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Growth and defence in young pine and spruce and the expression of resistance to a stem-feeding weevil

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Abstract Defence in young trees has been much less studied than defence in older ones. In conifers, resin within ducts in bark is an important quantitative defence, but its expression in young trees may be influenced by developmental or physical constraints on the absolute size of the resin ducts as well as by differential allocation of resources to growth and resin synthesis. To examine these relationships, we used nitrogen fertilisation of 1- and 2-year-old pine and spruce to produce trees of different sizes and measured the effect on the number and size of resin ducts and the amount of resin they contained. All of these variables tended to increase with stem diameter, indicating a positive relationship between resin-based defence and growth of 1- and 2-year-old trees. In pine, however, the mass of resin flowing from severed ducts was much lower relative to duct area in 1- than in 2-year-old trees, suggesting that the older trees allocated a higher proportion of the carbon budget to resin synthesis. Resin-based defence in 1-year-old pines appears to be both positively related to growth and resource limited. In spruce, resin production was generally lower, and age-related differences were not observed, suggesting that resin-based defence is less important in this species. Bio-assays of 2-year-old trees with the pine weevil, *Hylobius abietis*, emphasised the importance of resin as a defence against this bark feeding insect. Nitrogen fertilisa-

tion had a limited influence on resistance expression. One-year-old trees remained susceptible because of their small size, low resin production and limited response to fertilisation. The strong growth response of 2-year-old trees to fertilisation increased resin-based defence, but most spruce trees remained susceptible, while most pines were resistant at all levels of fertilisation.

Keywords *Hylobius abietis* · Pine · Plant defence · Resin ducts · Spruce

Introduction

Defence against herbivory in relation to plant age or developmental stage has been observed in a number of tree-pest interactions (Boege and Marquis 2005; Bryant et al. 1994; Bryant and Julkunen-Tiitto 1995; Fritz et al. 2001; Goodger et al. 2004; Kearsley and Whitham 1989; Spiegel and Price 1996). The causes of this ontogenetic change are often not well understood and, in particular, defence has been much less studied in younger trees than in older ones (Boege and Marquis 2005; Hanley and Lamont 2002). Herbivory is a strong selective force on young plants (Watkinson 1997), but so is competitive ability and, as a result, there could be a trade-off between growth and expression of quantitative defences. Trade-offs between growth and defence are evident in some trees or for some carbon-based secondary chemicals (CBSC) but not others (Donaldson et al. 2006; Mutikainen et al. 2002; Osier and Lindroth 2006; Rosner and Hannrup 2004). These interactions are frequently discussed in the context of resource-availability models of defence (Herms and Mattson 1992). While such models can predict total allocation to CBSC (Koricheva et al. 1998), they provide an inadequate description of the underlying

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