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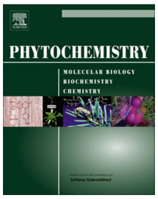

Differences in shoot and root terpenoid profiles and plant responses to fertilisation in *Tanacetum vulgare*

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ABSTRACT

Intraspecific chemical diversity is a common phenomenon especially found in shoots of essential oil-accumulating plant species. Abiotic factors can influence the concentration of essential oils, but the effects are inconsistent and little is known in how far these may vary within an individual and within species between chemotypes. *Tanacetum vulgare* L. occurs in various chemotypes that differ in the composition of mono- and sesquiterpenoids in their shoot tissues. We investigated how far shoot chemotype grouping is mirrored in root terpenoid profiles. Furthermore, we studied whether different fertilisation amounts influence the plant growth and morphological traits as well as the constitutive terpenoid concentration of leaves and roots of three chemotypes, trans-carvyl acetate, β-thujone, and camphor, to different degrees. Shoot terpenoids were dominated by monoterpenoids, while the roots contained mainly sesquiterpenoids. The clear grouping in three chemotypes based on leaf chemistry was weakly mirrored in the root terpenoid composition. Furthermore, the leaf C/N ratio and the stem height differed between chemotypes. All plants responded to increased nutrient availability with increased total biomass and specific leaf area but decreased C/N and root/shoot ratios. Leaf terpenoid concentrations decreased with increasing fertiliser supply, independent of chemotype. In contrast to the leaves, the terpenoid concentrations of the roots were unaffected by fertilisation. Our results demonstrate that aboveground and belowground organs within a species can be under different selection pressures.

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1. Introduction

Plants respond to varying environmental conditions by multiple morphological and chemical adaptations (Schoonhoven et al., 2007). Abiotic factors fundamentally influence the establishment and growth of plants. Thereby, plants under high fertilisation are able to synthesise higher concentrations of primary metabolites and may thus change their allocation of resources in the production of secondary metabolites used for defence compared to plants growing under low fertilisation. Several hypotheses were developed in the past addressing the question whether a trade-off exists between investment into growth and defence, assuming that the production of secondary metabolites can be costly (Stamp, 2003). Among these hypotheses, the growth differentiation balance hypothesis (GDBH) predicts that under low availability of resources for differentiation, carbon is shifted to the production of secondary metabolites whereas in nutritious soils, C-based secondary metabolism declines as allocation into growth processes receives priority (Herms and Mattson, 1992). In contrast, increasing light availability results in an increase of secondary metabolites (Stamp, 2003). Overall, the plants face a trade-off between investment in growth, increasing competitive abilities, and in defence against herbivores (Herms and Mattson, 1992).

Past studies on changes in metabolite profiles in response to environmental conditions investigated mainly shoot tissues. In contrast, changes in root chemical profiles due to different abiotic or biotic conditions are less understood (Rasmann et al., 2012; van Dam, 2009; Wenke et al., 2010). However, shoots and roots face a different herbivore and pathogen community and may therefore be subjected to different selection pressures. Studies on plant responses to environmental variation including root defence chemistry mainly focused on species, in which the chemical profiles of shoots and roots consist of the same class of compounds (Rasmann and Agrawal, 2008). Furthermore, individuals within a plant species may not necessarily show consistent responses to environmental changes but intraspecific variation and high phenotypic plasticity is increasingly acknowledged primarily in aboveground plant organs (Estell et al., 2013; Hol, 2011; Poelman et al., 2009).

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Terpenoids are the largest group of organic compounds in the plant kingdom. Especially within aromatic plants, a high intraspecific variation in the composition of terpenoids can be found, allowing discrimination into different chemotypes, which are defined by their major terpenoid compound (Crocoll et al., 2010; Grønberg Jensen and Ehlers, 2010; Holopainen et al., 1987; McConkey et al., 2000). The high compound diversity is mediated by terpene synthases, which act as primary enzymes that catalyse the synthesis of hemiterpenes (C_5), monoterpenes (C_{10}), sesquiterpenes (C_{15}) or diterpenes (C_{20}) (Gershenzon, 1994; Tholl, 2006). Many of these terpene synthases are able to catalyse the formation of multiple products from a single substrate, leading to complex product mixtures (Tholl, 2006). Terpenoid biosynthesis should be influenced by nutrient availability because a lack of nutrients negatively affects formation of amino acids and enzymes (Taiz and Zeiger, 2010) which are essential for terpene production. Furthermore, the production of terpenoids is assumed to be costly (Gershenzon, 1994) and thus, the GDBH may hold for this compound class. However, the reactions of terpenoids to different nutrient treatments are inconsistent and mainly tree species were investigated (Burney et al., 2012; King et al., 2006; Mihaliak and Lincoln, 1989; Ormeño and Fernandez, 2012). High concentrations of terpenoids in above- and belowground tissues might be advantageous because several terpenoids have allelopathic properties (Grøndahl and Ehlers, 2008; Johnson et al., 2010). Moreover, terpenoids are known to act antagonistic against pathogens and to repel generalist herbivores but can also attract specialists to their hosts (Burney and Jacobs, 2011; Langenheim, 1994; Müller and Hilker, 2001).

Common tansy (*Tanacetum vulgare* L., Asteraceae, synonymous *Chrysanthemum vulgare* (L.) Bernh.) is an aromatic plant that predominantly stores monoterpenoids in its leaves. It shows an unusually high variation in shoot terpenoid profiles between individuals, forming thus at least 30 different chemotypes which are defined by the main terpenoid(s) of the aboveground tissue and are genetically fixed (Lokki et al., 1973). The progeny of a given parental *T. vulgare* plant can be composed of different chemotypes, as the species is outcrossing (Lokki et al., 1973). However, not all chemotypes can hybridise with each other (Holopainen et al., 1987). To our knowledge, the variation of the root terpenoid composition in relation to the shoot chemistry has not been studied in this species. *T. vulgare* is native to Europe and Asia and has become established in North America, where it is invasive in some areas (Schmitz, 1998). Contrary to many other invaders it is also very successful and considered a weed in its native range (Gassmann et al., 2006; Rebele, 2000), although it is not always successful in competitive interactions on certain soil types (Rebele, 2000). Nowak and Komor (2010) investigated the effects of several fertiliser concentrations on sugar and amino acid contents in the phloem of *T. vulgare*. To our knowledge, fertilisation effects on growth and secondary chemistry in dependence of the chemotype have not been considered in this species.

In the present study we investigated the differences between shoot and root terpenoid profiles in three common chemotypes of *T. vulgare*. Furthermore, we determined the effects of low and high fertilisation supply on growth, morphological traits, and on constitutive terpenoid concentrations *vs.* profiles in leaf and root tissues of these chemotypes. In detail, we asked whether the responses to fertilisation may be chemotype-specific. According to the GDBH, we hypothesised a reduction in terpenoid concentration in plants with high fertilisation supply. Different responses in plants of various chemotypes might thereby reflect different costs of the involved enzyme cascades. Our comparative and comprehensive approach, investigating shoot and root responses in different chemotypes, led to an increased understanding of the complexity of intraspecific natural variation and phenotypic plasticity.

2. Results and discussion

The terpenoid composition of the roots of *T. vulgare* differed from that of the leaves, with only a weak grouping in chemotypes in the roots. No significant interaction was discovered between the factors fertilisation and chemotype for the different traits measured. Therefore, these factors are discussed separately.

2.1. Terpenoid compositions of leaves and roots are different

Based on the leaf chemistry, the seedlings of five seed families of *T. vulgare* were assigned to three chemotypes, namely trans-carvyl acetate, β-thujone, and camphor. In 9-week old plants, in total 51 terpenoids were found in the leaf tissues of all plants, with different abundances in the three chemotypes (Table S1). Monoterpenoids predominated in the leaves and only few sesquiterpenoids were present, which is in accordance with the literature (Abad et al., 1995; Rohloff et al., 2004; Wolf et al., 2011). However, our results may have been slightly biased towards the less volatile terpenoids due to our extraction procedure. Nevertheless, the three chemotypes could be clearly separated by leaf metabolite profiles in a PCA (Fig. 1A) and separation was explained by the main monoterpenoids trans-carvyl acetate, β-thujone and camphor, respectively (loadings in PCA, Fig. 1B). In accordance, the total leaf terpenoid composition based on the relative amounts of all terpenoids differed significantly between chemotypes (two-factorial PERMANOVA, factor chemotype: $df = 2$, $F = 573.68$, $P < 0.001$, factor fertilisation discussed below). The numbers of leaf terpenoids did not differ significantly between chemotypes (trans-carvyl acetate chemotype: 19 ± 5.7, mean ± SD, β-thujone chemotype 18 ± 3.4, camphor chemotype: 21 ± 3.9; one-way ANOVA: $F = 2.3$, $df = 2$, $P = 0.06$). Similarly, no differences were found in the total leaf terpenoid concentration (Fig. 3G, Table 2), which is mirrored in the fact that the three chemotypes showed also comparable numbers of glands and trichomes (Fig. 3E, Table 2).

Contrary to the leaf terpenoid composition, non-lignified roots contained a significantly lower diversity of terpenoids with 16 terpenoids in total (Table 1) (Wilcoxon rank sum test, $W = 1830$, $P < 0.001$). Furthermore, roots contained mainly sesquiterpenoids and only traces of the monoterpenoid isoborneol (Table 1). The three sesquiterpenoids germacrene D, bicyclogermacrene and (*E*)-β-caryophyllene occurred in both leaves and roots but not necessarily in the leaves and roots of the same plants. Some of the sesquiterpenoids found in *T. vulgare* roots have been also described to occur in roots of other plant species, such as β-farnesene and α-isocomene in chamomile (Asteraceae), germacrene D and bisbolene in *Senecio altissima* (Asteraceae) and (*E*)-β-caryophyllene in maize (Poaceae) (Irmisch et al., 2012; Johnson et al., 2010; Rasmann et al., 2005). As in the leaves, the number of root terpenoids in *T. vulgare* and the total root terpenoid concentrations were comparable between chemotypes (number of terpenoids: trans-carvyl acetate chemotype: 8 ± 2.6, β-thujone chemotype 9 ± 3.1, camphor chemotype: 9 ± 2.7; one-way ANOVA: $F = 1.96$, $df = 2$, $P = 0.15$; concentrations see Fig. 3H, Table 2). A higher number of terpenoids may involve higher production costs due to a more complex enzymatic machinery but also oxygenation status of terpenoids may influence production costs (Gershenzon, 1994). Thus, other *T. vulgare* chemotypes with a more complex pattern of terpenoids may be more cost-intensive than chemotypes with a lower number or different composition of terpenoids.

The clear grouping in three chemotypes based on leaf chemistry (Fig. 1 A and B) was only weakly mirrored in the root terpenoid

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