



**HAL**  
open science

# Colonisation by native species of abandoned farmland adjacent to a remnant patch of Mediterranean steppe

Elise Buisson, Thierry Dutoit

► **To cite this version:**

Elise Buisson, Thierry Dutoit. Colonisation by native species of abandoned farmland adjacent to a remnant patch of Mediterranean steppe. *Plant Ecology*, 2004, 174 (2), pp.371-384. 10.1007/BF03543067 . hal-04825667

**HAL Id: hal-04825667**

**<https://hal.science/hal-04825667v1>**

Submitted on 8 Dec 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# Colonisation by native species of abandoned farmland adjacent to a remnant patch of Mediterranean steppe

Elise Buisson\* and Thierry Dutoit

UMR-CNRS 6116 Institut Méditerranéen d'Ecologie et de Paléocécologie, Université d'Aix-Marseille III, FST Saint-Jérôme, case 461, 13397 Marseille Cedex 20, France; \*Author for correspondence (tel.

+33.4.42.90.84.86; fax. +33.4.42.90.84.48; e-mail: elise.buisson@univ.u-3mrs.fr)

Received 9 August 2002; accepted in revised form 5 March 2004

**Key words:** Historical ecology, Land-uses, Restoration, Seed bank, Seed rain, Succession

## Abstract

We studied plant distribution at the margins (0–10 m) of three formerly cultivated plots adjacent to a remnant patch of the only Mediterranean steppe of France: La Crau. We sampled above-ground vegetation, seed bank, seed rain and seed dispersal by ants in order to assess the colonisation of steppe species at margins. Our results showed that (1) present day above-ground vegetation of formerly cultivated plots is influenced more by former agricultural practices (duration of melon cultivation, fertilisation) and time since abandonment than their position in relation to the steppe. (2) An edge effect was identified as the vegetation of the steppe (e.g. *Thymus vulgaris*, *Salvia verbenaca*, *Linaria arvensis*) colonises the formerly cultivated plots (coefficients of similarity between vegetation on margins and steppe vegetation decreased with distance from boundaries ( $r = 0.65$ ,  $p < 0.001$ ). (3) Permanent deep seed bank (10–20 cm) did not contribute to either site or edge effects and was characterised by weed species from previous melon cultivation (e.g. *Chenopodium album*, *Kicksia elatine*, *Portulaca oleracea*, *Solanum nigrum*). (4) Seed rain density decreased with distance from edges ( $r = 0.39$ ,  $p < 0.001$ ) and seemed positively correlated to *T. vulgaris* cover. (5) The number of seeds in ant-traps seemed correlated to *T. vulgaris* cover. We concluded that after 19 years of abandonment, only about half of the steppe species have colonised just the few meters of the margins of the formerly cultivated plots and that restoration from seed bank, seed rain or seed dispersal by ants is unlikely. Our results are thus discussed within the context of restoring the steppe plant community on formerly cultivated plots.

## Introduction

Past agricultural land-uses have affected the composition and structure of the herbaceous ecosystems throughout the landscape around the Mediterranean Sea (Grove and Rackham 2001). Most studies on the effects of past agricultural practices, such as ploughing and the fragmentation of herbaceous ecosystems, are undertaken in dry grasslands because they are considered 'hot spots' of biological diversity in Europe (Hillier et al. 1990). Formerly ploughed areas are often difficult to locate because they are masked by the effects of a high number of wild fires. Fires eliminate some species characteristic of arable land leading to similar vegetation on all fields (Trabaud and Galtie 1996). This is part of the reasons why the effects of former ploughing on present day vegetation have received so little study in the Mediterranean area in comparison with North-western Europe (Austrheim and Olsson 1999).

Two scales can be identified in experimental methods used to study the impact of former ploughing on present day vegetation: (1) The landscape scale is usually used to identify the extent and distribution of former agricultural practices, and the order of events, which may play an important role in the creation of present vegetation patterns of dry grasslands. These studies in historical ecology (Sheail 1980; Rackham 1986; Russel 1997; Egan and Howell 2001) compare old maps, postcards and county records with present

data (Bruynseels and Vermander 1984; Gibson and Brown 1991; Molnar and Biro 1996; Pärtel et al. 1999; Debussche et al. 1999). Most of these studies showed that large tracks of grasslands were ploughed in the 19<sup>th</sup> century and used for different types of cultivation such as cereals, vineyards or even dye plants in complex rotational systems (Smith 1980; Rosén and Borgegard 2001). They also showed that, as cultivation in dry soils became less and less viable, sites were abandoned or spontaneously forestated in the 20<sup>th</sup> century (Crompton and Sheail 1975; Poschlod and WallisDeVries 2002). (2) At the plant community scale, the short-term (Austrheim and Olsson, 1999) and long-term (Cornish 1954; Wells et al. 1976) effects of ploughing on present day vegetation were also clearly identified. Formerly cultivated plots showed a decrease in species-richness and changes in their botanical composition compared with adjacent grazed dry grasslands. For example, arable weeds can persist for a long time in above ground vegetation and below ground (seed bank) and can be used as biological indicators of former land-uses (Dutoit et al. 2003a; Poschlod and WallisDeVries 2002). Ploughing does not only impact plant species-richness and botanical composition but also the direction taken by post-cultural plant succession compared with that of post-pastoral succession (Gibson and Brown 1991). These effects can be linked to an increase in soil fertility in the formerly cultivated plots because of fertiliser applications during the cultivation period (Gough and Marrs 1990; Marrs 1985) and the presence of ruderal species (*sensu* Grime, 1974), which are known to have seeds with long-term viability in the soil seed bank (Graham and Hutchings 1988a,b; Dutoit and Alard 1995; Dutoit et al. 2003b). In this study, we focused on the interactions between the history of formerly cultivated plots (landscape scale) and the position around a remnant patch of a steppe (plant community scale) in order to identify the colonisation pattern from the steppe to the formerly cultivated plots. Understanding the progression of colonising plants at the margins of abandoned fields is particularly important from a restoration ecology point of view because it is from the edge that autogenic restoration occurs from the steppe to formerly cultivated plots (Hutchings and Booth 1996a). The aims of this study were (1) to identify the agricultural history of three formerly cultivated plots, which were all adjacent to the same remnant patch of a steppe. (2) to correlate the differences observed in present day vegetation of formerly cultivated plots with the changes induced by ploughing, fertilising and time since cultivation abandonment in soil characteristics (chemical and physical composition) and with changes in the seed bank (3) to identify the colonisation pattern at the margins between formerly cultivated plots and the remnant patch of the steppe by studying plant distribution, seed bank, seed rain, and seed dispersal by ants and (4) to apply our results to the restoration of plant species-rich steppe vegetation

on formerly cultivated plots.

### *Study area*

In South-eastern France (Bouches-du-Rhône), La Crau, a large plain of steppe formation (11,500 ha) located between the Rhône Delta and the Berre Lagoon, is a site of great biological and ecological importance. This plain is the ancient delta of the Durance River, and the steppe vegetation has been shaped over centuries by (1) a dry and windy Mediterranean climate (mean annual temperature 14 °C; mean annual precipitation 500 mm/year, more than 3000 hours of sunshine/year and very strong winds blowing 334 days/year); (2) an extremely flat topography with rounded siliceous stones covering 50% of the soil surface, the average soil depth is 40 cm (Devaux et al. 1983) overlying a 5 to 25 meter thick layer of impermeable conglomerate making the alluvial water table inaccessible to the roots of plants (Colomb and Roux 1978); (3) itinerant sheep grazing since very ancient times (2 000 BP, Badan et al., 1995). In the 1950s, direct pumping of the water table allowed the development of early-season melon agricultural production, later replaced by fruit orchards. These activities contributed to fragmentation of the formerly homogenous steppe landscape, and now this plain resembles a sort of archipelago, where the islands are the remnant patches of steppe in a matrix of cultivated areas. Up to now, little consideration has been given to the interactions between the remnant patches of steppe and the matrix from a restoration ecology perspective (Etienne et al. 1998), except for birds (Wolf et al. 2001). Moreover, confounding effects of fires are not an issue here as shepherds have not traditionally used fire in the plain of La Crau (Fabre 1997). Thus, this site gives us a good opportunity to study the effects of ploughing on plant community patterns in a Mediterranean context. Our study site is in the centre of the plain, on the Nature Reserve of Peau de Meau in the largest patch of remaining steppe (43°33'E 4°50'N, elevation 10m, 6 500 ha) dominated by perennial *Brachypodium retusum* and *Thymus vulgaris*. This Nature Reserve is 163 ha (Figure 1), with about 25% of steppe and 75% of formerly cultivated plots in 2001. Amongst these plots, 55% have been cultivated with melons and row crops; the rest was cultivated with cereals (Masip 1991). We selected three formerly melon-cultivated plots, all adjacent to the same remnant patch of steppe, and we used aerial photographs (IGN, Institut National de Géographie) from 1944 to 1989 to document past impacts in each formerly cultivated plot. The type of cultivation (non-cultivated, cereal cultivation, melon cultivation) was thus distinguished in the aerial photos for 1944-1989. The first set of aerial photos available was for 1944, taken by the U.S. Air Force and the last set necessary was for 1989 as all types of cultivation had stopped by that time in the research area. Historical ecology methods (bibliography and questioning

farmers) contributed to a better understanding of former agricultural practices for melon and row crops.

Plot (A) is northwest of the steppe (Figure 1). It was most probably cultivated with melons for the first time in 1971 under small plastic tunnels (1.7 m wide, 0.7 m high, Borrey 1965). Because *Fusarium oxysporum* *F. sp. melonis*, a fungus harmful to melon plants, developed in the soil in the first year of cultivation (Odet 1991), plots were cultivated for one year only and melon cultivation continued the following year on new plots. Plots were usually left barren for 10 to 15 years after a one-year cultivation with cereals before being cultivated with melons again (Borrey 1965; Le Gloru 1956). Plot (A) may have been used to grow cereals between 1972 and 1979 and was then abandoned.

Plot (B) is west of the steppe. It was cultivated with cereals for the first time between 1960 and 1965. Melons were grown under small plastic tunnels in 1972. Cereals were then cultivated again in 1973 immediately before the plot was abandoned.

Plot (C) is south of the steppe. It was first cultivated with cereals between 1960 and 1965 and then with melons under small plastic tunnels in 1968. This plot was then cultivated with cereals in 1969. It was cultivated with melons again several years in a row between 1979 and 1984. As a fungus resistant plant had been created by then, melon and row crop continued in greenhouses (8 m wide ( 2 m height) during this period.

In the mid 80's melon cultivation stopped after an over-production and because human conditions in La Crau were too difficult. Melon cultivation was very destructive for three reasons: (1) until a fungus resistant plant was available, cultivated plots were moved every year, destroying a lot of steppe surface (Masip 1991); (2) the ploughing was deep (Masip 1991) and reached the bedrock bringing pieces of conglomerate into the soil; (3) the plots were watered, fertilised (2500 kg/ha K at the time of ploughing and 250 kg/ha 5-8-8 N, P, K at the time of setting) and treated against red spiders, aphids and powdery mildew (Borrey 1965). After abandonment, grazing occurred on the plots at the same stocking-rate as on the steppe (Fabre 1998).

Plot (D) is the remnant patch of the steppe, adjacent to all three formerly cultivated plots and has not been cultivated between 1944 and 2001.

## Methods

### *Experimental lay-out*

On each formerly cultivated plot, we set three transects perpendicular to the edge of the steppe. Each transect measured 10 meters because visible steppe vegetation colonisation on plots, indicated by encroaching *T. vulgaris* and *B. retusum*, never exceeded 10 meters. To keep transects independent, we placed them 10 meters apart because most herbaceous species do not disperse over more than a few

meters (Verkaar et al. 1983a). We collected all data from points set one meter apart along these transects starting at the edge between the steppe and formerly cultivated plots. For each transect, 11 points were sampled (from 0m to 10m), 33 per plots and 99 in total. Sampling points are named as follows: the first number is the distance from the edge in meters (0 to 10), the letter is the plot (A, B or C) and the second number is the transect number (1, 2 or 3) (e.g., 8A1: sampling points located 8 meters from the boundary, on field A, transect 1).

### *Vegetation sampling*

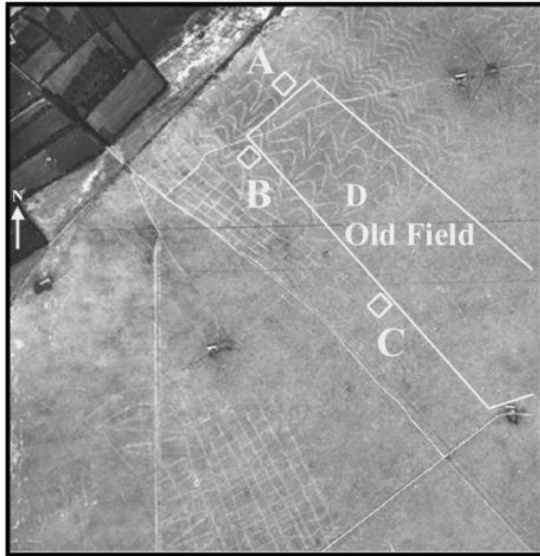
The vegetation was recorded on one side of the transects in 10 quadrats of 40 (40 cm (16000 cm<sup>2</sup>) at each sampling point in May 2001. To avoid disturbing the vegetation, all other samples (soil, seed bank and seed rain) were taken on the other side of the transects. The percent cover of *T. vulgaris* and *B. retusum*, two dominant species of the steppe, as well as the percent cover of stones, vegetation and bare ground were estimated in each quadrat. We also sampled all other species in each quadrat using the presence/absence method.

### *Soil sampling and analyses*

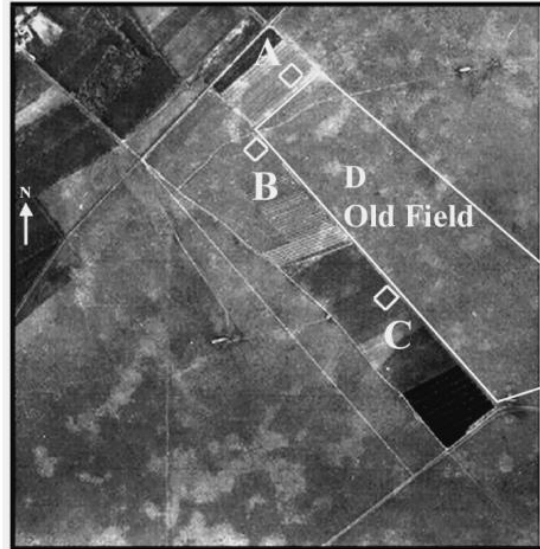
Soil sample (200 g) was taken at sampling points 0, 5 and 10 meters along each transect in February 2001. Samples were dried and sieved (200  $\mu$ m). N was measured using the Kjeldahl method, P<sub>2</sub>O<sub>5</sub> using the Olsen method and C using the Anne method (Baize 2000). The concentrations of CaO, K<sub>2</sub>O and MgO available to plants were measured using the Shollenberger and Dreibelbis method (Aubert 1970). The pH of soil was also determined.

### *Seed bank*

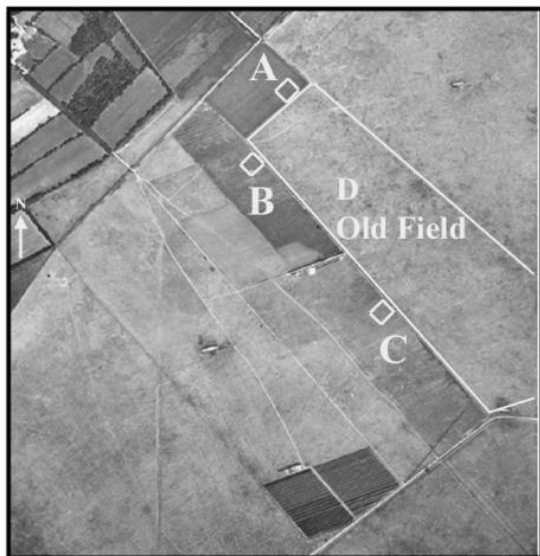
In order to look at the effects of old disturbances, the permanent seed bank (5 years in the soil, Thompson et al. 1997) was sampled in January 2001. Bakker et al. (1996) proposed to sample at two depths. We selected two depth classes: 0-10 cm and 10-20 cm (ploughing stopped around 20 cm deep). Two 500 cm<sup>3</sup> containers, each corresponding to a depth class, were filled with soil after removing stones bigger than 2 cm. The volume of soil sampled was 500 cm<sup>3</sup>/point/depth (198 samples total). This should allow the species present in the seed bank to be detected, as Bakker et al. (1996) recommended 1200 cm<sup>3</sup> and Hayashi and Numata (1971) 600 cm<sup>3</sup> and as the combined volume plot/distance from the edge/depth would be 1500 cm<sup>3</sup>. Each of the 198 samples was placed in water for 30 minutes and then passed through a 200  $\mu$ m mesh before being spread in flats filled with a 2 cm thick layer of vermiculite (inert substrate) topped with medical compresses. Flats were kept in a greenhouse. They were moved around in the greenhouse several times to randomise germination conditions. Flats were left in the greenhouse for four months and the soil was lightly disturbed after three months to increase the total number of germinations (Thompson and Grime 1979). Seedlings were identified using Muller (1978) and Mamarot (1997), counted and removed. When they could not be easily identified, seedlings were potted and grown in a growth chamber (16h day at 25 °C : 8h night at 20 °C) until identifiable using the standard text (Jauzein, 1995). Seed bank data used for statistical analyses were numbers of seedlings of each species at each sampling point and for each depth (numbers of seedlings for 500 cm<sup>3</sup>).



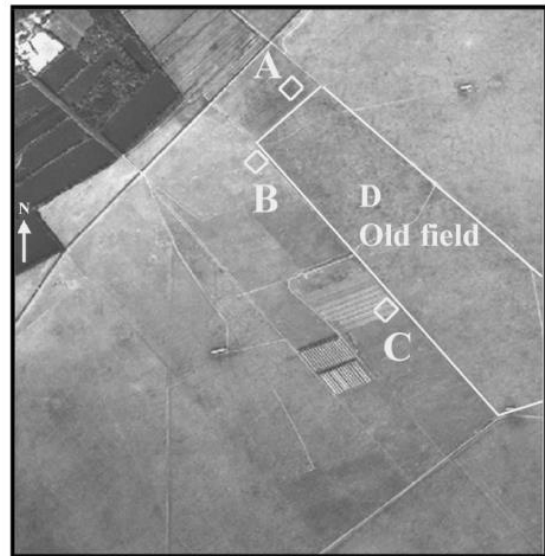
**1947**  
**A, B and C before cultivation**  
**D: Old field**



**1971**  
**A: Melon cultivation in plastic tunnels**  
**B: Ex-cultivated cereal plot**  
**C: Plot after melon cultivation in plastic tunnels**  
**D: Old field**



**1975**  
**A: Cereal cultivation**  
**B: Plot after melon cultivation in plastic tunnels**  
**C: Ex-cultivated plot**  
**D: Old field**



**1984**  
**A and B after cultivation**  
**C: Plot after melon cultivation in greenhouses**  
**D, the old field, was not cultivated between 1944 and 2002**

*Figure 1.* Historical trajectories of 4 plots A, B, C and D (old field (steppe) of the Nature Reserve of Peau de Meau (43°33'E 4°50'N) investigated with aerial photos for 1944 to 1984 (scale 1/25000, IGN- Institut Géographique National).

### *Seed rain*

The seed rain was sampled from April 15<sup>th</sup> to May 15<sup>th</sup> 2001 at the peak of the seed dispersal season (Bourrelly et al. 1983). Sticky traps, made of paper filters coated with grease and placed in 14cm diameter petri dishes, were fixed with pegs at all sampling points along the transects. Sticky papers were

changed once, early May. Seeds were identified to the species level under a dissecting microscope using a reference collection put together by Borrel and Palluel (1984) in Cerdan et al. (1986). Seed rain data used for statistical analyses were numbers of seeds of each species at each sampling point (trap (153.89 cm<sup>2</sup>)).

### *Seed dispersal by ants*

In order to assess ant seed dispersal from the steppe to the formerly cultivated plots, ant traps were set at all sampling points along the transects. These traps, consisting of 5 cm diameter × 10 cm high containers filled with a non-attractive liquid 50%, 49% water, 1% acetic acid and a few drops of tensio-active detergent, were placed in the soil at the end of March 2001. The traps were left closed until April 15<sup>th</sup> so that ant behaviour would not be influenced by trap setting. The traps were opened at the peak of the ant harvest season on April 15<sup>th</sup> 2001 (Cerdan et al. 1986) and changed once early May. The seeds-dispersed-byants data used for statistical analyses were numbers of seeds of each species at each sampling point (trap = 19.63 cm<sup>2</sup>).

### *Statistical analyses*

In order to describe the vegetation composition at the margins between the steppe and plots, CAs (Correspondence Analyses; STATOS software) were performed on the (99 points × 96 species) matrix vegetation data. The relative contribution of each point (sampling points and species) to an axis, was indicated in brackets in the results (= distance of point to the origin of the coordinate system / ( contributions of all points to an axis). The relative contribution of a point indicates whether or not, and to what extent, the respective point contributes to the overall inertia (a relative contribution is considered high if superior to twice the average relative contribution ). It is particularly useful in the case of CAs for which the correspondence map location may represent a point very well but the same point may not contribute much to the overall inertia (Garson 2003). In order to explain the composition of the vegetation with environmental variables, a PCA (Principal Component Analysis; STATOS software) was performed on the (27 points ( 25 variables) matrix, containing the following variables: (1) soil condition variables: C, N, P<sub>2</sub>O<sub>5</sub>, K<sub>2</sub>O, NaO, CaO, MgO, pH, C/N, percent covers of stones and of bare ground; (2) vegetation variables: vegetation, percent covers of *T. vulgaris* and *B. retusum*, vegetation species richness, seed rain, seed bank species richness and density for the two depth classes, number of seeds found in the ant traps and number of ants; (3) historical variables: cultivation time, time since abandonment. Also, ANOVAs were run on the soil variables in relation to the distance from the steppe edges. To analyse the seed bank, CAs were performed on the seed bank data with the two depth classes considered separately: 0-10cm (99 points × 33 species) matrix and 10-20 cm (99



points × 31 species) matrix.

Coefficients of similarity (Sorensen Index) were calculated for each distance from the edge and for each formerly cultivated plot using the formula  $S.I. = 2j/A+B$  ( $j$  = number of species occurring on both steppe and the formerly cultivated plot,  $A$  = number of species occurring in the steppe (Straub 1996; Römermann 2002),  $B$  = number of species occurring on the formerly cultivated plot).

In order to understand the spatial distribution patterns of the most represented species, possible correlation between the frequencies of these species with the distance from the edge were investigated. Possible correlation between percent cover of *T. vulgaris*, seed rain or seed dispersal by ants with the distance from the edge and possible correlation between each of these three set of data were also investigated.

## Results

The CA performed on the vegetation data (Figure 2) distinguished each formerly cultivated plot and showed that each was characterised by some particular species. Axis 1 (10.8%; mean relative contribution for sampling points: 10.05, for species: 10.39) was strongly influenced by the points of plot A, particularly 8A2 (contribution 34) and 1A3 (contribution

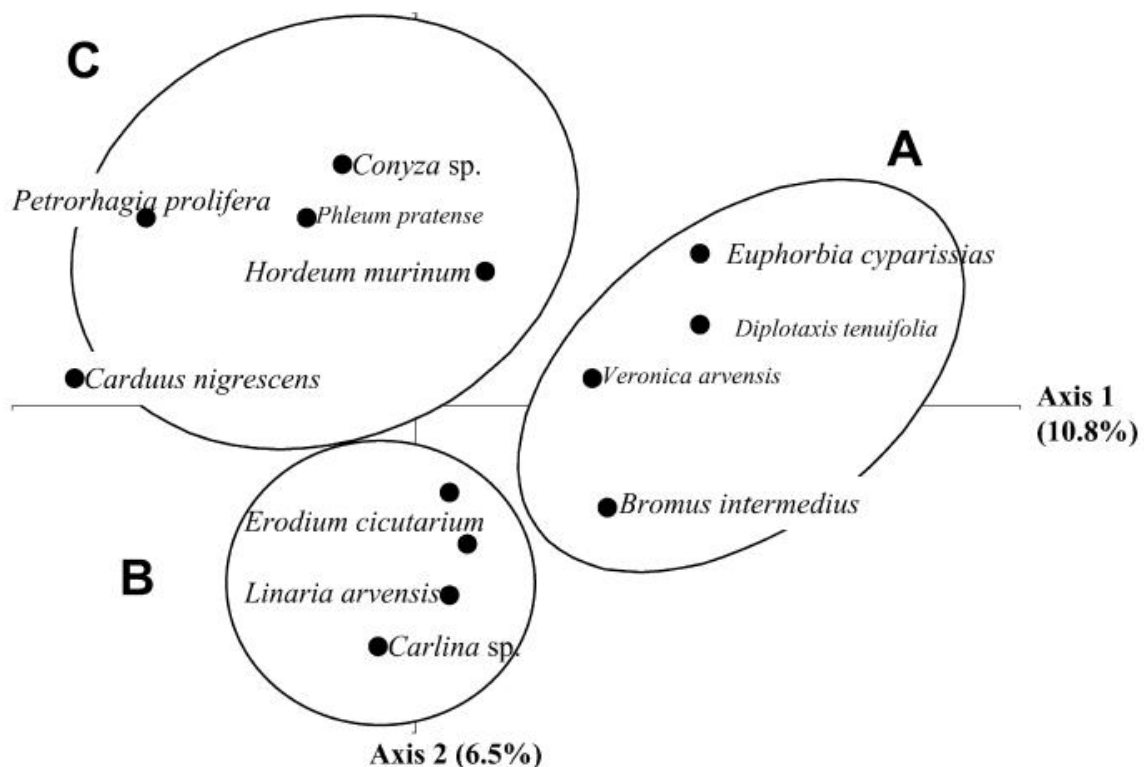


Figure 2. CA performed on the vegetation data for the three formerly cultivated plots (A, B and C) (99 points x 96 species). Only the species showing a high contribution to the axes are presented on the Figure. The 33 sampling points of each plot are circled.

30), correlated with species *Diplotaxis tenuifolia* (82), *Euphorbia cyparissias* (60), *Bromus intermedius* (34) and *Veronica arvensis* (33). On axis 1, plot A

contrasted with plots B and C correlated with *Carthamus lanatus* (34) and *Medicago rigidula* (30). Axis 2 (6.5%; mean relative contribution for sampling points: 10.02, for species: 10.4) placed plot B opposite plot C. Indeed, point 6C3 (83) correlated with *Conyza* sp. (64), *Phleum pratense* (49), *Hordeum murinum* (44) and *Petrorhagia prolifera* (32) was placed opposite points 0B1 (48) and 3B2 (57) correlated with *Carlina* sp. (63), *Linaria arvensis* (36) and *Erodium cicutarium* (32). This site effect was confirmed by the CA on the surface seed bank (0 to 10 cm) data but with different species (plot A e.g. *Anagalis foemina* and *Sideritis romana*, plot B e.g. *Calamintha nepeta* and *Lithospermum arvense* and plot C e.g., *Chenopodium album*). At the opposite, this site effect was not observed in the deep seed bank (10 to 20 cm). Therefore, the surface persistent seed bank consists of few steppe species and distinguished each formerly cultivated plot characterised by some particular species, while the deep persistent seed bank consists of arable weed species (*Kickxia elatine*, *Portulaca oleracea*), ruderal and nitrogen-loving species (*C. nepeta*, *Lobularia maritima*, *Polygonum aviculare*, *Senecio vulgaris*, *Solanum nigrum*) (see Appendix).

The PCA performed on the environmental, historical and vegetation variable matrix also distinguished between plots. The first two axes accounted for 43.2% of the total variation: 26.7% for axis 1 and 16.5% for axis 2 (Figure 3). Axis 1 was strongly influenced by points 10C1 and 5C1 correlated with the longest cultivation time (2 years) and higher K<sub>2</sub>O, CaO and P<sub>2</sub>O<sub>5</sub> concentrations. Conversely, plots A and B were correlated with earlier times of abandonment (1974-1978). The PCA shows that each plot is characterised by an own unique historical trajectory (conditions of melon cultivation, time since abandonment, cultivation time).

Although the CA and the PCA distinguished a strong site effect and failed to assess the vegetation patterns at the margin, there were observable trends of environmental variables and of vegetation composition changing with the distance from edges that

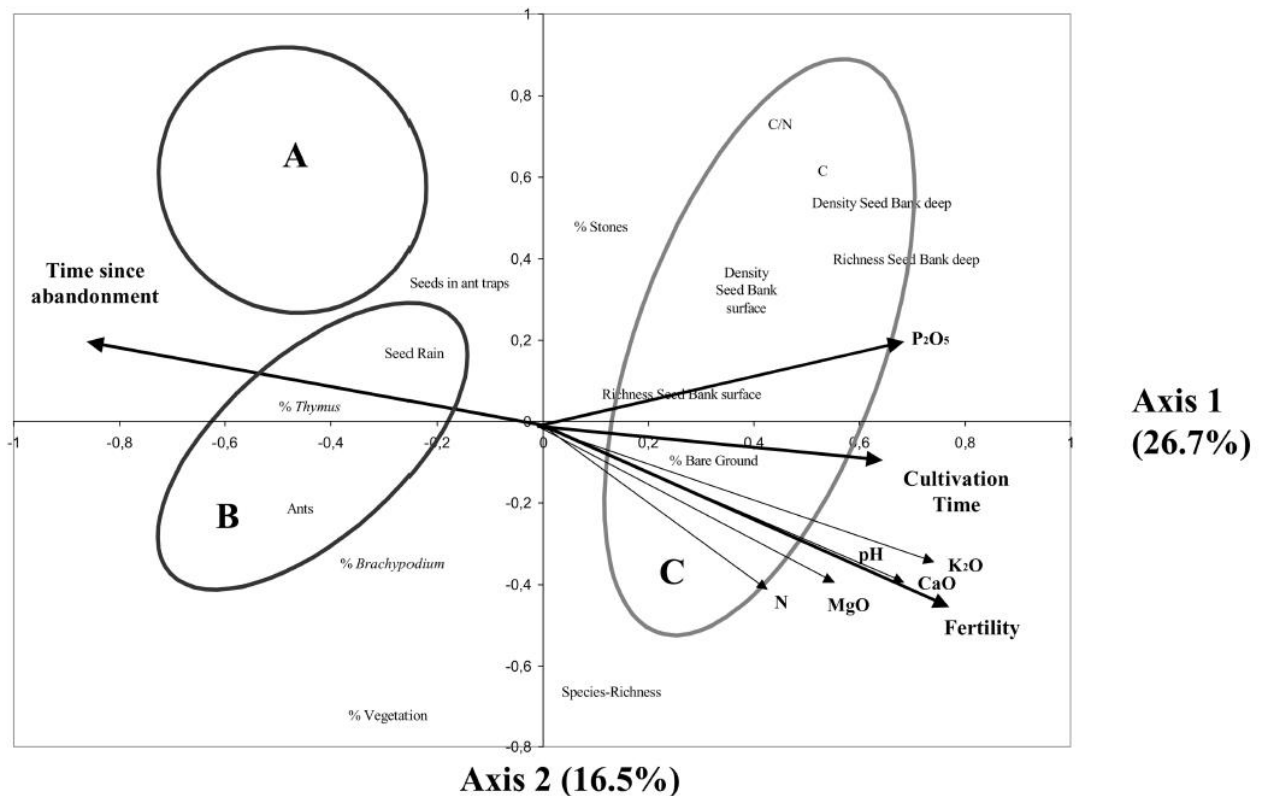


Figure 3. PCA performed on the environmental, historical and vegetation matrix for the three formerly cultivated plots (A, B and C) (27 points x 25 variables).

were comparable within the three plots. ANOVAs run on soil conditions and vegetation variables showed that only P<sub>2</sub>O<sub>5</sub> concentrations and percent covers of stones increased significantly with the distance from the steppe edges (F=6.95 for p<0.05 and F=13.33 for p<0.001 respectively). Close to edges, there were more species characteristic of the steppe vegetation e.g *B. retusum*, *T. vulgaris* and *Salvia verbenaca* and far from edges there were more arable weed species such as *C. nepeta*, *H. murinum* and *Bromus* sp.. The values of the coefficients of similarity between the vegetation at each sampling points and the vegetation of the steppe decreased significantly with the distance from edges ( $r=-0.65$  p<0.001) (Figure 4). We found that the spatial patterns of some of the most represented native steppe species (*T. vulgaris*, *Polycarpon tetraphyllum*, *Linaria arvensis*, *Linum strictum*, *Galium murale*, *Galium parisiense*, *Geranium molle*, *Hedypnois cretica*, *Hypochaeris glabra*, *Euphorbia exigua*, *Logfia gallica*) followed the same distribution, with higher number of individuals close to edges of the formerly cultivated plots than far from the edge (Table 1). Thus, steppe species decreased significantly with the distance from edges and species of the fields increased with the distance from edges (Table 1). The distribution of species such as *Bromus* sp. and *D. glomerata* on margins appeared to be unrelated to the distance to edges. *T. vulgaris* and *C. nepeta*, respectively decreased or increased with the distance to edges depending on where the seed source is located (respectively steppe or field).

Simple linear regressions showed that the number of seeds in the seed rain decreased with the distance from edges ( $r = 0.39$ ,  $p < 0.001$ ). Other significant correlation tests (ant-borne seeds and distance; *T. vulgaris* cover and number of ants; *T. vulgaris* cover and number of ant-borne seeds; *T. vulgaris* cover and quantity of wind-borne seeds) had low  $r$  values.

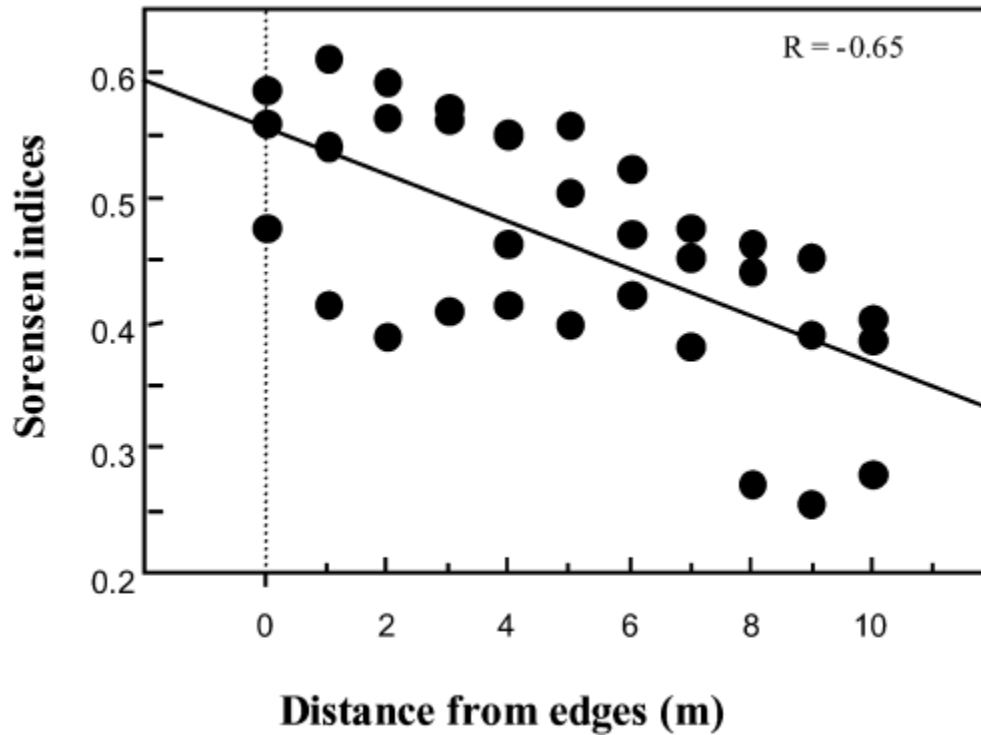


Figure 4. Relation between Sorensen indices and distance from edges ( $r = 0.65$ ,  $p < 0.001$ ).

Table 1. Coefficient of regression ( $r$ ) of correlation tests between variables (species frequency and distance to edges). <sup>x</sup> native steppe species, \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ , n.s. non significant. Species  $r$

Species	$r$
<i>Thymus vulgaris</i> <sup>x</sup>	-0.48***
<i>Polycarpon tetraphyllum</i> <sup>x</sup>	-0.44***
<i>Linaria arvensis</i> <sup>x</sup>	-0.30**
<i>Linum strictum</i> <sup>x</sup>	-0.60***
<i>Galium murale</i> <sup>x</sup>	-0.23*
<i>Galium parisiense</i> <sup>x</sup>	-0.67***
<i>Geranium molle</i> <sup>x</sup>	-0.22*
<i>Hedypnois cretica</i> <sup>x</sup>	-0.29**
<i>Hypochaeris glabra</i> <sup>x</sup>	-0.41***
<i>Bromus rubens</i>	n.s.
<i>Dactylis glomerata</i>	n.s.
<i>Calamintha nepeta</i>	0.38***
<i>Euphorbia exigua</i> <sup>x</sup>	-0.66***
<i>Logfia gallica</i> <sup>x</sup>	-0.58***

## Discussion

The CA performed on the vegetation data and the persistent surface seed bank data showed that the three plots are characterised by some particular species. Plot A is characterised by arable weeds, plot B by steppe species and plot C by mesophilous species. However, the three plots are geographically close together and adjacent to the same remnant patch of steppe. Despite the dominant wind direction (north west – south east), passing over both plots B and C after the remnant patch of steppe, all plots still have different dominant species. Thus, the site effect cannot be explained by the position of the plots in relation to the steppe or by a present climate gradient. The PCA clearly showed that the below and aboveground vegetation of each plot is characterised by its own unique historical and agricultural trajectory. For example, plot C has been cultivated for a longer time (melons for two years minimum) and has been abandoned more recently (last melon cultivation between 1978 and 1984).  $K_2O$ , N and  $P_2O_5$  concentrations (chemicals contained in fertilisers) are still high on this plot. Past ploughing reached the bedrock, mixing the calcareous conglomerate into the soil. This is observable because of the high CaO and MgO concentrations and an increase of soil pH that may be responsible for the presence of mesophilous species on plot C. Austrheim and Olsson (1999) also showed that floristic differences of several grasslands close together can be explained by differences in times of abandonment (older abandonment 39 years). Wells et al. (1976) showed as well that the floristic differences of such grasslands can be explained by differences in historical trajectories: cultivation time, time of abandonment (older abandonment 100 years) and type of cultivation. In our study, we show that these plots, all cultivated for melons, are floristically different because of differences in historical and agricultural trajectory: the dates and duration of cultivation are specific to each plot and the conditions of melon cultivation were different (cultivation in tunnels (plot A and B) or in tunnels and then in greenhouses (plot C)).

Independently of the various historical impacts and of the differences in number of species found on each field (Table 2), we observed comparable spatial distribution patterns on the three plots: 1) The distribution of forbs found on the fields, such as *C. nepeta*, which is dispersed by barochory and myrmecochory, increased with the distance to edges because the seed source are on the fields. 2) The distribution of grass species found on the fields, such as *Bromus* sp., was unrelated to the distance to edges although seed sources are on fields because grasses disperse further than forbs (Hutchings and Booth 1996a). 3) The similarity between the vegetation of formerly cultivated plots with that of the steppe decreased with the distance from the edge. In order to explain this change of flora and the decrease of steppe species, we made two assumptions. There was either an environmental

gradient (ecocline), which creates a new habitat between the two adjacent ecosystems (Van der Maarel 1990) or an ‘edge effect’ (Frochot 1987), here shown by the more mature ecosystem (the steppe) colonising the formerly cultivated plots (younger ecosystem).

*Table 2.* Total number of species in the vegetation (per 52.8 m<sup>2</sup>). Total number of species and of germinations in soil seed bank to a depth of 20 cm (per 0.033 m<sup>3</sup>). Total number of taxa and of seeds in the seed rain (per 0.51 m<sup>2</sup>) and in ant traps (per 0.065 m<sup>2</sup>).

Vegetation:	A	B	C	Total
Total number of species in the vegetation	63	66	83	94
Soil seed bank: 198 soil samples in 1 sampling event at both depths				
Number of species in permanent seed bank (0-20 cm)	27	28	21	39
Number of germinations in permanent seed bank (0-20 cm)	691	375	497	1563
Seed rain in 198 traps sampled in 2 sampling events				
Number of taxa	25	12	17	27
Number of seeds	812	735	790	2337
Seeds in ant traps in 198 traps sampled in 2 sampling events				
Number of taxa	19	13	17	24
Number of seeds	255	265	198	718

The increasing P<sub>2</sub>O<sub>5</sub> concentrations with the distance from the edge suggest that there is an environmental gradient. Indeed, fertilisers were particularly applied under tunnels and greenhouses and not at the margins of the plots that served as vehicular access tracks. Gough and Marrs (1990) and Austrheim and Olsson (1999) showed that phosphorus is negatively correlated with species richness. Indeed, phosphorus excess has a negative effect on mycorrhizae, reducing the competitiveness of species associated with them (Grime et al. 1987); 92% of dry grassland species have such associations. Moreover, phosphorus excess has a positive effect on ruderal species by increasing their competitiveness to the detriment of dry grassland species (Gough and Marrs 1990). Although such a phosphorus gradient exists, it may not explain the degree of vegetation change we observed. Indeed, Janssens et al. (1998) showed that in meadow ecosystems, 5 mg/100 g of extractable phosphorus in soil is a threshold above which there are very few species (less than 20 species per 100 m<sup>2</sup>), but the concentrations we observed in La Crau were not high enough.

We also observed that the spatial distribution patterns of some of the most represented native steppe species, mainly forbs, were similar on the three plots: more individuals grew close to the edge of the plots than far from the edge, which is consistent with Verkaar et al. (1983b) who have shown that dispersal distances of forbs are very limited (0.3 to 3.5 m). Thus, steppe species are colonising formerly cultivated plots and there is an ‘edge effect’ within just a few meters. Because of Mediterranean conditions, passive restoration may be much slower than observed by Critchley and Fowbert (2000) on 50 set-aside sites randomly selected in England (species richness increased after 5 years, especially close to the site edge). Moreover, it is incomplete since the

best coefficient of similarity obtained was 0.61 (plot C, sampling point 1 m from the edge).

Since the environmental gradient observed may not explain the change of flora, it may be better explained by the vegetation dynamics itself (e.g., neighbouring effect). Indeed, *T. vulgaris* seed dispersal and germination may be particularly linked with ants as found with *Lavandula latifolia* seeds (Cerdan et al. 1986). Ants may disperse *T. vulgaris* seeds with them as they colonise new areas. Also, *T. vulgaris* may be a structuring species of the community as *T. vulgaris* plants are the only topography of this extremely flat plain. They may play a role as windbreaks, stopping seed saltation from the steppe to the plots. Our study shows that *T. vulgaris* seemed positively correlated with number of ants, of ant-borne seeds and of windborne seeds. Another hypothesis is that plot vegetation is less heavily impacted by grazing at the margins as sheep activity is less intense there. Indeed, Dureau and Bonnefon (1998) showed that large sheep flocks did not graze evenly the corners and sides of two adjacent plots belonging to different owners (here, plot D does not belong to the same owner than plots A, B and C).

Seed rain and seed dispersal by ants seem limited to the margins (see Appendix). Restoration from the seed bank appears to be minimal, as well. Indeed, the deep persistent seed bank consists of arable weed species dating back from the time of melon cultivation. These species have long-term permanent seeds (>5 years, Thompson et al. 1997; Römermann 2002). Some of these species (e.g. *Portulaca oleracea* and *Solanum nigrum*) cannot be found in above ground vegetation because the conditions necessary to their growth no longer exist (ploughing, fertiliser, controlled climate, water etc.). In the surface persistent seed bank, few steppe species are present, even at the very edge between the steppe and formerly cultivated plots. Most of the steppe species have a transient seed bank (< 1 year, Thompson et al. 1997) because they co-evolved with grazing, which creates favourable conditions to the establishment of seedlings (Willems 1995). Therefore, to restore the formerly cultivated plots, steppe species may need to be reintroduced .

On October 8<sup>th</sup>, 2001, a large nature reserve was created in order to preserve the steppe vegetation of La Crau (Réserve Naturelles des Coussouls de la Crau, 7 412 ha). Cultivation, removal of stones and other modifications of natural habitat conditions is now prohibited (Boutin 2002). Some of this protected land is formerly cultivated plots, and so the restoration of these plots to steppe is necessary. In the present study, we show that after cultivation, a community composed of arable weed establishes on the plots, even when adjacent to a remnant patch of steppe. In this particular case, passive restoration is limited to a few meters along the edge between the steppe and formerly cultivated plots and restoration is extremely slow and incomplete, contrary to Etienne

et al.'s (1998) assessments.

Restoration by sowing has been attempted in Europe (Wells 1991; Hutchings and Booth 1996b).

However, it would be interesting here to investigate the facilitative roles that some species may have for recolonisation: only a few species may have to be sown to restore the full species diverse community. Indeed, we noted some positive correlation between the percent cover of *T. vulgaris* and the number of ants and the number of seeds they carry as well as, the quantity of seeds dispersed by wind. Thus, *T. vulgaris*, a dominant species of the steppe, could be a structuring species of the community. Future research could focus on controlling its establishment (sowing and transplanting) and documenting its role in the restoration of formerly cultivated plots.

## Acknowledgements

This study was financed with a grant from the French Department of Ecology and Sustainable Development (Ministère de l'Écologie et du Développement Durable), program 'Espaces Protégés'. We gratefully acknowledge the Conservatoire-Etudes des Ecosystèmes de Provence and the team of the Eco-Musée de Crau. We are grateful to Markus Bernhardt, Paola Bottone, Eric Gerbaud, Christiane Rolando, Christine Römermann, Franck Torre and Elise Trivelly for technical support and field assistance. We also would like to thank Marjorie Sweetko and Grey Hayes for proof reading and language checking draft manuscripts.

## References

- Aubert G. 1970. Méthodes d'analyses des sols. CRDP, Marseille, France.
- Austrheim G. and Olsson E.G.A. 1999. How does continuity in grassland management after ploughing affect plant community patterns? *Plant Ecology* 145: 59–74.
- Badan O., Brun J.P. and Congès G. 1995. Les bergeries romaines de la Crau d'Arles. Les origines de la transhumance en Provence. *Gallia* 52: 263–310.
- Baize D. 2000. Guide des analyses en pédologie. INRA, Paris, France.
- Bakker J.P., Poschlod P., Strykstra R.J., Bekker R.M. and Thompson K. 1996. Seed banks and seed dispersal: important topics in restoration ecology. *Acta Botanica Neerlandica* 45: 461–490.
- Borrey M. 1965. Contribution à la connaissance des petites régions agricoles. La Crau. Ministère de l'Agriculture, Bouches-du-Rhône, France.
- Bourrelly M., Borel L., Devaux J.P., Louis-Palluel J. and Archiloque A. 1983. Dynamique annuelle et production primaire nette de l'écosystème steppique de Crau (Bouches-du-Rhône). *Biologie-Ecologie méditerranéenne* 10: 55–82.
- Boutin J. 2002. Plaine de la Crau. La réserve Naturelle des Coussouls de Crau. *Garrigues* 30: 4–5.
- Bruynseels G. and Vermander J. 1984. L'évolution de la végétation calcicole de Nismes à Vaucelles entre 1905 et 1982. *Parcs Nationaux* 39: 71–79.
- Cerdan P., Borel L., Palluel J. and Delye G. 1986. Les fourmis moissonneuses et la végétation de la Crau (Bouches-du-Rhône). *Ecologia Mediterranea* 12: 15–24.
- Colomb M. and Roux R.M. 1978. La Crau, données nouvelles et interprétations. *Géologie Méditerranéenne* 5: 303–324.
- Cornish M.W. 1954. The origin and structure of the grassland types of the Central North Downs. *Journal of Ecology* 42: 359–374.
- Critchley C.N.R. and Fowbert J.A. 2000. Development of vegetation on set-aside land for up to nine years from a national perspective. *Agriculture, Ecosystems and Environment* 79: 159–



- Crompton G. and Sheail J. 1975. The historical ecology of Lakenheath Warren in Suffolk, England: a case study. *Biological Conservation* 8: 299–313.
- Debussche M., Lepart J. and Dervieux A. 1999. Mediterranean landscape changes: evidence from old postcards. *Global Ecology and Biogeography* 8: 3–15.
- Devaux J.P., Archiloque A., Borel L., Bourrelly M. and Louis-Palluel J. 1983. Notice de la carte phyto-sociologique de la Crau (Bouches-du-Rhône). *Biologie-Ecologie méditerranéenne* 10: 5–54.
- Dureau R. and Bonnefon O. 1998. Etude des pratiques de gestion pastorale des coussouls. pp. 61- 89.. In: *Patrimoine Naturel et Pratiques Pastorales en Crau*. CEEP Ecomusée de Crau, Saint-Martin de Crau, France.
- Dutoit T. and Alard D. 1995. Permanent seed bank in chalk grassland under various management regimes : their role in the restoration of species-rich plant communities. *Biodiversity and Conservation* 4: 939–950.
- Dutoit T., Buisson E., Roche P. and Alard D. 2003a. Land use history and botanical changes in the calcareous hillsides of Upper-Normandy (North-Western France): new implications for their conservation management. *Biological conservation* 115: 1–19.
- Dutoit T., Gerbaud E., Buisson E. and Roche P. 2003b. Dynamique d'une communauté d'adventices dans un champ de céréale créé après le labour d'une prairie semi-naturelle: rôles de la banque de graines permanente. *Ecoscience* 10: 225–235.
- Egan D. and Howell E.A. 2001. *The historical ecology handbook: a restorationists' guide to reference ecosystems*. Island Press, Washington, USA.
- Etienne M., Aronson J. and Le Floch E. 1998. Abandoned lands and land use conflicts in southern France. *Ecological Studies* 136: 127–140.
- Fabre P. 1997. *Homme de la Crau, des coussouls aux alpages*. Cheminements en Provence. Eds: Clergeaud L. and Giard J.L.
- Fabre P. 1998. La Crau, depuis toujours terre d'élevage. pp. 34–44. In: *Patrimoine Naturel et Pratiques Pastorales en Crau*, CEEPEcomusée de Crau, Saint-Martin de Crau, France.
- Frochot B. 1987. Synergism in bird communities: a method to measure edge effect. *Acta Oecologica* 8: 253–258.
- Garson G.D. 2003. Correspondance analysis. (pages html). CHASS NCSU. <http://www2.chass.ncsu.edu/garson/pa765/correspondence.htm> (last checked in December 2003).
- Gibson C.W.D. and Brown V.K. 1991. The nature and rate of development of calcareous grassland in southern Britain. *Biological Conservation* 58: 297–316.
- Gough M.W. and Marrs R.H. 1990. A comparison of soil fertility between semi-natural and agricultural plant communities: implications for the creation of species-rich grasslands on abandoned agricultural land. *Biological Conservation* 51: 83–96.
- Graham D. J. and Hutchings M.J. 1988a. Estimation of the seed bank of a chalk grassland ley established on former arable land. *Journal of Applied Ecology* 25: 241–252.
- Graham D.J. and Hutchings M.J. 1988b. A field investigation of germination from the seed bank of a chalk grassland ley established on a former arable land. *Journal of Applied Ecology* 25: 253–263.
- Grime J.P. 1974. Vegetation classification by reference to strategies. *Nature* 250: 26–31.
- Grime J.P., MacKey J.M.L., Hillier S.H. and Read D.J. 1987. Floristic diversity in a model system using experimental microcosms. *Nature* 328: 420–422.
- Grove A.T. and Rackham O. 2001. *The nature of Mediterranean Europe : An ecological history*. Yale University Press: New Haven and London, UK.
- Hayashi I. and Numata M. 1971. Viable buried-seed population in the Miscanthus- and Zoysia-type grasslands in Japan. *Ecological studies in the buried-seed population in the soil related to plant succession VI*. *Japanese Journal of Ecology* 20: 243–252.
- Hillier S.H., Walton D.W.H. and Wells D.A. 1990. *Calcareous grassland: ecology and management*. Bluntisham Books, Bluntisham, UK.
- Hutchings M.J. and Booth K.D. 1996a. Studies on the feasibility of re-creating chalk grassland vegetation on ex-arable land. I. The potential roles of the seed bank and the seed rain. *Journal of Applied Ecology* 33: 1171–1181.

Hutchings M.J. and Booth K.D. 1996b. Studies on the feasibility of re-creating chalk grassland vegetation on ex-arable land. II. Germination and early survivorship of seedlings under different management regimes. *Journal of Applied Ecology* 33: 1182–1190.

Janssens F., Peeters A., Tallowin J.R.B., Bakker J.P., Bekker R.M., Fillat F. and Oomes M.J.M. 1998. Relationship between soil chemical factors and grassland diversity. *Plant and Soil* 202: 69–78.

Jauzein P. 1995. Flore des champs cultivés. *Sopra – Inra, Paris, France.*

Kerguélen M. 1999. Index synonymique de la flore de France. [\\_pages.html](http://www.inra.fr/Internet/Centres/Dijon/malherbo/dfd/acceuil1.htm)). INRA Dijon. <http://www.inra.fr/Internet/Centres/Dijon/malherbo/dfd/acceuil1.htm>. (October 1999 ; last checked in May 2003).

Le Gloru P. 1956. Le melon en Crau. *Compte rendu des journées maraîchères méridionales. Chateaufort-19 juin 1956. Salon de Provence, France.*

Mamarot J. 1997. Mauvaises herbes des cultures. ACTA: Paris, France.

Marrs R.H. 1985. Techniques for reducing soil fertility for nature conservation purposes: a review in relation to research at Roper's heath, Suffolk, England. *Biological Conservation* 34: 307–332.

Masip A.C. 1991. Le peuplement végétal de la réserve de Peau de Meau. Données pour la gestion. Ph.D. Thesis, University of Barcelona, Barcelona.

Molnar Z. and Biro M. 1996. Vegetation history of the Kardoskut area (S. E. Hungary). I. Regional versus local history, ancient versus recent habitats. *Tiscia*: 15-25.

Muller F.M. 1978. Seedlings of the north-western European lowland. A flora of seedlings. Junk: The Hague, The Netherlands.

Odet J. 1991. Le melon. CTIFL: Paris, France.

Pärtel M., Mändla R. and Zobel M. 1999. Landscape history of a calcareous (alvar) grassland in Hanila, western Estonia, during the last three hundred years. *Landscape Ecology* 14: 187–196.

Poschlod P. and WallisDeVries M.F. 2002. The historical and socio-economic perspective of calcareous grasslands- lessons from the distant and recent past. *Biological Conservation* 104: 361–376.

Rackham O. 1986. The history of the countryside. Phoenix Giant: London, UK.

Römermann C. 2002. The effects of historical melon and cereal cultivation on the actual vegetation structure of a dry steppic grassland: the example of the Crau (South-eastern France). Master Thesis, University of Marburg.

Rosén E. and Borgestad S.O. 2001. The open cultural landscape. *Acta. Phytogeographica Suecica* 84: 113–134.

Russel E.M.B. 1997. People and the land through time: linking ecology and history. Yale University Press: New Haven, USA.

Sheail J. 1980. Historical Ecology: the documentary evidence. Institute of Terrestrial Ecology, Huntingdon, UK.

Smith C.J. 1980. Ecology of the English chalk. Academic Press: London, UK.

Straub B. 1996. La végétation de la Crau sèche (Peau de Meau). CEEP Ecomusée de la Crau, Saint-Martin de Crau, France.

Thompson K. and Grime J.P. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology*. 67: 893–921.

Thompson K., Bakker J. and Bekker R. 1997. The soil seed bank of North West Europe: methodology, density and longevity. Cambridge University Press, Cambridge, UK.

Trabaud L. and Galtie J. 1996. Effects of fire frequency on plant communities and landscape pattern in the Massif des Alpilles (Southern France). *Landscape Ecology* 11: 215–224.

Van der Maarel E. 1990. Ecotones and ecoclines are different. *Journal of Vegetation Science* 1: 135–138.

Verkaar H.J., Schenkeveld A.J. and Brand J.M. 1983a. On the ecology of short lived forbs in chalk grasslands: micro-site tolerances in relation to vegetation structure. *Vegetatio* 52: 91–102.

Verkaar H.J., Schenkeveld A.J. and van der Klashorst M.P. 1983b. The ecology of short-lived forbs in chalk grasslands: dispersal of seeds. *New Phytologist* 95: 335–344.

Wells T.C.E., Sheail J., Ball D.F. and Ward L.K. 1976. Ecological

studies on the Porton Ranges: relationships between vegetation, soil and land-use history. *Journal of Ecology* 64: 589–626.

Wells T.C.E. 1991. Restoring and re-creating species-rich lowland dry grassland. In: Goriup P.D., Batten M.A. and Norton J.A. (eds), *Conservation of Lowland Dry Grassland Birds in Europe*. Joint Nature Conservancy Committee, Peterborough. pp. 125–132.

Willems J.H. 1995. Soil seed bank, seedling recruitment and actual species composition in an old and isolated chalk grassland site. *Folia Geobotanica Phytotaxonomica*. 30: 141–156.

Wolff A., Paul P.J., Martin J.L. and Bretagnolle V. 2001. The benefits of extensive agriculture to birds: the case of the little bustard. *Journal of Applied Ecology* 38: 963–975.