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The implications of seed rain and seed bank patterns for plant succession at the edges of abandoned fields in Mediterranean landscapes

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Abstract

Some environmental variables and above-ground vegetation, seed rain, ant-borne seeds and seed banks were studied on three abandoned fields, at the margins between these fields and a remnant patch of a native steppe vegetation of a high value for nature and species conservation. While the fields were the same size, were adjacent to the same patch of remnant steppe and were cultivated with the same crop, site-specific environmental variables contributed to 23% of the vegetation patterns; each site was characterised by its unique historical trajectory and thus, by a particular set of species. Distance from boundaries contributed to 10% of the vegetation patterns. Species characterising the surrounding steppe were found close to boundaries; species characterising abandoned fields were found further away. Winter seed banks and summer deep seed bank did not contribute much to either effect and were characterised by species dating back from past cultivation. Conversely, summer surface seed bank greatly contributed to (83%) the differences in species composition between the three fields. Seed rain contributed to differences in species composition between fields (91%) and distance (76%). Ant-borne seeds largely contributed to the differences between fields (87%). The colonisation of steppe species on field margins occurs mainly through seed rain and is very slow and incomplete. In a semi-arid fragmented open-landscape, patches of native vegetation do not play a great role in colonisation processes, and itinerant sheep grazing is insufficient to initiate recovery.

Keywords: Ants; Dry grassland; Mosaic of herbaceous communities; Seed bank; Seed rain; Steppe

1. Introduction

While many studies on grazing, mowing and burning regimes have been carried out to plan conservation management for individual grasslands (Hillier et al., 1990; Poschlod and WallisDeVries, 2002), only few studies plan for long-term management within fragmented open-landscapes and studies on secondary succession and edges have yet to be relevant to long-term management. Studies focusing on edges assessed either the influence of agriculture-related factors on field-margin vegetation (Kleijn et al., 1997) or the influence of field-margin vegetation on crops (Dutoit et al., 1999; Von Arx et al., 2002).

Investigating colonisation processes at edges of abandoned fields is important (Wilson and Aebischer, 1995) because the field potential to recover via long-term seed bank or long-distance seed rain has often been found to be relatively low in Northern Europe (Graham and Hutchings, 1988; Hutchings and Booth, 1996a; Kalamees and Zobel, 2002). Studying edges is even more important in dry climates, where drought induces conditions that dramatically slow down successional processes (Blondel and Aronson, 1999). Results may have important conservation

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implications, particularly in the Mediterranean basin where grasslands harbour a high proportion of endangered taxa (Médail and Quézel, 1999).

The hypothesis of this research was that remnant patches of vegetation are a source of seeds for the colonisation of abandoned fields either by seed rain or ant dispersal. The aims of the present study were (1) to describe the colonisation processes on abandoned field margins over a complete growing season in order to determine how steppe vegetation re-establishes at the margins between abandoned fields and a remnant patch of steppe in order (2) to provide information for the long-term management of abandoned fields.

2. Methods

2.1. Study area

The study was carried out in the plain of La Crau, located ~50 km north-west of Marseille in south-eastern France. The steppe vegetation of the plain evolved with: (1) a dry Mediterranean climate; (2) a shallow soil (<400 mm) and an impermeable bedrock; (3) itinerant sheep grazing since 3000 BP (Buisson and Dutoit, 2004). The steppe vegetation is dominated by the stress-tolerant species *Brachypodium retusum* and *Thymus vulgaris*, which represent ~50% of the biomass, and is composed of a great diversity of annual species (Buisson and Dutoit, in press). The remnant central patch of steppe was fragmented by row crop and melon cultivations between 1965 and 1985, after which all patches of steppe and fields were grazed by itinerant sheep from February to June.

Three abandoned fields (A, B, C) were selected on the sheepfold of Peau de Meau (43°33′E, 4°50′N, elevation 10 m), in the centre of the plain. All fields were adjacent to one same remnant patch of undisturbed steppe (D) in order to avoid confounding changes in the floristic composition on the margins of abandoned fields with differences due to species composition of steppe patches (Römermann et al., 2005). However, fields had varied cultivation periods, dates of abandonment and locations given in Table 1.

2.2. Sampling

On each studied field (A, B, C), three transects (1, 2, 3) were set out perpendicular to the field boundary. Each transect started at the boundary and stretched towards the centre of abandoned fields and measured 10 m because the visible gradient of the typical steppe perennial species *T. vulgaris* % cover never exceeded 10 m. The three transects per field were laid 10 m apart because most herbaceous species do not disperse by wind over more than a few meters (Verkaar et al., 1983), especially in the plain were vegetation grow very low. Collection points were set 1 m apart along the transects starting at the field edge (point 0) between steppe and fields (0–10 m; 11 samples). All data were collected in 2001, a year with an average climate.

Above-ground vegetation was recorded in 10 sub-quadrats of 40 cm × 40 cm at each sampling point totalling 990 sub-quadrats, in May 2001. *T. vulgaris* and *B. retusum* % cover, as well as stones, vegetation and bare ground % cover were visually estimated by one observer in each quadrat. All other species were sampled in each quadrat using the presence/absence method. To avoid disturbing the vegetation, other sampling was taken on the other side of the transects.

Two hundred gram of soil was taken at sampling points 0, 5 and 10 m along each transect in February 2001 (27 samples total). Samples were dried and sieved through a 200 μm mesh sieve. Total nitrogen was measured using the Kjeldahl method, phosphorus using the Olsen method and total carbon using the Anne method (Baize, 2000). The concentrations of calcium, potassium and magnesium available to plants were measured using the Shollenberger and Dreibelbis method (Baize, 2000). The soil pH was also measured in H_2O (Baize, 2000).

The persistent seed bank, seeds that persist in the seed bank >1 year, (Thompson et al., 1997) was sampled in February 2001 before the input of fresh seeds and after

Table 1
Cultivation history of the three abandoned fields A, B, C and the steppe on the sheepfold of Peau de Meau

Sites	Type of cultivation	Duration of cultivation and year of abandonment	Field location
Field A 5 ha	Melons (small tunnels) Cereals and alfalfa	1 year in 1971 1 year in 1972	N-NW of the steppe patch (D)
Field B 5 ha	Cereals and alfalfa Melons (small tunnels)	From 1960 to 1966 1 year in 1971	W of the steppe patch (D)
Field C 5 ha	Cereals and alfalfa Melons (small tunnels) Cereals and alfalfa Melons, courgettes, aubergines, peppers (large tunnels)	1 year in 1972 1 year in 1968 1 year in 1969 From 1979 to 1984	W-SW of the steppe patch (D)
Steppe D 6500 ha	Not cultivated	na	na

After abandonment, grazing occurred on all fields, as on the steppe, by itinerant sheep from February to June.