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Identification of windows of emergence and seedling establishment in a pine Mediterranean forest under controlled disturbances

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Abstract

The regeneration phase is a critical step in plant population dynamics, but is still incompletely understood owing to the intricacy and complexity of the factors concerned. We investigated the role played by pine emergence, survival and growth in the recruitment process of a Mediterranean pine forest under disturbances of various intensities. Disturbances were produced by site treatments including mechanical chopping, soil scarification, and controlled fire of low or high intensity. Pine seedling emergence, survival, dimensions and the relative cover of bare soil, grasses and shrub were monitored on 580 1 m² plots over 6 years in a mature Aleppo pine forest (*Pinus halepensis* Mill.).

Seedlings did not emerge continuously and regularly with time, but mostly in bursts, which were particularly marked in the rainy autumnal seasons. This specific pattern defined a 'window' of emergence characterised by the length of time during which seedlings emerged, the number of emerged seedlings and the shape of the window. Survival and growth decreased from the youngest cohort to the oldest cohort. Emergence, survival and growth did not respond in the same way to treatments and soil surface conditions. In particular, scarification treatments were most favourable to emergence, whereas the high-intensity controlled fire treatment was most beneficial to survival. Shrub cover was detrimental to emergence, but positively influenced survival and growth.

We conclude that environmental factors controlling survival, emergence and growth processes differ, and that their importance varies over time. A detailed understanding of the processes involved in seedling recruitment can be helpful for selecting the types and intensities of the controlled disturbances to be applied to successfully regenerate forest stands.

Keywords: recruitment; emergence; survival; growth; soil treatments; seedling; microsite; *Pinus halepensis*

Introduction

Seedling establishment is critical for the persistence of plant populations, and their distribution and composition (Grime 2001). It is also a challenging step in managed forest systems when renewing ageing populations of trees and adapting the ecosystem to changing environmental conditions. However, birth rate and transition from a seed to a recruit are complex phenomena influenced by a myriad of factors (Harper 1977; Grubb 1977).

At local scales, successful seedling establishment requires overcoming successive ecological filters (Clark, Macklin, & Wood 1998; Muller-Landau et al. 2002). A first filter is seed limitation: absence or dearth of seedlings results from limited seed supply. This may be due to insufficient seed availability and/or high post-dispersal predation. A second filter is emergence limitation, which depends closely on suitable microsites. A last filter is survival limitation: the number of seedlings can be limited through time due to mortality caused by a variable set of biotic and abiotic factors. Although the theoretical importance of these processes on recruitment is well-established for ecological dynamics (e.g. Harper 1977, Hurtt & Pacala 1995; Silvertown 2004; Paine et al. 2012), quantifying their relative importance and interactions remains a challenge.

Seed limitation has particularly marked impact on seedling population dynamics of systems where both fecundity and dispersal can limit establishment, such as old-field successions, tree colonisation or migration, or shrub encroachment (e.g. Clark 1998; Dovčiak, Frelich, & Reich 2005). However, it may be of minor importance in some systems such as in managed pine forests, where seed sources are often nearby and abundant, and so seeds are produced well in excess of what is needed for successful recruitment (Clark et al. 1999). In this context, successful plant establishment is mainly controlled by emergence and survival processes that operate at different time scales. Emergence is often a non-continuous process occurring in pulses during restricted time periods. For instance, studies on tree invasion or colonisation have emphasised the importance of 'waves' of recruitment due to a conjunction of events, seeds entering an environment that becomes temporarily favourable to seedling establishment (Davis, Grime, & Thompson 2000; Prévosto, Coquillard, & Hill 2003; Dovčiak, Frelich, & Reich 2005). In forest management the use of controlled disturbances to create time-limited favourable conditions for stand regeneration has been widely recognised (see reviews by Balandier et al. 2006; Wiensczyk et al. 2011). These opportunities in seedling recruitment of natural or anthropogenic origin have been formalised through the concept of the 'window' (Gross 1980; Rankin & Pickett 1989; Myster 1993), defined as a period during which the community is open to plant establishment. However, studies characterising these windows of recruitment, such as their

durations, frequencies and intensities are scant, because they require following the dynamics of seedlings lengthily and at close intervals. By contrast, seedling survival has been widely investigated, and studies have emphasised the role of certain key factors and processes as major bottlenecks, including competition by vegetation (e.g. Nambiar & Sands 1993; Scholes & Archer, 1997; Castro, Zamora, & Hódar 2002), predation and herbivory (e.g. Gill & Marks 1991; Gómez & Hódar 2008), or climate events such as droughts (e.g. Gómez-Aparicio 2009).

Our study set out to gain a fuller understanding of the concept of windows of emergence and identify major constraints to seedling establishment occurring during the recruitment phase according to different site conditions. We also sought to disentangle the roles played by emergence, survival and growth in the success or failure of the regeneration process. To achieve these aims, we monitored the seedling dynamics over 6 years in a Mediterranean *Pinus halepensis* forest under various soil and vegetation treatments producing a gradient of disturbance intensity. More specifically, we addressed the following questions:

- How is emergence influenced by controlled disturbances through time? Based on our results, we propose an illustration and a refinement of the concept of ‘window’ of emergence.
- What is the contribution of survival to the success or failure of the recruitment process, and how is survival influenced by treatments and soil cover conditions? We also examined the effect of these factors on seedling growth.

Materials and methods

Study site

The study was set up in Southern France (43°54′01″- 4°44′55″), 80 km south-west of Marseille, on mature Aleppo pine woodland (altitude 105 m). The climate was meso-Mediterranean, annual mean temperature 14°C, annual mean rainfall 689 mm, with autumn the most rainy season (September–November: 240 mm) followed by spring (March–May: 170 mm). During the period of our observations, rainfall was below the long-term mean in 2005–2007 (respectively 485, 517 and 383 mm), and above or close to the mean in 2008–2010 (respectively 946, 672 and 729 mm). Soils were of the rendzina type, composed of an organic upper layer (5–10 cm), an alteritic second layer of variable depth (10–40 cm), and calcareous bedrock. For the first layer, mean C/N ratio was 15.2 and mean pH 7.9. The general topography was a north-oriented gentle slope. The combined effects of slope and soil depth variation produced fluctuating soil fertility at the local scale of 1 m.

Before treatments, the stand consisted of a dominant 90-year-old *Pinus halepensis* tree layer with scattered *Quercus ilex* trees in the subcanopy layer, a well-developed shrub layer dominated by *Buxus sempervirens*, *Quercus coccifera* and *Viburnum tinus*, and a sparse ground layer dominated by

Brachypodium retusum. The stand was thinned during the winter of 2004, leaving a basal area of 12 m².ha⁻¹ and a density of 210 trees.ha⁻¹. Mean tree height was 12.8 m and mean girth was 89 cm.

Treatments and experimental design

A randomized block design was set up inside the thinned stand using five soil and vegetation treatments. The treatments, originally applied in winter and spring 2005 to enhance pine seedling establishment, consisted of (i) mechanical chopping of ground vegetation (noted 'chopping'), (ii) chopping followed by scarification in one direction loosening forest floor and top soil to depth ≈20 cm (noted 'scarification'), (iii) chopping followed by scarification in two perpendicular directions (noted 'scarification2'), (iv) controlled fire of low intensity (noted 'low fire'), (v) controlled fire of high intensity due to the presence of logging slash on the ground (noted 'high fire'), and (vi) control, *i.e.* no vegetation or soil treatment (see Prévosto & Ripert, 2008 for more details).

The treatments were replicated four times using forty 14 m × 14 m plots (eight plots/treatment except for low and high fire treatments four plots/treatment). Plots were distributed in four 34 m × 82 m blocks. Plots were separated from each other by a buffer zone of at least 2 m.

All trees of the site were located by their *x*, *y* coordinates, and their height and girth were measured. No seed rain measurements were made, but basal area did not vary with the treatments used in this study (mean basal area 12.2 ± 0.9 m².ha⁻¹, *F* = 1.02, *P* = 0.42). Considering that basal area is often used as a surrogate for seed rain (e.g. Greene & Johnson 1994; Dovčiak, Frelich, & Reich 2005) we assumed that seed rain was comparable among the treatments. In addition, light measurements performed during three consecutive clear days in June 2005 using a total of 40 solarimeter tubes (300–3000 nm, Delta-T Device) distributed among the different treatments and two tubes left in full light conditions did not reveal any significant differences among the treatments in light transmittance (mean: 0.70 ± 0.03, *F* = 1.41, *P* = 0.25).

Measurements

In each plot, 15 subplots of 1 m² were evenly spread along five transects of length 12 m except in plots with the control treatment, where only 10 subplots were established. In each of the 580 subplots of the experiment, pine seedlings were counted, their status (dead/living) noted and their height measured. They were also located using a 1 m² grid divided into 25 squares 20 cm × 20 cm and accurately mapped in order to monitor the individual fate of each seedling. Counting took place twice a year in June and January in 2006 and 2007, *i.e.* after each rainy period (autumn and spring),

and then in January from 2008 to 2011. Previous studies had shown that Aleppo pine emergence usually occurs during the rainy season, mostly in autumn under Mediterranean climates (e.g. Ne'eman, Goubitz, & Nathan 2004). Although the precise cause of mortality was not determined, seedlings that turned brown and dried out during the summer with no visible damage were assumed to have been killed by drought.

Soil surface description of subplots was carried out at the end of each growing season. Cover of bare soil, grass, shrub were visually estimated using an abundance dominance coefficient derived from the Braun-Blanquet method: 0, < 5%, [5–25%[, [25–50%[, [50–75%[, [75–100%]. For subsequent computations the centre of each class was used.

Data analysis

Pine density data exhibited over-dispersion and an excessive number of zeros. Previous analyses (not shown) demonstrated that density was adequately modelled by a negative binomial distribution. We therefore ran generalised linear models using a negative binomial relationship (procedure 'glm.nb' of the 'MASS' package, R software) to test the effects of treatment (categorical variable), time (continuous variable) on pine density and pine emergence and the interaction between treatments and time. We also developed models to test the influence of soil cover conditions used as quantitative variables.

To analyse survival data we computed, for each cohort (= seedlings emerged in the same period) and each treatment, the survival rates defined as the percentage of seedlings surviving from emergence to the period of observation. Only the first four cohorts were considered to correspond to the seedlings that emerged in the autumn of years 2005 and 2006, and spring of years 2006 and 2007. To describe the relationship between survival time (time elapsed between the emergence and death of the seedling) and the explanatory variables, we developed linear-mixed effects models (procedure lmer, packages lme4 and lmerTest of R) by separating fixed effects (treatments and cohorts) from random effects (subplots nested in plots and blocks). To analyse changes in seedling height we used generalised linear models followed by Tukey *post hoc* tests to detect significant differences ($P < 0.05$) after checking for ANOVA assumptions. When conditions of ANOVA were not met, we used the non-parametric Kruskal-Wallis test followed by non-parametric multiple comparisons according to the method proposed by Siegel and Castellan (1988) to detect significant differences ($P < 0.05$) among the factors tested (procedure 'kruskalmc' of the 'pgirmess' package, R software).

Results

Density of emerged and living seedlings

Results of the generalised linear models indicated that time and treatments strongly and positively influenced the density of emerged and living seedlings (Table 1). By contrast, interactions between time and treatment were not significant or less so, except for the high fire treatment, which positively enhanced seedling density through time, whereas the chopping treatment showed the opposite trend on emerged seedlings. However, changes in densities with time and treatments differed between these two variables (Fig. 1). Emergence peaked at 8, 20 and 44 months, corresponding to the end of the first, second and fourth autumn after the end of the treatments (Fig. 1A), while there were only two less pronounced peaks for the density of living seedlings at 25 and 44 months (Fig. 1B). Moreover, emergence decreased with time, very low densities of newly emerging seedlings being observed on the last counting date (0.12 seedling.m⁻² all treatments together), while densities of living seedlings tended to stabilise at higher levels (1.26 seedling.m⁻²). Densities increased with disturbance intensity for both emerged and living seedlings, the lowest density being recorded for the control treatment. Maximal emergence was always recorded in the scarification treatments, followed by the high fire treatment (Fig. 1C). By contrast, densities of living seedlings after 30 months were lower in the former than in the latter, and at the end of the period of observation ($t = 68$ months), the high fire treatment had more seedlings (2.35 seedling.m⁻²) than the double scarification (1.26 seedling.m⁻²) or single scarification (1.54 seedling.m⁻²) treatments.

Table 1. Analysis of variance summaries for generalised linear models testing the variation in density of emerged seedlings or of living seedlings explained by time, treatments and interactions.

Variable name	Density of emerged seedlings		Density of living seedlings	
	Estimate	<i>P</i>	Estimate	<i>P</i>
Time	-0.018	<0.001	0.023	<0.001
Chopping	1.156	<0.001	1.137	<0.001
Scarification	1.681	<0.001	1.749	<0.001
Low fire	1.196	<0.001	1.233	<0.001
High fire	1.289	<0.001	1.522	<0.001
Scarification2	1.761	<0.001	1.611	<0.001
Time × Chopping	-0.002	0.740	-0.007	0.007
Time × Scarification	0.011	0.010	-0.005	0.034
Time × Low fire	-0.001	0.880	-0.006	0.043
Time × High fire	0.025	<0.001	-0.005	0.112
Time × Scarification2	0.010	0.032	-0.002	0.504

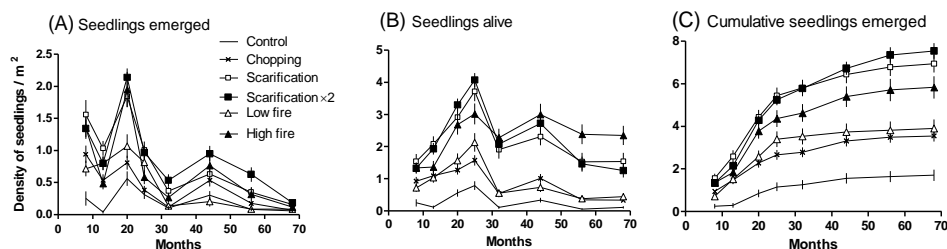


Fig. 1. Changes in seedling densities (mean \pm SE) over time for six different treatments: (A) Emerged seedlings, (B) Living seedlings and, (C) Cumulative number of emerged seedlings. Time 0 refers to the end of the treatment applications in May 2005.

On examining the influence of soil surface conditions on seedling densities (Table 2), we found a clear negative effect of grass cover through time on densities of both emerged and living seedlings. Shrub cover also showed a negative effect on emergence, but its effect on seedling density was less marked. Bare soil cover positively influenced the densities of emerged and living seedlings, although this effect was not significant for emergence.

Table 2. Analysis of variance summaries for generalised linear models testing the variation in density of emerged seedlings or of living seedlings explained by time and percent cover of grass, shrub and bare soil.

Variable name	Density of living seedlings		Density of emerged seedlings	
	Estimate	<i>P</i>	Estimate	<i>P</i>
Time	0.003	0.03	0.025	0.032
Grass cover	-0.018	<0.001	-0.005	<0.001
Shrub cover	-0.004	0.022	-0.009	<0.001
Bare soil cover	0.011	<0.001	0.003	0.103

Survival

We modelled seedling survival time as a function of treatment, type of cohort, and both factors (Table 3). The combined model was preferred on the basis of the Akaike information criterion. It showed that survival was significantly increased by the treatments, especially the scarification and

high fire treatments. Successive cohorts of seedlings (*i.e.* cohort 1 to cohort 4) exhibited an increasing risk of mortality indicated by the negative values of the estimates; this effect was especially marked for the last cohort.

Table 3. Results of linear mixed-effects models (survival time) including the null model (random effects only), the model with treatments (mod1) and the model with treatments and cohorts (mod2). Results of this last model are shown (Cohort 1: January 2006, Cohort 2: June 2006, Cohort 3: January 2007 and Cohort 4: June 2007).

	Df	AIC	P
modnull	4	18345	
mod1 (treatments)	9	18302	<0.001
mod2 (treatments, cohorts)	12	18179	<0.001

mod 2 (Variable name)	Estimate	t	P
Chopping	4.87	1.96	0.05
Scarification	8.48	3.58	<0.001
Low Fire	4.19	1.54	0.012
High Fire	15.40	5.86	<0.001
Scarification2	9.84	4.17	<0.001
Cohort 2	-6.92	-6.68	<0.001
Cohort 3	-5.82	-6.75	<0.001
Cohort 4	-11.73	-11.18	<0.001

Variations in the rate of survival for the different treatments and cohorts (Fig. 2) showed that the high-intensity controlled fire was the treatment most favourable to survival. This effect was especially marked in the last three cohorts. By contrast, the favourable influence on survival of the intense scarification treatment noted in the first cohort was clearly reduced in the following cohorts. The least beneficial effects were observed in the control treatment, and to a certain extent in the chopping and low fire treatments.

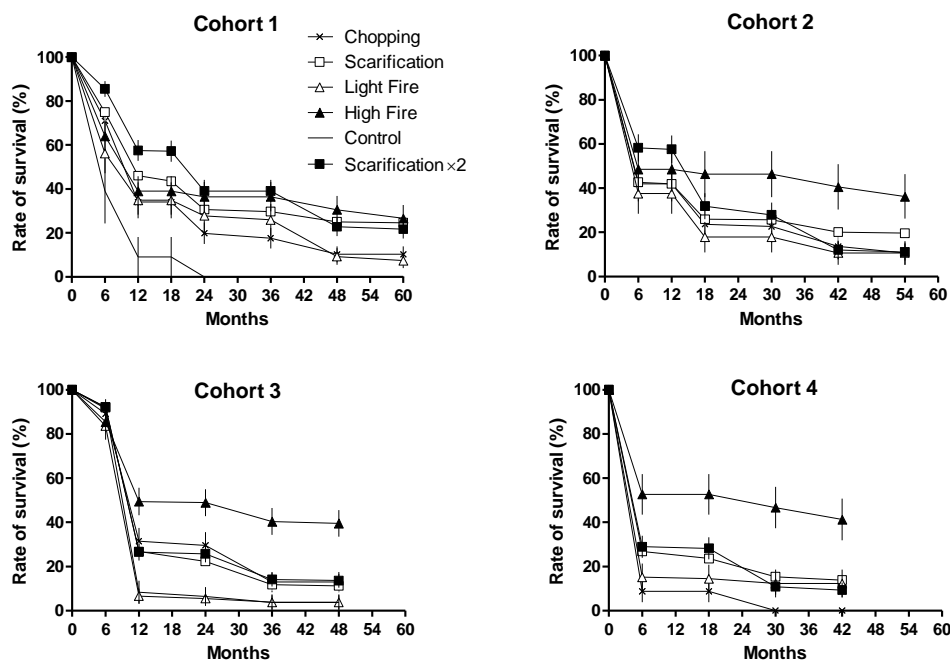


Fig. 2. Changes in survival rates (mean \pm SE) over time for the successive cohorts of seedlings under six different treatments (Cohort 1: January 2006, Cohort 2: June 2006, Cohort 3: January 2007 and Cohort 4: June 2007).

These results can in part be explained by the variations in the soil surface cover conditions for the different treatments (see Appendix A: Fig. 6). Cover of bare soil, which dramatically decreased with time, from 24% after treatment application to less than 1% 68 months later, was in fact produced in higher abundance in the high fire and then in the scarification treatments compared to the other treatments. By contrast, grass cover increased steadily with time (from 4% to 43%) in all treatments, but remained lowest in the high fire treatment. Shrub cover also regularly increased (from 11% to 35%) in all treatments (with the exception of the control), but at the end of the experiment shrub cover was more abundant in the high fire treatment than in the other treatments (45% vs. 32%, control excepted).

Soil surface conditions had a significant influence on survival time (Fig. 3). Bare soil and shrub cover had a positive effect on survival, whereas grass cover had a detrimental effect.

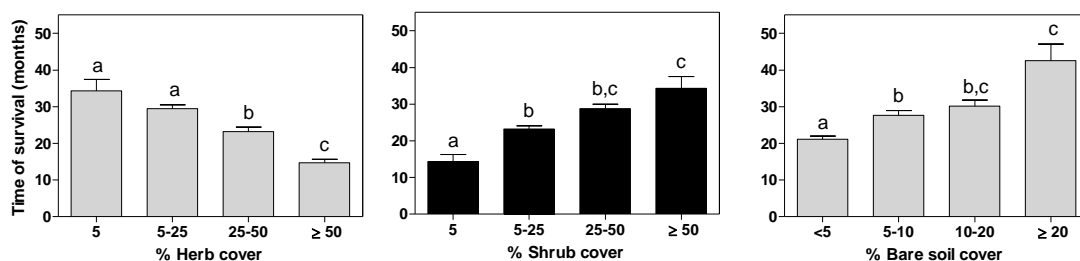


Fig. 3. Time of survival (mean \pm SE, all cohorts combined) as a function of the mean percent cover of grass, shrub and bare soil computed over the study period. Letters indicate significant differences at $P < 0.05$ (multiple comparisons test after Kruskal-Wallis test).

Growth

Analysis of the final height of the seedlings showed a highly significant effect of the treatments, cohorts, shrub cover, a moderate effect of herb cover and no significant effect of bare soil cover (see Appendix A: Table 4).

As expected, height decreased for the successive cohorts (defined here by year) at a given date. For instance, for the last year seedling mean height was 59.7 ± 2.1 cm for cohort 1 but only 10.2 ± 1.1 cm for cohort 4. More interestingly, the comparison of height across cohorts at the same age showed that seedling height significantly increased with the cohort number, especially between the first and the following cohorts (Fig. 4A). This shows that seedlings of the first cohort developed in better conditions and then grew better than seedlings of the following cohorts. Height was also positively influenced by the scarification treatments (Fig. 4B) and by shrub cover (Fig. 4C).

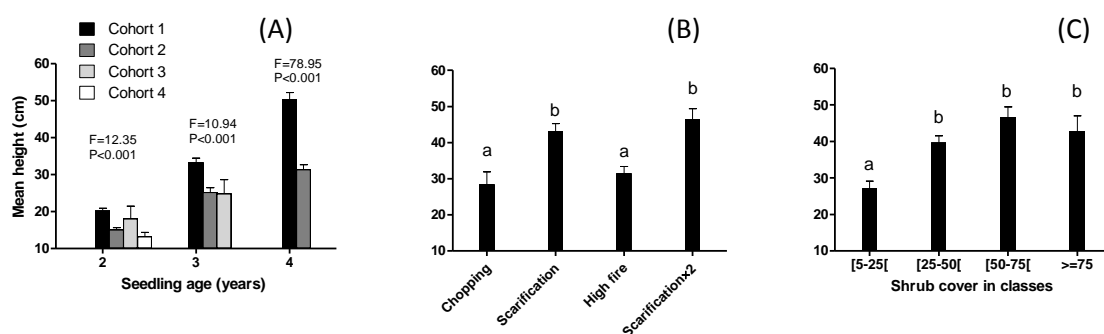


Fig. 4. Seedling height (mean \pm SE) changes: (A) with age according to the different cohorts (all treatments combined), (B) with treatments in the last year of the study period, all cohorts combined

(only treatments with more than 30 seedlings are presented), (C) with shrub cover in the last year of the study period, all cohorts combined. Cohorts 1 to 4 correspond to years 2006 to 2009.

Discussion

Although the importance of processes driving recruitment is well-established (Harper 1977), their intricacy and interdependence make their quantification a challenge (Grubb 1977).

The extensive sampling effort in both space and time required to disentangle the processes at work in recruitment has been recognised as a clear limitation. For instance, Clark et al. (1999) reported in a survey of the literature on recruitment limitations in forests that studies on early recruitment are usually short, most spanning a single year and only a few covering more than five years. We therefore set out to study recruitment over a relatively long period (six years) with a high sampling effort (580 subplots). In this study, not all processes were analysed; in particular, seed dispersal and availability were not measured, and were assumed not to vary among the different treatments or over time. The assumption of no variation of seed distribution in space is supported by the regular distribution of adult trees and similar basal areas among the treatments (Greene et al. 1999; Greene & Johnson 1994). The assumption of no variability in seed production over time is less sure, although we were not aware of any mast years in Aleppo pine during the study period. Taking these constraints into account, we next examine the role played by emergence, survival and growth in the recruitment process.

Emergence: refining the concept of 'window'

We found that seedling emergence was not continuous and regular over time, but resulted mostly from temporal pulses (see Fig. 1). Many studies have shown that temporal pulses in seedling community are mainly driven by temporal fluctuations in seedling recruitment (De Steven 1994; Delissio et al. 2002; Norden et al. 2007), but studies disentangling emergence and survival are scant. We also showed that emergence was strongly influenced by treatment intensity, emphasising the key role of disturbance in regenerating forest systems composed of pioneer species like Aleppo pine (Ne'eman, Goubitz, & Nathan 2004; Osem et al. 2013).

In Fig. 5 we propose a schematic diagram illustrating the forming of a window of emergence producing a pulse of seedlings. Disturbances modify values of environmental factors (abundance of suitable microsites, light availability, soil moisture content, seed arrival, etc.) allowing seedling emergence. These variations produce for each factor a window of potential emergence, *i.e.* a time interval during which conditions are favourable or highly favourable for seedlings to emerge. The combination of these windows results in an overall window of effective emergence that can be

characterised by attributes such as duration, intensity (*i.e.* maximum emergence) and shape (*e.g.* one or several peaks). As multiple factors can be involved in the emergence process, and as variations of these factors with time can be cyclic rather than linear, the window's attributes can also vary greatly. For instance, pulses of seed availability or temporary periods of favourable climatic conditions can produce fragmented rather than continuous windows of emergence. Considerable variation in seedling establishment over time has, for instance, been reported as the consequence of community-wide masting events in seed production (Kelly 1994; Koenig et al. 1994).

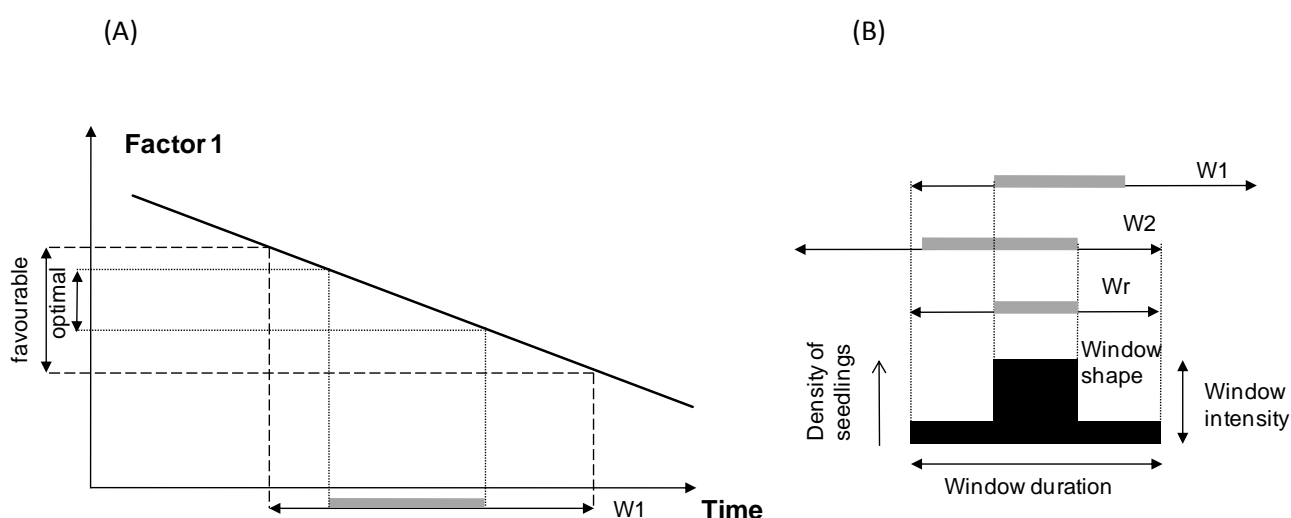


Fig. 5. Formation of a window of emergence controlled by two factors. (A) For a given factor, emergence is possible during a specific time interval (denoted "favourable") and peaks within this interval (denoted "optimal"). A window of time is thus produced (denoted W1 for factor 1) including a time interval of potential maximum emergence (indicated by the thick grey line). (B) For two factors, two windows (W1, W2) are produced, the combination of which results in an effective window of emergence (Wr), which defines the emergence response. This window can be characterised by its duration (duration of emergence), its intensity (maximal emergence) and its shape.

However, in our study, recruitment occurred in a relative short period (six years) and peaked at the end of the first and second year following site treatments. Such a pattern has been quite frequently observed in monospecific stands composed of pioneer species. Studying age structure of *Pinus ponderosa* stands in the southwestern US, Savage, Brown and Feddema (1996) found that the vast majority of trees originated in one or a few years, and attributed this remarkable temporal coherence in germination to the conjunction of favourable climatic conditions and human

disturbances (precipitous cessation of grazing in particular). Similarly, Rankin and Pickett (1989) showed that 90% of *Acer rubrum* trees had established in an old field within the first seven years after land abandonment, and Myster (1993) emphasized the role of temporal variations in “windows” of recruitment to explain the colonisation of old fields by deciduous trees in New Jersey, USA. Such temporal windows were also identified by Dovčiak, Frelich and Reich (2005) in colonisation of abandoned fields by *Pinus strobus* in the prairie-forest ecotone of the north-central United States. The fluctuations of emerged seedling number with time were remarkably consistent through the different treatments. In our study, the two main peaks detected corresponded to the two first autumns following the end of the treatments. This result was perfectly in line with previous results on seedling emergence in post-fire or fire-free conditions for the same species (Daskalidou & Thanos 2004; Nathan & Ne’eman 2004; Osem et al. 2013), reporting maximal emergence in autumn due to high seed availability (seeds are released in summer) at the start of the rainy season. The absence of emergence in autumn 2007 was explained by a particularly dry year (–44% of the mean rainfall). Variations in emergence among the treatments can be explained by large changes in the amount of suitable microsites after treatment application. The most intense treatments (scarification, high-intensity fire) were also the most efficient for creating sites free of ground vegetation favourable to seedling emergence. By contrast, less intense treatments (chopping, low-intensity fire) with lower impacts on soil and ground vegetation were also less efficient in promoting emergence. Ground vegetation, in particular herbaceous vegetation, has in fact been reported to be detrimental to the emergence of coniferous species mainly because it forms a physical barrier against germination (Prach, Lepš, & Michàlek 1996; Castro, Zamora, & Hódar 2002). Because of the recovery of the herb and shrub vegetation, conditions become less favourable, leading to the ‘closure’ of the window of emergence.

Influence of survival and growth in the recruitment process

When examining densities of emerged seedlings and live seedlings through time, clear differences appeared (Fig. 1). In particular, the end of the period of observation was characterised by a very low emergence (0.12 seedling.m⁻² at $t = 68$ months) compared with the much higher density of living seedlings (1.26 seedling.m⁻²). Density of living seedlings as observed at a given date resulted from the combination of two different processes: emergence and survival.

We found differences in survival of the cohorts in the treatments. Survival decreased with the successive cohorts, an effect that was particularly visible between the first and the last cohort. A first reason was that seedlings in the first cohort benefited from more favourable soil surface conditions. Grass cover in particular (mainly *Brachypodium retusum*) was much less developed when the first

cohort was established (4% vs. 27% for the last cohort) and competition for water by grasses is known to affect woody seedling survival negatively (Neary et al. 1999; Pausas et al. 2003). In addition, mortality is also a size-dependent process (e.g. Escudero 1999; de la Cruz et al. 2008), and the larger seedlings in the first cohort were likely to be better able to withstand summer drought than the smaller seedlings in the last cohort. Larger seedlings benefited from a more developed root system, leading to a more efficient uptake of water. By contrast, the smaller seedlings of the last cohort established in a less favourable environment (*i.e.* with more developed ground vegetation) exhibited a lower probability of survival and reduced growth.

Treatments also had differential effects on survival, emergence and growth processes. In particular, survival was higher in the high-intensity fire treatment than in the scarification treatments, whereas the reverse was true for emergence and growth. From these results, we can conclude that environmental factors controlling survival, emergence and growth processes differ, and that their importance is likely to fluctuate with time. A clear illustration of this was given by the contrasting role played by shrubs, which exerted a negative influence on emergence but a positive one on survival and growth. On the one hand, shrubs produce litter, which often constitutes a barrier to emergence by preventing the radicle of the seedling from reaching the bare soil (Sayer 2006). On the other hand, shrubs can provide shelter and alleviate the harsh climatic conditions prevailing in open conditions, thus favouring seedling survival (Gómez-Aparicio 2009; Castro et al. 2004) and to a certain extent height growth.

Conclusion

Disturbances, by modifying availability of suitable microsites, can open windows of emergence that are time-limited and depend on the type of disturbance. Disturbances that are the most efficient in producing bare soil and in removing ground vegetation cover, such as intense scarification or high-intensity controlled-fire treatments, are also the most efficient in enhancing emergence, and more generally the whole process of recruitment. We found seedling survival and growth to be time-dependent processes, the youngest cohort of seedlings surviving and growing better than the following cohorts. They were not necessarily influenced by the same factors as emergence. This was shown by the contrasting role of shrub cover, limiting emergence on the one hand but enhancing survival and growth on the other. A better understanding of the processes involved in recruitment is therefore a key step for determining what silvicultural treatments (*e.g.* application of controlled disturbances) are best adapted to successfully regenerating forest stands.

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Appendix A

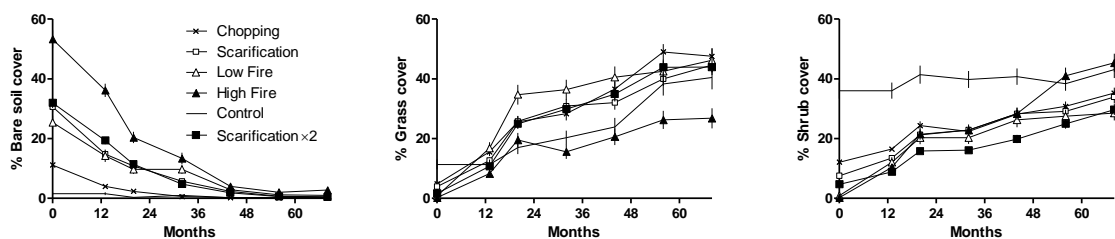


Figure 6. Changes in bare soil, grass and shrub cover (mean \pm SE) over time for the different treatments

Table 4. Analysis of variance summaries for the generalised linear model testing the variation in height of the last year explained by treatments, cohorts and soil cover conditions.

	Df	Deviance	P-value
Treatments	5	21146	<0.001
Cohorts	4	143426	<0.001
Bare soil cover	1	632	0.28
Grass cover	1	1321	0.09
Shrub cover	1	5269	<0.001