Science of the Total Environment 547 (2016) 39–47

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

The effect of warming and enhanced ultraviolet radiation on gender-specific emissions of volatile organic compounds from European aspen

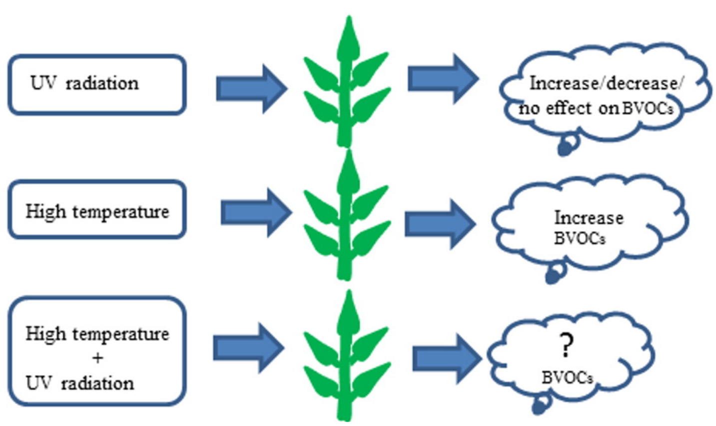
Mengistu M. Maja [a,*], Anne Kasurinen [a], Toini Holopainen [a], Riitta Julkunen-Tiitto [b], Jarmo K. Holopainen [a]

[a] University of Eastern Finland, Department of Environmental Science, P.O.Box 1627, 70211 Kuopio, Finland
[b] University of Eastern Finland, Department of Biology, P.O. Box 111, 80101 Joensuu, Finland

HIGHLIGHTS

- We measured VOC emissions from European aspen under UV and warming stress.
- Warming induced isoprenoid emission from European aspen.
- Warming also modified VOC emission response of European aspen to UV-radiation.
- UV radiation had little effect on VOC emission rate but it affects VOC blend.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 18 August 2015
Received in revised form 22 December 2015
Accepted 23 December 2015
Available online xxxx

Editor: D. Barcelo

Keywords:
Climate warming
European aspen
Gender
UV-radiation
Volatile organic compounds

ABSTRACT

Different environmental stress factors often occur together but their combined effects on plant secondary metabolism are seldom considered. We studied the effect of enhanced ultraviolet (UV-B) (31% increase) radiation and temperature (ambient +2 °C) singly and in combination on gender-specific emissions of volatile organic compounds (VOCs) from 2-year-old clones of European aspen (*Populus tremula L.*). Plants grew in 36 experimental plots (6 replicates for Control, UV-A, UV-B, T, UV-A + T and UV-B + T treatments), in an experimental field. VOCs emitted from shoots were sampled from two (1 male and 1 female) randomly selected saplings (total of 72 saplings), per plot on two sampling occasions (June and July) in 2014. There was a significant UV-B × temperature interaction effect on emission rates of different VOCs. Isoprene emission rate was increased due to warming, but warming also modified VOC responses to both UV-A and UV-B radiation. Thus, UV-A increased isoprene emissions without warming, whereas UV-B increased emissions only in combination with warming. Warming-modified UV-A and UV-B responses were also seen in monoterpenes (MTs), sesquiterpenes (SQTs) and green leaf volatiles (GLVs). MTs showed also a UV × gender interaction effect as females had higher emission rates under UV-A and UV-B than males. UV × gender and T × gender interactions caused significant differences in VOC blend as there was more variation (more GLVs and trans-β-caryophyllene) in VOCs from female saplings compared to male saplings. VOCs from the rhizosphere were also collected from each plot in two

* Corresponding author.
E-mail address: mengistu.maja@uef.fi (M.M. Maja).

http://dx.doi.org/10.1016/j.scitotenv.2015.12.114

exposure seasons, but no significant treatment effects were observed. Our results suggest that simultaneous warming and elevated-UV-radiation increase the emission of VOCs from aspen. Thus the contribution of combined environmental factors on VOC emissions may have a greater impact to the photochemical reactions in the atmosphere compared to the impact of individual factors acting alone.

1. Introduction

Depletion of the stratospheric ozone layer has increased the level of ultraviolet (UV-B, 280–320 nm) radiation that reaches the troposphere (Hegglin and Shepherd, 2009; Zhang et al., 2014). UV-B radiation can damage plant tissues and cause morphological, physiological and biochemical changes in plants (e.g. Jansen et al., 1998; Caputo et al., 2006). Although the stratospheric ozone layer is now recovering due to reduction in the emissions of ozone depleting substances as a result of the Montreal protocol (Assessment for Decision-Makers: Scientific Assessment of Ozone Depletion, 2014; Bais et al., 2015), it has not fully recovered. Moreover, chemicals that were not historically linked to ozone layer damage (such as short-lived bromine substances (Hossaini et al., 2015) and substitutes of ozone depleting substances (Assessment for Decision-Makers: Scientific Assessment of Ozone Depletion, 2014)) contribute to the slow recovery process. Increased emission of nitrous oxide (N_2O) also plays a role in slowing down ozone recovery (Ravishankara et al., 2009).

The increased UV-B radiation triggers a diverse range of responses including changes at physiological, biochemical and molecular levels in organisms (Guruprasad et al., 2007). High doses of UV-B radiation can destroy amino acid residues and lead to the inactivation of proteins and enzymes involved in biochemical processes (Stapleton, 1992; Hollosy, 2002), and thus affect primary and secondary metabolism (Krupa, 2000; Holopainen, 2011). UV effects on plant secondary metabolism are often associated with changes in the concentration of flavonoids, particularly in defence against high levels of UV-B radiation (e.g. Stapleton, 1992; Bidart-Bouzat and Imeh-Nathaniel, 2008). However, studies about the effect of UV-radiation on the emission of plant volatile organic compound (VOCs) are not voluminous (Loreto and Schnitzler, 2010), and responses vary depending on plant species, VOC type and level of UV stress (Holopainen, 2011). While some studies found enhanced terpenoid emission (Filella and Peñuelas, 1999), in others UV-B radiation caused no change (Blande et al., 2009) or reduced VOC emission (Ambasht and Agrawal, 1997) from different plant species. Supplemental UV-B on sweet basil (*Ocimum basilicum* L.) increased emission rates of monoterpenes (MTs) and sesquiterpenes (SQTs) (Johnson et al., 1999). Similarly, isoprene emission rates from gambel oak (*Quercus gambelii* Nutt.) were reported to have increased as a result of supplemental UV-B radiation representing 30% of stratospheric ozone layer depletion (Harley et al., 1996). On the other hand, increased doses of UV-A (320–400 nm) radiation enhanced the magnitude of isoprene emission from hybrid poplar (*Populus* × *canadensis*) saplings (Pallozzi et al., 2013).

In addition to increased UV-B radiation, forests face also high temperature regimes (Niinemets, 2010). Recent projections indicate that average global surface temperature is expected to rise (IPCC, 2013), thus causing more temperature-induced stress that leads to the emission of VOCs (Holopainen, 2004). VOCs, particularly isoprene provide protection against high temperature (Peñuelas et al., 2005; Velikova and Loreto, 2005) and oxidative stress (Velikova et al., 2012) that might damage photosynthetic machinery. Environmental stresses often appear simultaneously, and may have overlapping effect on the emission rates of different VOCs (Holopainen and Gershenzon, 2010). Therefore, these stresses can have additive or antagonistic effects such that the multiple environmental factors may amplify or suppress VOC emission responses of plants (Gouinguene and Turlings, 2002; Himanen et al., 2009). In the face of rising temperature and uncertain fate of future levels of UV-B radiation in the biosphere, it is necessary to assess the VOC emission responses to the combined stresses of these two factors, which will give clues to the future VOC emissions of plants exposed to multiple abiotic stresses.

European aspen (*Populus tremula* L.) is a widespread tree species in Europe (Worrel, 1995) and known emitter of MTs, isoprene (Hakola et al., 1998) and SQTs (Zhang et al., 1999). It is an important model species (Ingvarsson, 2005) having two genders, with a male-biased sex ratio of 2:1 (Myking et al., 2011). Males and females often invest their resources differently leading to sex-related differences in plant growth and defence (e.g. Obeso, 2002; Nybakken et al., 2012) as female plants usually allocate more resources to reproduction and defence than growth, whereas male plants have better growth and are more prone to herbivore damage than females (Lloyd and Web, 1977; Dawson and Ehleringer, 1993). Sex-related differential resource allocation could affect plant VOC emission rates and profile in the presence of multiple environmental factors. Understanding the VOC emission responses of European aspen is important because any change in VOC emissions in this species due to changing UV-A, UV-B, temperature or combination of these factors may affect the isoprenoid pool, and thereby affect the reaction chemistry of the atmosphere (Wiedinmyer et al., 2014). Although some studies have explored the effect of warming (Hartikainen et al., 2009) and UV-radiation (Pallozzi et al., 2013) on some defensive traits of aspen, the combined effects of UV-radiation and warming are not well known.

The aim of this study was to assess whether enhanced UV-B, UV-A radiation (as a control for UV-B exposure) and elevated temperature, singly or in combination, affect the emission rate and composition of VOCs from the shoots and rhizospheres of European aspen. In order to assess the effect, VOC measurements were carried out from aspen plants at an experimental field. UV-B and warming effects on growth, phenolic concentrations as well as fungal infection were studied from the same plants (Randriamanana et al., 2015). The hypotheses tested in this study were that 1) VOC emission rates are affected by UV-radiation and temperature enhancements, 2) VOC emission responses to combined enhancement of UV and temperature differ from their separate effects, 3) female plants emit more VOCs than male plants in response to warming and UV-radiation, and 4) VOC emission from the rhizosphere of aspen are influenced by warming and UV-B treatments.

2. Materials and methods

2.1. Plant material and experimental setup

A field experiment was established using 12 (six genotypes of each sex) European aspen genotypes that were acquired from different locations in eastern and southern Finland (see Randriamanana et al., 2014 for detailed information on the locations of the genotypes). Twigs were collected from adult trees far apart from each other during January to February 2011. Axillary buds from each mother tree were aseptically micropropagated and acclimated in greenhouse to photoperiod of 18 h, a daytime temperature of 26–30 °C, a night-time temperature of 15 °C and an air relative humidity of 41–78% (Randriamanana et al., 2014).

This experiment was established in 2012 in the experimental field located at the Botanical Garden of Joensuu, eastern Finland (62°30 N, 29°46 E). The experimental site was divided into 36 plots and above each plot there was an aluminium frame (1.5 m wide and 3 m long, effective area was 1.20 m × 2.40 m) fixed to iron posts to secure the UV lamps and infrared heaters in position. Before the planting of the plantlets to the plots, a 10 cm layer of composted organic soil (Puutarhan