Article

Characterizing and Quantifying Water Content in 14 Species of Bryophytes Present in Azorean Native Vegetation

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Abstract: Bryophytes are an important component of plant diversity, may be found from sea level to mountaintops, and are particularly conspicuous on the Azores islands. These plants rely on environmental water, which acquires intercepting rain and dew (liquid water) and uses fog (water vapor), and transports both externally, by capillary forces, and internally, in different cells (specialized or not). This study characterizes and quantifies the ability of six liverworts and eight mosses to retain water, through different pathways, and to lose water by evaporation. Twelve replicates of each species were collected in Azorean native vegetation during the summer of 2016. The absolute water content (AWC) was obtained through measurements of specimens saturated, without free water, and completely dry. Most of the 14-target species showed an ectohydric behavior pattern retaining more than 60% of water through gametophyte surface. The AWC value ranged from 646% in *Polytrichum commune* to 5584% in *Sphagnum subnitens*. The water loss by direct evaporation showed, for most of species, an exponential decay curve along time. Understanding how much native bryophytes, acquire, store, and release water into the system contributes not only to the knowledge of native vegetation resilience but also to potential impacts on the availability and quality of water—a major ecosystem service performed by bryophytes.

Keywords: ectohydric; endohydric; external conduction; internal conduction; elevational gradient; mosses; liverworts

1. Introduction

Unlike vascular plants, most bryophytes do not have an efficient internal water-conducting system [1] and absorb water over their entire surface [2]. Furthermore, they do not any have specific mechanisms to regulate water loss [3,4]. They are considered poikilohydric organisms, which means that their associated amount of water fluctuates in concert with the availability of water from their surroundings [5]. For bryophytes, their first contact with water starts when the tips of their stems and leaves contact with rain, fog, or dew [6], unlike vascular plants, where effective water contact starts with the root tips, in the soil, and is dependent of the soil's water availability. However, bryophytes are able to optimize their water uptake and use: when water is accessible, they quickly become hydrated and metabolize; when that resource is not available, they dry out and become dormant [5], but after rewetting, bryophytes recover their normal physiological activities [7]. Thus, in spite of their lack of mechanisms to retain water, their tolerance to desiccation is remarkable since many species possess tissues that can withstand complete desiccation without suffering injury [7], hence enforcing an effective survival strategy.

According to water relations (absorption and conduction), bryophytes have been distinguished into three physiological groups: endohydric, ectohydric, or myxohydric

species [8]. Endohydric species are more similar to vascular plants; they mainly absorb and conduct water internally, using a well-developed conducting strand and basal rhizoidal system (e.g., *Polytrichaceae*, some thallose liverworts) [8], achieving turgidity slowly [2]. Ectohydric species mostly absorb and conduct water externally, by the entire plant surface, through capillary forces (e.g., leafy liverworts and the majority of mosses) and they usually are hydrated within a few seconds [6,9]. Myxohydric species present features of both endohydric and ectohydric systems [8].

The total water content (WC: wet weight relative to dry weight) of bryophytes may be divided into two fractions, external and internal, and the latter subdivided into apoplast and symplast water. Externally, the water absorption and conduction are facilitated by several specialized surface characteristics of gametophytes [10] as leaf characteristics (e.g., length, sheathing base, concavity, divergence/spacing from the stem, margin rolling, orientation/disposition, nerve extension; papilla and mammilla) [8,11,12], creating an interconnecting network of capillary spaces [12]. This water could be seen as surface films on the leaves and as droplets in the leaf axils [10]. Internally, the water is located in the symplast, where it is held within the cytoplasm by osmosis [13–15] or in the apoplast, outside cell membranes, which includes all free space inside the plants (e.g., meatus, dead, empty cells), and also cell walls [16], where water is supported by matric forces. When desiccation occurs, bryophytes gradually lose water starting with external, apoplastic, and symplastic water. Authors refer to water held in cell walls as the most difficult water to be lost [17]. According to Proctor [15] the proportions of these components vary greatly among different bryophytes, and each species may present different water retention abilities.

The distribution and movement of water within bryophytes, as well as water loss, is variable and may be influenced by several structures and traits. Externally, it is determined by the organization of the plant, as the colony size and density, and also by branching patterns and leaf arrangements [10]. Internally, the water distribution and movement are partly determined by the geometry of the capillary spaces [13]. These may differ even among species since many species have plasticity, meaning they are able to perform structural adaptations, such as adjust shoot density, branching intensity and many other traits in response to environmental conditions [12,18]. These adaptations facilitate the movement of water and its absorption and reduce its loss [6]. For instance, species of the genus *Polytrichum* present denser patches, with small shoots as an adaptation of reduced water availability [19,20], and like many other mosses, they closely appress their leaves to stem, avoiding water loss [21]. Thus, water content varies among species, reflecting habitat preference and architecture.

The literature shows that bryophytes store most of their water externally (see revision in Proctor [15,17,22]). In the particular case of *Sphagnum* spp., plants have arrangements of shoots, branches, and leaves that enable them to conduct external water efficiently [13,23]; internally, they possess hyaline porose cells that hold large amounts of water [24]. Some species have other arrangements, differing in their ability to store water. Working with 20 species (although not *Sphagnum* spp.), Dilks and Proctor [13] found that, at full saturation (excluding external water), the water content of mosses varied between 141% (*Anomodon viticulosus* (Hedw.) Hook. and Taylor) and 516% (*Hookeria lucens* (Hedw.) Sm.) while the values for liverworts varied between 210% (*Bazzania trilobata* (L.) Gray) and 1180% (*Pellia epiphylla* (L.) Corda) of dry weight (dw). More recently, an experiment by Zotz and colleagues [25] with a desiccation-tolerant species, *Grimmia pulvinate* (Hedw.) Sm., showed that when the plant was air-dried it presented water content values around 22% dw, and when fully saturated the same cushions reached up to 730% dw. On the other hand, a hydrophilous species such as *Brachythecium austro-salebrosum* (Müll. Hal.), may reach water content values around 3560% dw [26].

The hydration status of bryophytes will depend both on the amount of water stored and the rate at which that water is lost since bryophytes do not regulate evaporation rates [27]. In fact, the hydration status of these plants depends on factors such as air temperature, relative humidity, vapor pressure deficit, radiation, and wind speed of habitats, as

well as the plant phenology and water use efficiency [12,28,29]. However, many species are able to retard water loss, growing in complex structures that help to maintain humidity [30]. Köhler and colleagues [31] studied the water storage dynamics of several epiphytes recording bryophytes' water content values ranging from 36% to 418% dw. Starting with 3 days of sunny weather without rain or fog, the drying out and water contents decreased by 251% dw [31].

The Azores are not often associated with water shortage due to the high average annual precipitation (1930 mm/yr), which far exceeds the average annual evapotranspiration (581 mm/yr) [32,33]. In addition, the presence of peatlands at mid-elevation in the central part of most islands is important for water storage, and for releasing water into the environment in times of drought (summer months) [34]. Nevertheless, the drainage system is influenced by factors such as geology or vegetation integrity. Due to the geological structure of the subsoil (young volcanic lava), an important amount of water is lost by runoff. In addition, human impacts on vegetation may directly influence the soils infiltration, ability, and the micro-topography of the land [34], and some of the Azorean islands, such as Terceira, have repeatedly suffered from water shortages (e.g., 1992; 2005) [35].

In the face of climate change, future scenarios indicate that on islands, not only is temperature predicted to increase but also rainless periods are predicted to become more frequent [36], with serious consequences for biodiversity. Recently Patiño and colleagues [37] assessed the potential distribution of the 35 Macaronesian endemic bryophytes under present and future (2070) climate conditions; those projections show the potential extinction of six Macaronesian endemic species, while some of the now commonest species would fall into vulnerable (VU) or endangered (EN) IUCN categories.

Bryophytes are prevalent in Azorean vegetation, where they present higher richness of indigenous species than vascular plants [38,39]; nevertheless, they are comparatively less studied, although their role in several ecosystem processes, namely water retention, is of paramount importance. Understanding how much native bryophytes store and lose water will contribute to the knowledge of how resilient the native vegetation will be in face of climate change and the potential impact on one major ecosystem service performed by these plants: the availability and quality of the water resource. Thus, this work focuses on the plant community level, where the external water is extremely important, and not on the plants themselves and their individual cells, which various studies have previously investigated [12,13,15,40].

This study aims to characterize and quantify the ability of fourteen indigenous bryophytes (six liverworts and eight mosses) common and abundant in native Azorean vegetation, to retain water, through different pathways, and to lose water by evaporation. The main question of the present study is: Can water relations and evaporation in bryophytes be explained by their morphological features/body architectures (internal and external structures)? While the specific research questions are:

1.　How will absolute water content (AWC) vary among the selected species?
2.　Which pathway, ectohydric (external) or endohydric (internal), retains the most water? How are these pathways related to the morphological features of the species?
3.　How fast do bryophytes lose their water through direct evaporation and how much do they lose?

A standardized procedure/methodology from the field to the lab is proposed (Appendix C) for the measurements of absolute water content (AWC), internal water content (WCInt), and external water content (WCInt).

2. Materials and Methods

2.1. Study Sites

This study was conducted on Terceira Island (38°40′ N; 27°20′ W; 0.4 MY [41]), the third largest (402 km^2; 1021 m a.s.l) and the second most populated [42] of the nine islands of the Azores (Portugal). This volcanic archipelago is located in the North Atlantic Ocean, between the European and the North American continents [43]. Terceira Island presents

55% of its surface below 300 m a.s.l., 42.5% between 300 m and 800 m, and 1.9% above the 800 m a.s.l. [34].

Samples were collected on three sites, along an elevational gradient, located on the western side of the island, within the limits of the Natural Park of Terceira [44]. The Natural Park encloses the best-preserved native vegetation areas, avoiding highly disturbed and modified areas, and has a rich and diverse bryophyte flora. The three collection sites were: Farol da Serreta (FS, 40 m a.s.l.); Pico da Lagoínha (PL, 683 m a.s.l.); and Serra de Santa Bárbara (SSB, 1012 m a.s.l.) near the highest point of the island. At lowland, Farol da Serreta, presents a coastal vegetation of relatively low stature (up to 300 cm), with monostratified and poor floristic communities composed mostly of *Erica azorica* with *Frullania acicularis* and *Trichostomum brachydontium* growing on basaltic rock. Average annual precipitation at Farol da Serreta is 95.98 ± 29.48 mm and average mean temperature is 17.21 ± 3.12 °C [43]. The mid-elevation site, Pico da Lagoínha, presents a *Laurus* submontane forest of relatively high stature (up to 800 cm), dominated by *Laurus azorica*, *Juniperus brevifolia,* and *Ilex azorica,* covered with *Plagiochila bifaria* and *Myurium hochstetteri*, among many others. Average annual precipitation at Pico da Lagoínha is 265.91 ± 108.29 mm and average mean temperature is 12.64 ± 3.30 °C [43]. The highest-elevation site, Serra de Santa Bárbara, exhibits dense patches of dwarfed (up to 160 cm), semi-prostrate *J. brevifolia* specimens, covered with different mosses and liverworts, such as *Scapania gracilis* and *Herbertus azoricus*. Average annual precipitation at this site is 326.46 ± 150.69 mm and average mean temperature is 10.74 ± 3.24 °C [43]. A thorough description of each site may be found in Henriques and colleagues [45].

2.2. Study Species

Fourteen indigenous species were selected for this study: six leafy liverworts, division Marchantiophyta—class Jungermanniopsida; and eight mosses, division Bryophyta—class Sphagnopsida (one species), class Polytrichopsida (one species), and class Bryopsida (six species) (*cf.* Table 1; Appendix A). Apart from taxonomic diversity, it was aimed to represent some of the most common and abundant bryophytes of native Azorean vegetation, not only to achieve a good representation of the species of the system but also to ensure that the populations were able to sustain the collecting pressure. Locally, each species represented the highest bryophyte biomass present on site, and could non-negligibly contribute to important ecosystem services, such as water retention and storage.

Table 1. Classification of the 14 Azorean species selected for this study. Classification is presented according to division (Div.), class, order, family, species, status of colonization according to Gabriel et al. (2010) [38] (END, endemic species to the Azores; MAC, endemic species to Macaronesia; NAT, native non–endemic species) and Sampling sites (FS, Farol da Serreta; PL, Pico da Lagoínha; SB, Serra de Santa Bárbara).

Div.	Class	Order	Family	Species	Colonization Status	Sampling Sites	Life Forms
Marchantiophyta							
	Jungermanniopsida						
		Jungermanniales	Herbertaceae	*Herbertus azoricus* (Steph.) P.W.Richards	END	SB	turfs
			Lepidoziaceae	*Bazzania azorica* H.Buch and Perss.	END	SB	wefts
				Lepidozia cupressina (Sw.) Lindenb. Subsp. *cupressina*	NAT	SB	wefts
			Plagiochilaceae	*Plagiochila bifaria* (Sw.) Lindenb.	NAT	PL, SB	turfs
			Scapaniaceae	*Scapania gracilis* Lindb.	NAT	PL, SB	wefts
		Porellales	Frullaniaceae	*Frullania acicularis* Hentschel and von Konrat	NAT	FS, PL, SB	mats
Bryophyta							
	Sphagnopsida						
		Sphagnales	Sphagnaceae	*Sphagnum subnitens* Russow and Warnst.	NAT	PL	turfs
	Polytrichopsida					SB	
		Polytrichales	Polytrichaceae	*Polytrichum commune* Hedw.	NAT		turfs

Table 1. *Cont.*

Div.	Class	Order	Family	Species	Colonization Status	Sampling Sites	Life Forms
	Bryopsida						
		Dicranales	Leucobryaceae	*Campylopus brevipilus* Bruch and Schimp.	NAT	FS	cushions
				Campylopus shawii Wilson	NAT	SB	turfs
			Pottiaceae	*Trichostomum brachydontium* Bruch	NAT	FS	turfs
		Hypnales	Lembophyllaceae	*Isothecium prolixum* (Mitt.) M.Stech, Sim-Sim, Tangney and D.Quandt	MAC	PL	wefts
			Myuriaceae	*Myurium hochstetteri* (Schimp.) Kindb.	NAT	PL	mats
			Thuidiaceae	*Thuidium tamariscinum* (Hedw.) Schimp.	NAT	PL	wefts

Due to a time-consuming cleaning procedure in the lab to obtain field weight (described in Section 2.4) and the time constraint of this study, only 14 species were selected, including 12 replicates, manageable for this first study on the quantification of water content of bryophyte in the Azores.

All records were confirmed in the lab, and exsiccated samples are kept in the Cryptogams' collection of the University of Azores (Herbarium code: AZU).

2.3. Sampling Procedure

In June 2016, 12 replicates of *c.* 25 cm^2 of the 14 selected bryophyte species were taken from the three field stations. Specimens were gathered as they were, either wet or dry, into sealed polyethylene vials, previously marked and weighed. Mosses were mostly collected from soil and rocks, except *Isothecium prolixum* and *Myurium hochstetteri*, growing on *Laurus azorica*, while liverworts were all epiphytic, growing on bark of the three commonest tree species (*L. azorica*, *Juniperus brevifolia*, and *Ilex azorica*).

2.4. Processing Samples in the Laboratory

The identifications of all the bryophyte specimens were confirmed in the laboratory by the first two authors, M.C.M.C. and R.G., with the aid of a stereo microscope (Leica Mz12.5), a light-microscope (Leica DM750), and different floras and identification keys [46–51]. Nomenclature follows the latest Azorean checklist [38], with taxonomic updates [52].

In the laboratory, after cleaning fresh green shoots under a stereomicroscope to remove the non-target materials (e.g., other bryophyte species, vascular fragments, soil, and litter) thus avoiding overestimating water content, samples were weighed on an electronic scale (COBOS A-150-SX, precision 0.001 g) to obtain the field weight. This process was necessary since, mostly in the richest sites, bryophytes usually grow intertwined with other species, making it difficult to find pure populations. During the cleaning stage, the species evaporated a few milligrams of water, but this was acknowledged, and due corrections were made (*cf.* Appendix B).

After cleaning, samples were submersed in water (*c.* 12 consecutive hours) to reach full turgor. Then, the specimens were left to drain the excess of water over 4–6 wires, about 15 cm from the table, until they dripped less than a drop per minute [28]. When they reached this stage, each specimen was weighed to obtain saturated weight (Ms), which accounted for all the water retained in the external capillarity spaces, as bryophytes are able to do in their colonies.

The Internal water content weight (Ma) was determined by weighing the samples after gently blotting them with absorbent paper to remove external water until no droplets of water were seen on the shoots [53]. According to Santarius [54] blotting generally gives more reliable estimates of full-turgor water content than centrifuging. Finally, samples were oven-dried for 48 h at 100 °C and weighed to determine specimens' dry weight (Md) [55].

All species were photographed in order to better visualize the architectural organization of space for water (*cf.* Appendix A).

A summary of these procedures may be seen in Appendix C (Table A1).

2.5. Data Analysis

2.5.1. Water Content

The water content expresses the amount of water retained, in different fractions, by each species in percent of dry weight (dw). Water content determination was adapted from Watkins and colleagues [53] and presented as a % of dry weight, as follows:

$$\text{Absolute Water Content (AWC; \% dw)} = Ms/Md \times 100 \tag{1}$$

In which, Ms is the saturated weight and Md is the dry weight after drying the plants in oven (100 °C during 48 h). This variable expresses the maximum water content supported by the whole plant in percent of dry weight.

$$\text{Internal Water Content (wCint.; \% dw)} = Ma/Md \times 100 \tag{2}$$

In which, Ma is the weight after absorption of external water through blotting and Md is the dry weight after drying the plants in oven (100 °C during 48 h). This variable expresses internal content of water supported by each species in percent of dry weight.

In which, Ms is the saturated weight and Md is the dry weight after drying the plants in oven (100 °C during 48 h). This variable expresses the maximum water content supported by the whole plant in percent of dry weight.

$$\text{External Water Content (wCext.; \% dw)} = (\text{AWC} - \text{wCint.}) \times 100 \tag{3}$$

In which, AWC is absolute water content and wCint. is internal water content. This variable expresses the external water content supported by each species in percent of dry weight.

2.5.2. Direct Evaporation Rate

The bryophytes' water loss by direct evaporation was estimated by recording the weight changes in samples. A set of five replicates per species was collected on April 2017 in the same places and circumstances as in the previous essay. Field samples, were fully hydrated (24 h) and exposed to ambient room temperature (21 °C $\pm$ 1 °C) and ambient room relative humidity (55% $\pm$ 5%) while weights were recorded at set time intervals (0′, 1′, 3′, 5′, 7′, 10′, 15′, 30′, 45′, 60′, 90′, 150′, 720′ [12 h], 1080′ [18 h], 1440′ [24 h], 2160′ [36 h], 2880′ [48 h] and 3600′ [60 h]). In the end, samples were oven-dried for 24 h at 100 °C. The observed differences in sample weight and oven-dry weights allowed the determination of the corresponding water loss (g) and respective evaporation rate (g/min).

2.5.3. Statistical Analysis

Since assumptions of normality were not satisfied for all water content values, even when using a logarithmic transformation of the data, the differences within and between the two pathways among the studied species were tested using multiple comparison tests through the non-parametric ANOVA—Kruskal–Wallis test.

Spearman rank correlation (rs) was calculated among AWC, wCint. and wCext. Kruskal–Wallis tests and Spearman rank correlation (rs) analyses were performed using SPSS (IBM SPSS Statistics 24).

3. Results

A total of 72 specimens of liverworts and 96 specimens of mosses were collected from the three studied native vegetation sites.

3.1. Absolute Water Content in Azorean Native Bryophytes

The absolute water content (AWC) of bryophytes varied among the selected species, ranging from 646% dw (*Polytrichum commune*) to 5584% dw (*Sphagnum subnitens*), almost a 10-fold difference; the other species lie between these values.

Within Marchantiophyta (Figure 1), *Herbertus azoricus* and *Lepidozia cupressina* showed the lowest and highest value of AWC, respectively, and these values were significantly different ($p < 0.05$) from all other liverworts.
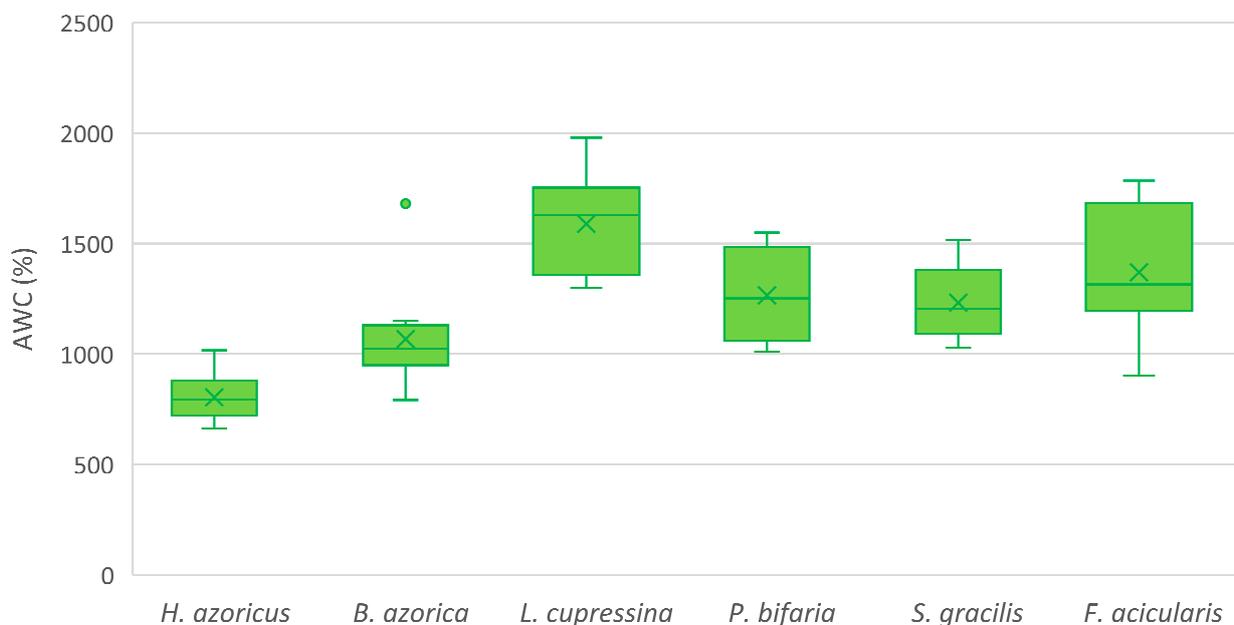
Figure 1. Boxplot of absolute water content (AWC) for the six selected leafy liverwort species (division Marchantiophyta). Values were estimated from 12 replicates per species, collected at Serra de Santa Bárbara, Terceira Island (1012 m a.s.l.).

The liverworts *Bazzania azorica*, *Plagiochila bifaria*, and *Frullania acicularis* did not show significant differences in their AWC ($p > 0.05$) among them.

Within Bryophyta (Figure 2), the moss *Sphagnum subnitens* (class Sphagnopida) presented the highest ability to hold water ranging from 4752% to 6354% while the moss *Polytrichum commune* (class Polytrichopsida) showed the lowest ability to hold water, showing a range of values from 481% to 825%. Within class Bryopsida, the pleurocarpous mosses *Isothecium prolixum* and *Myurium hochstetteri* presented, respectively, the lowest and the highest AWC values, which were always significantly different ($p < 0.05$) from the AWC of the remaining species. In fact, the moss *Myurium hochstetteri* (AWC = 2201% dw) exhibited the second highest value of AWC, following *Sphagnum subnitens*, although presenting less than half of *S. subnitens*' water-holding ability.

Of the 168 collected specimens, a quarter had an AWC below 1000% dw and around 60% had an AWC between 1000–2000% dw. Only 14% of specimens showed an AWC above 2000% and all replicates of *S. subnitens* belong in this range.
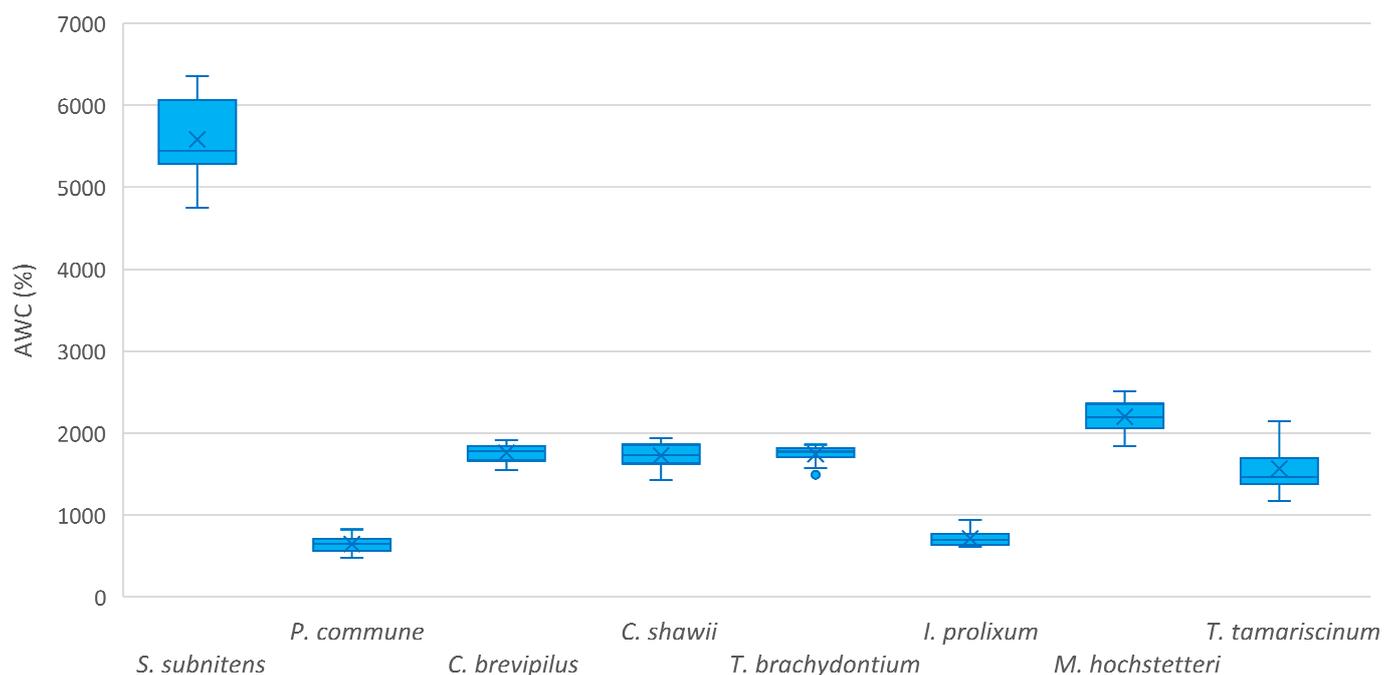
Figure 2. Boxplot of absolute water content (AWC) for the eight selected moss species (division Bryophyta). Values were estimated from 12 replicates per species. Acrocarpous mosses *Campylopus brevipilus* and *Trichostomum brachydontium* were collected at Farol da Serreta (40 m, a.s.l.); *Campylopus shawii* was collected at Serra de Santa Bárbara (1012 m a.s.l.); and remaining species were collected at Pico da Lagoínha (683 m a.s.l.), Terceira Island.

3.2. Internal and External Water Content in Azorean Bryophytes

All species showed a higher ability to hold water externally than internally (Figure 3). The mosses, that included the extremes of this distribution, were *Sphagnum subnitens* and *Myurium hochstetteri* which retained externally about 90% of the total water, while on the other hand *Polytrichum commune* and *Isothecium prolixum*, held externally around 60% of total water. The amount of external and internal water sustained by the six liverwort species is remarkably similar among them.

Among the analyzed species, the internal water content (wCint.) and the external water content (wCext.) were significantly different ($p < 0.05$) between classes Jungermanniopsida, Sphagnopsida, Polytrichopsida and Bryopsida, within each pathway (Table 2). The highest average wCint. values were recorded for Sphagnopsida and the lowest ones for Polytrichopsida. The six species of class Jungermanniopsida exhibited higher values of wCint. than the six species of class Bryopsida, and rather close for all species. For wCext., Sphagnopsida and Polytrichopsida kept the pattern with the highest and the lowest average values recorded, respectively. The class Bryopsida presented higher average wCext. values than Jungermanniopsida class.
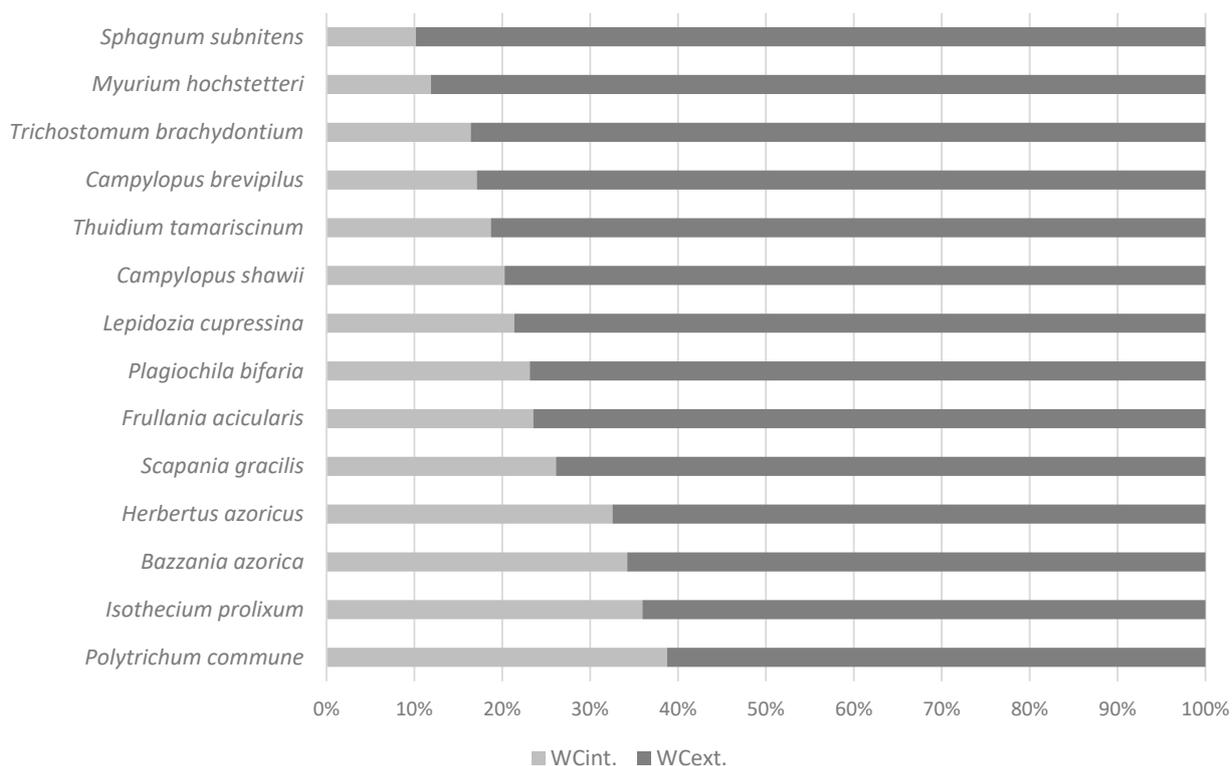
Figure 3. Percentage of internal water content (wCint.) and external water content (wCext.) per dry weight of each species collected from three different sites on Terceira Island, Azores.

Table 2. Average and standard deviation (StD) of absolute water content (AWC), internal water content (wCint.) and external water content (wCext.) per dry weight of each species (*n* = 12), collected from three different sites on Terceira Island. Species are identified by division and class.

Div.	Class	Species	AWC ± StD (%)	wCint. ± StD (%)	wCext. ± StD (%)
Marchantiophyta					
	Jungermanniopsida				
		Herbertus azoricus (Steph.) *p.*W.Richards	804 ± 103	262 ± 20	2542 ± 099
		Bazzania azorica H.Buch and Perss.	1067 ± 217	365 ± 65	702 ± 166
		Lepidozia cupressina (Sw.) Lindenb.	1589 ± 215	340 ± 13	1250 ± 214
		Plagiochila bifaria (Sw.) Lindenb.	1265 ± 200	301 ± 21	999 ± 232
		Scapania gracilis Lindb.	1232 ± 163	322 ± 17	910 ± 164
		Frullania acicularis Hentschel and von Konrat	1370 ± 293	322 ± 35	1048 ± 276
Bryophyta					
	Sphagnopsida				
		Sphagnum subnitens Russow and Warnst.	5584 ± 471	567 ± 47	5017 ± 455
	Polytrichopsida				
		Polytrichum commune Hedw.	646 ± 104	250 ± 13	395 ± 98
	Bryopsida				
		Campylopus brevipilus Bruch and Schimp.	1761 ± 113	301 ± 11	1460 ± 109
		Campylopus shawii Wilson	1727 ± 154	356 ± 12	1400 ± 213
		Trichostomum brachydontium Bruch	1743 ± 111	286 ± 08	1457 ± 109
		Isothecium prolixum (Mitt.) M.Stech, Sim-Sim, Tangney and D.Quandt	714 ± 95	282 ± 19	503 ± 253
		Myurium hochstetteri (Schimp.) Kindb.	2201 ± 199	261 ± 12	1939 ± 197
		Thuidium tamariscinum (Hedw.) Schimp.	1568 ± 313	293 ± 28	1275 ± 299

Within class Jungermanniopsida, *Herbertus azoricus,* and *Bazzania azorica* presented the lowest and highest wCint., respectively. Regarding wCext. the minimum value was also registered for *Herbertus azoricus*, while the maximum was achieved by *Lepidozia cupressina* (Table 2). Among the species of class Bryopsida, *Myurium hochstetteri,* and *Campylopus shawii* presented the lowest and highest wCint., respectively. The minimum wCext. was recorded for *Isothecium prolixum* while *Myurium hochstetteri* showed the maximum value (Table 2).

3.3. Rate of Water Loss

When subject to air temperature (21 °C ± 1 °C) and ambient room relative humidity (55% ± 5%), the water content of the selected bryophyte species showed, for most of them, an exponential decay curve along time (Figure 4).

All species showed the highest evaporation rate in the first minute of air exposition. At one minute the evaporation rate within each class was 0.76 g/min for Jungermanniopsida, 0.84 g/min for Sphagnopsida, 0.04 g/min for Polytrichopsida, and 0.52 g/min for Bryopsida (Appendix D). At 60 min, the evaporation rate within each class was 0.02 g/min for Jungermanniopsida, 0.05 g/min for Sphagnopsida, 0.01 g/min for Polytrichopsida, and 0.03 g/min for Bryopsida (Appendix D). The mosses *Sphagnum subnitens* and *Polytrichum commune* kept the pattern, losing more and less water, respectively. The liverworts (Jungermanniopsida) exchanged with mosses; they lost less water than Bryopsida.

The percentage of water loss, in relation to the initial water content, during air exposition is variable among species. The moss *Polytrichum commune* was the species that lost less water at the beginning (minute 1: 1%) and at the end (minute 3600: 83%) of the experiment (Appendix D). The moss *Thuidium tamariscinum* started to lose the highest amount of water (minute 1: 12%) among the remaining species, but the highest amount of water lost at the end was recorded for the liverwort *Scapania gracilis* (minute 3600: 98%) (Table A2), meaning it was almost totally dehydrated.

The moss *Sphagnum subnitens* retained its free water for the second longest time; after 150 min it had only lost a quarter of its water content (26%), while most of the other species had already lost more than 40% of their water contents (Tables A2 and A3).

After 60 min of air exposition, bryophytes from different classes diverged among water content lost: 36% (Jungermanniopsida), 20% (Sphagnopsida), 11% (Polytrichopsida), and 31% (Bryopsida) (Table A3).

Within each class, significant differences ($p < 0.05$) in weight were recorded between minute 1 and minute 1440 (Figure 4). Regarding sites, the water content showed to be significantly different ($p < 0.05$) between species collected from Pico da Lagoínha and Serra de Santa Bárbara. The water loss was significantly different ($p < 0.05$) between Farol da Serreta—Pico da Lagoínha and between Farol da Serreta—Serra de Santa Bárbara. The evaporation rate showed significant differences ($p < 0.05$) between Pico da Lagoínha and the remaining sites.
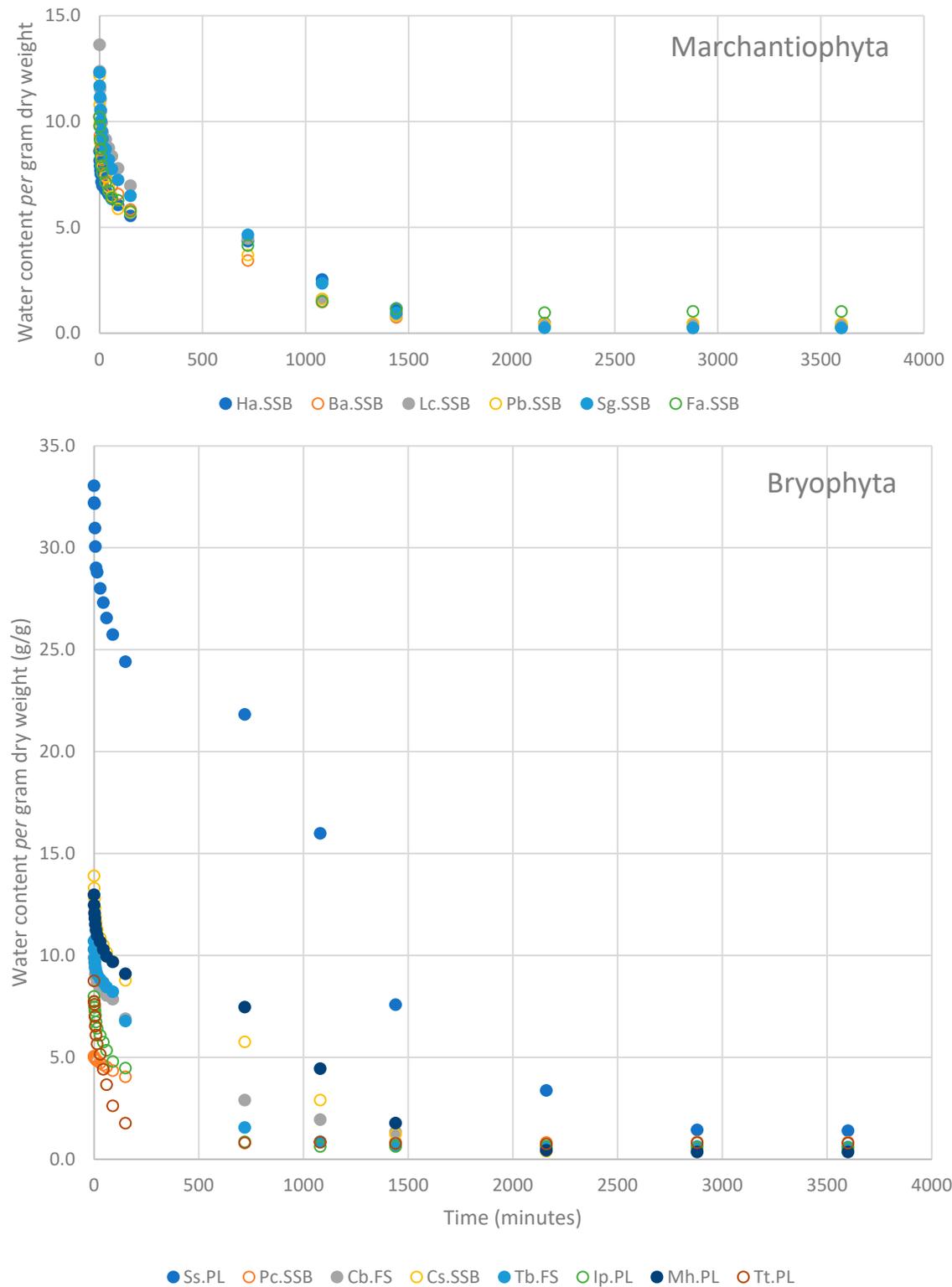
Figure 4. Water content decay of different liverwort (Marchantiophyta) and moss (Bryophyta species. Data represent the average of five replicates per species collected from three different sites (FS: Farol da Serreta; PL: Pico da Lagoínha; SSB: Serra de Santa Bárbara) on Terceira Island, Azores. Species abbreviations are made with the first letter of the two-word Latin name and sites.

4. Discussion

All bryophyte species can hold an important amount of water through a variety of internal and external structures. A selection of 14 bryophyte distinct species, commonly occurring in native vegetation on the oceanic Azorean Islands, from two divisions and four classes were analyzed regarding their water relations with the aim of assessing the range of their absolute water content (AWC) and which pathway—external or internal (including apoplast and symplast)—was favored by each species.

As expected, results regarding AWC vary widely in accordance with the different species. They are bound by the values presented by *Polytrichum commune* (AWC = 646% $\pm$ 104%) and *Sphagnum subnitens* (AWC = 5584% $\pm$ 471%), but the values of Jungermanniopsida and Bryopsida are much more similar among themselves, suggesting a taxonomic convergence in bryophytes' ability to hold water. In the present study, all species exhibit AWC values above 600%, which are much larger than the values reported in the literature for the same (or congeneric) species that range from 95–125% (*p. commune*) to 1225% (*S. subsecundum* Nees) (revision in Glime [56]), although other studies present higher values for other Sphagnaceae (e.g., Jauhiainen and colleagues [57]). Other species, present different values, from 434% (*Bazzania azorica*) to 790% (*Myurium hochstetteri*) [58]. The correlation between AWC values provided by different studies is high between same studied species (R^2 = 99.96%; *n* = 4 species [56]; R^2 = 69.48%; *n* = 5 species [58]; R^2 = 78.54%; *n* = 8 species (combined studies)). These differences are probably related to methodological procedures, namely the method used to stabilize the plants' weight, since there is not a common standardized method to calculate the saturated weight of samples, neither for the blotting procedure to assess the W_{int}. Some authors, aiming at establishing the ecological role of bryophytes on the ecosystems, use dripping to estimate the equilibrium water held externally—a soft method that allows the full occupation of the external network within and between the shoots (e.g., Ref. [28]). In other studies, species were gently blotted with tissue paper (e.g., Refs. [59,60]) or centrifuged (e.g., Refs. [13,26]) to obtain their full-turgor value, which remove part of the external water associated with the patch, while focusing on the plant's intrinsic characteristics. This study measured both the water absorbed within and the water retained on the surface of the thallus or leaves. Hence, the AWC values of the bryophytes reported here are higher than the average water-holding capacities reported in the literature, and possibly more in tune with what happens in the ecosystems.

The cellular structure and the complex architecture of some bryophytes may reinforce the internal and external water-holding ability of the species. For instance, among the 14 analyzed species, *S. subnitens* plants far exceed all others for water held, both externally and internally. The efficiency of the "external compartment" is likely to be related to the high number of ramifications of each shoot, which include an apical *capitulum* of short branches, as well as pendent and divergent branches along the stem (*cf.* Appendix A, A07 item), thus allowing water molecules to occupy this network of external space. Moreover, its growth in dense cushions increases the water retention ability and decreases water evaporation [61]. The very well-known and important ecological role played by *Sphagnum* species (e.g., Ref. [62]) is a consequence of their biological structure and architecture. Not only do the external traits of *Sphagnum* promote an extraordinary water-holding ability, but also its internal structure, with hyaline cells, most of them with pores (interruptions of the cell wall), dead and empty at maturity, are also very well adapted to hold water [63]. Other studies found that most of the water blotted from *Sphagnum* samples is inside the hyaline cells (90% [64]; 53–77% [23]).

In the present study, external water content represents 90% of the water-holding ability of *S. subnitens* (Figure 3), meaning that its external capillary water fraction considerably exceeds the other fractions. The remaining 10% of water is required for the functioning of chloroplasts for photosynthesis (Proctor, 2000a). This amazing ability to hold water is shared by different species of the same genus and was reported in several studies that indicate values of maximum water content per dry weight (dw), which are of the same order of magnitude as the results presented here. For instance, at the beginning of the

20th century Nichols specified values of 2200% dw for *Sphagnum* pads, used as bandages in World War I [65]. Values from 1812% dw were reported for *S. fuscum* (Schimp.) H. Klinggr. and 3410% dw for *S. papillosum* Lindb. [66]. However, a recent study of Hajek and Beckett [23] did not record such high values (421% dw in *S. cuspidatum* Ehrh. ex Hoffm. to 774% dw in *S. magellanicum* Brid.).

According to the evidence gathered in this study, AWC appears to be remarkably constant within the genus *Campylopus*, since the two species (*C. brevipilus* and *C. shawii*) showed no significant differences in their AWC, even considering that their habitat is quite distinct (coastal and forest, respectively), and they have different life forms (cushion and turf). In fact, some of their internal structures are similar, such as the structure of the shoot, cells, wall's length, etc. (*cf.* Appendix A, A09 and A10 items) indicating the conservation of these traits within the genus. In view of this information, and also in view of what has been described in the literature with Sphagnaceae and Polytrichaceae, it is hypothesized that there is a conservation of water relations at the taxonomic level.

The acrocarpous moss *Polytrichum commune* expressed the lowest ability to hold water, both internally and externally. This species behaves as an endohydric plant, with a well-developed internal conducting system and a complex cuticle (*cf.* Appendix A, A08 item). These characteristics make Polytrichaceae more similar to vascular plants, when considering their water relations [17,67]. The moss *P. commune* was expected to be the species that would achieve the highest internal water content because of its well-developed internal central strand, with specialized hydroids, that several authors propose as water conducting cells [14,67]. According to Hébant (Ref. [68]; see also [4]) the highest internal water conduction recorded, in Polytrichaceae, was 67% of the total conduction (at 70% relative humidity). Indeed, the internal water fraction achieved by this species represents almost 40% of its total water retention; the highest value associated with endohydric water conduction (Figure 3). The lowest external water content was also expected due to the presence of water-repellent wax cover on leaves [14], which decreases the ability to absorb high amounts of water externally; this would also lead to the hypothesis that *P. commune* shoots would evaporate water slower. According to Bayfield [69] both of the water conduction pathways are important, and their functioning is influenced by environmental conditions; if the atmosphere is dry and evaporation is high, the internal conduction will be the most important, while in a wet atmosphere with abundant soil water, the external pathway will be the most used. The full-turgor water content values showed by *P. commune* corroborate the values obtained on Fowbert [26] experiments for *P. alpestre* Hoppe (maximum water content 620% dw) but differ from the values found by Proctor [17] for *P. commune,* at full turgor, (179% water content per dw).

Leafy liverworts generally present a more delicate cellular structure than mosses (*cf.* Appendix A) and their AWC range was less pronounced than among mosses. For example, the samples of *Bazzania azorica*, exhibit AWC values of 1067%, which is in accordance with other studies where *Bazzania* spp. from coniferous forests in North America [70] or cloud forests in the Mascarenes [71] achieved values of 1300% dw and 1074% dw, respectively. However, Proctor [40] observed a maximum AWC achieved by *B. trilobata* as only 253% dw. The WCint. and WCext. of *B. azorica* seems also to be in accordance with Cleavitt and colleagues [72], where *B. trilobata* holds internally around 84% dw and externally around 126% dw. Another weft-forming liverwort, *Lepidozia cupressina*, exhibited the highest AWC values among liverworts, holding around 1589% of its dry weight, a value higher than that found in Australian ash forests (990% dw) [73]. Records of *Frullania tamarisci* AWC from Proctor and colleagues [17] are much lower (134% dw) than those obtained in this study for a closely related species, *F. acicularis* (1370% dw), although both species possess tightly overlapping leaves as well as sac-like lobules that help in holding water (*cf.* Appendix A, A06 item).

In general, the species that showed the highest ability to hold water have a more complex architecture, that allows them to increase the water stored by the creation of an interconnecting network of capillary spaces (*cf.* Appendix A). Further than *S. subnitens*, the

species *Lepidozia cupressina*, *Frullania acicularis*, *Campylopus brevipilus* and *Myurium hochstetteri* grow in dense mats, cushions, or patches. The liverwort *L. cupressina* presents pinnately branched stems with appressed and overlapping leaves [46]. The moss *Campylopus brevipilus* has long, straight, and erect leaves (when moist) with a wide nerve near the base, and *Myurium hochstetteri* presents concave leaves on erect and swollen branches [47,51].

The studied bryophytes species exhibit differences in their water loss but overall follow the same pattern of an exponential decay curve with time. This could be related to their complex structures and that, after a first loss of superficial (free) water, the species will release water in a constant but not linear way.

The bryophyte species with a more extensive surface area in contact with air are, on one hand, better suited for intercepting water but on the other hand, they will lose water more easily [74]. This pattern was observed for the mosses with loose and open structures, namely *Polytrichum commune*, *Isothecium prolixum,* and *Thuidium tamariscinum* which reduced most of their water content in the first 150 min of air exposition. *Sphagnum subnitens* was the second longest species to lose water. In addition to the large water-holding capacity, *Sphagnum* spp. is capable of supplying the top parts (capitulum) with water from below by capillary rise [75]. Its architecture together with its compact and dense growth form may influence water loss. This species also possesses large hyaline cells and is therefore less affected by the direct evaporation of the free water on its surface. In the study by Heijmans and colleagues [75] major differences in moss evaporation between the species were recorded mainly in dry moments where the *Sphagnum* moss presented the largest loss.

Within the Azorean forests, bryophyte communities probably would take more days to dry out completely because apart from the density of the surrounding vascular vegetation and the favorable climate variables (average high levels of humidity (RH > 90%), annual regular precipitation (>3000 mm), mild temperatures (*c.* 12 °C), low radiation inputs and vapor pressure deficit (<32 Pa)), their most complex architecture (e.g., cushions of mixed species with mixed growth forms) results in greater water holding capacity and lower evaporation rate [76,77]. Heijmans and colleagues [75] found that the habitat had a very strong influence on moss evaporation (0.3, 0.9, and 1.5 mm/day in the dense forest (*Hylocomium*), open forest (*Hylocomium* and *Sphagnum*), and bog (*Sphagnum*), respectively).

Summarizing, all the Azorean studied species demonstrated an ability to hold considerable amounts of water and lose it slowly by direct evaporation. *Sphagnum subnitens* champions water retention both internally and externally. The mosses *P. commune, I. prolixum*, and the liverwort *H. azoricus* showed a lower capability to hold water, but even as lower contributors to the water economy of the ecosystems, these species can potentially add respectively, 6, 7, and 8 g of water per gram of dry weight. These records are higher but in the same order of magnitude as those estimated by Frahm [78] which indicates values of water storage between 2.5 and 3.5 of dry weight, which may be related to the appraisal of different species, and their different storage ability. In addition, different approaches to measuring water content could have influenced the final results.

External water showed to be the highest fraction of water held by these 14 Azorean bryophyte species. It is important to the overall functioning of the plant more than to the internal functioning of the bryophyte because the variation takes place over a narrow range of near-zero water potentials, leaving cell function unaffected [15]. This means that species satisfy their own needs (metabolism of the individual cells) and then are able to promote a suitable habitat, making available this non-negligible fraction of water that benefits other plants, animals, and simply the habitat.

Further studies should demonstrate and quantify the importance of the structures and complex architecture of bryophytes (e.g., number of ramifications, gametophyte height, and width, presence or absence of hydroids and leptoids), as responsible for different water retention abilities among species. It would also be of paramount importance to test the hypothesis advanced in this study, that there is a phylogenetic conservation of retention of water-related traits. Another interesting study could examine the photosynthetic efficiency

of plants with the dry down curves, and how fast they recover, or if they recover totally or not after drying, their photosynthetic activity.

5. Conclusions

The main objective of this work was to characterize the physiological properties of some common bryophytes found in Azores. Knowledge of the water content is essential for physiological works, mainly pertaining to the effects of water stress on bryophyte metabolism. Bryophytes clearly behave as terrestrial sponges and besides their own water needs, the retention of additional external water will confer an overall positive effect on the ecosystem functioning.

Concerning the three original research questions it is possible to conclude that: (1) the absolute water content (AWC) of the selected species varied a lot, ranging from 646% of dry weight (dw) in *Polytrichum commune* to 5584% dw in *Sphagnum subnitens*; (2) all species showed a higher ability to hold water externally than internally, but both pathways are clearly important; (3) water loss showed an exponential decay curve along the time, where all bryophytes showed the highest rate of water loss in the first minute of air exposition reaching a water loss of 12% of *Thuidium tamariscinum* water content.

Differences in architecture and habit of the studied species may explain the differences in water content verified among them. In accordance with the literature, all species may be considered as preferentially ectohydric, so bryophytes typically maintain their internal water content constant by absorbing water from the external capillary spaces, as needed.

The data obtained in this study are of great ecological meaning since it shows the potential ability to absorb water and keep it within the ecosystem. The values found in this work mean that native and endemic bryophytes play an important role in the water resource retention of the native vegetation. After being stored, it may also be released, increasing the air humidity of the locations, and allowing other living beings to benefit from it. They are surely one of the key components that make native ecosystems more resilient in the face of climate change.

Appendix A

Species Studied—LIVERWORTS

A01—*Herbertus azoricus* (Steph.) P.W.Richards
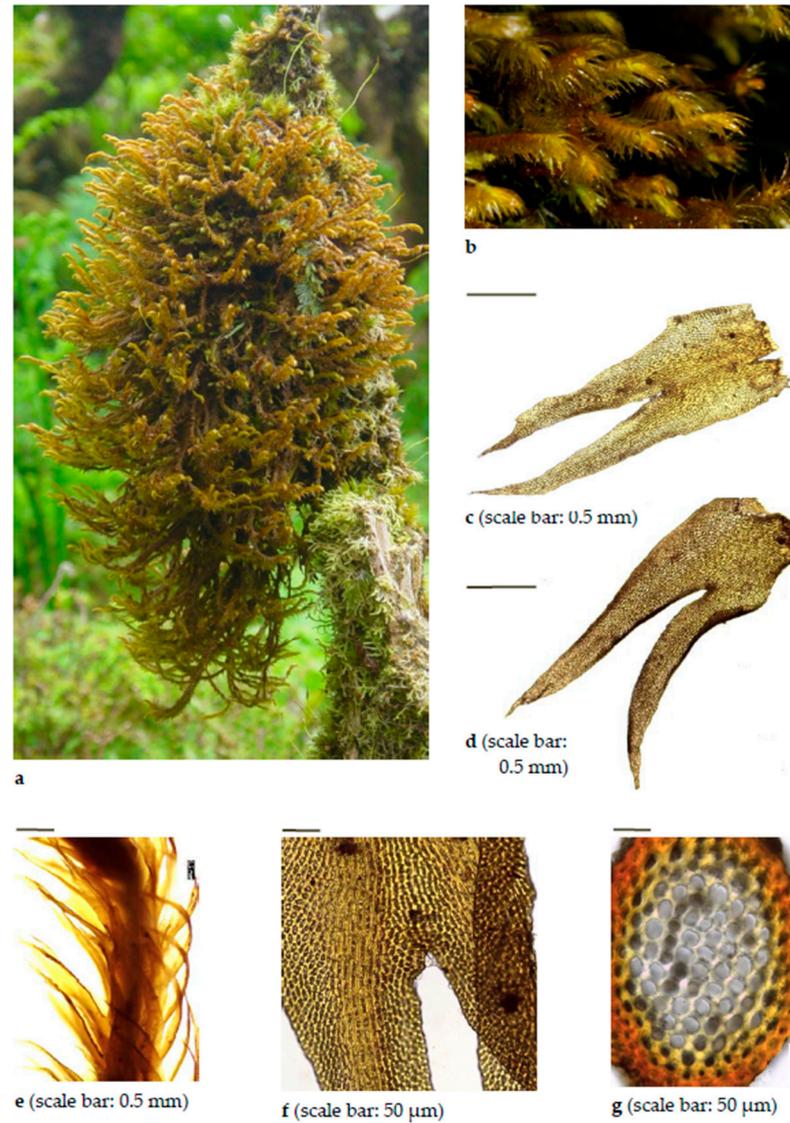
Figure A1. *Herbertus azoricus*: (**a**), habit, turfs; (**b**), shoots appear moss-like; (**c**), leaf, ventral side; (**d**), underleaf; (**e**), individual shoot; (**f**), vita with elongate cells of under leaf; (**g**), stem, transversal section. Photos: Rosalina Gabriel and Paulo A. V. Borges.

A02— *Bazzania azorica* H.Buch and Perss.

Figure A2. *Bazzania azorica*: (**a**), habit, shoots in the field; (**b**), shoot, dorsal side; (**c**), shoot, ventral side; (**d**), leaf cells; (**e**), leaves, dorsal side; (**f**), under leaves; (**g**), leaf, basal part; (**h**), leaf, apical part; (**i**), stem, transversal section. Photos: Rosalina Gabriel.

A03—*Lepidozia cupressina* (Sw.) Lindenb. subsp. *cupressina*

a

b

c (scale-bar: 200 µm)

d (scale-bar: 200 µm)

e (scale-bar: 50 µm)

f (scale-bar: 50 µm)
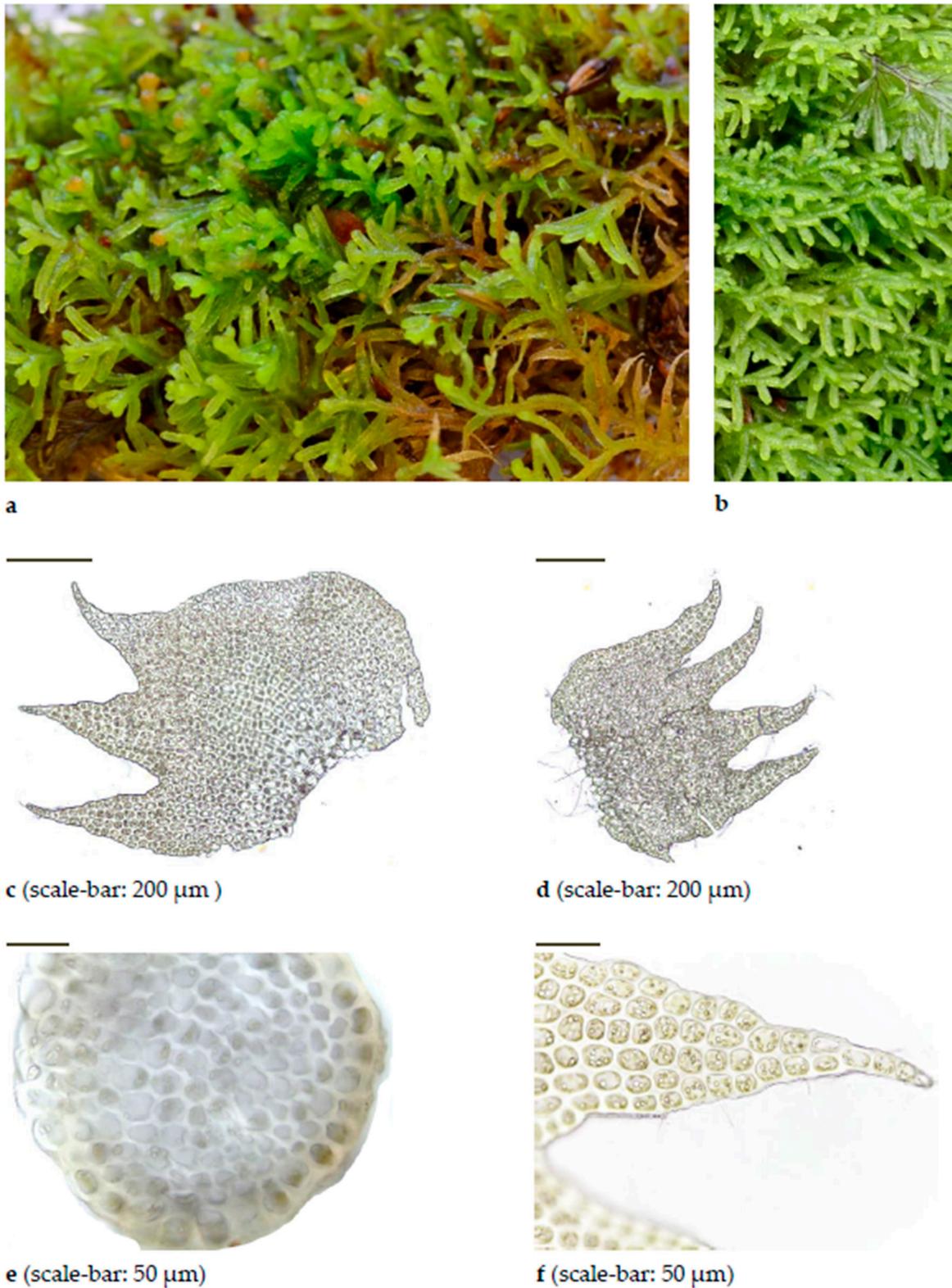
Figure A3. *Lepidozia cupressina* (Sw.) Lindenb. subsp. *cupressina:* (**a**), habit; (**b**), shoots, dorsal side; (**c**), leaf; (**d**), under leaf; (**e**), stem, transversal section; (**f**), leaf cells. Photos: Rosalina Gabriel and Paulo A. V. Borges.

A04—*Plagiochila bifaria* (Sw.) Lindenb.

Figure A4. *Plagiochila bifaria*: (**a**), habit; (**b**), shoots in the field; (**c**), leaves; (**d**), individual shoot; (**e**), shoot with sporophyte; (**f**), basal cells; (**g**), apical cells; (**h**), stem, transversal section. Photos: Rosalina Gabriel and Paulo A. V. Borges.

A05—*Scapania gracilis* Lindb.
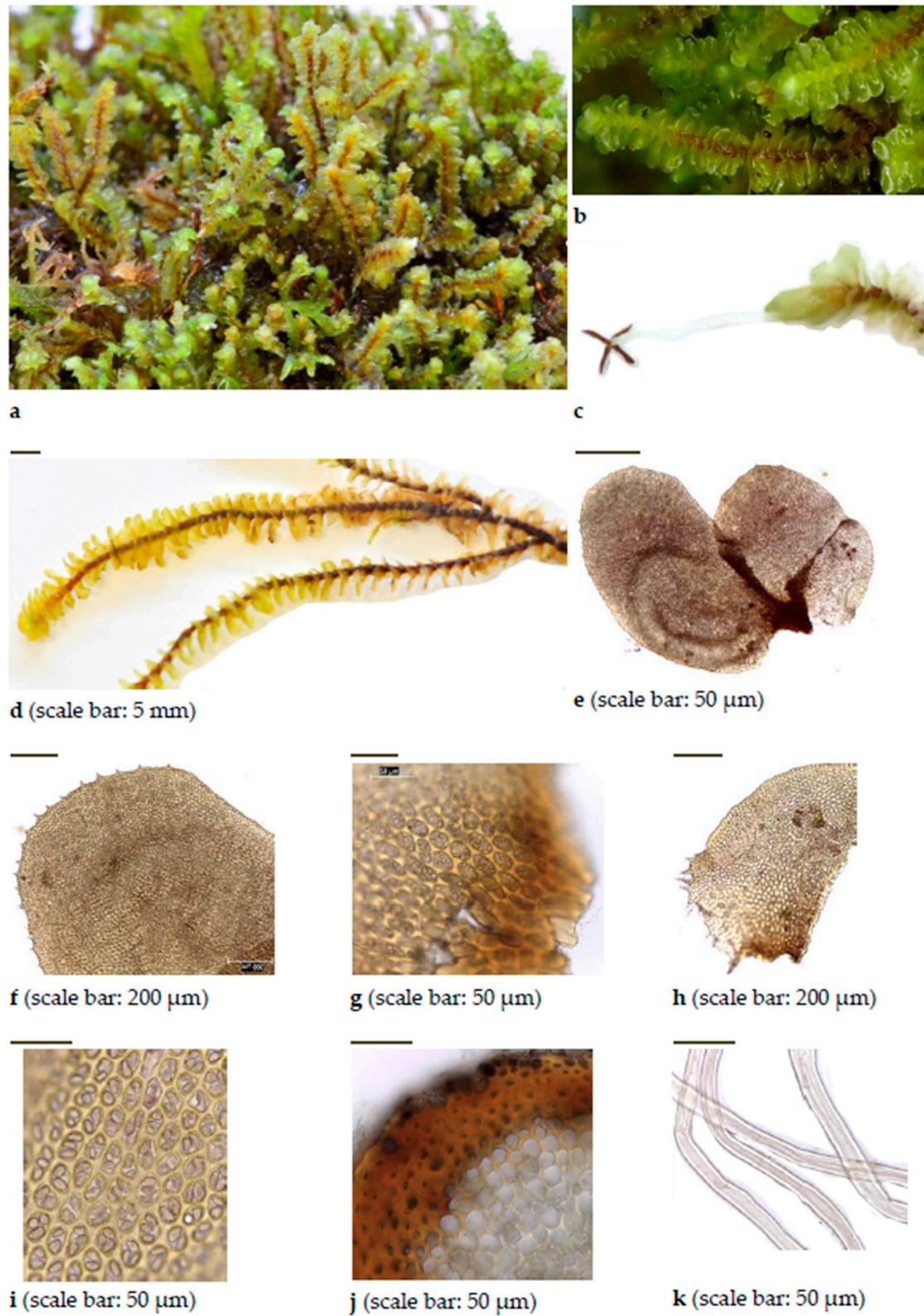
Figure A5. *Scapania gracilis*: (**a**), habit; (**b**), shoots in the field; (**c**), shoot with sporophyte; (**d**), individual shoot; (**e**), leaf, ventral and dorsal side; (**f**), leaf, apical part coarsely toothed; (**g**), leaf, basal part; (**h**), dorsal lobe dentate at base; (**i**), middle-leaf cells; (**j**), stem, transversal section; (**k**), rhizoids. Photos: Rosalina Gabriel and Paulo A. V. Borges.

A06—*Frullania acicularis* Hentschel and von Konrat

Figure A6. *Frullania acicularis*: (**a**), habit; (**b**), shoots in the field; (**c**), leaves, helmets and under leaves, ventral side; (**d**), leaves with occelli, dorsal side; (**e**), helmet with stylus; (**f**), underleaf; (**g**), stem, transversal section. Photos: Rosalina Gabriel and Paulo A. V. Borges.

Species Studied—MOSSES

A07—*Sphagnum subnitens* Russow and Warnst.
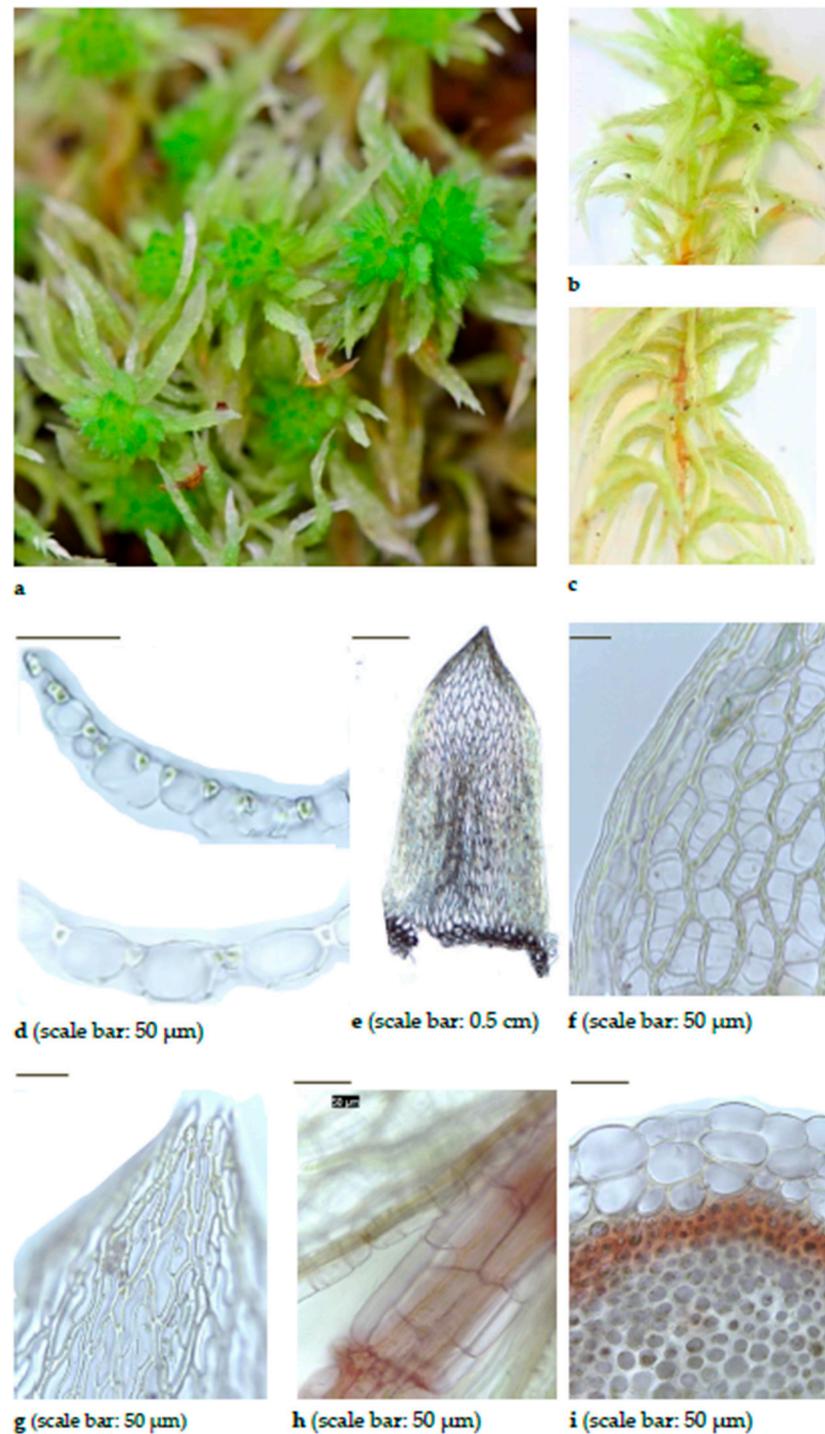
Figure A7. *Sphagnum subnitens*: (**a**), habit; (**b**), individual shoot with capitulum; (**c**), individual shoot; (**d**), branch leaf section; (**e**), stem leaf; (**f**), marginal cells of branch leaf; (**g**), cells of stem leaf apex; (**h**), branch; (**i**), stem transversal section. Photos: Rosalina Gabriel and Paulo A. V. Borges.

A08—*Polytrichum commune* Hedw.
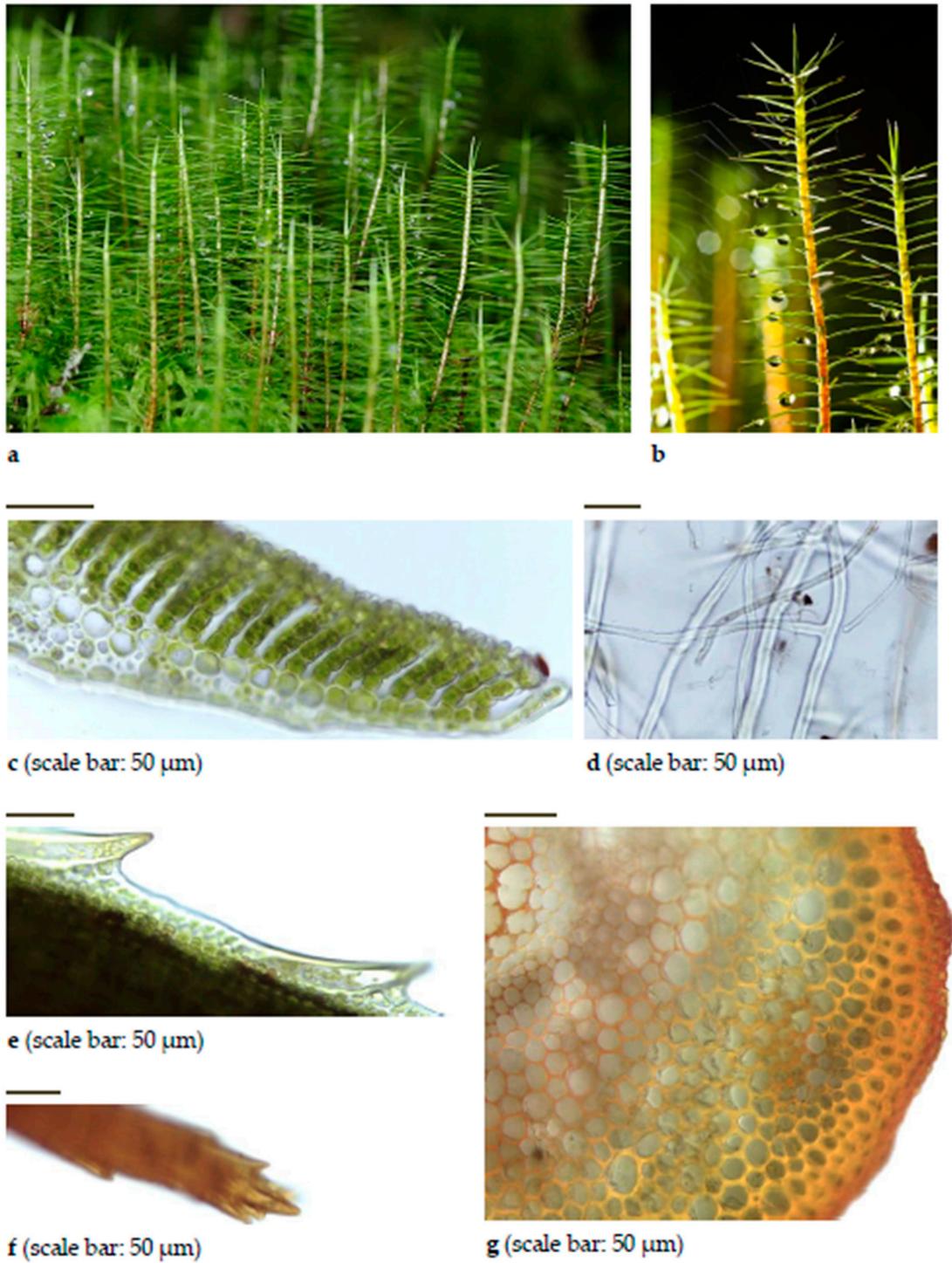
Figure A8. *Polytrichum commune*: (**a**), habit; (**b**), shoots in the field; (**c**), leaf section; (**d**), rhizoids; (**e**), leaf margin; (**f**), leaf apex; (**g**), stem transversal section. Photos: Rosalina Gabriel, Pedro Cardoso, and Ruben Tavares.

A09—*Campylopus brevipilus* Bruch and Schimp.

Figure A9. *Campylopus brevipilus*: (**a**), habit; (**b**), individual shoot; (**c**), leaves, (**d**), leaves, width nerve; (**e**–**g**), leaf section; (**h**), stem, transversal section. Photos: Rosalina Gabriel and Paulo A. V. Borges.

A10—*Campylopus shawii* Wilson
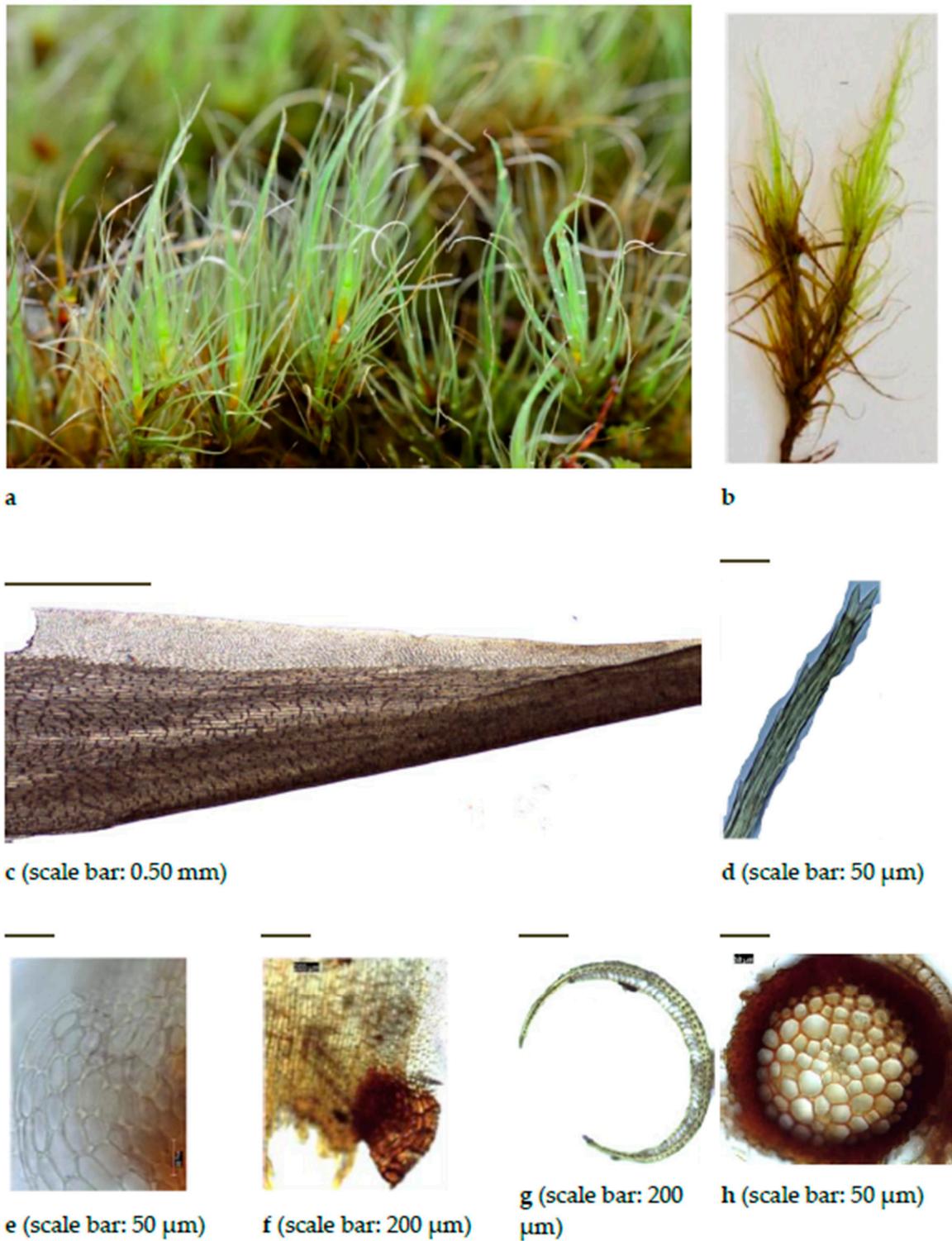
Figure A10. *Campylopus shawii*: (**a**), habit; (**b**), individual shoot; (**c**), leaf, (**d**), leaf apex; (**e**,**f**), alar cells with hyaline and reddish-brown auricles; (**g**), leaf section; (**h**), stem, transversal section. Photos: Rosalina Gabriel and Paulo A. V. Borges.

A11—*Trichostomum brachydontium* Bruch

Figure A11. *Trichostomum brachydontium*: (**a**), habit; (**b**), shoots in the field; (**c**), leaf, basal part; (**d**), leaf, apical part; (**e**), basal cells and nerve; (**f**), leaf apex; (**g**), stem, transversal section. Photos: Rosalina Gabriel and Paulo A. V. Borges.

A12—*Isothecium prolixum* (Mitt.) Stech, Sim-Sim, Tangney and D.Quandt.
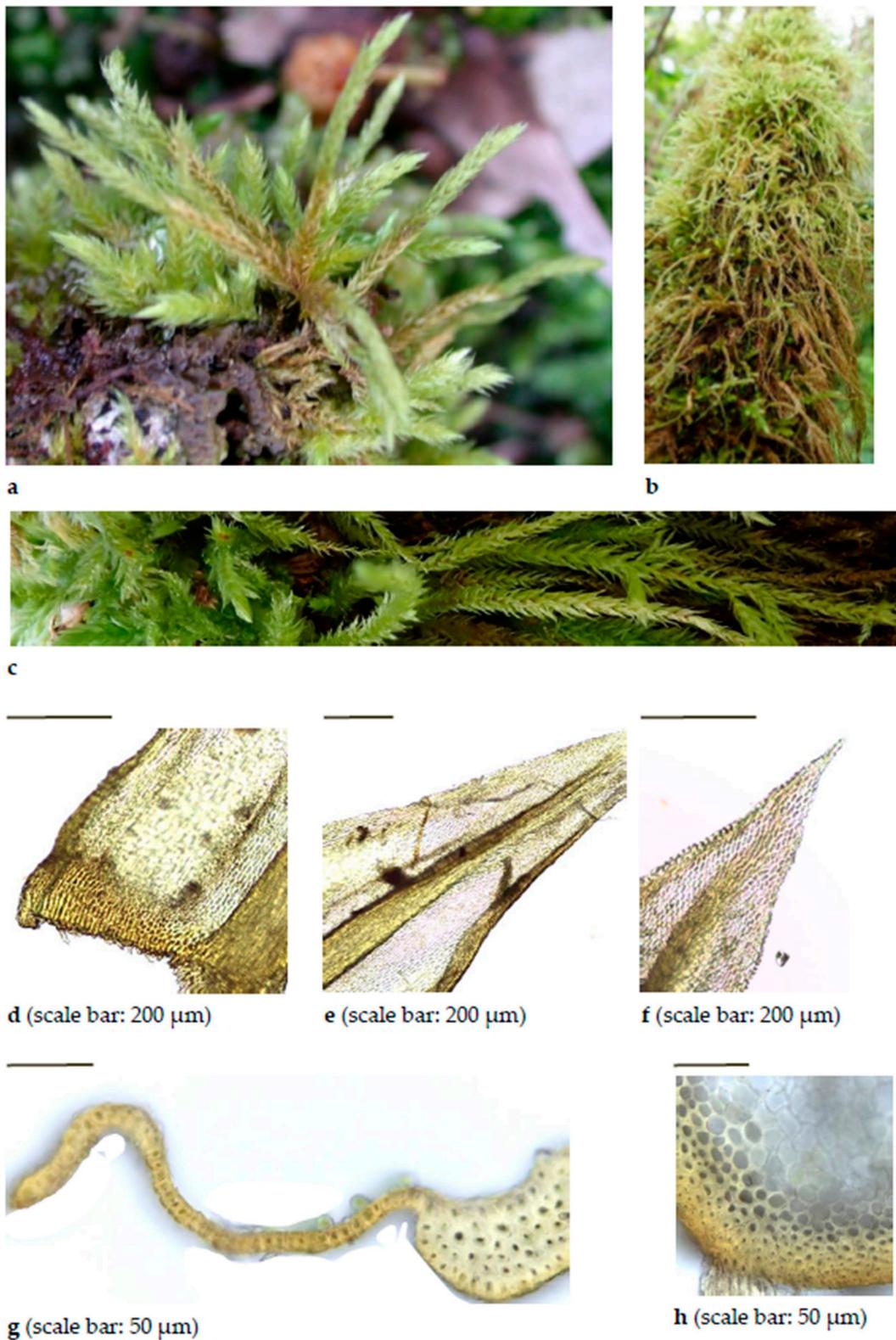
Figure A12. *Isothecium prolixum*: (**a**,**b**), habit, shoots in the field; (**c**), secondary, thin, shoots; (**d**), leaf base, alar cells, (**e**), middle leaf; (**f**), leaf apex, (**g**), leaf section; (**h**), stem, transversal section. Photos: Rosalina Gabriel.

A13—*Myurium hochstetteri* (Schimp.) Kindb.

a

b

c (scale bar: 500 µm)

d (scale bar: 200 µm)

e (scale bar: 200 µm)

f (scale bar: 50 µm)

g (scale bar: 50 µm)

h (scale bar: 50 µm)

i (scale bar: 50 µm)
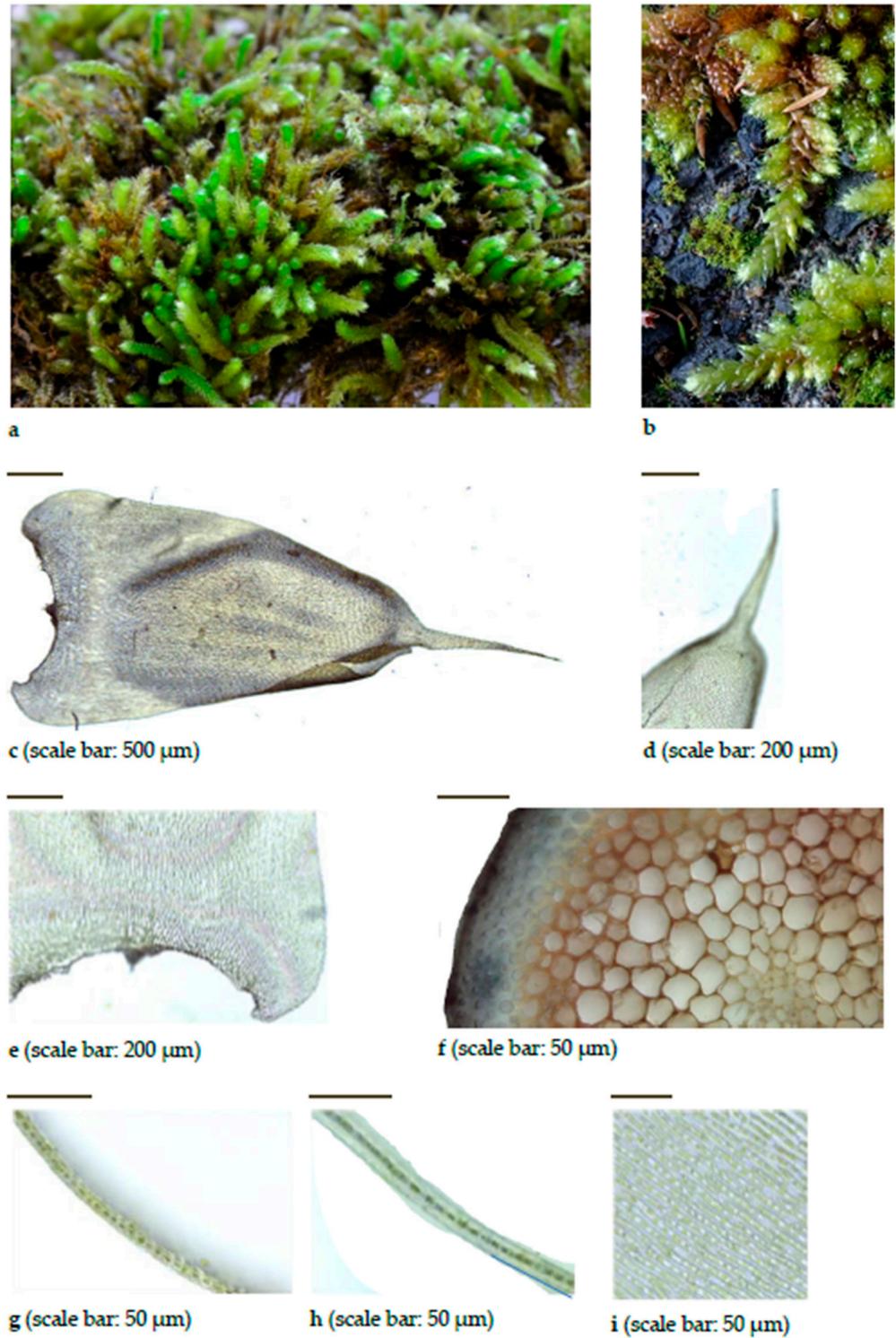
Figure A13. *Myurium hochstetteri:* (**a**), habit; (**b**), shoots in the field; (**c**), leaf; (**d**), leaf apex; (**e**), leaf, basal part; (**f**), stem transversal section; (**g**,**h**), leaf section; (**i**), leaf cells. Photos: Rosalina Gabriel and Paulo A. V. Borges.

A14—*Thuidium tamariscinum* (Hedw.) Schimp.

a

b

c (scale bar: 50 μm)

d (scale bar: 0.50 mm)

e (scale bar: 200 μm)

f (scale bar: 0.5 mm)

g (scale bar: 200 μm)

h (scale bar: 50 μm)
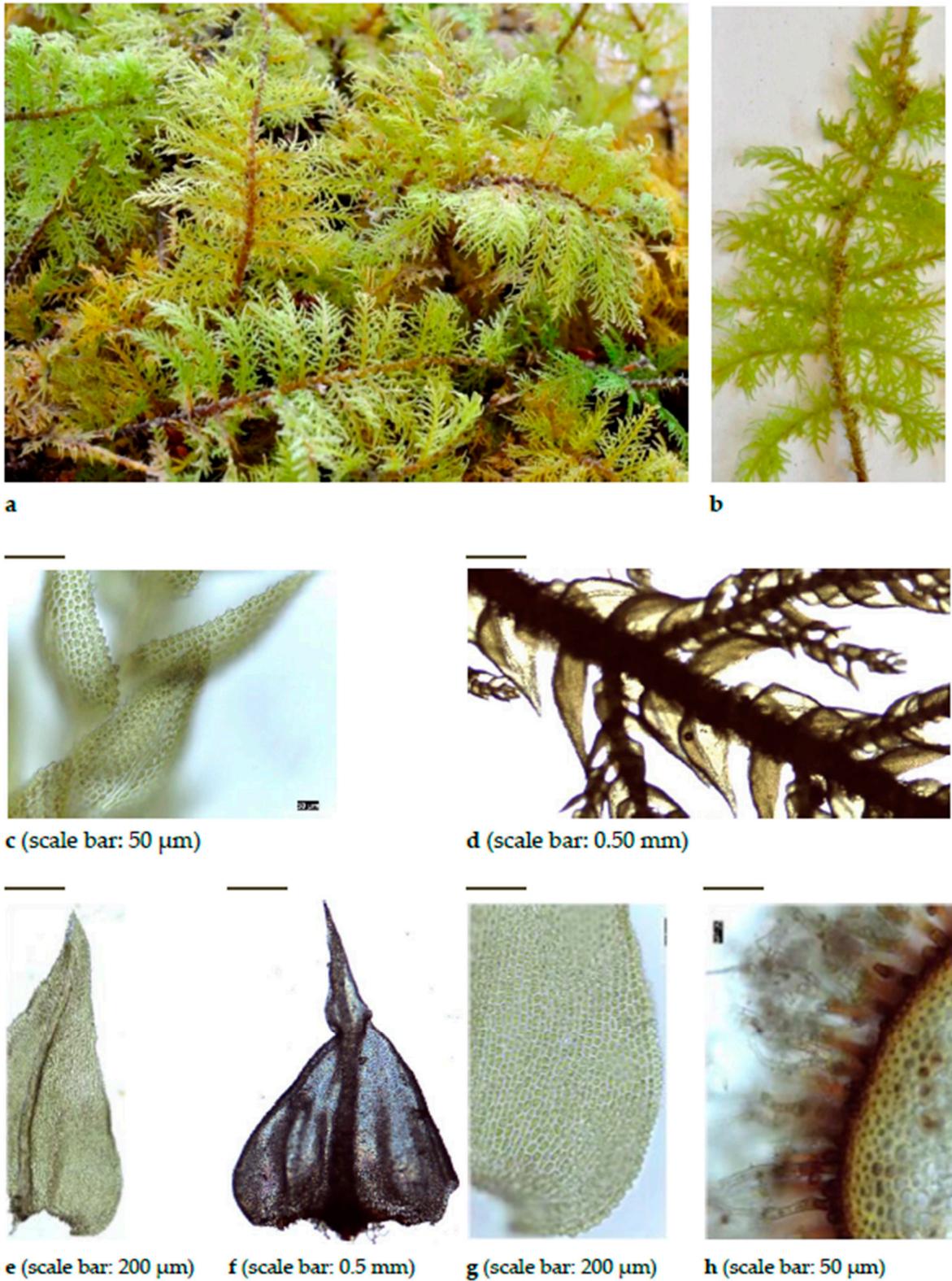
Figure A14. *Thuidium tamariscinum*: (**a**), habit; (**b**), shoot; (**c**), leaves; (**d**), stem; (**e**), branch leaf; (**f**), stem leaf; (**g**), leaf, basal part; (**h**), stem, transversal section, showing paraphyllia. Photos: Rosalina Gabriel and Paulo A. V. Borges.

Appendix B

Water Evaporation Curves—LIVERWORTS

Figure A15. *Cont.*

Figure A15. Graphs represent the calibration curves performed by each studied liverwort species in order to estimate the water evaporated from each specimen during cleaning stage of samples in the laboratory.

Water Evaporation Curves—MOSSES.

$y = 0.0049x + 0.032$
$R^2 = 0.9533$

◆ *Campylopus brevipilus*

$y = 0.046x + 0.2229$
$R^2 = 0.9689$

◆ *Campylopus shawii*

$y = 0.0701x + 0.2713$
$R^2 = 0.957$

◆ *Isothecium prolixum*

$y = 0.0552x + 0.2595$
$R^2 = 0.9761$

◆ *Myurium hochstetteri*

$y = 0.099x + 0.2942$
$R^2 = 0.9952$

◆ *Thuidium tamariscinum*

$y = 0.0053x + 0.1403$
$R^2 = 0.8809$

◆ *Trichostomum brachydontium*

Figure A16. *Cont.*
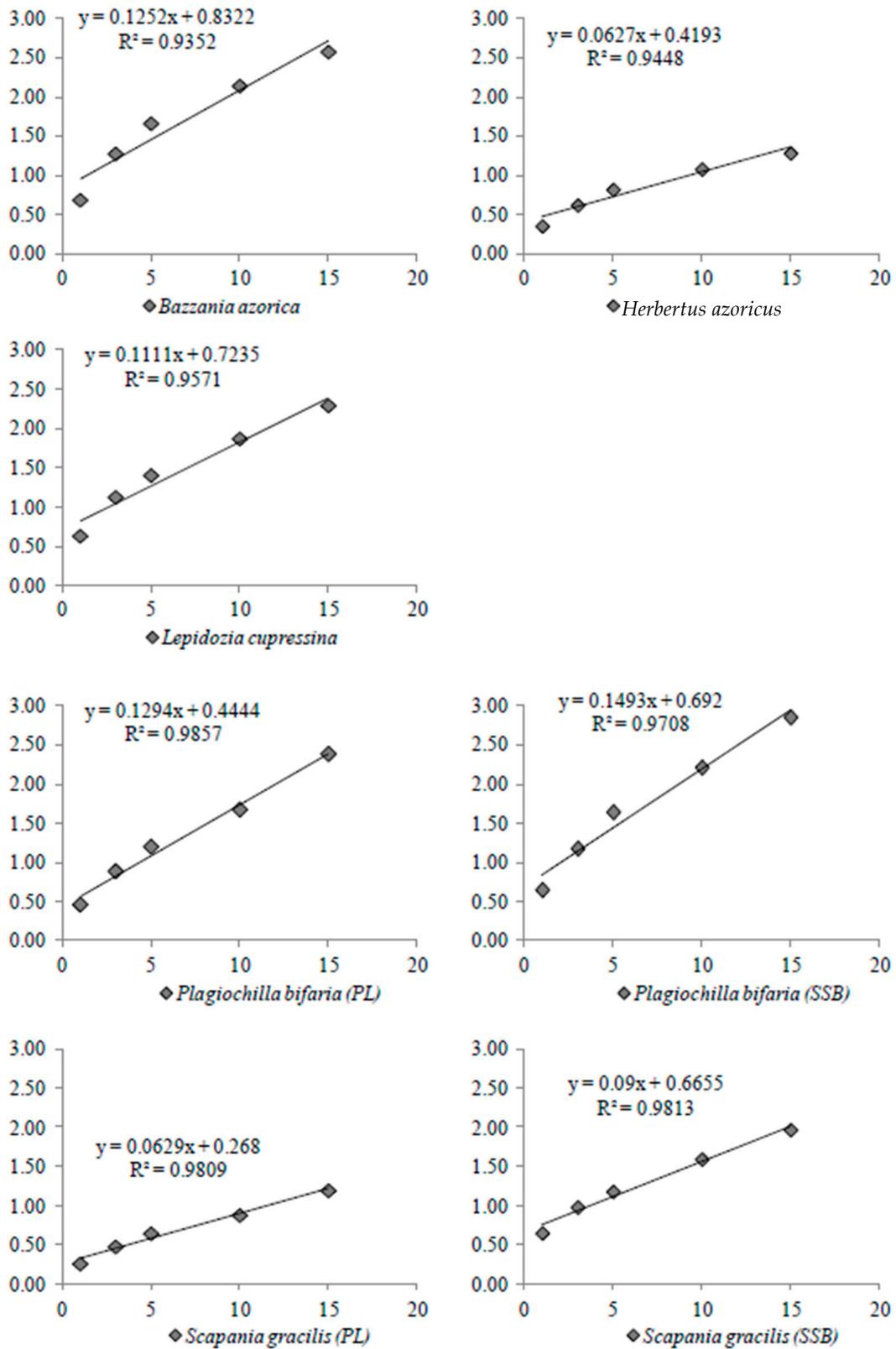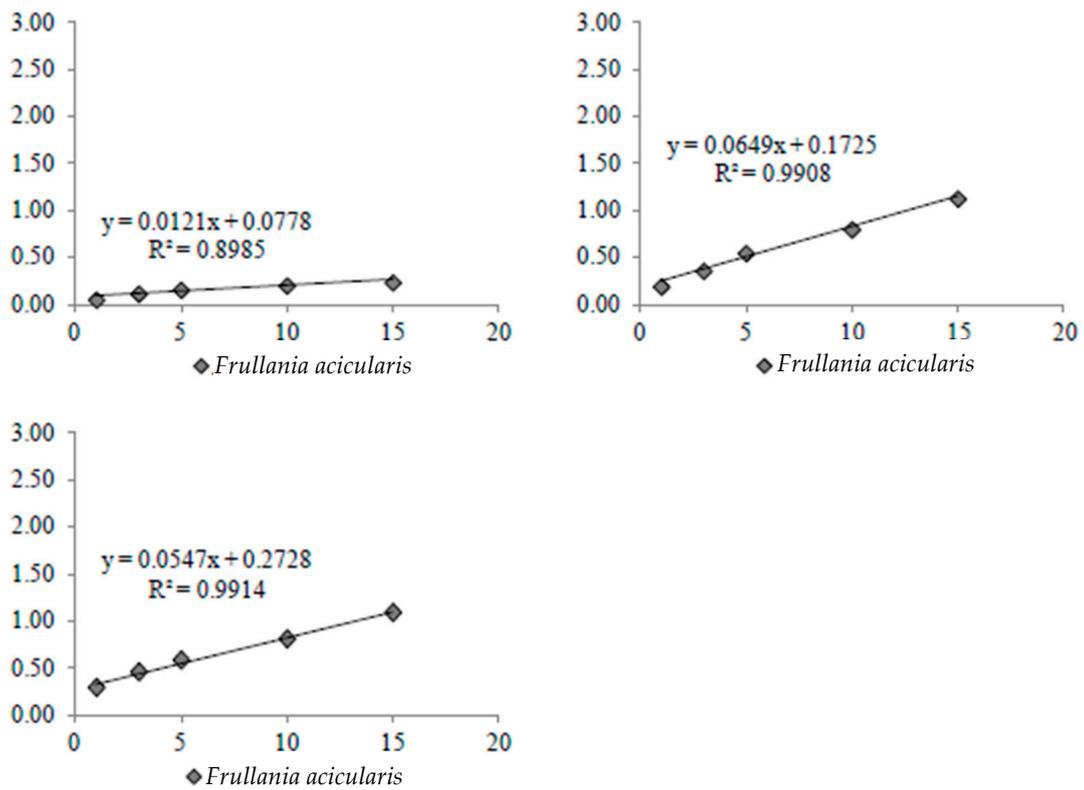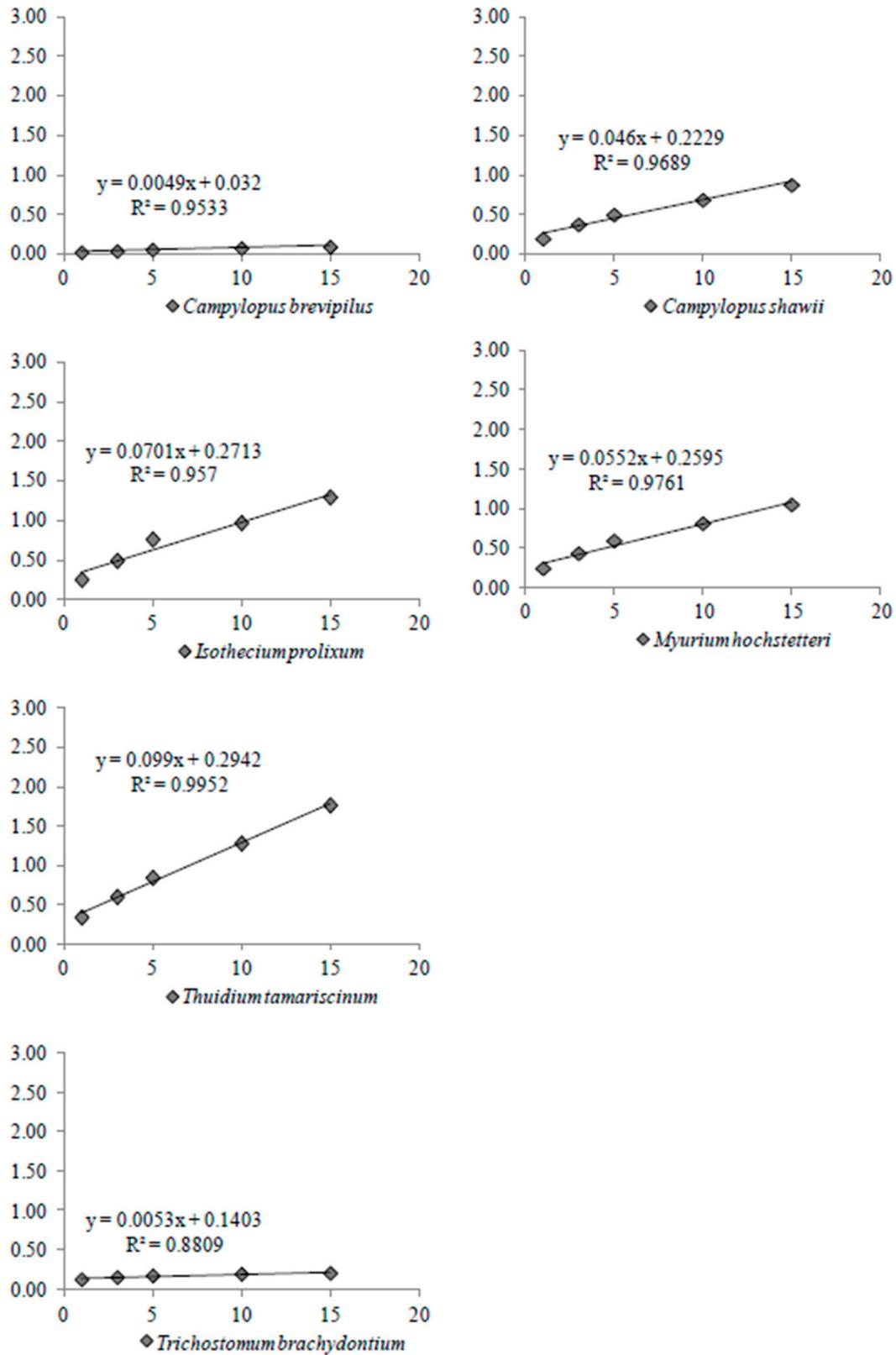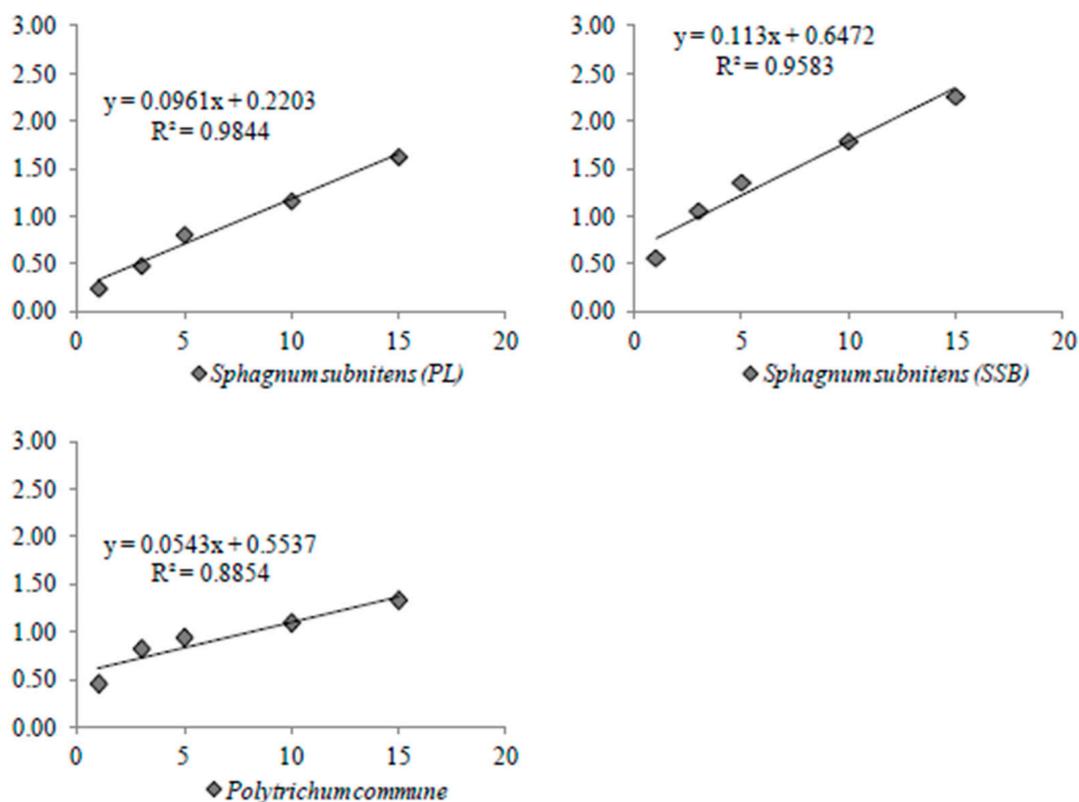
Figure A16. Graphs represent the calibration curves performed by each studied moss species in order to estimate the water evaporated from each specimen during cleaning stage of samples in the laboratory.

Appendix C

Table A1. Protocol to measure field weight, saturated weight, internal water content weight, and specimens' dry weight in bryophytes.

LOCATION	ACTION	OBSERVATIONS
In the field	Look for an appropriate area, with many large populations of the species you need to collect.	Assure yourself that you have the proper authorization to collect field samples. Assure yourself that the target species occurs in many different patches and that it is abundant in the area, before collecting.
	Gather an appropriate number of replicates of the target bryophyte species (e.g., 25 cm^2) to sealed polyethylene vials, previously marked and weighted.	Try to collect the purest populations, to diminish the cleaning time in the laboratory. Avoid collecting just the central part of the patch, to keep the integrity of the sample in the field, as much as possible.
	Collect a small Herbarium sample of each target-species to be able to confirm its identification and compare it with other reference material.	
In the laboratory	Confirm the identity of each species using a stereo microscope and a light-microscope, and different floras and identification keys.	
	Clean the fresh shoots/thalli under a stereo microscope to remove all non-target materials (e.g., other bryophyte species, vascular fragments, soil, and litter).	Try to preserve the structure of the patch as much as possible. Try to work fast in order to avoid undue evaporation.
	Weigh each sample on an electronic scale, in order to obtain the **field weight**.	This step is optional.
	Submerse each replicate in water to reach the full turgor (*c.* 12 consecutive hours).	

Table A1. *Cont.*

LOCATION	ACTION	OBSERVATIONS
	Leave the hydrated samples over a structure of 4–6 wires, assembled 15–20 cm from the bench, and let the samples drip the excess water.	Samples should keep the field structure, as much as possible.
	Weigh the samples only when plants drip less than one drop per minute. This is **the saturated weight** (Ms), which accounts for all the water retained in the external capillarity spaces, as bryophytes can do in their colonies.	
	Gently blot the samples using absorbent paper to remove external water. No droplets of water should be seen on the shoots.	It is also possible to centrifuge the samples, however Santarius (1994) affirms that blotting generally gives more reliable estimates of full-turgor water content than centrifuging.
	Weigh the blotted samples to obtain the **internal water content weight** (Ma)	
	Oven-dry each sample for 48 h at 100 °C.	
	Weighed the oven-dried samples to determine **specimens' dry weight** (Md).	

Appendix D

Table A2. Percentage of water loss and standard deviation (italic), in relation to the initial water content, by direct evaporation of different liverwort species (division Marchantiophyta). Data represent the mean of 5 replicates for 17 period times (minutes). Specimens were collected on Serra de Santa Bárbara, Terceira Island, Azores.

Time (min)	Ha.SSB	Ba.SSB	Lc.SSB	Pb.SSB	Sg.SSB	Fa.SSB
0						
1	5.1 ± 2.04	4.1 ± 1.35	8.8 ± 3.42	11.3 ± 5.28	5.1 ± 1.04	4.2 ± 0.81
3	8.1 ± 2.89	8.9 ± 2.46	14.7 ± 4.67	18.2 ± 5.72	9.4 ± 1.72	10.2 ± 3.84
5	10.5 ± 3.14	12.0 ± 3.65	18.3 ± 5.05	24.5 ± 6.51	14.2 ± 2.78	14.6 ± 4.04
7	12.7 ± 3.74	15.7 ± 4.67	22.3 ± 6.00	28.2 ± 6.43	18.3 ± 3.24	18.3 ± 4.66
10	16.9 ± 3.98	20.1 ± 5.54	26.2 ± 6.76	31.8 ± 5.97	22.2 ± 3.36	22.3 ± 4.98
15	19.0 ± 4.14	22.8 ± 6.17	29.4 ± 6.67	35.1 ± 5.44	25.2 ± 3.72	25.5 ± 4.90
30	21.4 ± 4.45	26.6 ± 7.32	32.0 ± 6.46	39.1 ± 5.31	29.2 ± 3.42	30.0 ± 4.67
45	23.8 ± 4.51	30.2 ± 7.93	35.0 ± 6.41	43.3 ± 5.02	33.2 ± 3.38	33.9 ± 4.57
60	26.2 ± 4.97	32.4 ± 8.04	37.9 ± 6.12	46.9 ± 5.02	36.9 ± 2.98	37.3 ± 4.55
90	29.5 ± 5.73	36.0 ± 8.69	42.2 ± 5.49	51.7 ± 4.06	41.0 ± 2.70	38.4 ± 4.61
150	35.5 ± 6.60	43.1 ± 9.92	48.2 ± 5.07	53.1 ± 5.09	47.3 ± 2.27	43.6 ± 4.56
720	49.1 ± 11.64	66.9 ± 16.66	66.5 ± 5.84	69.4 ± 5.12	62.3 ± 6.06	59.4 ± 8.78
1080	70.2 ± 10.67	86.0 ± 14.40	88.0 ± 2.45	86.6 ± 3.80	81.1 ± 5.14	85.6 ± 6.91
1440	86.3 ± 5.82	92.8 ± 5.72	94.0 ± 0.82	93.2 ± 1.30	92.3 ± 1.77	89.2 ± 4.99
2160	94.3 ± 4.13	96.3 ± 1.51	97.1 ± 0.56	96.4 ± 1.48	97.9 ± 0.38	90.9 ± 4.40
2880	96.3 ± 1.73	96.4 ± 1.35	96.8 ± 0.63	96.2 ± 1.47	98.0 ± 0.35	90.3 ± 4.33
3600	96.7 ± 1.28	96.4 ± 1.31	97.1 ± 0.57	96.3 ± 1.49	98.0 ± 0.33	90.3 ± 4.42

Table A3. Percentage of water loss and standard deviation (italic), in relation to the initial water content, by direct evaporation of different moss species (division Bryophyta). Data represent the mean of 5 replicates for 17 period times (minutes). Specimens were collected from three different sites on Terceira Island, Azores.

Time (min)	Ss.PL	Pc.SSB	Cb.FS	Cs.SSB	Tb.FS	Ip.PL	Mh.PL	Tt.PL
0								
1	2.5 ± *1.52*	0.8 ± *0.27*	3.6 ± *0.48*	4.2 ± *1.24*	3.6 ± *2.09*	3.4 ± *0.63*	3.9 ± *1.14*	11.8 ± *3.13*
3	2.7 ± *1.60*	1.5 ± *0.49*	6.3 ± *1.14*	8.0 ± *1.10*	7.8 ± *3.33*	6.7 ± *0.84*	6.9 ± *1.62*	13.6 ± *3.44*
5	6.3 ± *0.52*	2.1 ± *0.70*	8.6 ± *1.27*	11.3 ± *0.67*	9.6 ± *2.80*	9.0 ± *0.95*	9.0 ± *2.32*	20.7 ± *4.72*
7	9.0 ± *0.93*	2.7 ± *0.89*	11.6 ± *1.83*	14.3 ± *1.17*	11.6 ± *2.83*	11.6 ± *1.03*	11.2 ± *2.64*	26.1 ± *5.33*
10	12.2 ± *1.37*	3.5 ± *1.07*	13.4 ± *1.04*	16.4 ± *1.25*	13.5 ± *2.86*	15.3 ± *2.13*	13.3 ± *2.79*	31.3 ± *6.00*
15	12.9 ± *1.08*	4.7 ± *1.44*	15.8 ± *1.71*	18.8 ± *1.27*	15.1 ± *3.16*	19.3 ± *2.40*	15.3 ± *2.89*	36.4 ± *6.83*
30	15.3 ± *1.13*	6.9 ± *2.16*	18.2 ± *1.62*	21.8 ± *1.30*	17.3 ± *3.66*	23.6 ± *2.58*	17.7 ± *2.87*	42.4 ± *8.13*
45	17.4 ± *1.12*	9.0 ± *2.75*	19.8 ± *1.42*	24.3 ± *1.28*	18.9 ± *3.68*	27.8 ± *2.60*	20.6 ± *2.89*	51.0 ± *9.29*
60	19.7 ± *1.36*	11.1 ± *3.40*	21.9 ± *1.11*	26.9 ± *1.26*	20.9 ± *3.51*	32.7 ± *3.17*	23.3 ± *2.91*	59.9 ± *10.9*
90	22.1 ± *1.74*	14.8 ± *4.47*	23.7 ± *0.90*	30.2 ± *0.72*	23.1 ± *3.74*	39.6 ± *3.23*	25.3 ± *3.06*	72.1 ± *12.1*
150	26.2 ± *2.14*	21.3 ± *6.40*	32.9 ± *2.35*	36.9 ± *1.26*	36.5 ± *3.42*	43.8 ± *2.22*	29.9 ± *3.05*	82.3 ± *14.4*
720	33.8 ± *6.49*	82.2 ± *13.1*	71.5 ± *7.38*	59.0 ± *10.0*	85.2 ± *3.41*	89.4 ± *2.06*	42.5 ± *4.65*	90.7 ± *2.85*
1080	51.6 ± *6.79*	82.2 ± *12.9*	80.9 ± *7.20*	79.6 ± *8.69*	91.8 ± *2.52*	92.3 ± *1.59*	65.9 ± *7.29*	90.3 ± *2.83*
1440	77.2 ± *5.23*	82.7 ± *13.0*	86.8 ± *6.14*	91.3 ± *2.74*	93.5 ± *1.50*	92.3 ± *1.56*	86.4 ± *2.93*	91.0 ± *2.82*
2160	90.0 ± *4.94*	82.9 ± *13.0*	94.3 ± *1.46*	97.2 ± *1.02*	93.9 ± *1.35*	92.3 ± *1.55*	96.6 ± *0.96*	91.4 ± *2.81*
2880	95.8 ± *2.65*	82.3 ± *12.9*	96.0 ± *0.97*	96.9 ± *1.05*	94.1 ± *1.28*	93.0 ± *1.58*	97.3 ± *0.79*	90.6 ± *2.82*
3600	95.9 ± *2.66*	82.6 ± *13.1*	96.1 ± *0.93*	97.1 ± *1.03*	94.4 ± *1.27*	93.2 ± *1.58*	97.2 ± *0.81*	90.8 ± *2.85*

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