



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

Bernard Prévosto^{a,*}, Jordane Gavinet^{a,b}, Christian Ripert^a,
Catherine Fernandez^b

^a*Irstea, Ecosystèmes méditerranéens et risques, 3275 route Cézanne, CS 40061, 13612 Aix-en-Provence Cedex 5, France*

^b*Institut Méditerranéen de Biodiversité et d'Ecologie marine et continentale (IMBE UMR CNRS 7263), Aix-Marseille Université – Campus Saint-Charles, 3 place Victor-Hugo, 13331 Marseille Cedex 03, France*

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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.

Zusammenfassung

Die Regenerationsphase ist ein entscheidender Schritt in der Populationsdynamik von Pflanzen, aber sie wird aufgrund der Komplexität der beteiligten Faktoren noch nicht vollständig verstanden. Wir untersuchten die Bedeutung von Keimung, Überleben und Wachstum für den Rekrutierungsprozess in einem mediterranen Aleppokiefernwald (*Pinus halepensis* Mill.) bei Störungen unterschiedlicher Intensität. Die Störungen bestanden aus: Abschneiden der Bodenvegetation, Aufreißen des Bodens und kontrolliertem Brennen mit geringer bzw. hoher Intensität. Das Auflaufen der Kiefernkeimlinge, ihr Überleben

*Corresponding author. Tel.: +33 4 42 66 99 25; fax: +33 4 42 66 99 10.
E-mail address: bernard.prevosto@irstea.fr (B. Prévosto).

und Wachstum sowie der Deckungsgrad von nacktem Boden, Gras und Sträuchern wurden über sechs Jahre auf 580 1-m²-plots in einem reifen Kiefernwald beobachtet. Die Keimlinge erschienen nicht kontinuierlich, sondern meist in Schüben, die im regnerischen Herbst besonders ausgeprägt waren. Dieses artspezifische Muster definiert ein ‘‘Fenster’’ der Keimung, welches durch die Länge der Zeit, während derer Keimlinge erscheinen, die Anzahl der auftretenden Keimlinge und die Form des Fensters charakterisiert ist. Überleben und Wachstum nahmen von der jüngsten bis zur ältesten Kohorte ab. Keimung, Überleben und Wachstum reagierten unterschiedlich auf die Behandlungen. Insbesondere begünstigten Behandlungen mit Aufreißen des Bodens die Keimung, während kontrolliertes Feuer hoher Intensität für das Überleben besonders förderlich war. Bedeckung mit Sträuchern war ungünstig für die Keimung, beeinflusste aber Überleben und Wachstum positiv. Wir schließen, dass unterschiedliche Umweltfaktoren Keimung, Überleben und Wachstum kontrollieren und dass ihre Bedeutung im Lauf der Zeit variiert. Ein eingehendes Verständnis der Prozesse, die bei der Keimlingsrekrutierung eine Rolle spielen, kann bei der Auswahl von Art und Intensität kontrollierter Störungen für ein erfolgreiches Waldmanagement hilfreich sein.

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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, Wright, Calderón, Hubbell, & Foster 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; Hurr & 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 et al. 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, Collet, Miller, Reynolds, & Zedaker 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

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