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Shedding light through the smoke on the germination of Mediterranean Basin flora

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ABSTRACT

Natural and anthropogenic fires have historically been part of the Mediterranean Basin (MB). As a result of this long exposure to fires, MB flora has developed various strategies to persist under recurrent fires. One of these strategies is to survive and regenerate by resprouting and another is through post-fire seedling recruitment. For species that recruit seedlings after a fire there is evidence that fire-related germination cues are implicated in the process of triggering seedling emergence from soil-stored seeds. In some species, particularly in Cistaceae and Fabaceae, germination is stimulated by heat. Fire-related chemical germination cues, such as smoke, charcoal, and nitrogenous compounds (collectively termed 'smoke'), have also been recognised as promoting seed germination in MB flora. However, the role of smoke in the germination of MB plant species has received less attention and recognition than the role of heat-shock and is generally seen as having a relatively limited role as a post-fire germination cue in MB flora.

Our hypothesis is that this is due to the fact that research on smoke-stimulated germination in the MB region has been limited and poorly addressed, and this is biasing our view on the role of smoke in MB flora.

Using available literature, we first analyse the role of smoke in the germination of MB flora and discuss some of the issues that limit our understanding of its role on the flora of the region. We point to gaps in the literature and provide suggestions for further research.

We conclude that differences in evidence of smoke-stimulated germination in MB flora when compared with other Mediterranean regions may not reflect real ecological or evolutionary differences among these regions but are likely the consequence of the limited number of well-designed studies in the MB.

Contents

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1. Introduction

Most plant communities in the Mediterranean Basin (MB) are highly fire-prone and subject to recurrent fires (Pausas, 2004). Although currently most fires have an anthropogenic origin, fires remain a natural phenomenon in the region (Keeley et al., 2012). In fact, there is increasing evidence that fire has played an important role in shaping fire-related plant traits (He et al., 2012; Pausas et al., 2012) and in driving plant community assembly (Verdú and Pausas, 2007; Pausas and Verdú, 2008). As in other fire-prone ecosystems, many MB plant species have developed several traits to cope with recurrent fires, such as those related to resprouting and post-fire seedling recruitment (Pausas et al., 2004).

Resprouting is a widespread mechanism enabling individual plants to persist after fire; it is widespread in MB flora and many of the resprouting species of this region do not show post-fire seedling emergence or fire-stimulated germination (Paula and Pausas, 2008; Paula et al., 2009). The other mechanism is the accumulation of persistence seed banks in the canopy (serotiny; *Pinus halepensis, P. brutia, P. pinaster;* Hernández-Serrano et al., 2013) or soil. Seedling recruitment from soil-stored seedbanks is enhanced by fire because it acts as a germination cue, triggering emergence when resources are highly available. The most important fire-related germination cues are heat, and the chemical products resulting from biomass combustion during fire such as: smoke; charred wood; or nitrogenous compounds (for simplicity, all of these fire-derived chemicals are here termed 'smoke', e.g., smoke-stimulated germination).

In the MB, fire-stimulated germination and post-fire seedling emergence is common and has been extensively studied, especially in woody species with physical seed dormancy, such as in Fabaceae and Cistaceae (Paula et al., 2009). Seeds of these species have specialised structures in the seed coat (e.g., the strophiole in Fabaceae and the chalazal plug in Cistaceae) that move, or become disrupted, as a response to external factors, and so enable water to pass through the impermeable seed coat layer(s) (Baskin et al., 2000; Baskin and Baskin, 2014). In the MB, the regulation of dormancy release in these species with physical seed dormancy is typically linked to heat-shock resulting from fire (Herranz et al., 1998, 1999; Moreira and Pausas, 2012) and is similar to that which occurs in other fire-prone regions with Mediterranean-type climate (MTC), such as South Africa, California and southern Australia (Bell et al., 1993; Keeley, 1995; Keeley and Bond, 1997). However, post-fire seedling recruitment in MB flora is not limited to species with physical dormancy and is also widespread in species with water-permeable seed coats – such as Lamiaceae, Ericaceae, Asteraceae, and Poaceae (Paula et al., 2009). The role of fire in germination and post-fire seedling recruitment of these species is less clear; however, there is now evidence that both fire-related heat-shock and smoke are important germination cues (Moreira et al., 2010).

Despite recent efforts, the role of smoke in the germination of MB plant species has received less attention than the role of heat-shock (Paula and Pausas, 2008; Paula et al., 2009). It was assumed, based on a small sample size, that smoke-induced germination is less frequent in the MB than in other MTC regions; and that a substantial amount of post-fire recruitment is probably the result of opportunistic colonising species that use other (not strictly fire-related) cues to signal general disturbances, such as light and temperature. This would suggest that fire-stimulated germination results from seed characteristics that are not specialised for fire (Keeley and Baer-Keeley, 1999). Indeed, smoke is generally seen as having a relatively limited role as a post-fire germination cue in MB flora (Buhk and Hensen, 2006; Ne'eman et al., 2012). Our hypothesis is that this view is due to the fact that research on smoke-stimulated germination in the MB region has been limited and not properly addressed, and this is biasing our view on the role of smoke in MB flora. Here we summarise the role of smoke in the germination of the MB flora while highlighting some of the issues that limit our understanding in this topic. We also offer suggestions for further research. For this review, we included sites outside the region with typical mediterranean climate (sensu Olson and Dinerstein, 1998; Fig. 1) because of the local similarity in the flora (particularly, the studied species are also present in the mediterranean climate region) and in the local environment, and because fires are also frequent.

2. Methodological issues

Up to now, 24 studies have been published that perform germination (laboratory) experiments with fire-derived products on MB species; five used liquid smoke (Moreira et al., 2010; Tavşanoğlu, 2011; Çatav et al., 2012; Moreira et al., 2012; Çatav et al., 2014); six used aerosol smoke (Crosti et al., 2006; Reyes and Casal, 2006a;

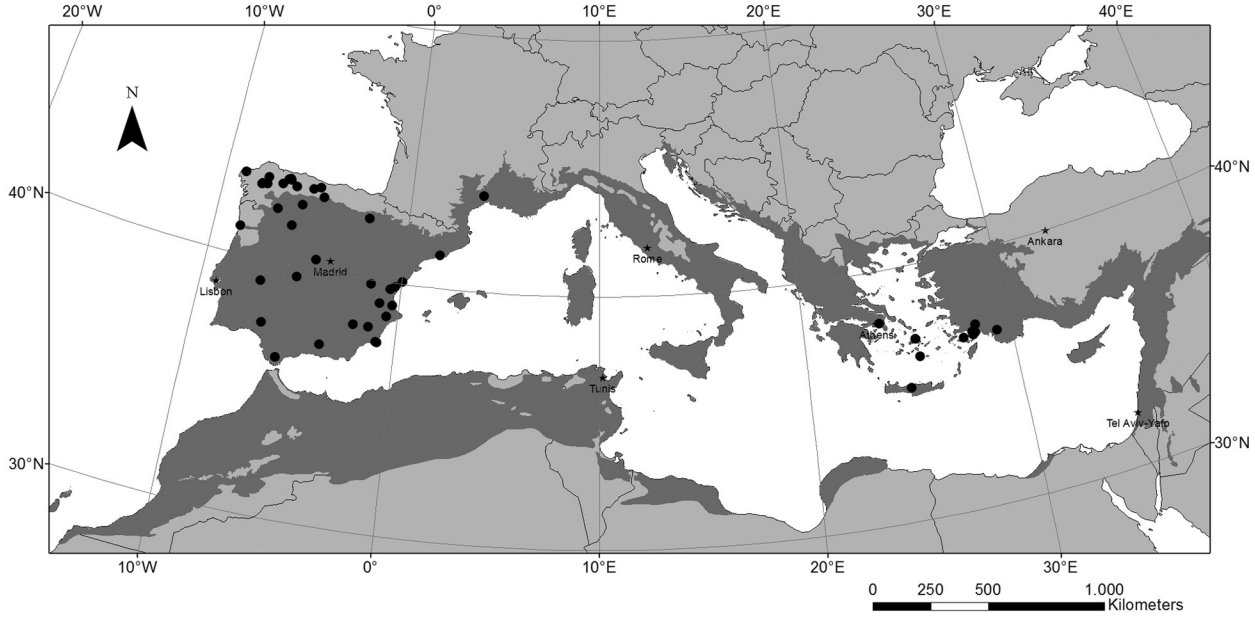

Fig. 1. Distribution of the sites where smoke-stimulated germination has been studied (black dots) in the Mediterranean Basin. Dark grey area represents the region with mediterranean-type climate (Olson and Dinerstein, 1998). Few sites outside of this region were also considered because of the local similarity in the flora (particularly, the studied species are present in the mediterranean climate region) and environment, and because fires are also frequent.

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