Available online at www.sciencedirect.com
ScienceDirect
Forest Ecology and Management 255 (2008) 1510–1515
Forest Ecology and Management
www.elsevier.com/locate/foreco

Does plant-derived smoke affect seed germination in dominant woody species of the Mediterranean matorral of central Chile?

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Received 13 January 2006; received in revised form 8 November 2007; accepted 9 November 2007

Abstract

Studies performed in the fire-prone Mediterranean-type climate shrublands of Australia, California, and South Africa have shown that plant-derived smoke enhances seed germination in many species. Unlike other areas with similar climate, central Chile stands out for the absence of natural fires, suggesting that smoke may not be expected to promote germination. However, anthropogenic fires have been frequent since several millennia, and the role of fire on shaping fire functional traits is not clear at this point. The aim of this study was to evaluate the effects of plant-derived smoke on seed germination of some predominant native woody species from the Mediterranean matorral of central Chile. We exposed seeds of 18 woody species to plant-derived smoke for 30 min and assessed their germination. Five species failed to germinate under either the experimental and control conditions. Smoke significantly stimulated germination in three species, while decreasing it in eight. Species showing smoke-inhibited germination tend to be major dominants in the Chilean matorral vegetation. The three smoke-stimulated species are known colonizers. This suggests that current human-caused fires could drastically change the structure of Chilean matorral. Although our results suggest fire have not played a major role in shaping adaptations for seed germination of woody species in the Chilean matorral, more investigation about ephemeral species is needed. This study provides the first results about smoke-related germination in the Mediterranean-type zone of central Chile, generating the opportunity to investigate the evolutionary context and distribution of smoke-stimulated germination in all the Mediterranean-type ecosystems.
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Keywords: Central Chile; Fire; Mediterranean; Seed germination; Smoke

1. Introduction

Recurrent fires are characteristic of Mediterranean-type climate shrublands in Australia, California, Mediterranean Basin, and South Africa (Keeley, 1995). Plant species in these fire-prone ecosystems show a wide variety of reproductive adaptations to fire, such as fire-stimulated flowering of many geophyte species (Le Maitre and Brown, 1992; Rundel, 1996; Lamont et al., 2000), or the presence of serotinous cones and fruits that release and disperse seeds only after fires (Bond and van Wilgen, 1996). Seed germination also shows particular adaptations to one or more of the physical cues provided by fire in these habitats. For instance, seeds of many species are stimulated to germinate by charred wood, nitrogenous substances, ash, or heat-shock (e.g., Keeley, 1987, 1991; Bond and van Wilgen, 1996; Keeley and Fotheringham, 1997; Herranz et al., 1998; Buhk and Hensen, 2006).

Smoke is another of the products generated as a consequence of wildfires, and since the 1990s substantial evidence has accrued for its effects on seed germination. Smoke-stimulated seed germination has been reported for many species in the South African fynbos (de Lange and Boucher, 1990; Brown, 1993; Brown et al., 1993, 1994, 2003; Pierce et al., 1995; Keeley and Bond, 1997). A positive germination response to smoke has also been extensively demonstrated for many species in Australia (Dixon et al., 1995; Roche et al., 1997; Read and Bellairs, 1999; Morris, 2000; Read et al., 2000; Lloyd et al., 2000; Tieu et al., 2001; Williams et al., 2003; Thomas et al., 2003) and Californian chaparral as well (e.g., Keeley and Fotheringham, 1997, 1998a,b). In the Mediterranean Basin,

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doi:10.1016/j.foreco.2007.11.006

however, although a positive response to smoke has been found for some species (Crosti et al., 2006), substantial evidence indicates that smoke-stimulated germination is poorly developed in this area (Buhk and Hensen, 2006; Reyes and Casal, 2006a,b; Rivas et al., 2006). The variation among Mediterranean-type ecosystems on the distribution of fire functional traits has been attributed to differential evolutionary processes (Pausas et al., 2006).

Smoke-stimulated species span different families and genera of gymnosperms, monocotyledons and dicotyledons; also embracing a range of plant forms from geophytes to phanerophytes (van Staden et al., 2000). This range of species from different continents and regions suggest that stimulation of germination by smoke or smoke-derived compounds may be common not only in Mediterranean fire-prone ecosystems. Indeed, plant-derived smoke also enhances germination of species from non-fire-prone habitats (Pierce et al., 1995). Among the chemical compounds of smoke, nitrogen oxides (Keeley and Fotheringham, 1997) and butenolide (van Staden et al., 2006; Flematti et al., 2007) have been proposed as the responsible for seed germination stimulation.

In the Mediterranean-type zone of central Chile, thousands of human-caused fires occur each year over the summer season, and the sclerophyllous vegetation (called the matorral) is the most damaged plant association (CONAF, 2003). Unlike other Mediterranean zones of the world, lightning-ignited fires are very rare in central Chile under current environmental conditions (Mooney, 1977; Armesto et al., 1995). The sedimentary records of charcoal and fossil pollen suggest that this has been true for millennia (Aravena et al., 2003). Due to the rarity of natural fires, it has been hypothesized that fire has not play an important role on plant species evolution in the Chilean matorral (Armesto and Gutierrez, 1978; Avila et al., 1981; Muñoz and Fuentes, 1989). However, anthropogenic fires have occurred since the first indigenous settlements (ca. 14,000 BP), with higher occurrences during pre-cultural periods (*agroalfarero* period, 2300 BP), and increasing exponentially their frequency since Spaniard colonization (1536–1542) to the present (Aravena et al., 2003). As a consequence, the importance of fire on shaping adaptive traits in native plant species of the Mediterranean-type zone of central Chile is not clear at this point.

There is not a great deal of literature on post-fire germination in the Mediterranean-type zone of central Chile, and the scarce researches conducted so far has been focused only on dominant woody species (Muñoz and Fuentes, 1989; Segura et al., 1998). For instance, the study of Muñoz and Fuentes (1989) experimentally assessed the effect of heat and fire-treated soils (ash-soils) on seed germination of several dominant species of the matorral. They found that ash-soil treatment failed to promote seed germination among the studied species, and only two out of seven species tested (*Muehlembeckia hastulata* and *Trevoa trinervia*), significantly increased their germination by heat (100 °C, 5 min). Segura et al. (1998) demonstrated a lack of viable seeds under shrubs burned by high-intensity fires. However, low-severity fires generally allowed native woody species to emerge, and species such as *M. hastulata* and *T. trinervia* increased their seed germination after low-intensity fires (Segura et al., 1998). This suggests that, after low severity fires, where the soil temperature is not lethal for seeds (<50 °C, Gómez-González et al., unpublished data), other fire-related cues, such as smoke, could trigger post-fire seed germination in the matorral. However, the effect of smoke on seed germination has not been evaluated in this ecosystem.

Our aim here was to experimentally explore the effects of plant-derived smoke on seed germination among predominant native woody species from the Mediterranean matorral of central Chile. This study provides the first information about germination responses to smoke in this Mediterranean-type zone of the world, generating an opportunity for investigating the evolutionary context and distribution of smoke-stimulated germination in all the Mediterranean-type ecosystems.

2. Materials and methods

2.1. Seed preparation

Bulk collections of mature seeds of 18 woody species (mostly trees and shrubs) (Table 1) were made in populations located in the Cordillera de Los Andes immediately east of the city of Santiago, and in the Coastal Range immediately to the west of Santiago. All seeds were collected over the period summer to autumn of 1998 and stored in paper bags at ambient temperature in the laboratory for 3 months. The plant species selected for this study included the main dominants of the typical lowland sclerophyllous matorral (e.g., *Lithrea caustica*, *Cryptocarya alba*, *Quillaja saponaria*) and montane sclerophyllous woodland (e.g., *Kageneckia angustifolia*, *K. oblonga*). Many of these species, in addition to being physiognomic dominants, are widely distributed in central Chile, and thus can be considered typical of the Mediterranean sclerophyllous vegetation of the region (Arroyo et al., 1995). Moreover, 50% of the species tested are endemic to Chile (Table 1).

Two sets (control and smoke treatment) of four replicates (50 seeds each) were prepared for each species, discarding any aborted and insect-damaged seeds. Seeds were placed on filter paper in petri dishes without any previous stratification or scarification because we were interested in detecting the effect of smoke *per se* on germination.

2.2. Smoke treatment

The smoke treatment was applied to dry seeds in open petri dishes in a sealed 1.7 m × 1.7 m × 0.3 m polyethylene chamber connected to a smoke source generated in a 50 l metal drum through combustion of plant material. The metal drum was connected to the sealed chamber by a 5-cm diameter, 1.6-m length metal tube, fitted with a serpentine water cooling system designed to cool the smoke such as to maintain the smoke-treated and control seeds at a similar temperature. The combusted material comprised a 50:50 mixture of dry litter and green foliage of *L. caustica* and *Q. saponaria*. These species

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