



Short-term carbon allocation dynamics in subalpine dwarf shrubs and their responses to experimental summer drought



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ABSTRACT

Carbon (C) allocation is a key determinant of plant functioning and ecosystem processes. Its dynamic responses to environmental conditions and global change are still poorly understood. This holds particularly true for dwarf shrubs, which are an important component of high mountain vegetation. We studied the short-term C allocation dynamics in two dominant dwarf shrub species, *Vaccinium myrtillus* and *Vaccinium uliginosum*, at two subalpine sites, in the Pyrenees and in the Alps, and additionally performed an experimental rain exclusion to simulate summer drought at the site in the Alps. We compared net assimilation rates (A_{max}), stomatal conductance (g_s) and shoot water potentials (Ψ_s) between the two species and carried out a ¹³C pulse labelling experiment to trace their C allocation dynamics, both under natural conditions and in the drought experiment. Under ambient conditions, *V. uliginosum* showed higher A_{max} and g_s and used recent assimilates as a respiratory substrate more slowly than *V. myrtillus*. C allocation dynamics in current-year shoots differed significantly between the species, showing a progressive decrease after the pulse labelling in *V. uliginosum* shoots but a progressive increase in *V. myrtillus* shoots. In the drought experiment, a significant reduction of soil moisture caused predawn Ψ_s below -1.2 MPa in both species, which is considered close to the turgor loss point. However, the stomatal conductance and the speed of transfer of newly assimilated C to belowground organs decreased in *V. uliginosum* only. We found a strong coupling in C allocation dynamics between xylem and phloem tissues of the rhizome, which was maintained under drought. Although both species were largely tolerant to the drought imposed, our results indicate a higher drought sensitivity of *V. uliginosum* compared to *V. myrtillus*, with potential implications for community composition and ecosystem C cycling in a future climate.

1. Introduction

Carbon (C) allocation from photosynthetically active plant parts to other plant compartments is a premise for plant growth and metabolic maintenance, and has important implications for ecosystem C cycling (Högberg and Read, 2006; Brüggemann et al., 2011). The study of plant C allocation patterns and their dynamics provides essential information on the transfer, use or storage of assimilates, and how these functions might change directly or indirectly due to environmental changes both at the longer (Litton et al., 2007; Poorter et al., 2012) and the shorter timescales (Epron et al., 2012). Recent methodological advances have allowed studying C allocation dynamics *in situ* with isotopic pulse chase labelling, conferring an understanding of the fate of assimilated C and

its responses to environmental changes. While the short-term C allocation dynamics have been studied in grasslands (e.g. Bahn et al., 2009; Burri et al., 2014; Fuchslueger et al., 2014; Hasibeder et al., 2015) and, for woody species mostly in trees (see review by Epron et al., 2012, and more recent studies by Streit et al., 2013; Krepkowski et al., 2013; Blessing et al., 2015; Hartmann et al., 2015; Hagedorn et al., 2016 and Desalme et al., 2017), the understanding of the environmental controls and responses to climatic changes is still limited. To date, very little is known on the short-term C allocation dynamics in dwarf shrubs (see Karlsson, 1985).

Dwarf shrubs are an important component of many subalpine plant communities (Körner, 2003; Ninot et al., 2008) and play a crucial role in treeline processes (Batllori et al., 2009; Grau et al., 2012, 2013; Liang

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et al., 2016). Climate and land-use changes have led to an expansion of dwarf shrub species in mountain areas, where they colonize abandoned pastures and herbaceous-dominated alpine sites (Tasser and Tappeiner, 2002; Dullinger et al., 2003; Sanz-Elorza et al., 2003). Shrub encroachment may have profound impacts on ecosystem structure and functioning (Eldridge et al., 2011; Prévosto et al., 2011; Ropars and Boudreau, 2012; Bragazza et al., 2013; Maestre et al., 2016). The genus *Vaccinium* contains ecologically important and widespread species across cold regions. *Vaccinium myrtillus* L. and *Vaccinium uliginosum* ssp. *microphyllum* (Lange) Tolm. or *Vaccinium gaultherioides* (hereafter *V. uliginosum*) are clonal dwarf shrub species of similar dimensions, deciduous leaf habit and with a complex and extensive network of subterranean rhizomes. Despite their similar leaf-habit and size, *V. myrtillus* bears photosynthetic shoots that remain green for some years after their formation, whereas *V. uliginosum* does not. Thus, green shoots of *V. myrtillus* represent a significant part of its total photosynthetic area, and remain functional for a longer period than the deciduous leaves, with so far unknown implications for C allocation dynamics.

Global change projections for the end of the century point to changing precipitation patterns with an increase of extreme events such as severe summer droughts (IPCC, 2013; Dai, 2013). Limited water supply alters photosynthesis and respiration and thereby drives major changes in ecosystem C balance (Giais et al., 2005; Zhao and Running, 2010; Reichstein et al., 2013; Frank et al., 2015; Yuan et al., 2016). Moreover, frequent and intense drought events may decelerate the expansion of forests and shrublands driven by land-use change and warming at high elevations (Barros et al., 2017). When facing water stress, most plants respond with stomatal closure, which reduces water loss at the expense of decreasing C uptake by photosynthesis (Chaves et al., 2002; Flexas et al., 2006). Some studies based on isotopic labelling experiments found that drought slowed down the transfer of recently assimilated C to belowground compartments (Ruehr et al., 2009; Barthel et al., 2011; Fuchslueger et al., 2014; Hasibeder et al., 2015), but other studies did not find such effects (Burri et al., 2014; Blessing et al., 2015; Hommel et al., 2016). Moreover, drought may reduce phloem transport through a reduction of water potential and non-structural carbohydrate availability, causing dysfunctions in the transfer of assimilates throughout the plant (Hartmann and Trumbore, 2016). Also xylem has been shown to transport C derived from an exchange between phloem and xylem (Gruber et al., 2013) or from refixed root-respired CO₂ (Aubrey and Teskey, 2009; McGuire et al., 2009; Bloemen et al., 2013a,b); drought may affect xylem C transport by affecting the above processes or by embolism formation and hydraulic failure (Tyree and Sperry, 1988; Brodribb and Cochard, 2009; Choat et al., 2012).

In our study, we aimed to determine the differences in the short-term C allocation between *V. myrtillus* and *V. uliginosum* at two subalpine sites differing in their background climate conditions, one in the Alps and one in the Pyrenees. Moreover, we studied the effects of an experimental summer drought on the short-term C allocation dynamics of both species. We hypothesized that (i) due to the photosynthetic capacity of its shoots, *V. myrtillus* would show higher C uptake per shoot biomass and faster turnover and transport to belowground organs; (ii) the dynamics of recently assimilated C would be slower and less pronounced for xylem than phloem; and that (iii) drought would slow down C allocation to rhizomes, with stronger reduction in tracer dynamics in xylem relative to phloem.

2. Materials and methods

The study aimed at comparing C-allocation dynamics of *V. myrtillus* and *V. uliginosum* *in situ*. We performed two separate pulse labelling experiments at two subalpine sites, in the Alps and in the Pyrenees. Despite their similar annual precipitation, rainfall during the summer months is distinctly higher at the site in the Alps than in the Pyrenees (see below). In the Alps, we also aimed at exploring the effects of

experimental drought on C allocation patterns of both species. A summary of the measurements taken at each study site is provided in Table A.1.

2.1. Study species

Vaccinium myrtillus and *V. uliginosum* grow in acidic substrates and often coexist, although their elevation distribution differs slightly at mid-latitude mountains. *Vaccinium myrtillus* can be found from the colline to the upper subalpine belt (although it also reaches alpine sites), whereas *V. uliginosum* grows at slightly higher altitudes than *V. myrtillus*, from the subalpine to the alpine belt (Aeschimann et al., 2004; Bolòs et al., 2005). *Vaccinium uliginosum* is more heliophilous, and can resist strong winds and the lack of snow cover (Jacquemart, 1996), contrarily to *V. myrtillus*, which needs snow protection in winter (Ritchie, 1956) and has a lower freezing resistance (Martin et al., 2010; Wheeler et al., 2014).

2.2. Study sites and experimental design

2.2.1. Stubai valley, Alps

The study site is located at a subalpine grassland colonized by dwarf shrub patches (1820 m a.s.l.) in the Stubai valley, Austrian Central Alps (47° 7' 45" N, 11° 18' 20" E). It is immediately adjacent to a site where previous pulse labelling and drought experiments have been performed on herbaceous vegetation (e.g. Bahn et al., 2009; Seeber et al., 2012; Fuchslueger et al., 2014, 2016; Hasibeder et al., 2015). Vegetation includes the dominant dwarf shrub species *Vaccinium myrtillus* and *Vaccinium uliginosum*, plus other less abundant dwarf shrub species (*Calluna vulgaris* and *Vaccinium vitis-idaea*) and numerous grasses and forbs (*Agrostis capillaris*, *Festuca ovina*, *Deschampsia flexuosa*, *Briza media*, *Luzula multiflora*, *Campanula scheuchzeri*, *Chaerophyllum hirsutum*, *Crepis conyzifolia*, *Hypericum maculatum* and *Potentilla erecta*, amongst others). The mean annual temperature of the site is 3 °C and the mean annual precipitation is 1100 mm; and summer precipitation (June–August) amounts to 548 mm.

A drought experiment was set up on 3 July 2014 and consisted of three blocks, each one with a drought plot and the corresponding control plot, all of them placed on mixed patches of the clonal dwarf shrubs *V. myrtillus* and *V. uliginosum*. Drought was simulated with rain-out shelters of 3 × 3.5 m basal area and 2.5 m height covered with transparent and UV-B transmissive plastic foil (UV B Window; Folitec, Westerborg, Germany; light transmittance ca. 95%, see Hasibeder et al., 2015). Inner ventilation was achieved through openings at the bottom and the top of the face sides of the rain-out shelter. At the centre of each rain-out shelter, an area of 1 × 1 m was established on which a 15-cm-high plastic frame was installed by inserting it ca. 3 cm into the soil. Plastic frames were also installed on the corresponding control plots. The frames served to place the ecosystem chamber airtight for measurements of ecosystem CO₂ fluxes and for pulse labelling. On the hillslope-facing side of each rain-out shelter the soil was trenched down to ca. 20 cm, and the trench was filled with waterproof plastic foil to avoid runoff water getting inside drought plots.

We installed two sets of sensors for light, air temperature and air moisture (HMP155 with radiation and precipitation shield DTR500; Vaisala, Helsinki, Finland), one outside the rain-out shelters and one inside one of the rain-out shelters. In addition, we installed one soil temperature sensor (S-TMB, Onset Computer Corporation, MA, USA) and one soil moisture sensor (EC-10; Decagon Devices, WA, USA) per plot. Data were recorded by dataloggers (HOBO micro station, Onset Computer Corporation, MA, USA).

2.2.2. Filià valley, Pyrenees

The study site is located at a low shrub heath in Filià valley, Pallars Jussà, Central Pyrenees, on a 28° steep N-facing slope at 1900 m a.s.l. (42° 27' 41" N, 0° 57' 40" E). The dominant shrub species are *Vaccinium*

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