FUNGAL ECOLOGY 6 (2013) 397–407

available at www.sciencedirect.com

SciVerse ScienceDirect

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

Water relation parameters of six *Peltigera* species correlate with their habitat preferences

Andrea NARDINI[*], *Ada MARCHETTO*, *Mauro TRETIACH*

Dipartimento di Scienze della Vita, Università di Trieste, Via L. Giorgieri 10, 34127 Trieste, Italy

ARTICLE INFO

Article history:
Received 15 September 2012
Revision received 13 March 2013
Accepted 26 April 2013
Available online 5 July 2013
Corresponding editor:
Peter D. Crittenden

Keywords:
Anatomy
Cell wall elasticity
Lichen
Osmotic potential
Pressure–volume curve
Turgor loss point

ABSTRACT

Water relation parameters were measured in six congeneric lichen species with different requirements for water availability and with green algae (*Peltigera aphthosa*, *Peltigera leucophlebia*, *Peltigera venosa*) or cyanobacteria (*Peltigera horizontalis*, *Peltigera praetextata*, *Peltigera rufescens*) as main photobionts. Pressure–volume analysis was performed with a dewpoint hygrometer and integrated with anatomical analyses. The *Peltigera* species typical of arid environments were characterized by relatively lower osmotic potential (π_0) and turgor loss point (Ψ_{TLP}), and higher values of bulk modulus of elasticity (ε). Both π_0 and Ψ_{TLP} were correlated with the size of medullary cells, while ε was negatively correlated with cell dimensions. The adaptive value of low Ψ_{TLP} might reside in the capability to maintain cell turgor for longer time intervals under dry conditions. High ε might allow xerophilous lichens to regain cell turgor more promptly even for small amounts of water uptake, thus enlarging the cumulative period of positive carbon balance in environments with fluctuating water availability. The influence of the photobiont type is also discussed.

Introduction

Water is essential for plant life. Because photosynthetic reactions are generally more sensitive to cellular dehydration than respiratory ones (Larcher, 2003), adequate water content is a fundamental pre-requisite for autotrophic organisms to run CO_2 fixation reactions and to maintain a positive carbon balance. In vascular plants, the water content of leaves and other organs is a function of soil moisture availability, transpiration rate, and water transport rate from the soil to the foliage (Kirkham, 2005). As homoiohydrous organisms, vascular plants tend to maintain their water content relatively constant independently of fluctuations of water availability in the surrounding environment (Proctor and Tuba, 2002). Although net primary productivity of terrestrial habitats is mainly contributed by vascular plants (Brodribb, 2009), the "homoiohydry" strategy is not always successful, because it depends on the more or less continuous and/or predictable presence of water in an adequate reservoir that is generally represented by the soil.

Terrestrial surfaces comprise large macro- and microhabitats where water is available in scarce and unpredictable quantities and/or soil is virtually absent, like deserts, tundras, alpine/nival areas, and hard surfaces like rocks and tree bark. These harsh environments are colonized by poikilohydrous organisms (Proctor and Tuba, 2002) represented by cyanobacteria (Büdel, 2011), aerial microalgae (Häubner et al., 2006), lichens (Lange and Matthes, 1981), mosses and liverworts (Tuba et al., 1996), and a few vascular plants (Porembski and Barthlott, 2000). In particular, lichens – an obligate

---

[*] *Corresponding author*. Tel.: +39 040 5583890.
E-mail address: nardini@units.it (A. Nardini).

1754-5048/$ – see front matter © 2013 Elsevier Ltd and The British Mycological Society. All rights reserved.
http://dx.doi.org/10.1016/j.funeco.2013.05.004

symbiosis between heterotrophic fungi and one or more populations of autotrophic algae and/or cyanobacteria – dominate approximately 8 % of the Earth's land surface and hence play a significant role in terrestrial carbon and water fluxes. Poikilohydrous organisms do not exert any apparent control on water loss comparable to that observed in vascular plants. They can gain and lose water very rapidly, surviving extreme desiccation states and recovering full metabolic activities within minutes to hours following rewetting (Smith and Molesworth, 1973; Lidén et al., 2010).

Water relations of vascular plants have been extensively studied during the past decades. Following the introduction of the pressure chamber (Scholander et al., 1965) as an effective, simple instrument for measuring the water potential of plant organs, the number of published articles dealing with plant water relations and based on robust thermodynamic bases (Tyree and Jarvis, 1982; Turner, 1988) has significantly increased (e.g. Cheung et al., 1975; Kubiske and Abrams, 1990). In particular, the introduction of 'pressure–volume' analysis of plant water potential components as a function of water content (Tyree and Hammel, 1972; Kikuta et al., 1985), has greatly enlarged our understanding of water relations at the cell, organ and plant level, as well as our knowledge of the functional significance of adaptive modifications of key parameters under drought stress conditions. As an example, it has been reported that osmotic potential at full turgor (π_0) is generally lower in cells of plant species adapted or acclimated to drought conditions than in those growing under high water availability (Dreyer et al., 1990; Salleo and Lo Gullo, 1990; Bartlett et al., 2012). Low π_0 in drought-adapted plants generally correlates with low values of water potential at the turgor loss point (Ψ_{TLP}) (Bartlett et al., 2012). In turn, Ψ_{TLP} correlates with minimum seasonal water potential (Ψ_{min}) as well as to other predictors of plant adaptation to water shortage, like vulnerability to drought-induced hydraulic dysfunction (Brodribb et al., 2003; Lenz et al., 2006). Finally, the bulk modulus of elasticity (ε) of leaf cells has been reported to undergo significant changes in response to acclimation/adaptation of plant species to drought conditions (e.g. Salleo and Lo Gullo, 1990; Saito and Terashima, 2004).

Examples of analysis of water relation parameters in poikilohydrous organisms, and specifically in lichens, are much less common (e.g. Beckett, 1995, 1997; Proctor et al., 1998), and lichen water relations are generally described in terms of water content (Lange et al., 2007; Hartard et al., 2009). This can partially be explained by the fact that accurate determination of water potential values of lichens requires the use of psychrometric techniques, which are more expensive in terms of laboratory equipment and significantly more time consuming than pressure chambers. Interestingly, pressure–volume curves obtained on leaf samples using psychrometers or dewpoint hygrometers yield results consistent with those obtained using the pressure chamber (Kikuta et al., 1985; Nardini et al., 2008). Analysis of water potential components of lichens would significantly contribute to the understanding of the biophysical basis of their ecological requirements as well as of relationships between water availability and metabolic activity. This knowledge, in turn, would favor the development of mechanistic models simulating the loss and uptake of water as a function of changes in environmental parameters (Jonsson et al., 2008).

In the present study, pressure–volume curves of congeneric lichen species with different requirements for water availability are reported. Our aim was to verify whether water relation parameters of lichens are related to species-specific ecological requirements. In particular, we hypothesized that xerophilous lichens should be characterized by a suite of water relations parameters (namely, low Ψ_{TLP} and π_0) that would favor turgor maintenance and positive carbon balance under low cell water content, as previously reported for vascular plants (Bartlett et al., 2012).

Materials and methods

Species studied

The study was carried out on six species of the genus *Peltigera*, which comprises some of the largest terricolous lichens of Europe. Most species in the genus have a heteromerous, foliose, lobed thallus with corticate upper side and ecorticate, rhizinate lower side, often with well-developed veins. The photobiont is a cyanobacterium (*Nostoc*; most species) or chlorococcoid (*Coccomyxa*; a few species), but in the latter case the thallus also contains *Nostoc* colonies in specialized external structures (cephalodia). *Peltigera* species generally occur on bare soil or in short turf, mossy lawns, bonfire sites, as well as on mossy tree trunks and fallen logs. The species (Table 1) were selected according to: (a) relative local commonness; (b) main photobiont type (*Nostoc vs. Coccomyxa*); (c) water requirement. The latter information was drawn from Ellenberg et al. (1991) in the form of a seven-class ordinal scale of xerophytism, from one (extremely hygrophilous), to seven (extremely xerophilous), allowing ordering of the species along a gradient, from *Peltigera aphthosa* to *Peltigera rufescens*. The analysis of the vegetation composition of the collection sites was consistent with this information (data not shown).

Material collection and preparation

Entire thalli were collected in the sites detailed in Table 1. Lichens were immediately transported to the laboratory, air-dried for 2 d, and then carefully cleaned by removing soil particles, mosses and organic detritus. Lichens were further air-dried in the laboratory for 4 d more. Five to ten samples per species were cut from marginal lobes of different thalli, and any apothecia were removed. Samples were placed in sample holders (40 mm diameter, 5 mm height) and further dried by inserting them into an air-proof plastic box containing silica gel. At the end of this procedure, samples were weighed to get their initial dry weight (ranging between 0.05 and 0.08 g) using a digital balance (BA110S, Sartorius).

Samples were then progressively rehydrated. Samples were first transferred to a transparent plastic box lined with wet filter paper and maintained for 2 hr at 20 °C, under artificial lighting (PPFD = 20 μmol m^{-2} s^{-1}). After this time, samples were immersed in deionized water for 4 min. They were then maintained in the humid box for 3 d and then re-immersed in deionized water for 12 min to complete the