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Effect of fire-derived chemicals on germination and seedling growth in Mediterranean plant species

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Abstract

The promoting effect of smoke-derived chemicals (e.g. karrikinolide and cyanohydrin) on germination in many plants from Mediterranean-type ecosystems such as South Africa and south-western Australia is well documented. However, very little is known about (1) the relative importance of different compounds and their possible interactive effects, (2) their role in enhancing seedling growth in wild plants, and (3) their effect on the germination of plants in the Mediterranean Basin. To fill these gaps in knowledge, we performed experiments to evaluate the effect of smoke water, karrikinolide, mandelonitrile (a cyanohydrin analogue), potassium nitrate and gibberellic acid on the germination and seedling growth of 37 species from the Mediterranean Basin. The results suggest that germination and/or seedling growth of 21 species are enhanced by at least one of the fire-derived chemicals. There were positive correlations between most of the compounds tested in terms of germination response, but synergetic and inhibitory effects were also detected. Stimulation of germination was most prominent in species with annual life cycles. Fire-derived chemicals were more effective in stimulating root growth than shoot growth. In conclusion, we provide novel evidence that the recruitment of different Mediterranean species may be enhanced by different smoke compounds, and that synergetic and inhibitory effects of chemical compounds are important in the germination ecology of plants.

Keywords: Fire; Germination; Smoke; Karrikinolide; Cyanohydrin; Annuals

Introduction

Fire is a common disturbance that affects a large proportion of ecosystems (Bond & Keeley 2005; Chuvieco, Giglio, & Justice 2008) and a significant driver of global plant diversity (Pausas & Ribeiro 2017). Even though most current fires have an anthropogenic origin, wildfires have affected plant community dynamics since the Paleozoic time (Glasspool, Edwards, & Axe 2004; Pausas & Keeley 2009). Therefore, wildfires have been recognized as a natural phenomenon in terrestrial ecosystems (Keeley, Bond, Bradstock, Pausas, & Rundel 2012), and many plant species have evolved adaptive traits to persist in fire-prone environments. Resprouting from basal lignotubers, serotiny, enhanced flammability, post-fire flowering

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and fire-stimulated seed germination are prominent examples of these adaptive traits (Keeley, Pausas, Rundel, Bond, & Bradstock 2011; Lamont & Downes 2011; Pausas, Alessio, Moreira, & Corcobado 2012). Specifically, fire-stimulated germination results from dormancy-breaking effects of heat or from combustion-related products (e.g. smoke and nitrogenous compounds). Heat can break the physical dormancy of many hard-seeded plants by affecting the permeability of seed coats and disrupting specific structures such as the chalazal plug and lens (Thanos, Georghiou, Kadis, & Pantazi 1992; Herranz, Ferrandis, & Martínez-Sánchez 1998; Baskin & Baskin 2014). On the other hand, even though the capacity to respond to smoke is notably dependent on various factors such as the type and level of seed dormancy, and the timing of germination (Merritt, Turner, Clarke, & Dixon 2007; Nelson, Flematti, Ghisalberti, Dixon, & Smith 2012), smoke-stimulated germination has been demonstrated in numerous species from a wide range of phylogenetic and ecological origins (Dixon, Roche, & Pate 1995; Pierce, Esler, & Cowling 1995; Keeley & Bond 1997; Adkins & Peters 2001; Moreira, Tormo, Estrelles, & Pausas 2010; Downes, Light, Pošta, & Van Staden 2015; Keeley & Pausas 2018).

Of the many compounds produced during biomass combustion, the first isolated germination cue was a butenolide (3-methyl-2*H*-furo[2,3-*c*]pyran-2-one) named karrikinolide (KAR_1) (Flematti, Ghisalberti, Dixon, & Trengove 2004; Van Staden et al. 2004; Dixon, Merritt, Flematti, & Ghisalberti 2009). Stimulation of germination in many smoke-responsive species by KAR_1 initially suggested that this compound is the main germination stimulant in smoke (Flematti et al. 2007; Chiwocha et al. 2009; Light, Daws, & Van Staden 2009). However, there is increasing evidence that smoke-stimulated germination is far more complex (Keeley & Pausas 2018). The existence of smoke-responsive species that do not respond to KAR_1 (Downes, Lamont, Light, & Van Staden 2010; Flematti et al. 2011) led to the discovery of a new germination cue, the cyanohydrin glyceronitrile (2,3-dihydroxypropanenitrile) (Flematti et al. 2011). Furthermore, the stimulatory effects of cyanohydrin analogues, such as glycolonitrile, acetone cyanohydrin, 2,3,4-trihydroxybutyronitrile and mandelonitrile (hereafter ‘MAN’), on germination have also been determined in several studies (Flematti et al. 2011; Baldos, DeFrank, & Sakamoto 2015; Tavşanoğlu et al. 2017).

In addition to their positive effect on germination, smoke and KAR_1 are known to stimulate seedling growth in various plants (Sparg, Kulkarni, Light, & Van Staden 2005; Van Staden, Sparg, Kulkarni, & Light 2006; Daws, Davies, Pritchard, Brown, & Van Staden 2007). This is an ecologically-important factor because growing fast in post-fire environments provides a competitive advantage and thus has strong implication for fitness (Brown & Van Staden 1997; Hanley & Fenner 1998). However, most studies on this topic have focused on the smoke-induced seedling growth in agriculture (Jain & Van Staden 2006; Kulkarni, Sparg, Light, & Van Staden 2006; Van Staden et al. 2006; Singh, Kulkarni, & Van Staden 2014), whereas little is known about smoke’s impact on wild plants (Moreira et al. 2010).

In comparison with other Mediterranean-type ecosystems (e.g. South Africa and Australia), there is limited knowledge regarding the effect of smoke and smoke compounds on plants in the Mediterranean Basin (reviewed by Moreira & Pausas 2018). For instance, whereas smoke-stimulated germination is mainly observed in annual plants (Keeley & Bond 1997; Keeley & Fotheringham 1998), most species tested in the Mediterranean Basin are perennials and many are woody. Such studies in the Mediterranean Basin include many species with physically dormant seeds (e.g. Cistaceae, Fabaceae), in which the germination cue is more likely to be heat than smoke. Furthermore, there is lack of information about the effects of specific smoke-derived compounds (KAR_1 and cyanohydrin) on the germination of Mediterranean plant species except *Chaenorhinum rubrifolium* (Tavşanoğlu et al., 2017). These shortcomings limit our ability to understand the evolutionary aspects of fire in the Mediterranean Basin and correctly frame this region among other Mediterranean-type ecosystems worldwide (Moreira & Pausas 2018).

Our hypothesis is that smoke, acting through a diversity of compounds, enhances plant fitness (increasing germination or seedling growth) in a range of plants from fire-prone Mediterranean Basin region. Specifically, we aim to test that whether (1) the germination of many Mediterranean plants is sensitive to smoke-derived compounds with a stimulation effect similar to species from other Mediterranean-type ecosystems; (2) this effect is especially common in annual plants; (3) different smoke compounds have different effects on germination, including synergetic effects; (4) germination responses to a smoke compound do not necessarily imply smoke-stimulated germination; and (5) smoke-derived compounds are effective in enhancing the seedling growth of some Mediterranean plants. To achieve these goals, we carried out two experiments to examine the effects of smoke water, specific smoke chemicals and nitrate on the germination and seedling growth of 37 plant species native to the Mediterranean Basin. In addition to these compounds, we also applied gibberellic acid (GA_3), a phytohormone that is considered to have a similar effect to KAR_1 (Merritt et al. 2006; Cembrowska-Lech & Kępczyński 2016).

Materials and methods

Study area, study species and seed collection

Fruits of 37 plant species were collected from their natural habitats in fire-prone areas of Muğla Province, southwestern Turkey, eastern Mediterranean Basin (36.8°–37.2° N, 22.4°–28.2° E). The study area has the typical Mediter-