



Effect of limited water availability on foliar plant secondary metabolites of two *Eucalyptus* species



Adam B. McKiernan^{a,b,*}, Mark J. Hovenden^a, Timothy J. Brodribb^a, Brad M. Potts^{a,b}, Noel W. Davies^c, Julianne M. O'Reilly-Wapstra^{a,b}

^a School of Biological Sciences, University of Tasmania, Private Bag 55, Hobart, TAS 7001, Australia

^b National Centre for Future Forest Industries, University of Tasmania, Private Bag 55, Hobart, TAS 7001, Australia

^c Central Science Laboratory, University of Tasmania, Private Bag 74, Hobart, TAS, Australia

ARTICLE INFO

Article history:

Received 28 December 2013

Received in revised form 16 March 2014

Accepted 21 April 2014

Keywords:

Water stress

Eucalyptus

Secondary metabolite

Drought

Terpene

Phenolic

ABSTRACT

Plant secondary metabolites (PSMs) have many ecological roles such as influencing decomposition, flammability and herbivory. PSM concentrations are genetically determined, but are also affected by environmental factors. Drought periods are predicted to become more frequent in many regions, and may have widespread impacts on PSM-mediated ecological interactions. We used two dominant tree species to investigate the impact of multiple levels of water availability on leaf PSM concentrations. Juvenile *Eucalyptus globulus* and *Eucalyptus viminalis* plants were subjected to one of three glasshouse watering regimes (high [control], moderate or low water availability) and the effect on leaf PSMs was investigated between species, treatments, and within-plant foliage age classes. Moderate and low water availability decreased total phenolic concentrations of both species, and decreased the C:N of *E. globulus* leaves. Low water availability reduced the concentrations of two terpene compounds, but only in specific foliage age classes. Overall, the majority of terpenes were unaffected by decreased water availability, as were two formylated phloroglucinol compounds and condensed tannins. We conclude that water limitation had little impact on overall leaf PSM concentrations, and that juveniles of these two eucalypt species generally maintained PSM concentrations while plant growth declined, eluding to both direct impacts of water limitation and within-plant resource prioritization.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

Plant secondary metabolites (PSMs) play diverse ecological roles including mediating plant/herbivore (O'Reilly-Wapstra et al., 2004; Wiggins et al., 2006a) and tri-trophic level interactions (Cory and Hoover, 2006), promoting plant flammability (Ormeño et al., 2009) and influencing rates of leaf litter decomposition (Lindroth, 2010). Many of these and other examples in the literature show that the effects of PSMs can extend past the traditional phenotype of the individual and affect dependent communities and ecosystem processes (Lindroth, 2010; Whitham et al., 2003, 2012). Changes to PSM concentrations can occur due to variation in a range of environmental conditions including nutrients (Gleadow and Woodrow, 2002), carbon dioxide (CO₂), ozone (O₃) (Peltonen et al., 2010), light (Mooney et al., 2009) and temperature (Wahid et al., 2007).

For example, increased temperature can lead to up-regulation of PSM synthesis (Wahid et al., 2007), and nitrogen availability affects concentrations of phenolics (Gleadow and Woodrow, 2002; O'Reilly-Wapstra et al., 2005). Furthermore, the quantity of a resource that is available to a plant (e.g. high, intermediate and low availability) can differentially affect the concentration of individual PSMs (Gutbrodt et al., 2012a). As such, experiments utilizing multiple levels of resource availability will be more informative than experiments investigating the effect of a single resource level (i.e. control and one experimental treatment) on PSM concentrations.

Drought is receiving increased attention in the literature due to the impact of recent drought periods (Choat et al., 2012), and the predicted decrease in rainfall across many regions (Meehl et al., 2007). Water limitation is problematic for plants as it inhibits plant access to resources used in photosynthesis, due to stomatal closure and reduced within-plant water transport (Bréda et al., 2006). As such, when water is limited plants elicit morphological, physiological and biochemical changes in order to tolerate water stress, or because water deficit has impaired normal plant function (Blackman et al., 2009; Mitchell et al., 2013). Changes to

* Corresponding author at: School of Biological Sciences, University of Tasmania, Private Bag 55, Hobart, TAS 7001, Australia. Tel.: +61 362262563.

E-mail address: A.B.McKiernan@utas.edu.au (A.B. McKiernan).

plant biochemical profiles may have significant effects outside the plant, especially if the plant species is dominant in the community (Whitham et al., 2012). Yet, despite the ecological consequences of changes to plant biochemical traits, surprisingly little is known about the effects of water stress on PSM expression in many dominant plant species.

Eucalyptus is a species-rich tree genus in Australia (over 700 species) that commonly dominates the continent's woodlands and forests (Brooker, 2002). Eucalypt foliage contains a diversity of PSMs that vary qualitatively and quantitatively between species (Li et al., 1996; McKiernan et al., 2012; Moles et al., 2013). PSM concentrations are also known to vary between leaves on individual eucalypt trees, and this is often associated with leaf age (Silvestre et al., 1997) and ontogenetic stage (O'Reilly-Wapstra et al., 2007). Plant secondary metabolites in eucalypts influence many ecological interactions. For example, formylated phloroglucinol compounds (FPCs) are important anti-feedants against marsupial herbivores (O'Reilly-Wapstra et al., 2010; Wiggins et al., 2006a; Youngentob et al., 2011), essential oil concentration affects plant flammability (Holmes, 2009) and phenolics influence litter decomposition (Horner et al., 1988). However, few studies have investigated the effects of reduced water availability on PSM concentrations in *Eucalyptus* (Doran and Bell, 1994; Gleadow and Woodrow, 2002; King et al., 2004; Leicach et al., 2010; Stone and Bacon, 1994). Most of this work has targeted a single PSM class (e.g. terpenes) and, to our knowledge, no previous study has linked multiple PSM classes in eucalypts to water availability.

Here, we use juvenile *Eucalyptus globulus* Labill. and *Eucalyptus viminalis* Labill. to investigate the effect of three levels of glasshouse-based water availability on a range of foliar PSMs. *E. globulus* and *E. viminalis* are classified in sub-genus *Symphomyrtus*, section *Maidenaria* (Brooker, 2000) and are, therefore, phylogenetically closely related within the diverse genus *Eucalyptus*. *E. globulus* is of interest as it is dominant in forest stands in south-eastern Australia and is the most widely planted hardwood species in temperate regions of the world (Potts et al., 2004). Understanding *E. globulus* responses to water limitation is, therefore, of global importance. *E. viminalis* is also widespread throughout south-eastern Australia (Williams and Potts, 1996) and both species are important food source for the regionally vulnerable koala (*Phascolarctos cinereus*) (Moore and Foley, 2005; Moore et al., 2005). *E. viminalis* was selected due to its close phylogenetic and geographic proximity to *E. globulus* (Duncan, 2005). As such, these eucalypts were ideal for understanding how two closely related species are affected by limited water availability.

The specific aims of this research were to determine: (1) if water limitation affects *E. globulus* and *E. viminalis* PSM concentrations and if the response varies between levels of water availability, (2) if water limitation differentially affects PSM concentrations of juvenile leaves divided into within-plant foliage age classes. We predicted that water limitation would decrease PSM concentrations due to limited photosynthetic carbon assimilation and within-plant transport of resources (Bréda et al., 2006). We also expected that leaf C:N would decrease due to constrained carbon assimilation and increased amino acid accumulation (Lawlor and Cornic, 2002), and that young leaves would contain the greatest concentrations of many PSMs (Silvestre et al., 1997).

2. Materials and methods

2.1. Plant material

E. globulus seed (Forestry Tasmania seed lot 100000325; 42.38°S, 146.60°E; 380 m asl; 1164 mm mean average rainfall) and *E. viminalis* seed (Forestry Tasmania seed lot 100002291; 41.75°S, 146.88°E; 400 m asl; 601 mm mean average rainfall) were

germinated and grown for 1 month in a naturally lit glasshouse. Uniform size (cotyledons and 1 leaf pair) seedlings (12 per species) were selected and transplanted into individual plastic pots (base 38 mm × 38 mm, top 50 mm × 50 mm, height 118 mm). Potting mix contained eight parts composted fine pine bark: three parts coarse river sand, and N:P:K [19:2.6:10] at 1 g/L potting mix. The pH was adjusted to approximately 6.0 with the addition of dolomite lime at 3 kg/m³. Seedlings were grown for 3 months, then re-potted into larger pots (base 115 mm diameter, top 138 mm diameter, height 169 mm) containing equivalent potting mix with the addition of fertilizer (5 g Osmocote® 3–4 month [N14:P6.1:K11.6] per pot). Plants were moved to a controlled environment glasshouse (16/8 h light at 18 °C/15 °C respectively) where they were watered daily and randomized weekly. Chelated iron (1 ml/L water) was added once to all seedlings. Plants were grown for a further five weeks before experimental treatments were applied.

2.2. Experimental treatments

Four individuals of each species were allocated to a control group (watered to field capacity), four to a moderate water treatment (50% replacement of water required to reach field capacity), and the remaining four to a low water treatment (25% replacement of water required to reach field capacity). Each potted plant was initially watered to saturation, then left to drain for 15 min to remove excess water (field capacity). A capped section of PVC pipe (120 mm long, 40 mm diameter) was placed on the potting mix surface parallel with each stem. Each pot was wrapped in a plastic bag (Shvaleva et al., 2006) which was secured around the stem below the first leaf pair and the PVC pipe in order to prevent evaporation from the potting mix but to facilitate continued watering through the pipe. Pots were then weighed to provide total mass at field capacity.

At the beginning of the experiment, water was withheld from six month old plants of both species in both water limitation treatments (not including controls) until each plant was beginning to wilt. Once wilted, pots were re-weighed to establish pot weight at wilting, and replacement water mass calculated for each individual pot (Ma et al., 2010). Control plants were watered every 2 days, drought treatment plants every 3 days, with transpirational water loss measured gravimetrically. Control plants were not watered daily as the sealed pots retained sufficient water over a two day period to not require re-watering. Leaf water potential (Ψ_{leaf}) of each plant was measured on a single leaf using a Scholander pressure chamber (PMS, Albany, OR, USA) on the third day of the watering cycle prior to harvesting (Blackman et al., 2009) (treatment means = control -0.16 MPa; moderate water -0.33 MPa; low water -1.14 MPa). Due to these watering regimes, the moderate water plants showed signs of turgor loss, and the low water plants were heavily wilted every third day prior to re-watering. Control plants never wilted. All pots were randomized weekly within the glasshouse, and treatment duration was 3 months.

2.3. Sample collection

Leaf harvesting from all plants occurred at the end of the three month experimental period on day three of the watering cycle when pots contained the least water. Plant height was measured from the soil surface to the base of the apical bud. For each plant, leaves were divided into young (new growth, not fully expanded, developed during treatment), intermediate (fully formed juvenile foliage, developed before and during treatment) and old (tougher dark colored juvenile leaves at base of stem and branches, developed prior to treatment) age groups based on leaf size, color and location on plant (Close et al., 2005). Leaves in each leaf class were removed from the stem of a single plant and pooled (total of three sample bags per plant). A random sub-sample of leaves from

Download English Version:

<https://daneshyari.com/en/article/4554354>

Download Persian Version:

<https://daneshyari.com/article/4554354>

[Daneshyari.com](https://daneshyari.com)