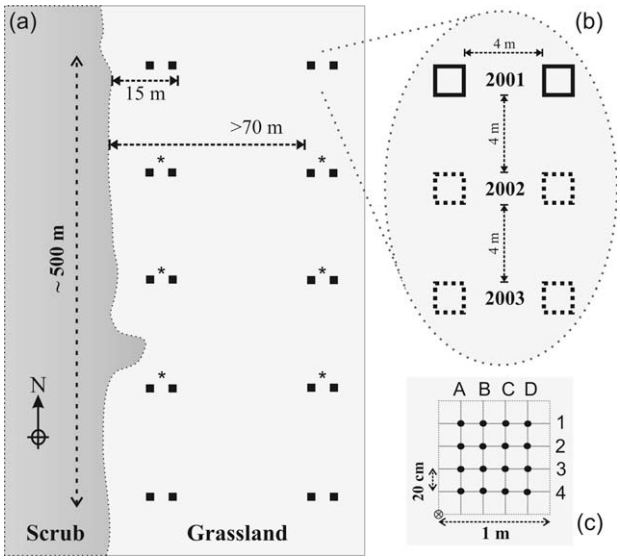

Fig. 1. Experimental layout. Spatial arrangement of the sowing sites (a) where hazelnuts were buried. Five sowing sites were placed close (<15 m) to the scrub edge and five were far away (>70 m) from it. Two 1 m^2 quadrats 4 m apart were sown per site per year (b). At each 1 m^2 quadrat, 16 nuts were buried in a 4×4 grid (c), 20 cm apart. A permanent peg marked the SW corner of each quadrat. An additional quadrat protected by a squirrel- and bird-proof cage was sown with nuts at each of the 6 sites marked with an asterisk in 2001 (see text).