Biol Invasions (2010) 12:1023–1029
DOI 10.1007/s10530-009-9519-z

ORIGINAL PAPER

Soil disturbance, vegetation cover and the establishment of the exotic shrub *Pyracantha coccinea* in southern France

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Received: 19 December 2008 / Accepted: 1 July 2009 / Published online: 18 July 2009
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Abstract We evaluate the mechanisms that determine the establishment of the non-indigenous shrub *Pyracantha coccinea* (Rosaceae) in the Montpellier region of southern France. *P. coccinea* establishes in abandoned agricultural fields in this region; yet, despite its high propagule pressure, it has not become a widespread invasive. We hypothesized that the disturbance conditions prevailing in abandoned agricultural fields right after abandonment may enhance the emergence, survival and growth of *P. coccinea*, but that shortly after abandonment colonizing vegetation prevents further establishment of this species. We conducted a field experiment to evaluate this hypothesis, studying the response of seedling emergence and growth of *P. coccinea* to soil and vegetation disturbance. Our results show that both lack of vegetation cover and soil disturbance promote the emergence of seedlings of *P. coccinea*. Thus, the disturbance conditions prevailing in abandoned agricultural fields seem crucial to allow establishment of this species. However, other factors such as lack of summer dormancy and seed predation might explain why this species has not become a widespread invasive.

Keywords Disturbance · Germination · Herbicide · Mediterranean region · Plant competition · Plant invasions

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Introduction

Successful invasions require the arrival, establishment and persistence of exotic species in self-sustaining populations and the subsequent spread into the recipient community (Rejmánek 2000). Establishment and persistence depend in part on the characteristics of the invaded ecosystem, particularly the availability of sites for establishment and resources for seedling development (Hobbs 1989; Lozon and MacIsaac 1997; Shea and Chesson 2002; Hierro et al. 2006).

Competition from native vegetation can influence such availability, conferring resistance against invasions to the recipient community (Elton 1958; Hobbs 1989; Myers and Bazely 1999). Through soil tillage and removal of plant cover, human disturbance may thus increase resource availability for invaders (Di Castri 1989; Hobbs 1991; Alston and Richardson 2006).

Here we evaluate the mechanisms that determine the establishment of the non-indigenous shrub *Pyracantha coccinea* (Rosaceae) in the Montpellier region of southern France. *P. coccinea* produces fruits profusely and is widely used in gardens and hedges in this region (Debussche and Isenmann 1990; Malric 2004), which makes it a widely available resource for frugivorous birds. In fact, *P. coccinea* is the most frequent food item in the gizzard contents of the main bird dispersers in the Montpellier region (Debussche and Isenmann 1990, 1994), which suggests that opportunities for seed dispersal are great. *P. coccinea* establishes frequently in abandoned agricultural fields (hereafter "old fields") and forest edges in this region (Debussche and Isenmann 1990; Malric 2004), and is known to behave as invasive in other parts of the world (Grau and Aragón 2000; Chytry et al. 2009). However, in spite of its high propagule pressure and its occasional establishment in old fields, *P. coccinea* has not become a widespread invasive. We hypothesize that the disturbance conditions prevailing in old fields right after abandonment may enhance the emergence, survival and growth of *P. coccinea*, but that shortly after abandonment colonizing vegetation prevents further establishment of this species. A prediction of this hypothesis is that both removal of vegetation cover and soil disturbance (the conditions prevailing in recently abandoned agricultural fields) are necessary for the establishment of *P. coccinea* in old fields.

To evaluate the above prediction we conducted a field experiment in which we measured the effect of the presence of herbaceous vegetation cover and soil disturbance on the emergence, survival and growth of *P. coccinea* seedlings. In addition to this field experiment designed to evaluate our hypothesis, we conducted two greenhouse experiments to evaluate the need of seed coat scarification for germination and the residual effect of the herbicide used to remove vegetation in the main experiment.

Materials and methods

Study species

Pyracantha coccinea (Rosaceae) is a thorny perennial shrub native to SE Europe and Asia, widely used in gardening and landscaping around the world. Blooming occurs in the spring. The orange to dark red fleshy fruits ripen in the fall, when they are eaten by frugivorous birds (Debussche 1985). Seeds usually germinate in spring, after cold stratification (Olmez et al. 2007).

Study area

We worked in the northern Montpellier region of southern France (43° 39′N, 3° 51′E), where *P. coccinea* is found commonly in gardens and hedges. The climate is Mediterranean type, subhumid to humid with cool to cold winters. Annual precipitation varies between 950 and 1,350 mm, with mild winters; average temperature in the coldest month varies between −1.5 and 0.5°C, and in the warmest between 26 and 30°C (Debussche and Escarré 1983). The dominant rock bed is limestone (Debussche and Lepart 1992).

The region is dominated by a mosaic of old abandoned agricultural fields and farmlands; the main crops are cereals and grapevine. Old fields have a recent history of abandonment mostly as consequence of the rural exodus (Debussche and Lepart 1992), and are subject to high propagule pressure of ornamental exotic plants because of their proximity to suburban gardens (Alston and Richardson 2006). Thus, soil and vegetation disturbance resulting from recent agricultural activities and the high propagule pressure make old fields especially vulnerable to invasions by exotic plants (Goldberg and Gross 1988; Di Castri 1989).

Experiments

Seed collection

Seeds used in all experiments were collected from fruits from *P. coccinea* plants naturally established in the Montpellier region. Once extracted from fruits, seeds were placed in paper bags in a refrigerator until the start of the experiments.

Scarification study

Pyracantha coccinea is bird dispersed, and seeds may thus need seed coat scarification for germination resulting from the passage of seeds through the digestive tract of birds. We conducted a scarification study to evaluate the need of scarification for the other two studies (Soil and vegetation disturbance and residual effect of herbicide, described below), we conducted a scarification study to evaluate this possibility. To this end, 200 seeds were incubated for 21 days in a chamber with automatic control of temperature and photoperiod that simulated the average spring conditions in Montpellier: 20°C for 14 h (day), and 15°C for 10 h (night) (Debussche and Escarré 1983). One hundred seeds were scarified by a mechanical method to simulate natural scarification and stop dormancy. Iron filings were used as an abrasive scarification method. Another 100 seeds were incubated without scarification (control). Ten batches (five per treatment) of 20 seeds were grown on filter paper in a Petri dish and moistened daily with distilled water. The number of germinated seeds was recorded every 48 h. Germination was considered to have occurred once the size of the radicle had reached 2 mm. Germination rate G was calculated using Maguire's (1962) equation, $G = \sum n_t/t$, where n_t is the number of seeds at day t, counting from the start of the experiment.

Soil and vegetation disturbance study

This field experiment was conducted at the CNRS experimental fields in Montpellier. We worked in fields that had been abandoned for 10–15 years. This area has been naturally colonized by herbaceous vegetation (mainly grasses).

We used an incompletely crossed experimental design with two factors: vegetation cover (with and without elimination of herbaceous cover at the beginning of the experiment) and soil disturbance (with and without disturbance of soil surface). Fifteen plots were randomly assigned to each one of the following treatments: (1) untouched vegetation, no soil disturbance; (2) no vegetation, no soil disturbance; and (3) no vegetation, soil disturbance. The design was necessarily incompletely crossed because it was not feasible to disturb the soil without disturbing the vegetation.

Seeds of *P. coccinea* were planted in 90 experimental plots (50 cm × 50 cm), separated from other plots by 20 cm bands of bare ground. Thirty-five seeds were sowed at each plot. The number of seeds planted (i.e., propagule pressure) in the experiment was determined using data on the seed rain of *P. coccinea* from a previous study in the CNRS experimental field (Lavorel et al. 1993). Soil disturbance consisted in manually turning the soil with a hand shovel to a depth of ~20 cm to emulate the action of a plough in an agricultural field. Vegetation cover was removed from undisturbed plots with a non-residual herbicide (Gliphosate 10%), which we applied to the plots 90 days before the start of the experiments, a period we considered long enough for the herbicide to dissipate. To evaluate the residual effect of the herbicide, a complementary experiment was designed, described below (see "Residual effect of herbicide").

Seeds were scattered on the surface of each plot and gently depressed into the soil or litter to prevent them from blowing away, following a regularly-spaced sowing pattern to minimize spatial seed interference. To reduce the effect of water stress on seedling establishment, all the experimental plots were watered 3 times a week throughout the study period (March–June 2005). The following variables were recorded weekly to evaluate the establishment success of *P. coccinea*: number of seedlings emerged, number of seedlings alive, height, and number of green leaves per surviving seedling.

Residual effect of herbicide

A second experiment under greenhouse conditions was conducted to evaluate if the residual effect of the herbicide used to eliminate the herbaceous cover affected seedling establishment and survival. Sixty pots with unvegetated, sterilized soil were randomly assigned to one of two treatments: herbicide and no herbicide. Ten seeds were planted per pot. Seedling emergence and survival were recorded weekly. Once the first true leaf had emerged, height and number of green leaves were measured weekly. Plots were watered twice a week for 3 months (March–June of 2005).

Statistical methods

Percent germination and germination rate of *P. coccinea* seeds and the effects of herbicide on seedling emergence, survival and growth were evaluated with *t* tests, after applying the arcsin square-root transformation to the original data. The effect of disturbance treatments on seedling emergence, survival, height and number of green leaves were evaluated with χ^2 tests with the data of all plots pooled, using the chisq. test function in *R* statistical software (http://www.r-project.org/). Because the observed frequency distribution among treatments violated the assumptions of a χ^2 test, we calculated the associated *P*-value by Monte Carlo simulations with 10,000 randomization replicates, using the simulate .p.value option of function χ^2 test.

Results

Scarification study

Percent germination was not significantly affected by the physical scarification of seeds of *P. coccinea*. Both scarified and unscarified seeds reached 75% of germination percentage after 21 days of incubation. Even though germination rate was slightly higher for unscarified (2.5 seedlings day^{-1}) than for scarified seeds (1.9 seedlings day^{-1}), this difference was not statistically significant ($t = 0.849$; $df = 1$; $P > 0.05$). Thus, the other two studies were conducted with unscarified seeds.

Soil and vegetation disturbance study

Seedling emergence occurred throughout the study period, although total emergence was low in all the treatments, never exceeding 10% of planted seeds. There was an overall effect of treatment on seedling emergence of *P. coccinea* ($\chi^2 = 86.65$; $df = 2$; $P < 0.001$). This effect was mainly due to the lack of seedling emergence in the untouched vegetation, undisturbed soil treatment. Where vegetation was totally eliminated, seedling emergence was significantly greater in the disturbed than in the undisturbed soil treatment ($\chi^2 = 5.77$; $df = 1$; $P = 0.023$) (Table 1).

Seedling survival was not affected by soil disturbance alone: it did not differ significantly between the two unvegetated treatments (undisturbed and disturbed soil) ($\chi^2 = 3.27$; $df = 1$; $P < 0.1014$) (Table 1). Similar results were obtained for the average height and number of leaves recorded in the surviving seedlings ($F_{2,29} = 2.63$; $P = 0.1170$ for seedling height, and $F_{2,29}) = 1.89$; $P = 0.1821$ for number of seedling leaves) (Table 1).

Residual effect of herbicide

Both seedling emergence and survival were generally low and did not differ significantly between treatments ($t = 0.0734$; $df = 19$; $P = 0.941$; and $t = 0.224$; $df = 19$; $P = 0.823$, respectively). Similarly, seedling height and number of leaves in surviving seedlings did not differ significantly between treatments ($t = 1.08$; $df = 19$; $P = 0.322$ for seedling height and $t = 0.85$; $df = 1$; $P = 0.432$ for number of leaves; Table 2).

Discussion

Our field experiment shows that soil disturbance and removal of vegetation cover promote the establishment of *P. coccinea* in our study area. The herbicide trial showed that these results cannot be attributed to the residual effect of the herbicide on the germination ability of *P. coccinea*. These results support our hypothesis, namely that the disturbance conditions

Table 1 Emergence (%), survival (%), height (cm) and number of leaves of *P. coccinea* seedlings in soil and vegetation disturbance experiment

Response variable	Untouched vegetation, undisturbed soil	No vegetation, undisturbed soil	No vegetation, disturbed soil
Emergence (%)	0 ± 0 a	6.0 ± 3.4 b	9.0 ± 3.4 c
Survival (%)	–	13.0 ± 8.2 a	18.0 ± 9.2 a
Height (cm)	–	1.7 ± 0.11 a	1.8 ± 0.07 a
Number of leaves	–	4.0 ± 0.3 a	4.1 ± 0.4 a

For a given response variable, values followed by the same letter are not significantly different between treatments ($\alpha = 0.05$)

Table 2 Emergence (%), survival (%), height (cm) and number of leaves of *P. coccinea* seedlings in pre-treated soil with and without herbicide

Response variable	With herbicide	Without herbicide
Emergence (%)	2.1 ± 1.0	5.0 ± 2.0
Survival (%)	75.0 ± 10.0	80.0 ± 15.2
Height (cm)	2.3 ± 0.2	1.9 ± 0.3
Number of leaves	8.8 ± 0.9	7.0 ± 0.8

For all response variables there were no statistically significant differences between the two treatments ($\alpha = 0.05$)

prevailing in old fields right after abandonment may enhance the emergence, survival and growth of *P. coccinea*, and that once old fields have been recolonized by vegetation further establishment of *P. coccinea* may be prevented.

The finding that both soil disturbance and lack of vegetation cover promote the establishment of invasive plants should not come as a surprise. Competition from native vegetation is one of the most important mechanisms conferring biotic resistance against invasions (Tilman 1993; Burke and Grime 1996; Lonsdale 1999; Prieur-Richard and Lavorel 2000; Bartha et al. 2003; Von Holle et al. 2003). Human disturbance creates patches of open ground and increases the availability of resources through the removal of natural vegetation (Di Castri 1989; Hobbs 1991; Alpert et al. 2000; Alston and Richardson 2006). The elimination of herbaceous cover thus seems to enhance establishment of *P. coccinea* owing to reduced competition by natural vegetation, increasing the availability of resources and sites for seedling establishment.

Given the extraordinary abundance of propagules of *P. coccinea* and the widespread occurrence of human disturbance in the Montpellier region, it may seem surprising that invasion by *P. coccinea* is not more widespread. Lack of invasion by fleshy-fruited, bird-dispersed plants is in fact generalized in the Mediterranean region of France (Debussche and Isenmann 1990). What prevents invasion by fleshy-fruited plants in this region? One possibility is what our hypothesis proposes, i.e., that colinizing vegetation soon after abandonment prevent further establishment of *P. coccinea*. The fact that we observed no seedling emergence in the untouched vegetation, undisturbed treatment is consistent with this hypothesis. Below we consider other, alternative explanations of the lack of widespread invasion of *P. coccinea* in the Montpellier region.

Debussche and Isenmann (1990) proposed that invasion by animal-dispersed plants is prevented by competition by the 65 native fleshy fruited plants. Under this hypothesis, the over-abundance of food resources offered by native fleshy-fruited species would detract vertebrate dispersers from feeding on fruits of exotic species. Although Debussche and Isenmann's conjecture is intriguing, some facts about the ecology of plant–frugivore interactions in general, and in the Mediterranean Basin in particular, suggest this mechanism may not be a sufficient explanation of the lack of invasion in the Montpellier region. Vertebrate seed dispersers are usually not highly specialized in terms of their feeding preferences, eating fruits from a variety of species (Jordano et al. 2003). This surely is the case in the Mediterranean Basin, where a subset of generalist bird species disperses seeds of the majority of the plant species (Herrera 1984). In fact, vertebrate dispersers are known to feed frequently on fruits of exotic species (Debussche and Isenmann 1990, 1994). Therefore, both in the Mediterranean and in most other ecosystems, it seems unlikely that these generalized frugivorous birds will discriminate against fruits of introduced species (Richardson et al. 2000). Other explanations must be considered, including limits to seedling survival caused by abiotic factors such as aridity, winter frosts and soil characteristics, as well as biotic factors such as competition, herbivory, seed predation and root symbioses.

Another potential explanation of the lack of widespread invasion by *P. coccinea* is its lack of summer dormancy. In Mediterranean-type ecosystems, post-germination establishment is severely limited by long, dry summer periods, particularly for woody species (Herrera 1992). Dormancy prevents seeds from germinating in the hot, dry season (Schültz 1999) and is a common trait in seeds of many species from mediterranean environments, such as *Prunus avium* (Oukabli and Mahhou 2007), *Virburnum tinus* (Karlsson et al. 2005) and *Ulex parviflorus* (Baeza and Vallejo 2006). *P. coccinea* lacks a marked seed dormancy mechanism, which increases its vulnerability to droughts and may thus hamper its establishment in our study region.

A final possibility is post-dispersal seed predation, which may have a considerable impact on plant populations and has been suggested as a potential mechanism controlling invasion and spread of exotic plant species (Maron and Vilá 2001). For instance, Nuñez et al. (2008) found that native seed predators, mainly rodents and birds, reduced the likelihood of establishment of nonindigenous Pinaceae in southern Andean forests. Similarly, the establishment of *Taxus baccata* in Spain is also restricted by ants and rodents except in predator-free sites (García and Obeso 2003).

Our study focused on one species that establishes in our study region but that has not become a widespread invasive in spite of the high abundance of its propagules, the frequent dispersal of seeds by bird dispersers and the demonstrated facilitation of establishment by soil and vegetation disturbance. This kind of system can give valuable information about the factors that limit the spread of invaders. Species like *P. coccinea*, which fails to invade in spite of having traits that make then good potential invaders, can give important insights about the factors that limit the spread of invaders.

Acknowledgments We thank Annabelle Dossantos and Juan del Río for help with experimental work, and Daniel Simberloff, Martín Nuñez and anonymous referees for valuables comments on the manuscript. AEV was supported by SGCyT, Universidad Nacional del Sur, Argentina. DPV was supported during the initial part of this work through a visiting scientist fellowship at the Centre d'Écologie Fonctionnelle et Evolutive of the CNRS, France.

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