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Water transport and gas exchange in the non-vascular plant *Dendroligotrichum dendroides* (Brid. ex Hedw.) Broth. (Polytrichaceae, Bryophyta)

Transporte de agua e intercambio de gases en la planta no vascular *Dendroligotrichum dendroides* (Brid. ex Hedw.) Broth. (Polytrichaceae, Bryophyta)

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RESUMEN

Se midió la conductancia hidráulica específica (Ks) y el intercambio de gases en individuos de *D. dendroides* (Polytrichaceae, Musci). Ks fue más alta que en algunas coníferas y comparable con algunas angiospermas leñosas, pero la fotosíntesis (Amax) fue relativamente baja. Los resultados muestran que una planta no vascular puede alcanzar altos valores de Ks, sugiriendo un funcionamiento "vascular" similar a las traqueófitas.

INTRODUCTION

Mosses are non-vascular plants, generally short, and lacking specialized vascular tissue. They are poikilohydric, meaning they are strongly dependent on environmental moisture (Proctor 1981). Mosses belonging to the Polytrichaceae present a conductive tissue analogous to xylem, and some species can reach 60 cm to ca. 1 m height. Several species of the Polytrichaceae have been studied regarding the anatomy of the stems and central strands (Tansley & Chick 1901, Hébant 1975). Despite the morpho-anatomical complexity of these mosses, functional studies are rare, and for some species non-existent (Longton 1981, 1988, Proctor 1981, 1982, 2000, Proctor *et al.* 2007).

Tall moss species like *Polytrichum*, *Dendroligotrichum* and *Dawsonia* are regarded as endohydric (Buch 1945, 1947). This is because water is internally conduced through the central strand, although some external water movement can occur through capillary spaces in the leaves (Proctor 2000). The leaf specific conductivity (Kl) has been evaluated in *Dawsonia superba* Grev. (Polytrichaceae) and can reach up to 2.79 mmol m^{-2} s^{-1} MPa^{-1}, comparable to some pteridophytes, but 10 to 20 times lower than an angiosperm (Brodribb *et al.* 2007). Nevertheless, specific hydraulic conductivity of the stems of Polytrichaceae has never been quantified.

There is a positive relationship between hydraulic conductance and carbon gain (Meinzer & Grantz 1990, Sperry & Pockman 1993, Hubbard *et al.* 2001). The photosynthesis rate in some mosses is lower than in most vascular plants (Brodribb *et al.* 2007), with the exception of *Polytrichum commune* Hedw. that reach values similar to gimnosperms (Brodribb *et al.* 2007). Many of the meassured mosses lack a central strand of conducting tissue or are relatively small in size.

D. dendroides is a Polytrichaceae with a central strand of vascular tissue (Fig. 1) that grows in Chile from Arauco Province in the Bío-Bío Region to Tierra del Fuego in the Magallanes Region (Müller 2009). It grows in the understory of the temperate rainforest forming a strata where it competes with seedlings of vascular plants and other mosses (Juan Larraín, personal communication). In the northernmost part of its distribution, *D. dendroides* can experience temporal dessication, specially in the summer (Atala, unpublished data). This moss can reach up to 60 cm height (samples in CONC herbarium, Universidad de Concepción).

The present study addresses the hydraulic conductivity of the stems of *D. dendroides,* and its gas exchange parameters. It is hypothesized that, given the size and anatomy of this moss, it could functionally behave as a vascular plant.

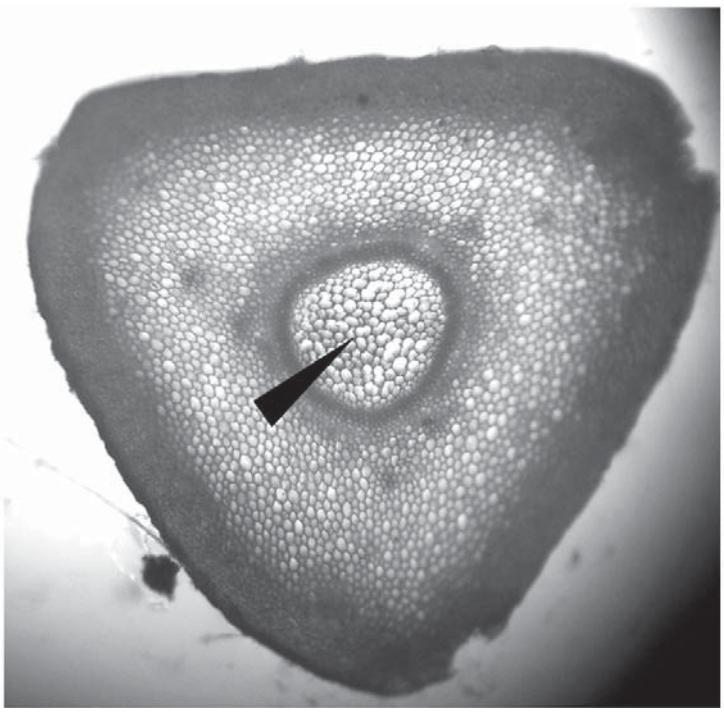

FIGURE 1. Cross section of the stem of *D. dendroides*. The arrow shows the central strand with hydroids. Photo taken at 100X.

FIGURA 1. Sección transversal del tallo de *D. dendroides*. La flecha indica el haz central con hidroides. Fotografía tomada a 100X.

MATERIALS AND METHODS

PLANT MATERIAL

Individuals of *D. dendroides* (Brid. ex Hedw.) Broth. were collected growing in the understory of Monumento Nacional Contulmo (protected area), in the border of Bío-Bío and La Araucania Regions of Chile. It corresponds to a temperate forest with rains usually falling in the winter, and summer rainfall usually dropping below 35 mm and with occasional droughts (Di Castri & Hajek 1976). Living plants were collected and then taken to the laboratory for analysis. Some individuals were put in a greenhouse for ecophysiological measurements.

SPECIFIC WATER CONDUCTIVITY AND GAS EXCHANGE

Individuals collected in the field were put in a greenhouse at Universidad de Concepción (Concepción, Chile) and were left for acclimatization for 2 weeks. They were maintained in constant moisture and under mild shade (40% full light) to avoid dehydratation and stress. Specific water conductivity (Ks) was determined for 10 individuals using a flowmeter with an integrated pressure-transducer. Plants were kept moist before and during the Ks measurements. We also measured leaf specific hydraulic conductivity (Kl) in the same individuals using the same instrument. To obtain Kl it was calculated the projected leaf area of a digital image of the plants using image measuring software (Sigmascan 5, SPSS, USA). Plants were hydrated when digitalized.

We conducted gas exchange measurements using an IRGA (CIRAS-II, PP Systems, Amesbury, MA, USA). Previous to measuring the maximum photosynthetic rate (Amax) we made light-response curves in 3 plants to obtain the amount of PAR radiation necessary to saturate carbon gain. We observed that 300 μmol m^{-2} of PAR were enough to reach Amax, and that PAR was used in the estimation of Amax in other 5 individuals of *D. dendroides*. We also obtained evapotranspiration (E) and stomatal conductance (g_s) in the same individuals. Instantaneous water use efficiency (WUE) was calculated as Amax/E. All measurements were conducted at 20°C. These plants do not have stomata on their leaves, and stomatal conductance would roughly represent leaf-air conductance.

The light compensation point (LCP) and dark respiration rate (Rd) were obtained from the light-response curves. Average values of the 3 individuals is reported.

Table I. Average ± S.D. of hydraulic traits of *D. dendroides*, *Sequoia sempervirens* (gymnosperm), and *Bahuinia variegata* (woody angiosperm). a = data taken from Ambrose *et al.* 2009. b = data taken from Zhu & Cao 2009.

Tabla I. Promedios ± D.E. de rasgos hidráulicos de *D. dendroides*, *Sequoia sempervirens* (gimnosperma), y *Bahuinia variegata* (angiosperma leñosa). a = datos tomados de Ambrose *et al.* 2009. b = datos tomados de Zhu & Cao 2009.

Trait	*D. dendroides* (Bryophyte)	*S. sempervirens* (Gymnosperm)[a]	*B. variegata* (woody Angiosperm)[b]
Ks (Kg s^{-1} Mpa^{-1} m^{-1})	1.78 ± 0.3	1.1 ± 0.1	2.07 ± 0.1
Kl x 10^{-4}(Kg s^{-1} Mpa^{-1} m^{-3})	0.41 ± 1.3	5.3 ± 0.8	6.33 ± 0.4

Table II. Average ± S.D. gas exchange traits of *D. dendroides*. WUE_i = instantaneous water use efficiency. LCP = Light compensation point. Rd = dark respiration.

Tabla II. Promedios ± D.E. de intercambio de gases de *D. dendroides*. WUE_i = eficiencia en el uso del agua instantánea. LCP = punto de compensación de luz. Rd = respiración oscura.

Trait	Average ± S.D.
Amax (μmol m^2 seg^{-1})	2.5 ± 0.39
E (mmol m^2 seg^{-1})	0.72 ± 0.05
g_s (mmol m^2 seg^{-1})	603.6 ± 551.24
WUE_i	3.47 ± 0.50
LCP (μmol m^2 seg^{-1} PAR)	15.22 ± 3.30
Rd	2.33 ± 0.06

RESULTS

The stems of *D. dendroides* can reach high Ks and Kl (Table I). These specific hydraulic conductivity measures were highly dependent on moisture status. After a few minutes plants began to dehydrate and Ks dropped rapidly. After re-hydration Ks values increased (data not shown). Despite the high water conductivities, gas exchange parameters were relatively low (Table II).

DISCUSSION

The moss *D. dendroides* is a non-vascular plant. Nevertheless, this plant has a specialized vascular tissue that can achieve very high hydraulic conductivity (Table I). The Ks values for this moss are higher than many conifers and comparable to some angiosperms (Table I, Ambrose *et al.* 2009, Zhu & Cao 2009). The high Ks could partially account for the large plant height (for a bryophyte). Biophysically, a plant without vascular tissue can only reach a few centimeters high, because of the diffusion limitations that increase with plant size (Vogel 2003).

Despite the high Ks, Amax values were relatively low, but comparable to other Polytrichaceae of similar size like *Dawsonia superba* (Brodribb *et al.* 2007). Both the Kl and Amax found in *D. dendroides* are within the range of other studied mosses (Brodribb *et al.* 2007). The low Amax and E could be due to plant mechanisms to reduce photosynthesis when water potential drops, since they lack stomata in the gametophyte leaves to control water loss (Zeiger *et al.* 1987). The lack of stomata could also explain the high gs values since water is loss trough the whole surface of the leaf. This plant is usually found in understory, in relatively shaded areas (Atala & Parra, unpublished data). The relatively low Amax, LCP, and Rd also suggest that this is a shade-tolerant species, usually presenting intrinsically low carbon gain rates (Givnish 1988; Valladares & Niinemets 2008).

This non-vascular plant has an organized conducting tissue with high specific hydraulic conductivity. In the field this plant could functionally behave as a vascular plant, competing and sometimes dominating the understory in the temperate forest of Chile. More functional and ecological studies are needed to fully understand the ecophysiology of Polytrichaceae, particularly of *D. dendroides*.

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