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Inducibility of chemical defences by two chewing insect herbivores in pine trees is specific to targeted plant tissue, particular herbivore and defensive trait

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ABSTRACT

There is increasing evidence that plants can react to biotic aggressions with highly specific responses. However, few studies have attempted to jointly investigate whether the induction of plant defences is specific to a targeted plant tissue, plant species, herbivore identity, and defensive trait. Here we studied those factors contributing to the specificity of induced defensive responses in two economically important pine species against two chewing insect pest herbivores. Juvenile trees of *Pinus pinaster* and *P. radiata* were exposed to herbivory by two major pest threats, the large pine weevil *Hylobius abietis* (a bark-feeder) and the pine processionary caterpillar *Thaumetopoea pityocampa* (a folivore). We quantified in two tissues (stem and needles) the constitutive (control plants) and herbivore-induced concentrations of total polyphenolics, volatile and non-volatile resin, as well as the profile of mono- and sesquiterpenes. Stem chewing by the pine weevil increased concentrations of non-volatile resin, volatile monoterpenes, and (marginally) polyphenolics in stem tissues. Weevil feeding also increased the concentration of non-volatile resin and decreased polyphenolics in the needle tissues. Folivory by the caterpillar had no major effects on needle defensive chemistry, but a strong increase in the concentration of polyphenolics in the stem. Interestingly, we found similar patterns for all these above-reported effects in both pine species. These results offer convincing evidence that induced defences are highly specific and may vary depending on the targeted plant tissue, the insect herbivore causing the damage and the considered defensive compound.

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1. Introduction

Because constitutive and induced plant defences are costly to produce and maintain, their concentration and distribution can vary considerably across plant tissues and within-plant parts differing in value, cost or risk of attack (Zangerl and Rutledge, 1996; Ohnmeiss and Baldwin, 2000). In particular, within-plant distribution of induced responses to herbivores may vary depending on the fitness value and the frequency of herbivore attack on each organ and/or tissue (Zangerl and Rutledge, 1996; Gutbrodt et al., 2011; Moreira et al., 2012). According to the Optimal Defence Theory, plants invest in high constitutive levels of defence and low inducibility for tissues that have high fitness value and are most fre-

quently attacked, and vice-versa (Zangerl and Rutledge, 1996; Ohnmeiss and Baldwin, 2000). On the other hand, there is also increasing evidence that plants responses to herbivores can be highly specific and rely on the recognition of the specific herbivore species causing damage (e.g. Mithöfer and Boland, 2008; Bingham and Agrawal, 2010; Halitschke et al., 2011; Karban, 2011; Bonaventure, 2012; Gutbrodt et al., 2012). Accordingly, these plant responses could differ among plant tissues or be restricted to particular tissues or plant parts in order to minimize costs of defence induction.

Over the past decade, it has become increasingly accepted that plant induced resistance to herbivores depends on plant and herbivore species-specific characteristics (e.g. Underwood, 1999; Agrawal, 2000; Mumm et al., 2004; Köpke et al., 2010; Halitschke et al., 2011; Carrillo-Gavilán et al., 2012). The biotic stimuli needed to elicit specific induced responses may include a direct recognition of the physical stimuli and specific molecular patterns of the

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enemies (denoted as herbivore-associated molecular patterns, Mithöfer and Boland, 2008). Moreover, this biotic stimuli may also include indirect clues such as the recognition of specific combinations of biogenic volatile compounds (reviewed by Kessler and Baldwin, 2002), and the independent and interactive effects of those exogenous triggering factors with damage-self recognition clues (damage-associated molecular patterns) from their own plant tissues after being damaged by the herbivores (Heil, 2009; Erb et al., 2012; Heil et al., 2012). The suite of triggering factors

elicited directly or indirectly by herbivore feeding could be shared to some extent within taxonomical insect groups or within herbivore feeding guilds. Plant responses to herbivory have been repeatedly shown, however, to vary depending on the insect diet breadth and insect feeding guild. It is well known, for example, that generalist and specialist herbivores can elicit different plant defensive responses (reviewed by Ali and Agrawal, 2012). On the other hand, herbivores from different feeding guilds vary in their salivary constituents, timing, intensity and pattern of damage, and may thus

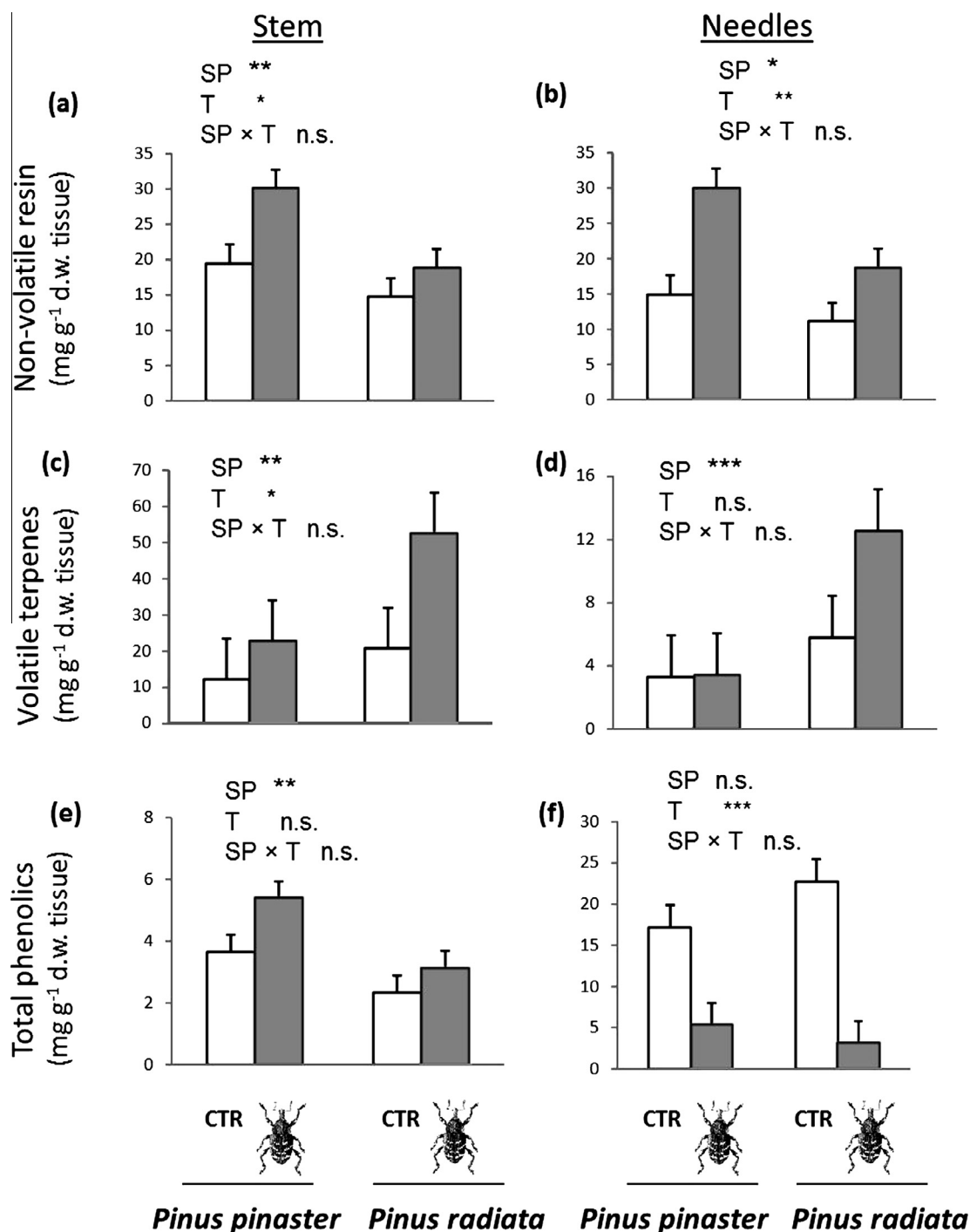


Fig. 1. Effects of the herbivory-induction by the large pine weevil *Hylobius abietis* (grey bars for the herbivore-treatment and white bars for the control) on the concentration of (a) non-volatile resin, (c) volatile terpenes and (e) total phenolics in the stem tissues; and (b) non-volatile resin, (d) volatile terpenes and (f) total phenolics in the needles of two pine species. Data are shown as LS means \pm s.e.m. $N = 10$. Asterisks indicate significant differences (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$) among pine species (SP), herbivore-induction treatments (T) and their interaction (SP \times T). n.s. = non-significant differences. F and P -values are shown in the Table 1.

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