

How does moss photosynthesis relate to leaf and canopy structure? Trait relationships for 10 Hawaiian species of contrasting light habitats

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Summary

- Mosses are an understudied group of plants that can potentially confirm or expand principles of plant function described for tracheophytes, from which they diverge strongly in structure.
- We quantified 35 physiological and morphological traits from cell-, leaf- and canopy-level, for 10 ground-, trunk- and branch-dwelling Hawaiian species. We hypothesized that trait values would reflect the distinctive growth form and slow growth of mosses, but also that trait correlations would be analogous to those of tracheophytes.
- The moss species had low leaf mass per area and low gas exchange rate. Unlike for tracheophytes, light-saturated photosynthetic rate per mass (A_{mass}) did not correlate with habitat irradiance. Other photosynthetic parameters and structural traits were aligned with microhabitat irradiance, driving an inter-correlation of traits including leaf area, cell size, cell wall thickness, and canopy density. In addition, we found a coordination of traits linked with structural allocation, including costa size, canopy height and A_{mass} . Across species, A_{mass} and nitrogen concentration correlated negatively with canopy mass per area, analogous to linkages found for the 'leaf economic spectrum', with canopy mass per area replacing leaf mass per area.
- Despite divergence of mosses and tracheophytes in leaf size and function, analogous trait coordination has arisen during ecological differentiation.

Abbreviations for traits (alphabetically within category): Photosynthetic light response traits: A_{area} , light-saturated assimilation rate per area ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$); A_{mass} , light-saturated assimilation rate per mass ($\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$); A_{N} , light-saturated assimilation rate per nitrogen ($\text{nmol CO}_2 (\text{g N})^{-1} \text{ s}^{-1}$); DSF, diffuse site factor (% daylight); I_c , compensation irradiance ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$); I_s , saturation irradiance ($\text{nmol photons m}^{-2} \text{ s}^{-1}$); QE_{area} , quantum efficiency area based ($\mu\text{mol CO}_2 \text{ m}^{-2} (\mu\text{mol photons m}^{-2})^{-1}$); QE_{mass} , quantum efficiency mass based [$\mu\text{mol CO}_2 \text{ g}^{-1} (\mu\text{mol photons m}^{-2})^{-1}$]; R_{area} , dark respiration rate per area ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$); R_{mass} , dark respiration rate per mass ($\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$). Leaf dimension traits: CCA, costa cross sectional area (mm^2); CL, costa length (mm); LA, leaf area (mm^2); LL, leaf length (mm); LT, lamina thickness (μm); LW, maximum leaf width (mm). Leaf shape traits: L/W, length/width; P²/A, perimeter²/area. Mid-lamina cell traits: CLA, cell lumen area (μm^2); CLH, cell lumen height (μm); CLL, cell lumen length (μm); CLW, cell lumen width (μm); CPA, cells per area (cells mm^{-2}); IWT, interior cell wall thickness (μm); LLA, lumen area fraction of leaf lamina; SWT, surface cell wall thickness (μm); XLA, cross sectional lamina lumen area fraction. Canopy structure and composition traits: CD, canopy density (g cm^{-3}); CH, canopy height (cm); CMA, canopy mass per area (g m^{-2}); LAI, leaf area index; LAR, leaf area ratio ($\text{m}^2 \text{ kg}^{-1}$); LMA, leaf mass per area (g m^{-2}); LMF, leaf mass per plant mass; N_{area} , nitrogen per area (g m^{-2}); N_{mass} , nitrogen per mass (%).

Introduction

Mosses vary strongly in structure and in physiology owing to phylogeny and adaptation (Hosokawa & Odani, 1957; Magdefrau, 1982; Pocs, 1982; Crum, 2001), but this diversity may be constrained by trait correlations, as has been shown for tracheophytes (Givnish, 1987; Sack *et al.*, 2003; Wright *et al.*, 2004). Determining the functional significance of moss trait variation is important because mosses reflect the condition of primitive plants, with simpler organization than tracheophytes, and are becoming a model for genetics, development and function (Cove, 2005; Thornton *et al.*, 2005; Cove *et al.*, 2006), even as they are increasingly recognized as a major contributor to ecosystem carbon cycling (Gorham, 1991; Lagerstrom *et al.*, 2007). The Hawaiian mosses present a wide range of morphological and ecological diversity (255 species; Staples *et al.*, 2004). For 10 wet forest species from a range of light habitats and life forms, we tested hypotheses for the correlations among structure, composition and photosynthetic function, focusing on 35 cell-, leaf- and canopy-level traits (Fig. 1; see the Supporting Information Table S1).

We first hypothesized that mosses would show traits associated with their distinctive growth form and adaptation. Mosses typically have leaves one cell thick, except at the midrib, without stomata to control water loss or extensive vascular tissue (Parihar, 1959; Schofield & Héban, 1984; Schofield, 1985). Consequently, mosses are poikilohydric, rapidly gaining and losing water according to availability in the immediate environment, coping with dry periods through desiccation tolerance (Watson, 1914; Proctor, 1984, 2000a; Kappen & Valladares, 1999; Proctor & Tuba, 2002; Oliver *et al.*, 2005; Glime, 2007; Proctor *et al.*, 2007). Given the potential limitations to carbon assimilation associated with this growth form, and with structural and biochemical tolerance of shade and desiccation, we expected mosses to have low light-saturated photosynthetic rates relative to tracheophytes, per area, per mass and per nitrogen invested (A_{area} , A_{mass} and A_{N} , respectively), low dark respiration rates per area and per mass (R_{area} and R_{mass}), low leaf mass per area (LMA), low nitrogen concentrations per area and per mass (N_{area} and N_{mass}), but high leaf area index (LAI) to maximize resource uptake.

We hypothesized that the 10 mosses would show similar relations of traits to light habitat as tracheophytes. Tracheophytes of higher irradiance tend to have higher A_{area} , A_{mass} , A_{N} , N_{area} , N_{mass} , R_{area} and R_{mass} , saturation and light-compensation irradiance (I_s and I_c), lower quantum efficiency (QE_{area} and QE_{mass}), and a morphology that maximizes CO_2 capture, including smaller, thicker leaves made up of smaller cells with thicker walls, with higher LMA, lower leaf mass fraction (LMF) and lower leaf area ratio (LAR;

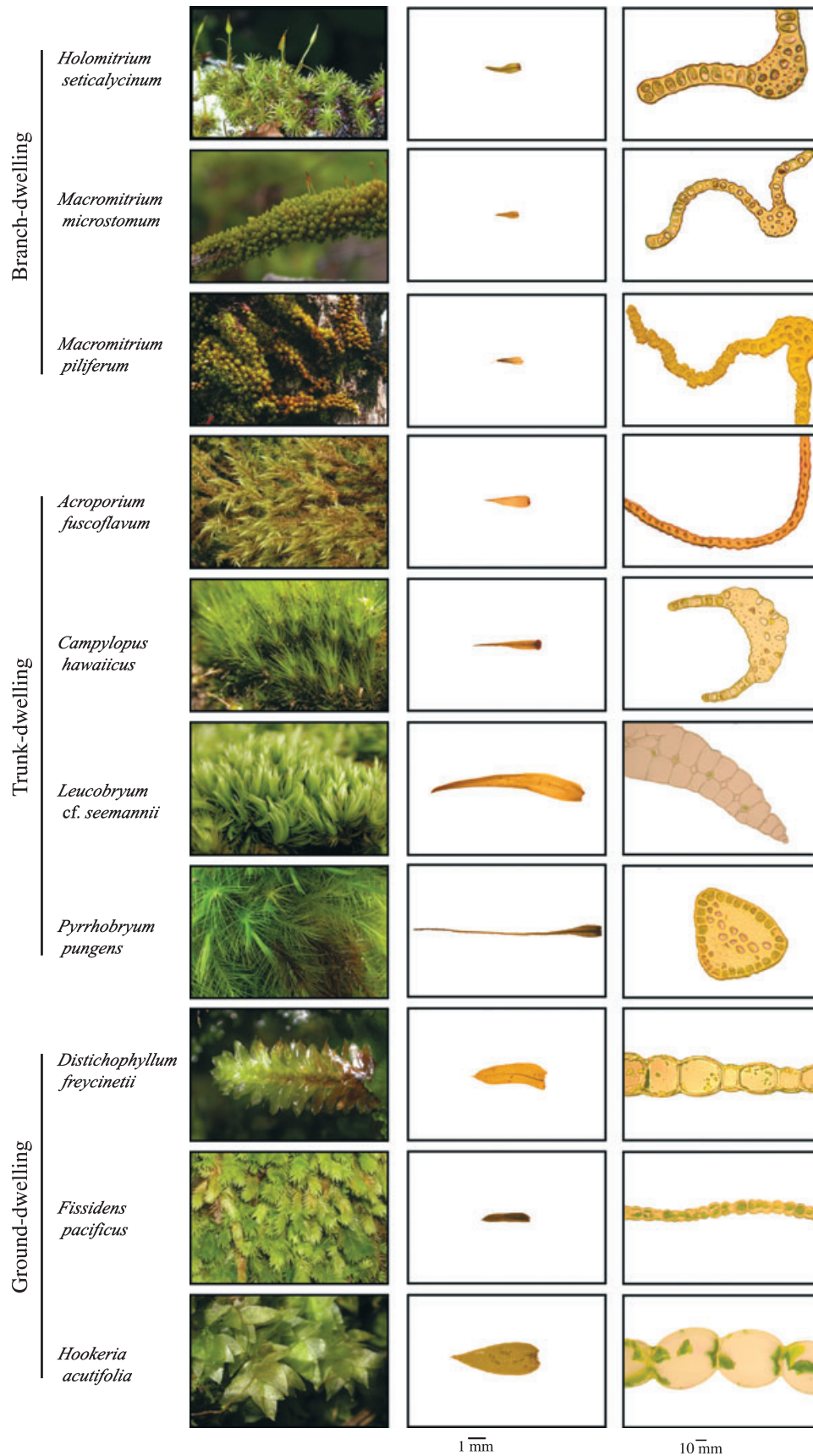
Givnish, 1987, 1988; Walters & Reich, 1999). Two previous studies showed lower I_c for shaded than exposed moss species of Japanese forest (Hosokawa & Odani, 1957; Miyata & Hosokawa, 1961).

Our third aim was to determine trait–trait correlations across the 10 moss species. Plant performance is optimized by the modification of functional trait ‘clusters’ (Ackerly & Reich, 1999; Niinemets & Sack, 2006; Poorter & Markesteijn, 2008). We expected to find correlations among traits within given categories (i.e. photosynthetic traits, cell-size related traits, leaf size traits and canopy-level traits). We also expected to find, as for tracheophytes, correlations among area-based traits and among mass-based traits that align with irradiance. Thus, for 11 species of Hawaiian lobeliads across light habitats, positive correlations were found among A_{area} , I_s , I_c , and R_{area} ; and among A_{mass} , R_{mass} and N_{mass} (Givnish *et al.*, 2004). We also tested for the ‘leaf economic spectrum’, by which traits related to high capacity for gas exchange are negatively correlated with traits related to leaf lifespan; A_{mass} correlates positively with N_{mass} and negatively with LMA across sets of tracheophyte species (Small, 1972; Field & Mooney, 1986; Givnish *et al.*, 2004; Hikosaka, 2004; Wright *et al.*, 2004; Karst & Lechowicz, 2007). We also tested whether moss canopies may be analogous to tracheophyte leaves, and thus whether canopy mass per area (CMA) might be analogous to LMA in physiological correlations. Finally, we hypothesized coordination of traits related to structural support. Across tracheophyte species, larger leaves tend to have higher LMA and lower N_{mass} because of a stronger investment in support tissues (Milla & Reich, 2007; Niinemets *et al.*, 2007; Niklas *et al.*, 2007; Arcand *et al.*, 2008).

Materials and Methods

Study species

Mosses were collected on Oahu, Hawaii (c. 21°20′ 43.01″ N, 157°48′12.79″ W) from lowland wet forest dominated by tree *Metrosideros polymorpha* (Myrtaceae) and mat-forming fern *Dicranopteris linearis* (Gleicheniaceae; Wagner *et al.*, 1990). This location had a modeled mean annual rainfall, temperature and relative humidity of 3329 mm, 19°C and 80%, respectively (T. W. Giambelluca and L. Cuo, unpublished). Ten of the most common moss species were selected, representing nine genera in six families, diverse in leaf and canopy morphology and ecology (Table 1; Fig. 1). We selected two of three branch-dwelling species in a single genus because they were by far the most common; two other branch-dwellers were observed, a *Cladopodium* sp. and a *Syrrophodon* sp., too rare at the study site to obtain replication.



1 mm

10 mm

Table 1 Moss taxa studied for leaf and canopy structure and function, arranged by microhabitat type, and leaf type and life-form (after Bates, 1998), and microhabitat diffuse site factor (transmitted irradiance as percent of irradiance above the forest canopy)

Genus and species	Family	Leaf type and life-form	Diffuse site factor (% daylight)
Ground-dwelling			
<i>Distichophyllum freycinetii</i>	Hookeriaceae	Wide leaves, rough mats	2.0 ± 0.3
<i>Fissidens pacificus</i>	Fissidentaceae	Narrow leaves, rough mats	3.0 ± 0.4
<i>Hookeria acutifolia</i>	Hookeriaceae	Wide leaves, rough mats	2.7 ± 0.8
Trunk-dwelling ¹			
<i>Acroporium fuscoflavum</i>	Sematophyllaceae	Small leaves, large cushions	14.4 ± 5.4
<i>Campylopus hawaiiicus</i>	Dicranaceae	Narrow leaves, large cushions	25.5 ± 6.7
<i>Leucobryum cf. seemannii</i>	Dicranaceae	Broad midrib, large cushions	8.1 ± 2.8
<i>Pyrrohobryum pungens</i>	Rhizogoniaceae	Narrow leaves, tall loose turfs	12.0 ± 0.9
Branch-dwelling			
<i>Holomitrium seticalycinum</i>	Dicranaceae	Narrow leaves, short turfs	13.3 ± 1.6
<i>Macromitrium microstomum</i>	Orthotrichaceae	Narrow leaves, short turfs	30.4 ± 6.7
<i>Macromitrium piliferum</i>	Orthotrichaceae	Narrow leaves, short turfs	15.5 ± 5.0

Species nomenclature follows Staples *et al.* (2004) except *P. pungens*, which follows Crosby *et al.* (2000); family nomenclature: Tropicos (<http://www.tropicos.org/>), Missouri Botanical Garden.

¹Usually <2 m above the soil.

Measurements – microhabitat irradiance and photosynthetic traits

Microhabitat irradiance was quantified for five colonies of each species. During overcast conditions, photosynthetically active radiation (PAR) was measured for the colony surface and simultaneously in an open area, using matched quantum sensors – LI-190/LI-250 (Li-Cor Inc., Lincoln, NE, USA) and HOBO H21-002 (Onset Computer Corporation, Cape Cod, MA, USA), to calculate the percentage of daylight diffuse PAR transmitted (i.e. the ‘diffuse site factor’ (DSF); Anderson, 1964).

Samples from each species were collected for measurement of photosynthetic light responses from January to March 2005 (see also Methods S1). We determined light-response parameters from plots of CO₂ assimilation rate (*A*) vs PAR. The dark respiration rate per mass (*R*_{mass}) was determined as the negative *A* at zero PAR, the light compensation point (*I*_c) as the *x*-intercept, the quantum efficiency (*QE*_{mass}) as the initial slope, and the saturation irradiance (*I*_s) as the irradiance at which 95% of the light-saturated carbon assimilation rate per mass (*A*_{mass}) was achieved (Marschall & Proctor, 2004; Rice *et al.*, 2008). Assimilation rate per nitrogen (*A*_N) was determined by dividing *A*_{mass} by N concentration per mass (*N*_{mass}; see Methods S1), and light-saturated assimilation rate, quantum efficiency, dark respiration rate and nitrogen per projected canopy area (*A*_{area}, *QE*_{area}, *R*_{area}, and *N*_{area}, respectively) by multiplying *A*_{mass}, *QE*_{mass}, *R*_{mass} and *N*_{mass} by the CMA; to be described later).

Measurements – leaf and cell morphological traits

Leaf and cell morphological traits were characterized from whole mounts and cross-sections of one mature leaf from each sample measured for photosynthesis (see Methods S1). We measured leaf area (LA), length (LL), length of costa (CL; i.e. the ‘midrib’ of the leaf), width (LW; perpendicular to the costa at the widest part of the leaf), perimeter²/leaf area (P²/A), and length/width (L/W). We measured costa cross-sectional area (CCA), and the lamina thickness (LT) midway between costa and leaf margin. In the center of whole mounts we measured cells per area (CPA), lamina lumen area fraction (LLAF; the ratio of cell lumen to lamina area) and average individual cell lumen area (CLA), length (CLL) and width (CLW). In cross-sections we measured cell lumen height (CLH), surface cell wall thickness (SWT), and interior cell wall thickness (IWT) (i.e. between adjacent mid-lamina cells). We measured cross-sectional lumen area fraction (XLAF) as the area of lumens divided by the lamina cross-sectional area.

Measurements – canopy traits

Canopy traits potentially linked with cell- and leaf-level structure and function were measured for three *c.* 25 cm² samples of each species. We determined LMA as leaf mass divided by leaf area, CMA as canopy mass divided by projected canopy area and canopy density (CD) as CMA divided by mean

Fig. 1 Diversity in form for the 10 Hawaiian moss species, including canopy, leaf, and mid-leaf cross sections in the first, second and third columns of images respectively. Note the absence of costa (midrib) in *Acroporium fuscoflavum* and *Hookeria acutifolia*. Also note that two species have atypical costae. In *Leucobryum cf. seemannii* the leaf is primarily a modified, flattened costa made of two layers of empty cells, with chlorophyllous cells embedded within; the cross-section shows only part of the leaf. In *Pyrrohobryum pungens*, the leaf is primarily made up of a large costa lacking lamina, with chlorophyllous cells making up the outer layer of the costa.

canopy height (CH). We determined leaf mass fraction (LMF) as total leaf mass divided by canopy mass and leaf area ratio (LAR) as total leaf area divided by canopy mass. We determined leaf area index (LAI) as total leaf area divided by projected canopy area (see Methods S1).

Statistical analyses

Statistical procedures were applied using R 2.6.1 (<http://www.r-project.org>). We tested differences in given moss traits using ANOVAs, nesting species within microhabitat. Data were log-transformed to improve normality and homoscedasticity (Zar, 1999). Multiple pairwise comparisons of traits among microhabitats were calculated with the Tukey Honestly Significant Difference test (HSD; Zar, 1999). A correlation matrix was determined to reveal the correlative structure of the traits; for a conservative assessment of trait correlations we considered these as significant only when $P < 0.05$ for both Spearman rank correlation and Pearson correlation coefficients (r_s and r_p ; Zar, 1999). When r_s was significant, and a relationship appeared nonlinear, r_p was calculated for log-transformed data (Sack *et al.*, 2003; Dunbar-Co *et al.*, 2009). We conducted principal component analysis (PCA) based on the correlation matrix to identify important axes of covariation among 18 traits, excluding redundant, highly correlated traits (see Results section); costa traits were also excluded because *Acroporium fuscoflavum* and *Hookeria acutifolia* commonly lacked costae (Bartram, 1933). We note that a potential weakness of our PCA analysis is the larger set of variables than the number of species, which can reduce the power to detect underlying components (Osborne & Costello, 2004). For traits related to leaf size, we also determined allometries by fitting standard major axes to log-transformed data, to account for error in both x and y -variables (using SMATR; <http://www.bio.mq.edu.au/ecology/SMATR>; Warton *et al.*, 2006), and tested whether the scaling was geometric (e.g. whether linear dimensions scaled with the 0.5 power of area), as expected if larger leaves maintained their shape proportionality and composition (Niklas, 1994).

Results

Substantial species differences in light habitat, photosynthetic traits and leaf and canopy traits

There was a 15-fold difference across species in microhabitat irradiance, as indicated by the diffuse site factor (DSF) ranging from 2.0% for ground-dwelling *Distichophyllum freycinetii* to 30.4% for branch-dwelling *Macromitrium microstomum*. Photosynthetic traits varied threefold to eightfold across the 10 species (Tables 2, S1, S2; Fig. 2). Mean assimilation per mass (A_{mass}) varied fivefold from 3.3 to 14.0 nmol g⁻¹ s⁻¹, from *Pyrrhobryum pungens* to *H. acutifolia* (Fig. 2), assi-

milation per area (A_{area}) varied twofold from 0.59 to 1.41 μmol CO₂ m⁻² s⁻¹ from *Leucobryum cf. seemannii* to *M. microstomum*, and assimilation per nitrogen (A_N) varied fivefold from 5.3 to 28.5 nmol CO₂ (g N)⁻¹ s⁻¹ from *P. pungens* to *M. microstomum*. Compensation and saturation irradiances (I_c and I_s) varied fourfold to sixfold respectively, from 5.4 to 32.6 μmol m⁻² s⁻¹ and from 69.2 to 253 μmol m⁻² s⁻¹. Quantum efficiency per mass and per area (QE_{mass} and QE_{area}) each varied sixfold. Dark respiration per mass and per area (R_{mass} and R_{area}) were the most variable photosynthetic traits, ranging eight- to 10-fold from 0.90 to 6.83 nmol CO₂ g⁻¹ s⁻¹ from *Macromitrium piliferum* to *Holomitrium seticalycinum* and from 0.085 to 0.850 μmol CO₂ m⁻² s⁻¹ from *Fissidens pacificus* to *H. seticalycinum*.

Species also differed strongly in all other categories of measured traits. Among the eight traits relating to leaf size and shape, leaf area (LA) was most variable, with a 28-fold difference between *M. microstomum* at 0.28 mm² and *Leucobryum cf. seemannii* at 7.7 mm². Among the nine traits relating to cell size, CLA was most variable, with a 300-fold difference between *M. piliferum* at 23 μm² and *H. acutifolia* at 6890 μm². Among the nine traits relating to canopy structure and composition, canopy height (CH) was most variable, with a 16-fold difference between *M. piliferum* at 0.30 cm and *P. pungens* at 4.8 cm.

Differences among microhabitats

The principal components analysis of trait data pointed to the distinctness of the ground-dwelling mosses from the trunk- and branch-dwelling mosses, which overlapped (Fig. S1). For 32 of 35 traits measured there were significant differences among microhabitats and among species nested within microhabitat (ANOVAs; Tables 2 and S2). For CMA and surface cell wall thickness (SWT), we found no significant species differences within microhabitats, and for one gas exchange trait, R_{mass} , we found significant differences among species but not among microhabitats.

For 16 of the 35 traits measured, the trait variation aligned with the microhabitat light and moisture gradient: the mean for trunk-dwellers was intermediate between those of ground- and branch-dwellers and for 14 of these cases there were significant contrasts between at least one pair of habitats (Tukey HSD; $P < 0.05$; exceptions were QE_{area} and R_{mass}). In many cases, the differences were consistent with sun vs shade adaptation in tracheophytes: for the photosynthetic traits, branch-dwellers had 24% lower QE_{area} and twofold to threefold higher A_N , I_c , I_s , R_{area} and R_{mass} than ground-dwellers (Tables 2, S1 and S2). Branch-dwellers had leaves 60–84% smaller in width (LW) and in LA than ground-dwellers, and 50% smaller in lumen area fraction (LLAF; Fig. 1). Leaves of branch-dwellers contained smaller cells, 87–98% lower in lumen length and area (CLL and CLA) and with twofold to threefold greater cells per area and

Table 2 Study traits, symbols, units, mean trait values for species of different microhabitats (ground-, trunk, and branch-dwellers) and the ranges of species means (minimum, mean and maximum values of species means)

Trait category/trait	Symbol	Units	Microhabitat	Species
Photosynthetic light response traits				
Diffuse site factor	DSF	% Daylight	2.5, 15.0, 19.7***	2.0, 12.7, 30.4**
Saturation irradiance	I_s	$\mu\text{mol photons m}^{-2} \text{s}^{-1}$	109, 119, 212***	69, 144, 253***
Compensation irradiance	I_c	$\mu\text{mol photons m}^{-2} \text{s}^{-1}$	5.6, 16.2, 17.8***	5.4, 13.5, 32.6*
Light-saturated assimilation rate per mass	A_{mass}	$\text{nmol CO}_2 \text{g}^{-1} \text{s}^{-1}$	10.7, 4.6, 10.3***	3.3, 8.1, 14.0*
Light-saturated assimilation rate per area	A_{area}	$\text{nmol CO}_2 \text{m}^{-2} \text{s}^{-1}$	0.82, 0.80, 1.22**	0.59, 0.93, 1.41**
Light-saturated assimilation rate per nitrogen	A_N	$\text{nmol CO}_2 (\text{g N})^{-1} \text{s}^{-1}$	8.4, 10.3, 18.6***	5.3, 12.2, 28.5***
Quantum efficiency, mass based	QE_{mass}	$\text{nmol CO}_2 \text{g}^{-1} (\mu\text{mol photons m}^{-2})^{-1}$	0.295, 0.131, 0.144***	0.079, 0.184, 0.451***
Quantum efficiency, area based	QE_{area}	$\mu\text{mol CO}_2 (\mu\text{mol photons})^{-1}$	0.0229, 0.0181, 0.0173*	0.0057, 0.0193, 0.0371***
Dark respiration, mass based	R_{mass}	$\text{nmol CO}_2 \text{g}^{-1} \text{s}^{-1}$	1.61, 1.96, 3.04	0.90, 2.18, 6.83**
Dark respiration per area	R_{area}	$\text{nmol CO}_2 \text{m}^{-2} \text{s}^{-1}$	0.124, 0.260, 0.372***	0.085, 0.253, 0.850(7)***
Canopy structure and composition traits				
Leaf mass per area	LMA	g m^{-2}	9.43, 16.3, 13.2**	6.4, 13.3, 31.4**
Leaf area index	LAI		6.1, 10.5, 8.4***	3.9, 8.6, 14.4**
Canopy mass per area	CMA	g m^{-2}	76, 177, 120***	68, 129, 235
Canopy height	CH	cm	1.65, 2.17, 0.44***	0.30, 1.49, 4.8***
Canopy density	CD	g cm^{-3}	0.0054, 0.0127, 0.0320***	0.0042, 0.0163, 0.0390***
Nitrogen per mass	N_{mass}	%	1.27, 0.54, 0.67***	0.24, 0.80, 1.51***
Nitrogen per area	N_{area}	g m^{-2}	96.9, 69.8, 80.4***	34, 81, 120***
Leaf mass per shoot mass	LMF		0.692, 0.807, 0.871***	0.650, 0.791, 0.913**
Leaf area ratio	LAR	$\text{m}^2 \text{kg}^{-1}$	8180, 6430, 7090***	2390, 7150, 11570**
Leaf dimension traits				
Costa length	CL	mm	3.24, 7.05, 1.91***	1.32, 4.17, 9.00***
Costa cross sectional area	CCA	mm^2	0.0026, 0.0314, 0.0015***	0.0006, 0.0130, 0.0856***
Leaf length	LL	mm	3.90, 5.96, 1.91***	1.32, 4.13, 9.00***
Maximum leaf width	LW	mm	1.15, 0.80, 0.44***	0.32, 0.80, 1.64***
Leaf area	LA	mm^2	3.52, 2.80, 0.56***	0.28, 2.34, 7.71***
Lamina thickness	LT	μm	30.6, 9.9, 14.1***	6.7, 18.2, 47.5***
Leaf shape traits				
Perimeter ² /area	P^2/A		24.8, 96.0, 37.1***	21, 57, 238***
Length/width	L/W		3.75, 8.64, 4.33***	2.8, 5.9, 17.3***
Cell traits				
Cell lumen area	CLA	μm^2	2660, 121, 46***	23, 943, 6890***
Lumen area fraction	LLAF		0.835, 0.474, 0.428***	0.351, 0.579, 0.884***
Cells mm^{-2} , cells per area	CPA	cells mm^{-2}	3370, 5790, 10680***	128, 6610, 15180***
Cell lumen length	CLL	μm	83.4, 32.2, 11.2***	6, 42, 195***
Cell lumen width	CLW	μm	29.7, 5.5, 5.9***	3.7, 13.7, 51.1***
Mid-lamina cell lumen height	CLH	μm	27.4, 6.4, 9.4***	2.7, 13.6, 42.9***
Surface cell wall thickness	SWT	μm	1.22, 1.83, 2.33**	1.16, 1.79, 3.56
Interior cell wall thickness	IWT	μm	1.21, 2.78, 3.10***	0.97, 2.41, 5.04***
Cross sectional cell lumen area/lamina area	XLAF		0.735, 0.332, 0.357***	0.145, 0.461, 0.827***

Asterisks represent the significance of analyses of variance for differences among microhabitats and species, with species nested within microhabitat: *, $P < 0.05$; **, $0.01 \geq P > 0.001$; ***, $P \leq 0.001$.

internal and surface cell wall thickness (CPA, IWT and SWT) than ground-dwellers. Branch-dwellers had most compact canopy form; leaf mass fraction (LMF) and canopy density (CD) of branch-dwellers were, respectively, 1.3-fold and sixfold higher than for ground-dwellers (Tables 2, S1, S2).

The relationships with light habitat, as quantified with DSF, confirmed the correlation of 12 traits with microhabitat irradiance. The QE_{mass} , LW, LA, LT, LLAf, CLA, CLW and CLH were correlated negatively with DSF, whereas A_{area} , CD, I_s and IWT correlated positively with DSF ($|r_p|$ and $|r_s| = 0.65\text{--}0.91$, $P = 0.001\text{--}0.04$).

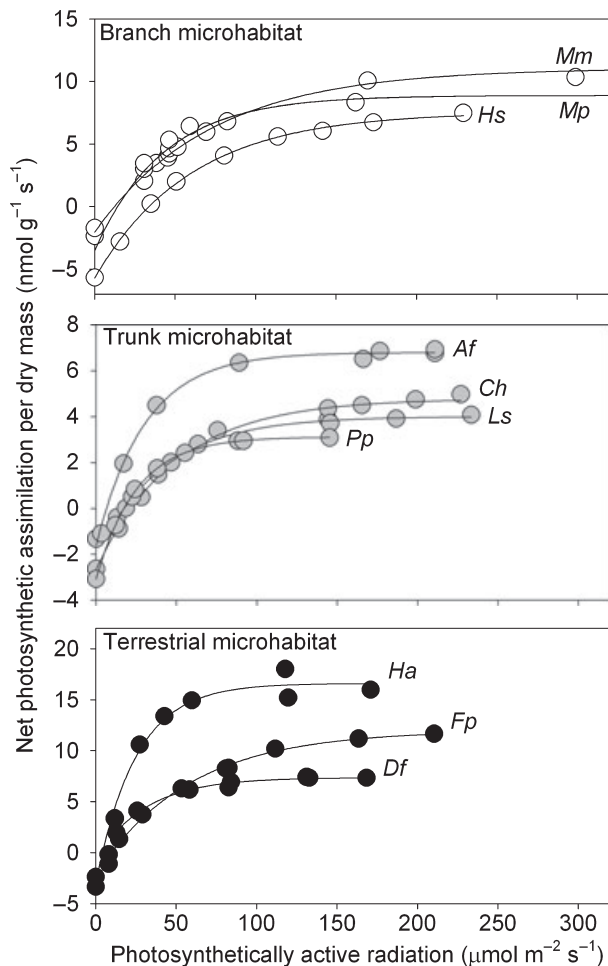


Fig. 2 Representative light response curves for 10 Hawaiian moss species from three microhabitats. An exponential rise to maximum was fitted for each species. Symbols: closed, ground-dwelling; tinted, trunk-dwelling; open, branch-dwelling; Af, *Acroporium fuscoflavum*; Ch, *Campylopus hawaiiicus*; Df, *Distichophyllum freycinetii*; Fp, *Fissidens pacificus*; Ha, *Hookeria acutifolia*; Hs, *Holomitrium seticalycinum*; Ls, *Leucobryum cf. seemannii*; Mm, *Macromitrium microstomum*; Mp, *Macromitrium piliferum*; Pp, *Pyrrhobryum pungens*. Measured values for *M. microstomum* (Mm) and *M. piliferum* (Mp) both continued at higher irradiances.

Comparison of key functional traits in the 10 Hawaiian mosses with values for tracheophytes

The functional traits of the Hawaiian forest mosses were broadly consistent with values compiled for 78 other moss species from 28 studies (Fig. 3), often spreading across mean values for tropical, polar and temperate moss species, and for a range of *Sphagnum* species (Fig. 3).

We found strong differences in functional traits between moss species and tracheophytes, based on a global compilation of tracheophyte data from tropical to tundra biomes (GLOPNET; Wright *et al.*, 2004). Values for A_{area} , A_{mass} , R_{mass} and N_{mass} for mosses in this study were substantially lower than those of tracheophytes (Fig. 3a–d), with mean values, respectively, 8%, 6%, 18% and 41% of those

compiled for all tracheophytes (Welch two-sample *t*-tests; $n = 274\text{--}2061$, $P < 0.001$), and, respectively, 12%, 8%, 14%, and 40% of values compiled for tropical rainforest tracheophytes ($n = 23\text{--}221$, $P < 0.001$). Similarly, the moss species LMA, with mean of 13.3 g m^{-2} , was lower than those of tropical rainforest tracheophytes and of tracheophytes overall ($P < 0.001$). Moss canopies had very large LAI, within the range of values for entire forest stands (Fig. 3f; Asner *et al.*, 2003), which do not typically include the moss layer (but see Bond-Lamberty & Gower, 2007). We found reports of moss LAI in three previous studies of seven temperate species; two studies reported values of 6–20 (Proctor, 1979; Vitt, 1990), which are similar to those in this study, and the other reported larger values of 44–129 (Simon, 1987).

Diversity in moss photosynthetic trait combinations

Across the moss species, photosynthetic light response parameters on an area or mass basis were typically uncorrelated, indicating a wide range of possible combinations of parameters ($|r_p|$ and $|r_s| = 0.01\text{--}0.66$; $P > 0.05$; Table S3; Fig. S2). The only significant relationships were positive correlations of QE_{area} with QE_{mass} , R_{area} with R_{mass} and a negative correlation of QE_{area} with I_s ($|r_p|$ and $|r_s| = 0.67\text{--}0.93$; $P = 0.0001\text{--}0.03$).

Bivariate trait correlations and trait clusters

The PCA and the correlation matrix highlighted trait clusters consistent with our hypotheses (Tables S3,S4; Fig. S1). The first PCA component explained 39% of the trait variance, and the first two components, 65% (Table S4). The first component was principally associated with traits related to the microhabitat gradient, and the second component with allocation to leaf and canopy-level structural support. The trait correlation matrix indicated many correlations within given trait categories (i.e. among leaf dimensions, among leaf shape traits, among cell traits and among canopy structure traits; grey cells in Table S3), but few among photosynthetic traits.

Trait correlations: traits linked with the light and moisture gradient

There were strong linkages among traits aligned with the microhabitat light and moisture gradient (Fig. S1). Traits most strongly related to this axis were CD, IWT, LMF, N_{mass} and QE_{mass} (Table S4). The clustering of traits with habitat was clear in the PCA; species of different habitats differed in scores of component 1 (ANOVA; $P = 0.0007$) but not of component 2 ($P = 0.10$). Species' scores of component 1 correlated tightly with their mean DSF ($r_p = -0.94$ for log-transformed DSF; $P < 0.001$).

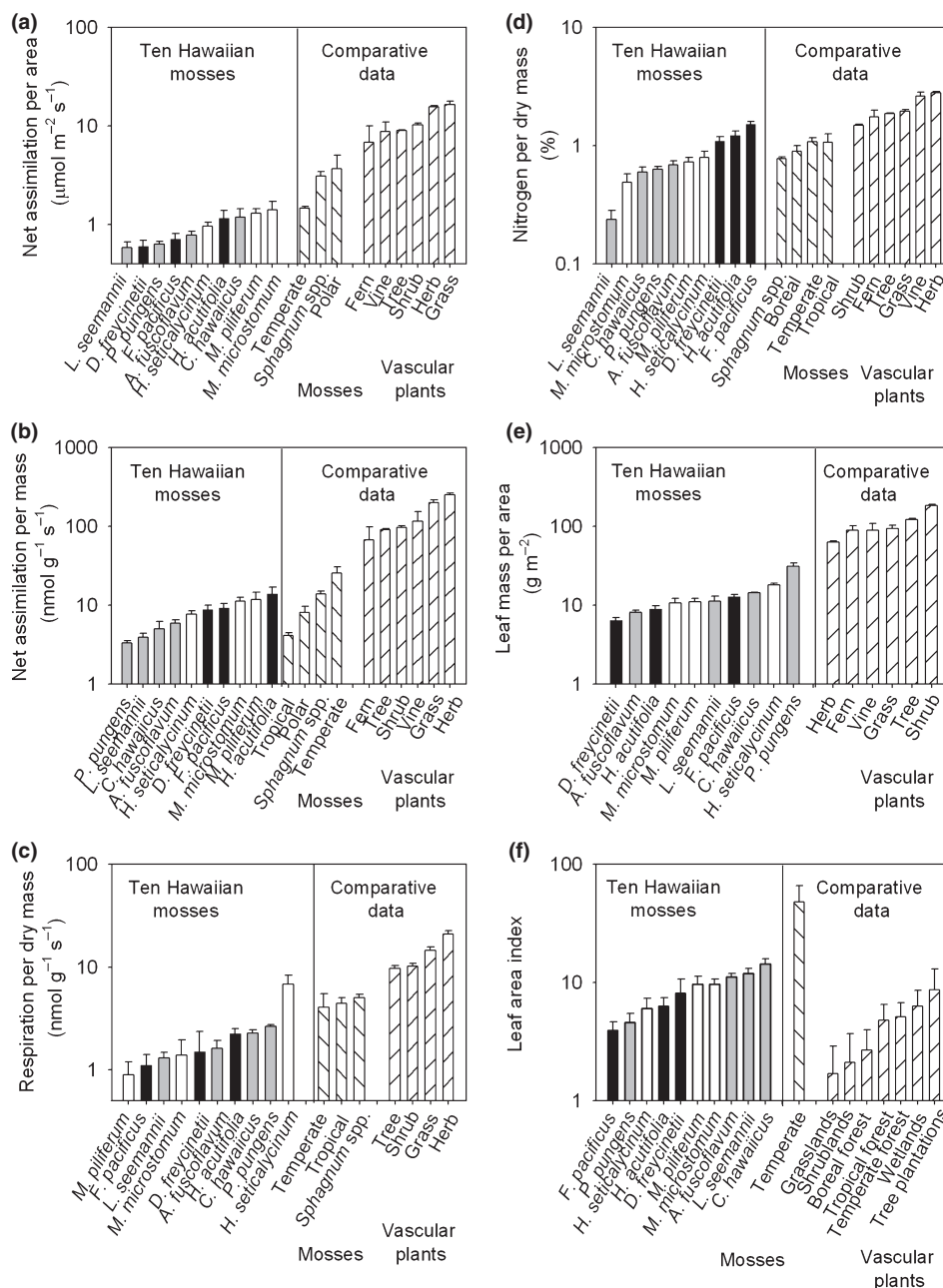


Fig. 3 Comparison of moss species in this study with compiled data for mosses and tracheophytes (vascular plants), for (a) light-saturated net photosynthesis per area, (b) light-saturated net photosynthesis per mass, (c) dark respiration per dry mass, (d) nitrogen per dry mass, (e) leaf mass per area and (f) leaf area index. Sources of comparative moss data: (a) temperate, 2 spp. (Silvola, 1985); *Sphagnum* spp., 12 spp. (Silvola, 1985; Rice *et al.*, 2008); polar, 3 spp. (Pannewitz *et al.*, 2005); (b) tropical, 11 spp. (Zotz *et al.*, 1997; Gabriel & Bates, 2003; Romero *et al.*, 2006); polar, 12 spp. (Longton, 1988; Davey, 1997); *Sphagnum* spp., 15 spp. (Titus & Wagner, 1984; Potter *et al.*, 1996; Schipperges & Rydin, 1998; Rice *et al.*, 2008); temperate, 21 spp. (Tobiessen *et al.*, 1979; Rundel & Lange, 1980; Alpert & Oechel, 1987; Potter *et al.*, 1996; Tuba *et al.*, 1996; Liu *et al.*, 1999; Martin & Adamson, 2001; Zotz & Rottenberger, 2001); (c) *Sphagnum* spp., 11 spp. (Titus & Wagner, 1984; Rice *et al.*, 2008); temperate, 7 spp. (Tobiessen *et al.*, 1979; Rundel & Lange, 1980; Tuba *et al.*, 1996); tropical, 11 spp. (Zotz *et al.*, 1997; Gabriel & Bates, 2003; Romero *et al.*, 2006); (d) *Sphagnum* spp., 16 spp. (Pitcairn *et al.*, 1995; Phuyal *et al.*, 2008; Rice *et al.*, 2008); boreal, 3 spp. (Startsev & Lieffers, 2006; Salemaa *et al.*, 2008); temperate, 13 spp. (Pitcairn *et al.*, 1995; Zotz & Rottenberger, 2001; Solga *et al.*, 2006; Britton & Fisher, 2007; Ozolincius *et al.*, 2007; Phuyal *et al.*, 2008); tropical, 8 spp. (Zotz *et al.*, 1997; Romero *et al.*, 2006; Liu *et al.*, 2008); (f) temperate, 7 spp. (Proctor, 1979; Simon, 1987; Vitt, 1990). Sources of comparative tracheophyte data: (a–e) 11–967 spp. per life form, except only 3 spp. each for ferns and vines in a–b (Wright *et al.* 2004); (f) 5–184 observations per vegetation type (Asner *et al.* 2003). Closed bars, ground-dwelling; tinted bars, trunk-dwelling; open bars, branch dwelling; bars with left cross-hatching, comparative moss data; bars with right cross-hatching, comparative tracheophyte data. Error bars, +1 SE.

We found two sets of partly interrelated trait clusters associated with light habitat: cell, leaf and canopy-level traits linked with leaf area (LA; Fig. 4a–e), and traits linked with canopy density (CD; Fig. 4f–j). Branch-dwellers had smaller leaves and cells than ground-dwellers, and LA correlated negatively with A_{area} , CD, CPA, I_s , and IWT, and positively with CH, CLA, LLA, LL, and LW ($|r_p|$ and $|r_s| = 0.64\text{--}0.96$, $P < 0.001$ to $P = 0.047$; Fig. 4a–e,i; Tables 2, S2, S3). We found that LL and LW scaled geometrically with LA, with coefficients not significantly different from the expected coefficient of 0.5 (95% CI = 0.35–0.96 and 95% CI = 0.41–0.96, respectively; Fig. 4e), consistent with shape variation being independent of leaf size. Other traits showed a relationship with leaf size that departed from power law scaling, consistent with adaptation to low irradiance in larger leaves; IWT did not increase with leaf size, as would have been expected from geometry, but instead decreased with a coefficient of -0.52 to an apparent minimum of approx. $1\text{--}2\ \mu\text{m}$ (Fig. 4d), CLA scaled with LA with a coefficient of 2.0, greater than the expected value of 1 (95% CI = 1.2–3.2), and CPA scaled with LA with a coefficient of -1.7 , less than the expected -1 (95% CI = -2.9 to -1.0 ; Fig. 4c). Consistent with these trends, LLA was not invariant with leaf size as expected from geometry, but increased in the largest leaves to *c.* 90%.

Other traits related to light habitat were linked with CD, which was greater for branch- than ground-dwellers. The CD correlated positively with I_s , A_{area} , A_N and LMF, and negatively with LLA, LL, LA and CH ($|r_p|$ and $|r_s| = 0.65\text{--}0.94$, $P < 0.001$ to $P = 0.046$; Fig. 4f–j; Table S3).

Trait correlations in mosses: traits linked with structural support allocation

The strong linkages among leaf, canopy and photosynthetic traits driving the second PCA axis were evidently related to structural support (Table S4; Fig. 5). These linkages arose because several of the species had high leaf allocation to costae, and leaves with longer and wider costae (i.e. with higher costa length (CL) and CCA), tended to have a higher leaf length/width ratio (L/W), as well as a greater LMA. Because longer costae were associated with the support of longer leaves on taller shoots, these traits also correlated with greater

CH and CMA, and with lower A_{mass} , presumably owing to increased self-shading and/or allocation to costa relative to photosynthetic cells. These trait linkages related to support thus included linkages with costa size (i.e. correlates of CL; Fig. 5a–c) and linkages with relative allocation to costa (i.e. correlates of L/W; Fig. 5d–f); CL and L/W themselves were weakly correlated, and negatively linked with A_{mass} ($|r_p|$ and $|r_s| = 0.71\text{--}0.93$; $P = 0.001\text{--}0.06$; Fig. 5a,d). In addition, CL correlated negatively with A_{area} and I_s and positively with CCA, CH, and LL ($|r_p|$ and $|r_s| = 0.76\text{--}1.00$, $P < 0.001$ to $P = 0.04$; Fig. 5a–c; Table S3), and L/W correlated positively with CMA, LMA and P^2/A (r_p and $r_s = 0.71\text{--}0.99$, $P < 0.001$ to $P = 0.03$; Fig. 5d–f; Table S3).

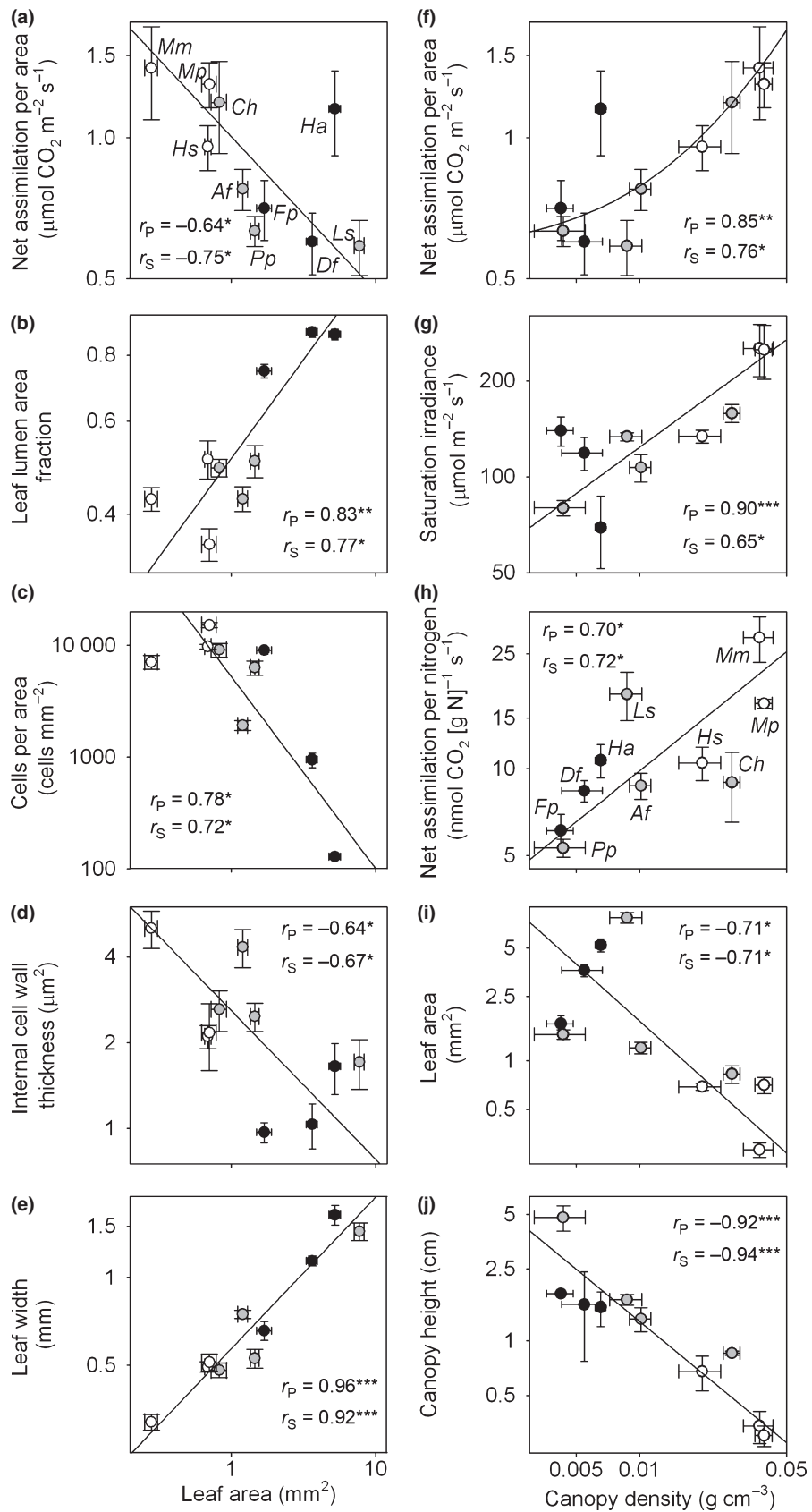
Trait correlations in mosses: the moss 'leaf economic spectrum'

We found correlations among moss traits analogous to those among leaf economics spectrum traits in tracheophytes (Fig. 6). While LMA was not significantly related to A_{mass} , A_{area} , N_{mass} or N_{area} , CMA correlated negatively with A_{mass} and N_{mass} (r_p and $r_s = -0.65$ to -0.76 , $P = 0.02\text{--}0.04$; Fig. 6a,b). However, the positive correlation between A_{mass} and N_{mass} found in tracheophytes was not apparent among the mosses of this study (Table S3). As reported for tracheophytes (Field & Mooney, 1986; Wright *et al.*, 2004), for mosses, the leaf economic spectrum relationships were stronger on a mass than an area basis. Thus, CMA was not significantly correlated with A_{area} or N_{area} , or A_{area} with N_{area} (Table S3).

Discussion

The 10 Hawaiian moss species exhibited strong physiological and structural variation. For example, species ranged 27-fold in LA, twofold in A_{area} , and fourfold to eightfold in N_{mass} , A_{mass} , I_s , I_c and R_{mass} . This species variation was greater than that in several previous moss studies, consistent with the wide range of habitat irradiances considered here. For example, mosses in a Japanese temperate forest and Panamanian rainforest, and bog *Sphagnum* species each varied 1.3-fold to threefold in A_{mass} , I_s , I_c or R_{mass} (Miyata & Hosokawa, 1961; Zotz *et al.*, 1997; Rice *et al.*, 2008). One

Fig. 4 Coordination of leaf area (LA) and canopy density (CD) with other leaf traits related to habitat irradiance: (a) light-saturated net photosynthetic rate per area (A_{area}), (b) lamina lumen area fraction (LLAF), (c) cells per area (CPA), (d) internal cell wall thickness (IWT), (e) leaf width (LW), (f) light-saturated net photosynthetic rate per area (A_{area}), (g) saturation irradiance (I_s), (h) net photosynthesis per nitrogen (A_N), (i) leaf area (LA), and (j) canopy height (CH). Symbols: closed, ground-dwelling; tinted, trunk-dwelling; open, branch-dwelling. Power laws were fitted as the standard major axes (SMA) of log-transformed data ($\log y = \log b + a \times \log(LA)$ for A–E and $\log y = \log b + a \times \log(CD)$ for G–J), except for F, in which a linear relationship was fitted as the SMA of untransformed data ($y = b + a \times CD$); A: $a = -0.331$ (95% CI: -0.599 to -0.183), $b = 1.01$; B: $a = 0.374$ (0.233–0.602), $b = 0.509$; C: $a = -1.72$ (-2.92 to -1.01), $b = 5272$; D: $a = -0.523$ (-0.945 to -0.290), $b = 2.60$; E: $a = 0.520$ (0.415–0.651), $b = 0.569$; F: $a = 22.8$ (10.9–47.8), $b = 0.561$; G: $a = 0.482$ (0.299–0.780), $b = 1140$; H: $a = 0.590$ (0.340–1.023), $b = 149$; I: $a = -1.17$ (-2.02 to -0.680), $b = 0.00798$; J: $a = -0.957$ (-1.32 to -0.694), $b = 0.0156$. Significance levels: *, $P < 0.05$; **, $0.01 \geq P > 0.001$; ***, $P \leq 0.001$.



study of four moss species in a North American forest also reported a fivefold to 10-fold range in A_{mass} and R_{mass} , driven by high values for the forest floor species *Plagiommium cuspidatum* (Tobiessen *et al.*, 1979).

Mosses differed strongly in functional traits from tracheophytes, which is unsurprising given their evolutionary divergence *c.* 430 million yr ago (Mishler *et al.*, 1994; Kenrick & Crane, 1997; Rensing *et al.*, 2008). The low moss physiological rates reflect constraints related to their growth form and the habitats in which they maintain dominance (Proctor, 2000a). The mosses also differed from tracheophytes in the correlations of photosynthetic traits and light habitat, but mirrored other important tracheophyte trends after accounting for differences in scale.

Low leaf mass per area, nutrient concentrations, and metabolic rates in mosses

Moss species' LMA values were low relative to tracheophytes, reflecting the presence of only one to two lamina cell layers. The lower LMA in mosses was also possibly related to their leaves requiring less allocation to structure because of their very small size, extending the trend for tracheophytes, in which small leaves can have low LMA, owing to lower allocation to vasculature and sclerenchyma (Milla & Reich, 2007; Niinemets *et al.*, 2007).

Moss canopies had distinctively low N_{mass} , A_{mass} , A_{area} and R_{mass} . The low A_{mass} would not arise from an inherently lower light harvesting efficiency; mosses and tracheophytes

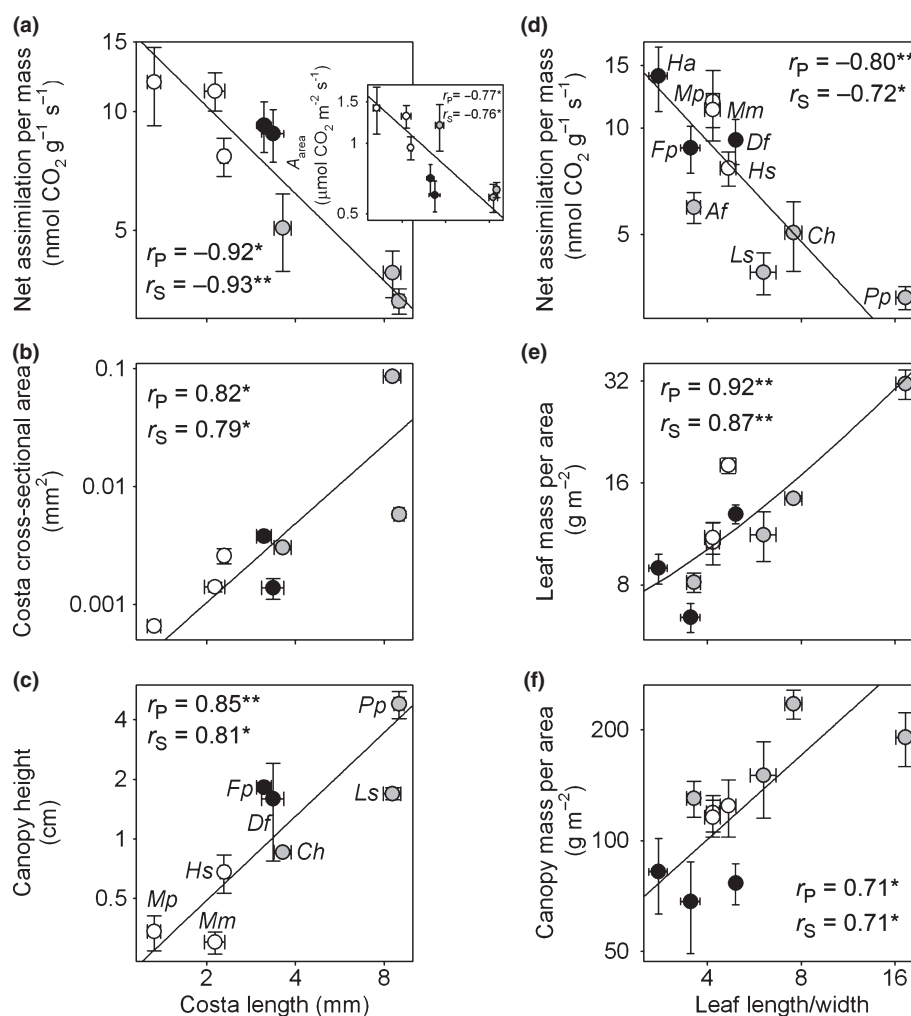


Fig. 5 Coordination of costa length (CL) and leaf shape (L/W) with other traits: (a) light-saturated net photosynthesis per dry mass (A_{mass}) and per area (A_{area} ; inset), (b) costa cross-sectional area (CCA), (c) canopy height (CH), (d) light saturated net photosynthesis per dry mass (A_{mass}), (e) LMA and (f) canopy mass per area (CMA). Symbols: closed, ground-dwelling; tinted, trunk-dwelling; open, branch-dwelling. Power laws were fitted as the standard major axes (SMA) of log-transformed data [$\log y = \log b + a \times \log(CL)$ for A–C, $\log y = \log b + a \times \log(L/W)$ for D and F], except for E, in which a linear relationship was fitted as the SMA of untransformed data ($y = b + a \times L/W$); A: $a = -0.732$ (95% CI: -1.072 to -0.500), $b = 17.1$; inset: $a = -0.553$ (-1.01 to -0.304), $b = 1.72$; B: $a = 2.22$ (1.28 – 3.84), $b = 0.000223$; C: $a = 1.41$ (0.85 – 2.33), $b = 0.184$; D: $a = -0.944$ (-1.510 to -0.590), $b = 34.0$; E: $a = 1.68$ (1.24 – 2.28), $b = 3.43$; F: $a = 0.762$ (0.442 – 1.312), $b = 35.0$. Significance levels: *, $P < 0.05$; **, $0.01 \geq P > 0.001$; ***, $P \leq 0.001$.

can have similar light-saturated photosynthetic rate per chlorophyll (Martin & Adamson, 2001). However, mosses may have low photosynthetic nitrogen-use efficiency; moss A_N values in this study averaged $12 \text{ nmol g}^{-1} \text{ N s}^{-1}$ (range $5\text{--}28 \text{ nmol g}^{-1} \text{ N s}^{-1}$) whereas a compilation of tracheophyte values averaged $66 \text{ nmol g}^{-1} \text{ N s}^{-1}$ ($6\text{--}255 \text{ nmol g}^{-1} \text{ N s}^{-1}$; Wright *et al.*, 2004). We suggest four possible explanations for the low A_{mass} , N_{mass} and R_{mass} of mosses. First, the low values may reflect shade adaptation; even branch-dwellers probably experience low irradiance during active periods when the tissue is hydrated under cloudy conditions (Rundel & Lange, 1980; Alpert & Oechel, 1987; Zotz & Rottenberger, 2001). Second, because of light attenuation by the high canopy leaf area, the lower leaf layers would have low A_{mass} (Zotz & Kahler, 2007), reducing the canopy integrated value. Third, water storage and desiccation tolerance may rely on allocation to cell wall material and/or osmoticum, and thus lead to lower A_{mass} , N_{mass} and R_{mass} . Fourth, mosses may experience strong limitation of photosynthesis because of the high resistance to CO_2 diffusion through liquid water on the leaf surface and in the cell

wall (Dilks & Proctor, 1979; Rundel & Lange, 1980; Rice & Giles, 1996). The evolution of specialized lamellae cells in the moss family Polytrichaceae to reduce this resistance and the carbon concentrating mechanisms in some hornworts point to the importance of this limitation (Proctor, 2005; Brodribb *et al.*, 2007; Meyer *et al.*, 2008).

Linkages of photosynthetic and structural traits with light habitat in mosses

Many traits in the Hawaiian mosses were aligned with light habitat, as reported for tracheophytes, whether for sun-acclimatized vs shade-acclimatized individuals, or for sun-adapted vs shade-adapted species (Givnish, 1988; Larcher, 2003). These sun-shade differences would contribute to functional and ecological segregation (Slack, 1990). We note that because the mosses in this study grew at different microsites, the species differences would include plasticity in addition to genetic differentiation. For branch relative to ground-dwelling mosses, leaves were smaller, composed of smaller cells with thicker cell walls, and lower in quantum efficiency (QE) and higher in A_{area} , A_N , I_c , I_s , R_{area} and R_{mass} . Smaller leaves may reduce heat loading (Vogel, 1968; Givnish, 1987). The higher A_{area} and I_s for branch-dwellers indicate increased capacity to utilize the greater available irradiance, and the higher R_{area} , R_{mass} and I_c would reflect an associated greater maintenance cost. Higher A_N for species of higher irradiance would result from greater nitrogen allocation to photosynthetic components (Givnish, 1988; Walters & Reich, 1999). These convergences between mosses and tracheophytes in the association of morphology with irradiance, despite ancient lineage separation and independent evolution of the leaf form, indicate robust principles of plant optimization to irradiance.

Despite these convergences, other important trends of tracheophyte sun-shade adaptation were not found for the 10 mosses, including the higher A_{mass} , N_{mass} and N_{area} typical of sun-adapted relative to shade-adapted tracheophyte leaves. The lack of these trends in the mosses may result from the same factors causing mosses to have low values for these traits. The general shade adaptation of mosses, their high LAI and the diffusion of CO_2 through water film may constrain A_{mass} in mosses (Dilks & Proctor, 1979; Rice & Giles, 1996), such that it would show limited increase with habitat irradiance. In addition, desiccation tolerance mechanisms that would lower A_{mass} , such as thick cell walls and osmotic adjustment, may be expressed more strongly in exposed habitats, with high irradiance, windspeed and vapor pressure deficit (Dilks & Proctor, 1979; Proctor, 1982). This expectation is consistent with smaller cells and thicker cell walls in branch-dwellers; these would 'dilute' the A_{mass} relative to species of shaded habitats.

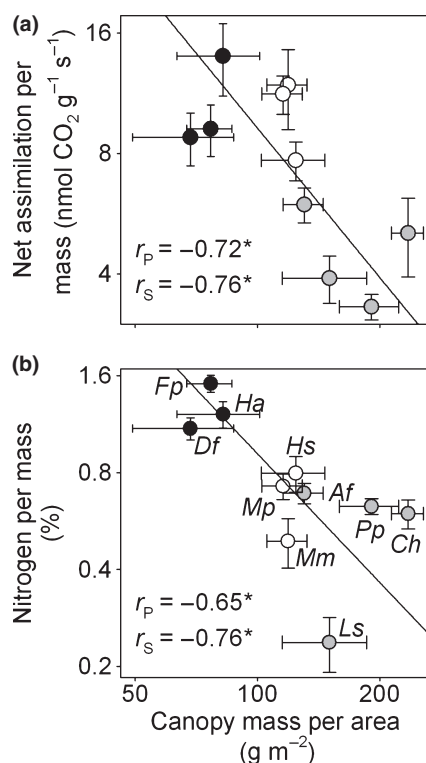


Fig. 6 Coordination of 'leaf economic' traits in mosses: (a) light-saturated net assimilation (A_{mass}) and canopy mass per area (CMA), (b) nitrogen per dry mass (N_{mass}) and CMA. Symbols for panels (a) and (b): closed, ground-dwelling; tinted, trunk-dwelling; open, branch-dwelling. Power laws were fitted as the standard major axes (SMA) of log-transformed data [$\log y = \log b + a \times \log(\text{CMA})$]: A: $a = -1.24$ (95% CI: -2.12 to -0.73), $b = 2786$; B: $a = -1.33$ (-2.38 to -0.740), $b = 413$. Significance levels: *, $P < 0.05$; **, $0.01 \geq P > 0.001$; ***, $P \leq 0.001$.

Trait–trait linkages in mosses: traits related to light, to structure, and to leaf economics

We found strong trait–trait linkages across the 10 species. Trait–trait correlations may indicate genetic or developmental linkages or coselection of traits that contribute to performance under similar conditions during evolution or ecological sorting (Reich *et al.*, 2003; Sack *et al.*, 2003; Givnish *et al.*, 2004; Wright *et al.*, 2004; Dunbar-Co *et al.*, 2009). In tracheophyte leaves, certain traits, such as LA and LMA, act as ‘hubs’, interlinked with many other traits (Sack *et al.*, 2003; Ackerly, 2004; Niinemets & Sack, 2006; Sack & Holbrook, 2006).

One striking finding was the lack in the mosses of the linkages (or trade-offs) among photosynthetic traits reported in tracheophytes, because moss species of higher irradiance did not necessarily have higher A_{mass} . However, other photosynthetic traits were linked with light habitat and showed numerous linkages with cell-, leaf- and canopy-level traits, especially correlating with LA and CD. Another cluster of trait correlations related to structural support, including CL, L/W, A_{area} , A_{mass} , CCA, CH, CMA and LMA.

Moss species also showed linkages analogous to the leaf economic spectrum in tracheophytes (Wright *et al.*, 2004). For the 10 mosses, CMA rather than LMA was linked with A_{mass} and N_{mass} . These relationships apparently arose from species variation in allocation to costa and cell wall, which simultaneously drove higher CMA and lower A_{mass} and N_{mass} , a similar mechanism to that found in tracheophytes (Niinemets, 2001; Shipley *et al.*, 2006). Notably, A_{mass} and N_{mass} were measured for canopies rather than for leaves, and it is possible that LMA would relate to A_{mass} and N_{mass} if all were measured for individual leaves; such relationships would likely vary with canopy layer (Zotz & Kahler, 2007) and, if they existed, did not hold at canopy-level, which is the most appropriate scale for considering whole-moss function. Notably, a study of 10 *Sphagnum* species found no correlation among A_{mass} , N_{mass} or CMA (Rice *et al.*, 2008), possibly reflecting their limited range of morphology and composition relative to the species in this study, as the *Sphagnum* species were all adapted to high light and high moisture (Clymo & Hayward, 1982).

How should one compare mosses and tracheophytes in their structure and function?

Our study extends the comparability of mosses and tracheophytes, despite fundamental structural differences. In our study we compared moss and tracheophytes leaves directly in their LMA. However, we also compared the moss canopy with the tracheophyte leaf in mass per area, in composition, and in gas exchange rates per area and per mass, because these two structures may be especially analogous (Proctor, 2000b). Moss canopy leaves may be

analogous to the layers of mesophyll cells within a tracheophyte leaf, with moss leaf area thus like internal mesophyll area. Indeed, moss canopy LAI values matched the 4–13 layers of mesophyll cells in tracheophyte leaves (Nobel, 1974; Roth, 1984).

The importance of CMA as a correlate of N_{mass} and A_{mass} also indicated the usefulness of comparing the moss canopy with the tracheophyte leaf. This comparison provides an indication of the possible convergence of structural and functional trait linkages for mosses and tracheophytes in the global leaf economics spectrum (Wright *et al.*, 2004), with the clear proviso that the full moss diversity has yet to be sampled (Fig. 7). The low values of moss species for A_{mass} , N_{mass} and LMA separated the mosses and tracheophytes when comparisons used LMA (Fig. 7; Hawaiian moss LMA values denoted with circles). However, when using CMA for the mosses, their values approached those of tracheophytes at the low A_{mass} and N_{mass} end of the spectrum (Fig. 7; Hawaiian moss CMA values denoted with diamonds). Notably, the *Sphagnum* species were located closer to the tracheophytes than the Hawaiian mosses, which had lower A_{mass} relative to their CMA (Fig. 7; *Sphagnum* CMA values denoted by triangles). The *Sphagnum* spp., which are typically well hydrated and exposed, may better optimize A_{mass} relative to structural allocation and desiccation tolerance. For a robust comparison of moss and tracheophyte function, data are needed for mosses of a yet wider range of morphologies (see also Notes S1 ‘Comparisons of bryophytes and tracheophytes’).

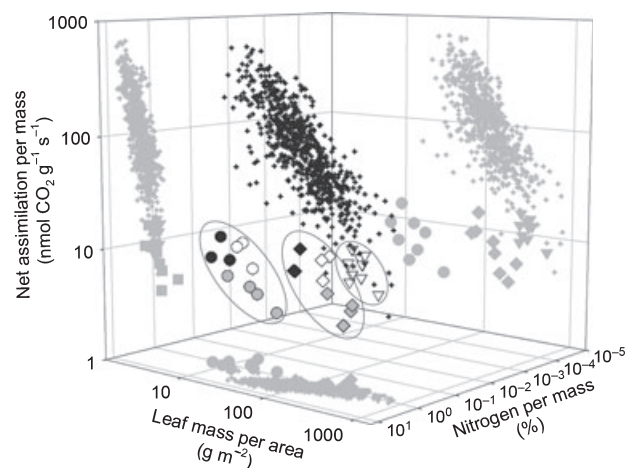


Fig. 7 The available data for mosses from two studies plotted as a first comparison with the global data compiled for the tracheophyte ‘leaf economic spectrum’: light-saturated assimilation rate per mass (A_{mass}), leaf mass per area (LMA), canopy mass per area (CMA) and nitrogen per mass (N_{mass}) for 10 Hawaiian mosses in this study, 10 *Sphagnum* species (data from Rice *et al.*, 2008) and tracheophytes (data from Wright *et al.*, 2004). Symbols: +, tracheophyte species; circles, LMA 10 Hawaiian moss species (closed, forest floor species; dark tint, trunk species; light tint, branch species); diamonds, CMA for 10 Hawaiian species (same colors as for habitats); triangles, CMA for *Sphagnum* spp.

Implications and needs for future study

Our understanding of moss biology is currently expanding, especially as genomic studies (e.g. of *Physcomitrella patens*; Rensing *et al.*, 2008) help clarify the evolutionary position and sequence similarity of mosses relative to other groups and as studies using mosses as model systems elucidate gene function (Cove *et al.*, 2006; Renzaglia *et al.*, 2007). Other studies have revealed that mosses can play essential roles in ecosystem carbon and water balance (Pocs, 1980; Skre & Oechel, 1981; Vitt, 2000; DeLucia *et al.*, 2003; Holscher *et al.*, 2004). This study highlights the high physiological and structural trait diversity in mosses, as well as trait linkages convergent with those reported for tracheophytes. Our findings support the proposal of Proctor (2000b) that the moss canopy can be used gainfully as the unit for measuring functional traits, such as photosynthesis, LMA and nutrient concentrations, and point to the practical ability to quantify key functional traits for bryophyte species within and across ecosystems (Cornelissen *et al.*, 2007). We found that, for example, CMA and CD, which are relatively simple to measure, are potential proxies for estimating canopy A_{mass} and A_{area} . Similarly, tight allometric relationships related leaf dimensions to harder-to-measure cell traits. These relationships need to be tested on additional species sets to ensure generality. Further work, sampling species within a phylogenetic context is needed to determine whether these trait correlations arise owing principally to adaptation or to ecological sorting. This study highlights the need for future work on the wide range of moss species for a full understanding of their function relative to tracheophytes. Detailed studies of the coordination among traits and environment and, ultimately, their genetic, developmental and structural bases, will reveal the degree to which leaf adaptation has occurred similarly across groups in which leaves evolved independently, for different scales and contexts.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Methods S1. Additional methods – photosynthetic traits, tissue nitrogen concentration, leaf and cell morphological traits, and canopy traits.

Fig. S1 Principal component analysis of 18 traits from 10 Hawaiian mosses.

Fig. S2 Independence of photosynthetic traits and light-saturated net photosynthesis per area.

Table S1 Mean values and standard error for each trait by species

Table S2 Study traits, symbols, and unit, and mean squares from one-way analyses of variance for differences among microhabitats and species, with species nested within microhabitat

Table S3 Correlation matrix of physiological and morphological traits at cell, leaf and clump-level for 10 Hawaiian moss species

Table S4 Factor-loadings of first two principal components for 18 traits determined for 10 Hawaiian moss species

Notes S1 Comparisons of bryophytes and tracheophytes.

Appendix S1 References for Additional Methods S1 and Notes S1.

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