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ORIGINAL PAPER

Terpene production and growth of three Pacific Northwest conifers in response to simulated browse and nutrient availability

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Abstract Natural variation in ungulate browsing behavior interferes with the understanding of plant morphological and biochemical responses to herbivory. To investigate mechanisms for recovery from herbivory, we examined growth patterns and biosynthesis of terpenoids under simulated browse (three clipping intensities) and supplemental mineral nutrition (four levels of controlled-release fertilization) for Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], western hemlock (*Tsuga heterophylla* Raf. Sarg.), and western red-cedar (*Thuja plicata* Donn *ex D. Don*) seedlings on a reforestation site in Northwestern Oregon, USA, that was fenced to exclude ungulates. Higher clipping intensities increased relative height growth (at cost of diameter growth) for all the species. Only western red-cedar showed a decline in monoterpene concentrations with increasing clipping severity, suggesting prioritization in biosynthesis of terpenoids for this species. Douglas-fir and western hemlock responded to fertilization mostly through increased growth. Western red-cedar growth responses to fertilization were less pronounced, but monoterpene concentrations were 2–3 times higher compared to non-fertilized trees. Douglas-fir and western hemlock browse recovery and responses to fertilization consisted primarily of increased growth, while western red-cedar balanced growth promotion with production of chemical defense compounds. Our data suggests the evolution of species-dependent resource allocation strategies in response to both browse and soil nutrient availability.

Keywords Fertilization · Herbivory · Plant defense compounds · Reforestation · Resource allocation

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Introduction

Ungulate browse reduces the photosynthetic capacity of a plant, thereby inhibiting functions such as growth and biosynthesis of secondary metabolites (Black et al. 1979; Mabry and Wayne 1997; Vourc'h et al. 2003). Browse tolerance is based on the ability of a plant to recover after damage. Recovery efforts vary by species whereby some plants allocate limited resources toward growth while others shift these toward production of alkaloids, phenylpropanoids, and terpenoids as biochemical defenses (Bazzaz et al. 1987; Strauss and Agrawal 1999; Bergvall and Leimar 2005). Terpenes have recently become of research interest due to the observed potential these collective and individual compounds have in deterring ungulate browse (Elliott and Loudon 1987; Duncan et al. 2001; Vourc'h et al. 2001; Nolte et al. 2004). Energy and resource costs to produce defensive compounds such as terpenes can be high; thus, the significance of these compounds in deterring browse may determine the degree of resources allocated toward their production and possibly away from plant growth (Bazzaz et al. 1987).

Supplemental mineral nutrition (i.e., field fertilization) may assist in recovery efforts to herbivory by adding to the total resource budget. For example, nitrogen fertilization has been observed to enhance the overall photosynthetic capacity of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] seedlings through addition of new chloroplastic cells