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Exploiting jasmonate-induced responses for field protection of conifer seedlings against a major forest pest, *Hylobius abietis*

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ABSTRACT

Herbivore damage commonly initiates an increased synthesis of chemical defensive compounds in attacked plants. Such induced defences are a vital part of plant defence systems, but when herbivore pressure is high, as frequently occurs in man-made ecosystems such as agricultural and forest plantations, plants may suffer considerable damage before adequate induced defences build up. To prepare the plants for such conditions their induced defence may be artificially triggered by the exogenous application of different phytohormones involved in damage signalling. This method is already employed in agriculture but within forestry systems it has so far been restricted to promising laboratory results. The pine weevil, *Hylobius abietis*, causes damage by feeding on the bark of young conifer plants and it is one of the main threats to successful regeneration in the Palaearctic region. Here we present results from a large scale field experiment where we triggered the induced defences of conifer seedlings using exogenous application of the chemical elicitor methyl jasmonate. To enhance the generality of the results different species were planted under extremely different environmental conditions; Maritime pine and Monterrey pine in Spain, and Scots pine and Norway spruce in Sweden. Weevil damage, chemical defences, and seedling growth were studied during the two growing periods following planting. In general, treated plants showed increased quantitative defences, and were less attacked, less wounded, less girdled and showed lower mortality rates than their untreated counterparts. Effects were mostly dose dependent, although some interactive effects with tree species were observed. The treatment initially caused a growth reduction but it was later compensated by the benefit, in terms of growth, of being less damaged. The measures that are currently taken to protect forest plantations against this harmful pest all around Europe have enormous economic costs and cause important environmental hazards. Elicitation of inducible defences in seedlings in the nursery appears to be an attractive alternative to these measures. To our knowledge, this is the first field study that explores the applicability of chemical elicitors of induced defences as a way to protect forest plantations against biotic threats.

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1. Introduction

In common with most plants, conifers defend against herbivores with a combination of physical and chemical mechanisms. Some defences are permanently expressed, irrespective of whether the plants are actually suffering damage (constitutive defences), while others are enhanced after the recognition of damage (induced defences) (Franceschi et al., 2005; Eyles et al., 2010). Induced defences are assumed to have evolved as a cost saving strategy in which the costs of producing resistance mechanisms are only incurred when defences are actually needed, i.e., after the damage or the risk of damage has been recognized (Sampedro et al., 2011a). Constitutive defences inhibit initial attacks but are sometimes insufficient to deter the attack or to avoid the proliferation of the damage. In such cases, induced defences, including increased synthesis of chemical defensive compounds already existing in healthy plants, synthesis of new chemical defences, and the formation of new physical structures can be vital for the plant to survive the attack (e.g., Zas et al., 2011; Zhao et al., 2011b; Schiebe et al., 2012).

In recent decades considerable progress has been made towards an increased understanding of the physiological mechanisms and metabolic pathways involved in the recognition, signaling and triggering of plant induced defences against biotic stressors (Heil, 2009; Erb et al., 2012). Different plant phytohormones such as jasmonates, ethylene and salicylic acid are now known to be involved in the activation of induced defensive responses in a wide array of different plant species (e.g., Creelman and Mullet, 1995; Halitschke and Baldwin, 2005). In particular, jasmonate signaling is thought to be involved in triggering

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defences against herbivores and necrotrophic pathogens in several plant taxa (Glazebrook, 2005). Accordingly, the methyl ester of jasmonic acid, i.e., methyl jasmonate (MJ) has been widely used as a chemical elicitor to simulate herbivory (Koo and Howe, 2009), with the exogenous application of MJ provoking responses similar to those occasioned by insect feeding (Franceschi et al., 2002; Rohwer and Erwin, 2008). In conifers, the exogenous application of MJ sprayed to aboveground tissues is known to have a large impact on the synthesis of both terpenoids and phenolics (Zulak et al., 2009), two of the main chemical defences of conifers against insect herbivores (Franceschi et al., 2005). Increased total amounts and/or alterations of the profile of these compounds have been reported following MJ application both in young seedlings (e.g., Martín et al., 2002; Heijari et al., 2005; Moreira et al., 2009; Erbilgin and Colgan, 2012) and adult trees (e.g., Erbilgin et al., 2006; Heijari et al., 2008; Erbilgin and Colgan, 2012), and for different conifer species (Hudgins et al., 2004) from boreal conifers such as *Pinus sylvestris* (Heijari et al., 2005, 2008) and *Picea abies* (Erbilgin et al., 2006; Zhao et al., 2011b; Schiebe et al., 2012) to Mediterranean pines such as *Pinus pinaster* (Moreira et al., 2009; Sampedro et al., 2011a) and *Pinus radiata* (Gould et al., 2008, 2009; Moreira et al., 2012b). Anatomical long-lasting responses such as the proliferation of traumatic resin canals are also well documented (Huber et al., 2005; Krokene et al., 2008).

In keeping with the enhanced defence status, MJ treated conifer seedlings have been reported to show increased resistance to a wide array of fungal pathogens and herbivore insects. Spraying *P. radiata* seedlings with a low concentration of MJ (<5 mM) has been shown, for example, to reduce *Diplodia pinea* infection by 60% (Gould et al., 2009), while spraying or fumigation of *P. abies* with MJ reduced the colonization of *Ceratocystis polonica* (Krokene et al., 2008) and protected seedlings against *Pythium ultimum* (Kozlowski et al., 1999). MJ application has been also shown to be effective against insect herbivores by reducing colonization, oviposition and/or damage levels of different insect feeding guilds, including phloem and bark feeders such as pine weevils (Heijari et al., 2005; Moreira et al., 2009), bark beetles such as *Ips typographus* (Erbilgin et al., 2006), and defoliators such as *Thaumetopoea pityocampa* (Moreira et al., 2013) and diprionid sawflies (Heijari et al., 2008). In some cases, MJ altered the attraction of the insect herbivores to the breeding or feeding sites due to changes in the emission of volatile organic compounds (e.g., Zhao et al., 2011a), while in others, the enhanced physical and chemical defences within plant tissues seem to be responsible for the reduced damage levels (e.g., Heijari et al., 2005; Moreira et al., 2009). Despite all these examples of positive results of MJ application protecting conifers against biotic stressors, negative results where MJ failed to protect seedlings or mature trees against particular enemies do also exist (Graves et al., 2008; Reglinski et al., 2009; Zhao et al., 2010; Vivas et al., 2012).

The responses of plants to jasmonates are not limited, however, to defence-related processes, but also include alterations of many other physiological traits related to growth and development (Cheong and Yang, 2003). Plants treated with MJ usually show reduced primary and secondary growth rates, either because of reduced photosynthetic activity (as observed by Heijari et al. (2005) after treatment with high doses (100 mM) of MJ) or just as a result of the physiological costs associated with boosting chemical defences (Sampedro et al., 2011a). This reduction in growth associated with MJ application has been outlined as a critical handicap for the practical applicability of this substance for protecting forest plantations against biotic aggressors (Holopainen et al., 2009). However, not all the growth-related responses to MJ are negative. MJ treated seedlings of *P. pinaster* have been found, for example, to have many more fine roots than control seedlings, and this enhancement of the root system may both help seedling establishment and increase the tolerance to herbivore damage (Moreira et al., 2012c). Additionally, as the effect of MJ on primary growth is usually greater than that on secondary growth (Heijari et al., 2005; Moreira et al., 2013), MJ treatment favors reduced height:diameter relationships, which is something that forest nurseries aim for since it increases seedling growth and survivorship after plantation (Willoughby et al., 2009).

Although our knowledge of the complex responses of conifers to MJ is still limited, there is increasing evidence that MJ application has potential for protecting forest plantations and nursery seedlings against pests and pathogens (Holopainen et al., 2009; Eyles et al., 2010; Moreira et al., 2012a). A particular harmful forest pest that potentially could be controlled by exogenous MJ application is the pine weevil, *Hylobius abietis* (L.), which significantly impacts the regeneration of conifer forests after clear cutting in large areas of Europe and Asia (Långström and Day, 2004). Adult pine weevils feed on the phloem and bark of conifer seedlings of many different species, causing stem girdling and high mortality rates (Örlander and Nilsson, 1999; Day et al., 2004). If no protection measures are carried out, weevil damage can cause up to 80% mortality (Petersson and Örlander, 2003). To date no definitive treatment is available, and a combination of different prophylactic measures, including soil scarification, retention of shelter trees, physical protection of the seedlings, delayed planting, and even insecticide treatments, is currently routinely applied (Petersson and Örlander, 2003; Nordlander et al., 2009, 2011). Most of these methods are expensive to apply and/or are environmentally hazardous; moreover they are frequently insufficient to reduce the level of damage and mortality to (economically) acceptable levels.

MJ application has been shown to reduce the damage caused by the pine weevil on pine seedlings of different species both *in vitro* (Moreira et al., 2009, 2013) and *in vivo* bioassays (Heijari et al., 2005; Sampedro et al., 2011b) under controlled conditions in the lab. Whether MJ can also be used to protect seedlings against the pine weevil under real field conditions is, however, yet to be tested. It is well known that a treatment that is highly efficient under controlled conditions in the lab is not always efficient under field conditions, where many interfering factors can potentially modulate its effects (Beckers and Conrath, 2007). Importantly, pine weevils are frequently a serious threat to seedlings not only immediately after planting but also during the second and following years. It is therefore important that the effect of any protecting treatment is long lasting. There are no previous studies where the effects of MJ application have been evaluated after two seasons, although for mature trees it has been shown that the effect of a MJ treatment can last for several years (Erbilgin et al., 2006; Zhao et al., 2010).

Here, we explore whether increasing defensive traits through MJ application at the nursery stage can be an efficient way to protect seedlings against this harmful forest pest in the field. We performed a field experiment with the two most commonly planted conifers in both northern (Sweden) and southern Europe (Spain). We investigated the effect of concentration and number of applications of MJ on chemical defensive traits, seedling growth and weevil damage during two growing seasons after planting. We aimed to gain insight into the viability of MJ application in the nursery to protect forest plantations against the pine weevil at field. The wide contrasts in ecological conditions between Spain and Sweden, with extreme differences not only in temperature and light conditions but also in forest functioning and insect behavior, should result in a high level of generality of the results of this study.

2. Materials and Methods

2.1. Plant material

Four conifer species were used in this study: Maritime pine (*Pinus pinaster* Ait.) and Monterrey pine (*P. radiata* D. Don) as

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