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Cushion size, surface roughness, and the control of water balance and carbon flux in the cushion moss *Leucobryum glaucum* (Leucobryaceae)[1]

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We explored the size dependence of water balance and carbon flux in the cushion moss *Leucobryum glaucum* (Leucobryaceae). Conductance to water vapor (g_a) was modeled empirically using 4–24 cm diameter cushions ($N = 14$) evaluated across wind speeds from 0.7 to 4.3 m/s in a wind tunnel. Model parameters included wind speed (u), kinematic viscosity (v), cushion diameter (L_d), and surface roughness (L_r). The model $g_a = -9.62(u/v)^{1.21} \cdot L_d^{-0.35} \cdot L_{r\text{-in}}^{-1.85}$ (where $L_{r\text{-in}}$ represents a dimensionless form of L_r; $R^2 = 0.88$) indicates negative relationships between g_a and both L_d and L_r. These predictions were evaluated during a 5-d field experiment where water loss and net carbon exchange (estimated by $\Delta F/F_m'$) were monitored. In the field ($N = 18$, 4–34 cm diameter cushions), L_r, but not L_d, controlled rates of evaporation due to additional turbulence that reduced size dependence of cushions along the forest floor. However, the duration of positive net carbon gain varied from 1.4 to 4.4 d and was significantly longer in larger diameter cushions. Thus, under field conditions, size-dependent changes in surface-area-to-volume relationships influence the duration of net carbon gain more than differences in water flux and lead to a strong size dependence of water balance and carbon flux.

Key words: allometry; boundary layer; bryophyte; growth form; Leucobryaceae; *Leucobryum glaucum*; life form; water budget.

In vascular plants, size affects light, water, and nutrient acquisition, thereby influencing growth, survival, reproduction, and ecological interactions (Donovan and Ehleringer, 1992; de Soyza et al., 1996; Zotz, 2000; Bonser and Aarssen, 2003). One of the principal effects occurs belowground where differences in root size cause differential access to soil water and mineral nutrients, thereby indirectly controlling leaf-level physiological responses that govern short- and long-term carbon gain. Although lacking roots and the ability to scavenge the environment effectively for water and nutrients, water and carbon balance in bryophytes is also dependent on plant size. During growth, changes in size and allometry alter the relative proportion of organs and tissues that control the fluxes and storage of water. Because the duration of favorable water status controls net carbon gain in bryophytes (Dilks and Proctor, 1979; Skre and Oechel, 1981; Proctor, 1990; Sveinbjornsson and Oechel, 1992; Tuba et al., 1998; Zotz and Rottenberger, 2001), canopy size should affect the length of the physiologically active period, and consequently growth rates and ecological interactions.

In lichens, increases in thallus size lead to reduced rates of evaporation, increased water storage, and prolonged periods of net carbon gain under laboratory conditions (Larson, 1984; Hestmark et al., 1997; Gauslaa and Solhaug, 1998). Similar patterns have been shown recently in bryophytes. Zotz et al. (2000) explored the size dependence of water and carbon budgets in the cushion moss *Grimmia pulvinata* (Hedw.) Sm. ex Sm. & Sowerby (Grimmiaceae). In their laboratory studies, increased cushion size was associated with lower rates of net photosynthesis on a mass basis. However, rates of evaporation declined and water storage capacity increased in larger cushions, leading to more favorable water balance. A carbon budget model developed from these relationships predicted that larger cushions should experience longer duration of positive carbon gain, and thus, enhanced growth rates. Unfortunately, although they evaluated the size dependence of evaporation rates in controlled conditions, they did not adequately explore this relationship across variation in one of the most important environmental factors that controls water fluxes in bryophytes: wind. Previous studies indicate that variation in wind speed causes between a 0.91 and 1.54 exponential increase in evaporation rates (Proctor, 1980; Rice et al., 2001). Thus, the mechanisms that underlie size dependence of water flux and consequently water budgets have not been well characterized. In addition, previous studies of size and wind dependence of water fluxes have been performed under laboratory conditions and there has yet to be an adequate field test of such phenomena for either lichens or bryophytes.

Unlike water flux in vascular plants, which is controlled physiologically by the opening and closing of stomata, water loss from most bryophytes is determined by canopy size and structural properties (i.e., ''life form'' sensu Mägdefrau, 1982; Bates, 1998) that influence the development of boundary layers adjacent to plant surfaces (Proctor, 1980, 1982, 2000; Rice and Schuepp, 1995; Rice et al., 2001). Boundary layers can be considered regions of still air that develop adjacent to surfaces due to friction (see Nobel, 1991; Jones, 1992; Schuepp, 1993; Campbell and Norman, 1998 for reviews). Water from leaves must move through boundary layers via molecular diffusion, and in bryophytes the boundary layer presents the major impediment to water loss (Proctor, 1980). In simple geometric shapes, like those of many vascular plant leaves, but also in spherical plant parts, boundary layer development is related functionally to linear dimensions. In general, as the linear size (i.e., organ diameter) increases, boundary layers thicken and evaporation rates decline by the −0.5 power both

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for flat (Schuepp, 1993) and spherical (Nobel, 1974) plant organs. In studies of bryophytes, this relationship has been assumed to have the same form as that which occurs in flat plates (Proctor, 1980). The scaling function that relates canopy diameter to water fluxes in bryophytes may not conform to that observed in previous studies. Unlike vascular plant organs that exist within a free air stream, many bryophytes persist on a substrate. Consequently, drag associated with the surface may submerge bryophyte canopies within thickened boundary layers or, alternatively, generate turbulence, both of which would reduce or eliminate the size dependence of water flux.

Fine-scale variation in branch and leaf structure also affects boundary layer properties in bryophyte canopies. Wind-tunnel measurements using 11 species performed by Rice et al. (2001) demonstrated that variation in the architecture of moss canopies alters boundary layer thickness and leads to differences in evaporation rates. This difference is caused by the generation of turbulence, by enhanced flow-through within canopies, and by increased exchange area in rough canopies, all of which increase mass transport from rough bryophyte surfaces. Overall, variation in surface properties as measured by a surface roughness metric (see below) causes a 0.33 power increase in rates of boundary layer conductance and evaporation.

Differences in canopy size will also affect water storage. Many bryophytes store water within external capillary spaces, in specialized hyaline cells and/or in decaying organic matter formed following tissue senescence. Within a given anatomical and structural type, differences in plant volume relate directly to variation in water holding capacity, and surface area-to-volume ratio (SA : V) characterizes the exchange area relative to storage capacity. When there are no allometric changes with increased size, water storage should increase to the third power of increases in canopy diameter and SA : V will scale to the power of -1 (Niklas, 1994). However, changes in canopy shape or leaf area ratio (leaf area per projected surface area) could increase or decrease the magnitude of that scaling function.

In this study, we employ a comprehensive approach to investigate the relationships among canopy size, canopy structure, wind, and the interaction between water and carbon balance in the common temperate forest floor moss species *Leucobryum glaucum* (Hedw.) Ångstr. ex Fries (the white or pin cushion moss; Leucobryaceae). We accomplish this by (1) measuring the size dependence of cushion morphology and relating it to properties that affect plant water budgets; (2) evaluating boundary layer conductance to water vapor of samples that vary in size in a laminar flow wind tunnel; (3) developing a boundary-layer conductance model based on cushion morphological attributes; and (4) evaluating predictions of the model during a 5-d drying course in the field.

MATERIALS AND METHODS

Study species—*Leucobryum glaucum*, an ectohydric, acrocarpous moss forms dense, semi-hemispherical cushions that expand in diameter and in height as they grow. Photosynthetic tissues are located along the outer 0.5–1.0 cm portions of the shoot apicies. With growth, tissues shaded within the cushion interior senesce and form a dense peat that functions in water storage. Leaves of *L. glaucum* contain 1–4 layers of physiologically inactive hyaline cells surrounding photosynthetic cells. These cells occupy over 75% of leaf volume and contribute to the ability of *L. glaucum* to hold up to 20 times its dry mass in water. *Leucobryum glaucum* commonly persists on duff, exposed roots, and soil in coniferous and mixed coniferous-deciduous forests throughout the temperate zone of the Northern Hemisphere (Crum and Anderson, 1981). In the study region, cushions often grow in sparsely vegetated understories. Consequently, interactions between the cushion and wind-flow adjacent to the forest floor should influence boundary layer and mass transfer properties.

Cushions of *L. glaucum* ranging from 4 to 34 cm in diameter were collected in a fully hydrated condition from a privately owned mature *Tsuga canadensis* (L.) Carrière (Pinaceae) forest near Cooperstown, New York, USA (42° 45.880 N, 74° 56.800 W). Discrete cushions across this size range were abundant on the sparsely vegetated forest floor at this site. Plants were removed from the substrate with a sharp knife. Samples for wind tunnel analysis (14 from 4 to 24 cm diameter, collected on 25 July 2002) were returned to the laboratory where they were maintained moist under full spectrum lamps over a 14-h day length. Plants used in the field study (18 from 4 to 34 cm diameter, collected on 6 August 2002) were transported to the field site (1 km distant) and kept moist under a 50% shade cloth on the forest floor for 2 d prior to the start of the field experiment.

Canopy structure—Each plant was assessed for diameter, surface area, volume, surface roughness, and leaf area. The surface roughness (L_r), a measure of the mean distance between high and low portions of the canopy, was derived from canopy depth profiles. A surface contact probe connected to a micromanipulator was used to measure canopy depth to the nearest 0.1 mm at 0.5 cm intervals along a 5 $\times$ 5 cm grid. The number of sample points varied from 121 to a minimum of 24 measurements on the smallest canopy. Larger scale shape pattern was removed from these data by performing a nonlinear regression using the formula for a parabola as employed by Hayward and Clymo (1983). Residuals from that regression were used in the analysis. The resulting data were used to calculate surface roughness with the semivariance method. In this analysis, surface roughness is measured from the maximal semivariance that characterizes the average of the squared differences between the mean and samples a given distance apart. In this case, the maximal semivariance occurred at $<$3 cm scale and reflects fine-scale variation in leaf and branch structure. The L_r parameter is calculated as the square-root of twice this value (see Rice et al., 2001 for more details on this method). The semivariance was calculated using VESPER software (Minasny et al., 1999) with the ''linear with sill'' algorithm.

Cushion surface area and volume were measured following the method of Zotz et al. (2000). Cushions were placed under the contact probe and cushion heights were measured at the central point and at 4–6 regularly spaced intervals along four radial transects in four principle directions. Each cushion was treated as a series of parts of a cone between two parallel cutting planes. The resulting shape is called a frustum and its surface area and volume were calculated from the formulas presented in Zotz et al. (2000). The total cushion surface areas and volumes were calculated as the sum of the frustum surface areas and volumes.

The surface area determined by this method assumes that the surface is flat. Leaf area was estimated for each sample by determining the empirical relationship between leaf area ratio (leaf area : projected surface area) and surface roughness in a subset of 12 samples and using that relationship to estimate leaf area for all cushions. Leaf area ratio was measured by excising a 1.5 $\times$ 1.5 cm portion of the canopy with a razor. Brown tissue and stems were removed with a scalpel while viewing under a dissecting microscope. Leaf tissue was dried at 65°C for 24 h and weighed to the nearest 0.1 mg. Leaf area was determined by multiplying leaf mass by specific leaf area (in square centimeter per milligram). This latter quantity was estimated by measuring the surface area of both sides of 60 leaves using a digital camera system equipped with a macro lens (Model VCS-10132, Pixera, Los Gatos, California, USA) and image processing program (Scion Image version 1.62c, Scion, Frederick, Maryland, USA). These leaves were dried and weighed to the nearest 0.01 mg. In *L. glaucum*, leaf bases are closely overlapping and contribute little to photosynthesis or evaporative area. Consequently, measures of leaf area were reduced by subtracting the fraction of leaf area that is occupied by the leaf base (58%). This was defined by the portion of the leaf from the base to the inflection point along the leaf margin and was measured on 25 leaves.

Boundary layer conductance—Rates of evaporation of water and boundary layer conductance were measured in a laminar flow wind tunnel (Model 402B, Engineering Laboratory Design, Lake City, Minnesota, USA). The working section measured 54 cm in length with a 30.5 × 30.5 cm cross section. Wind speeds ranged from 0.7 to 4.3 m/s and were measured above the sample in the middle of the flow field. Wind speed was assessed using a hot wire anemometer (Model 06-662-73, Control Company, Friendswood, Texas, USA) calibrated with a pitot probe and micromanometer (Dwyer Instruments, Michigan City, Idaho, USA).

Boundary layer conductance to water vapor (g_a) was evaluated by measuring evaporation of water. Cushions were sprayed with deionized water, weighed to the nearest 0.01 g, and placed within the wind tunnel. Samples remained inside the wind tunnel at a given wind speed until at least 0.10 g of mass were lost (3–16 min). The plants were removed and their mass recorded. At each of six wind speeds, evaporation was measured two times with the cushion placed at right angles in the two trials. Means of these values were used in the analyses.

During each trial, the relative humidity and air temperature were measured using probes on a photosynthesis system (see below) placed at the intake of the wind tunnel. Boundary layer conductance to water was calculated using the evaporation rates and environmental data following formulas presented in Jones (1992). Both evaporation rates and boundary layer conductance were expressed on a leaf area basis. Surface temperature was obtained by tying two 0.5 mm thermocouples (temperature to the nearest 0.1°C; Physitemp Instruments, Clifton, New Jersey, USA) to branches on the surface of the cushion. Due to the difficulty measuring cushion mass with the thermocouples attached, surface temperatures were measured in separate trials immediately following the evaporation ones.

A boundary layer conductance (g_a) model was constructed to relate g_a to variation in canopy structure. The model structure was derived from a dimensionless form that uses Sherwood (Sh), Schmidt (Sc) and Reynolds (Re) numbers. The Sh number characterizes conductance ($\mathrm{Sh} = g_a \times L \times D^{-1}$, where g_a, D, and L represent conductance, diffusivity of water in air, and characteristic length, respectively), Sc is a property of the fluid ($\mathrm{Sc} = v/D$, where v equals the kinematic viscosity of air), Re describes the flow environment ($\mathrm{Re} = u \times L \times v^{-1}$, where u is the wind speed). Under a wide range of conditions, these are related via the following relationship $\mathrm{ShSc}^{-0.33} = c\mathrm{Re}^n$, with c and n representing model parameters (Schuepp, 1993) that are estimated empirically.

This model requires the designation of a characteristic length (L). For spherical or cylindrical plant organs, the organ diameter has been used as a length scale to model flow and mass transfer. Under conditions when the geometry departs from a true sphere or cylinder, the diameter of the sphere or cylinder that has the same surface area has been employed as a length scale (Nobel, 1974). We follow this convention and calculate the diameter length (L_d) by multiplying this value by 0.81 to reflect the mean not maximal width in the direction of flow (Campbell and Norman, 1998). In rough surfaces, the magnitude of the roughness elements also determines boundary layer properties (Raupach et al., 1991) and correlates with mass transfer from bryophyte canopies (Rice et al., 2001). We included this in our model by adding surface roughness as a predictor variable. We converted the surface roughness (L_r) to dimensionless form by dividing it by the maximal L_r value in the study. We call this the surface roughness index ($L_{\text{r-in}}$).

These characteristic lengths may or may not scale with conductance similarly to each other or with changes in wind speed due to the effects of cushion geometry, sheltering, and turbulence generated by substrate roughness (Bandyopadhyay, 1987; Raupach et al., 1991; Krogstad and Antonia, 1999; also see Gurevitch and Schuepp, 1990 for discussion as applied to plants). Therefore, to allow these to influence boundary layer properties independently, we have factored them out of the Re number and assigned them individual scaling exponents. Thus, the complete mass transfer model is represented by $\mathrm{ShSc}^{-0.33} = c \times (u/v)^n \times L_d^{n'} \times L_{\text{r-in}}^{n''}$, where the Sh number employs L_d as a length scale. When this is solved for g_a, the model becomes $g_a = C \times (u/v)^n \times L_d^{(n'-1)} \times L_{\text{r-in}}^{n''}$. The parameter C is the product of the constants D, $\mathrm{Sc}^{0.33}$, and the variable c. The exponents n, $n' - 1$, and n'' and the C parameter were estimated by performing a multiple linear regression following log transformation. Given that each of the 14 samples was evaluated across a range of six wind speeds, sample points in this analysis were not independent and confidence intervals derived using parametric statistics would not be appropriate. Thus, the significance of the exponents and their 95% confidence intervals were calculated using bootstrap analysis on 1000 resampled data sets using SIMSTAT software (Provalis Research, Montreal, Quebec, Canada).

Physiological characteristics—Chlorophyll fluorescence parameters were compared to rates of net photosynthesis and dark respiration during drying at a range of temperatures under laboratory conditions; the resulting relationships were used to estimate physiological states in the field. Twelve 7–8 cm diameter cushions were collected on 1 September 2002 and maintained hydrated under 100 μmol · m^{-2} · s^{-1} light from full spectrum lamps over a 14-h day length. Beginning on 5 September, net photosynthesis and dark respiration were measured using a closed-chamber photosynthesis system (LI-COR 6200, LI-COR, Lincoln, Nebraska, USA) connected to a 1.1-L chamber enclosed within a circulating water bath constructed for the purpose. Net photosynthesis was measured as net CO_2 uptake expressed on a leaf area basis during 40-s measurement intervals where CO_2 concentrations changed between 0 and 15 ppm. Initial CO_2 level within the chamber was 380 ppm and relative humidity values ranged from 75 to 90%, with lower values present in dehydrated samples. Measurements were performed at a light intensity of 220 μmol · m^{-2} · s^{-1} provided by a 50-W halogen source filtered through 2 cm of water. Between measurements, plants were maintained under similar light conditions at the measurement temperature. This light intensity is within the range of common light in the natural environment and provided 75% of maximal rates of photosynthesis determined from four additional samples over a range of light intensities from 20 to 900 μmol · m^{-2} · s^{-1}. Cushions were exposed to wind from a fan to facilitate drying; drying from a fully hydrated state to negligible net photosynthetic rates took between 29 and 36 h. Two groups of four samples were used to characterize photosynthesis across a range of temperatures that occurred in the field. During measurements, surface temperatures ranged from 20° to 24°C in the first group and from 25° to 29°C in the second. Higher temperatures occurred with dry samples in each group, a pattern also evident in the field. Rates of dark respiration were measured over 40–80 s intervals at similar temperatures periodically during the course of the drying cycle.

Parameters derived from chlorophyll fluorescence measurements correlate with rates of photosynthesis and photosynthetic capacity. The effective quantum yield (Φ_{PSII}) can be estimated under ambient light conditions by measuring the ratio of the additional fluorescence yield achieved above the steady state value relative to the maximal yield ($\Phi_{PSII} = \Delta F/F_m'$; Genty et al., 1989; Maxwell and Johnson, 2000). Variation in $\Delta F/F_m'$ relates to differences in net photosynthesis in bryophytes (Tuba et al., 1997; Csintalan et al., 1999; Marschall and Proctor, 1999). This parameter was measured using a 5.5-mm fiber optic probe interfaced with a modulated fluorometer (MINI-PAM Fluorometer, Walz, Effeltrich, Germany) at three sample points on each cushion following each photosynthesis measurement. The probe, conducting saturating pulses, measuring and actinic light, was held 1.2 cm from the surface at a 60° angle using a standard leaf clip. Light intensity was the same as occurred during photosynthesis (220 μmol · m^{-2} · s^{-1}) and was evaluated at the plant surface.

Field water and net CO_2 exchange—Predictions of the boundary layer conductance model on evaporation and on the duration of positive net carbon gain were evaluated in a field experiment. The field site was 1 km from the collecting site and within a young *Acer rubrum* L. (Aceraceae) stand adjacent to Muskrat Pond, Otsego County, New York, USA. *Leucobryum glaucum* was present at the site, but was not abundant enough across a range of canopy sizes to provide samples for the study. Rates of evaporation were assessed during a 5-d drying course on 18 cushions that varied in diameter between 4 and 34 cm. Cushions were set on flat plastic trays on a raked carpet of commercial pine bark mulch (5.1 × 2.9 × 1.8 cm mean dimensions) within an open area of the forest floor. Plants were at least 3 m from the nearest tree bole and were distributed evenly around two concentric circles. Twelve cushions were placed in the outer circle and six in the inner one. Cushions were

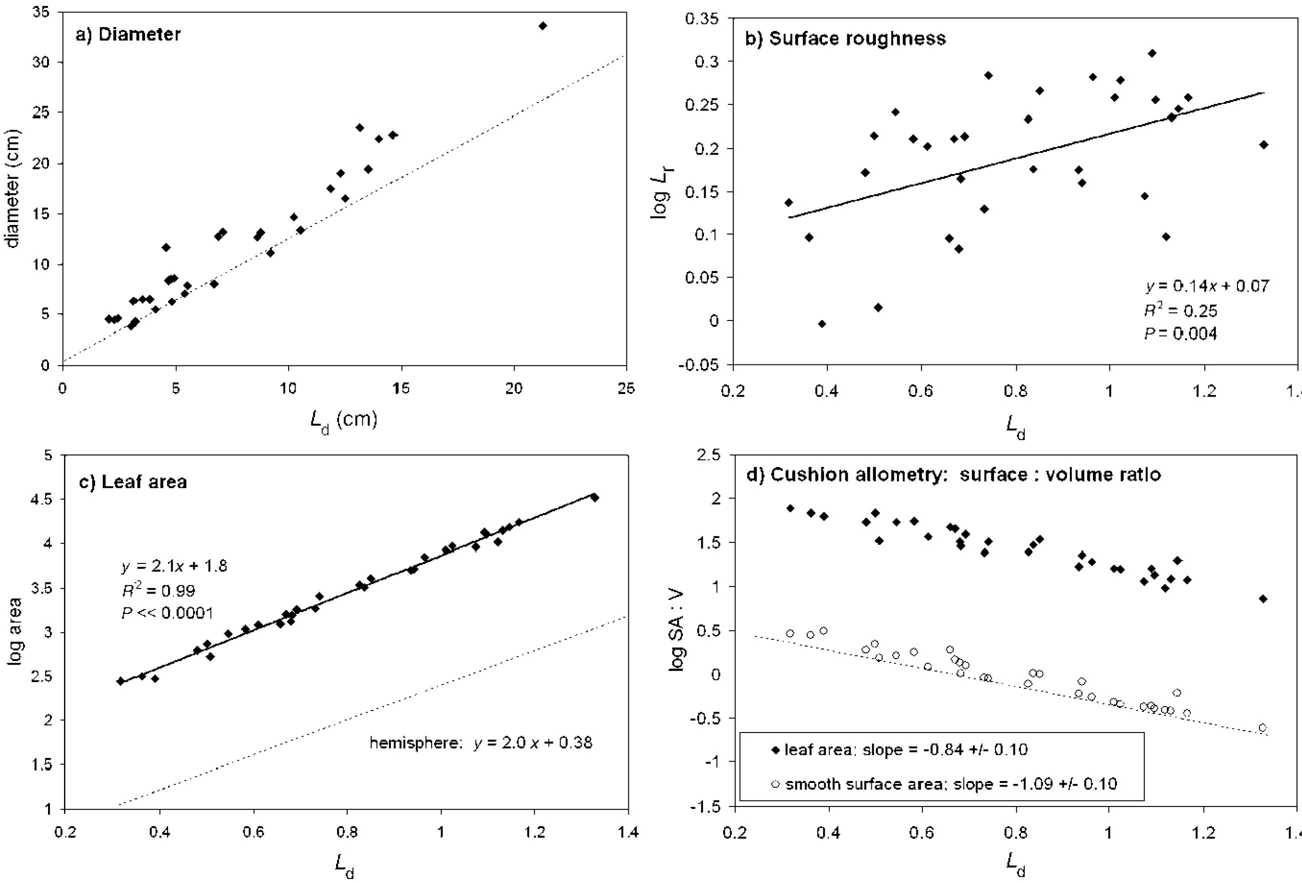

Fig. 1. Allometric relationships in *Leucobryum glaucum*. Relationships are shown between diameter length (L_d) calculated as 0.81 times the diameter of a hemisphere of the same surface area as the cushion and (a) cushion diameter; (b) surface roughness (mm); (c) leaf area (cm^2); and (d) surface area : volume ratio (cm^{-1}). In (a), (c), and (d), the dashed lines represent the relationship for a hemisphere. In the latter, the open circles show the SA : V where the cushions are assumed to have a smooth surface and the closed diamonds show the variable using leaf area. Slopes and their 95% confidence intervals are shown. Data points ($N = 32$) combine cushions employed in both field and laboratory studies.

all at least 1 m apart, and locations were rearranged arbitrarily at each sampling time.

Air temperature, relative humidity, and wind speed were measured 30 cm above the forest floor and 60 cm from the outer circle using a weather station connected to a data logger (RM Young Wind Sentry with a cup-type anemometer, interfaced with a CR10X Datalogger, Campbell Scientific, Logan, Utah, USA). Surface temperature was measured using two temperature probes placed in a hydrated *L. glaucum* cushion near the weather station. This cushion was comparable in size to the largest cushion in the sample. Environmental data were sampled at 2-min intervals and represent averages taken at 10-s periods over the course of each interval.

Plants were collected moist and kept hydrated at the field site under a shade cloth for 1 d prior to the start of the experiment. Beginning at 0600 the first day and at approximately 90-min intervals throughout each day, samples were weighed to the nearest 0.1 g to assess rates of evaporation.

Initially, plants were assessed for the Fv/F_m fluorescence parameter following dark adaptation, which correlates well with photosynthetic capacity (Tuba et al., 1997; Csintalan et al., 1999; Maxwell and Johnson, 2000). This was accomplished by performing measurements on cushions at night at the beginning of the experiment. Three Fv/F_m measurements (instrument described above) were performed within the middle one-half of each cushion with a minimum of 10 min dark adaptation between measurements. During the remainder of the field experiment, $\Delta F/F_m'$ was measured. This was preferred because it does not require dark adaptation and correlates well with photosynthetic performance under particular light and temperature regimes. This parameter was measured at 0900 the following morning and again at 1600 and continued for 5 d. On the last day, only the 1600 measurement was obtained. The $\Delta F/F_m'$ parameter was measured on three evenly spaced sample points within the top one-half of each cushion. Surface temperature and light intensity were recorded using a leaf clip attachment to the fluorometer (model 2060B, Walz). Light intensity for the measurements was maintained at 220 $\mu mol \cdot m^{-2} \cdot s^{-1}$ using a 50-W halogen light dispersed through a diffuser. Measurements were collected within a covered shelter to control light intensity. In addition, at the fluorescence sampling times and at approximately 90-min intervals throughout each day, samples were weighed to the nearest 0.1 g to assess water status and rates of evaporation.

The boundary layer conductance model makes predictions about the size dependence of evaporation in the field. The degree of size dependence during each sampling interval in the field was evaluated by relating L_d and L_r to rates of evaporation using multiple linear regression for each day and night interval during the study.

RESULTS

Canopy structure—Morphological features associated with water balance in *L. glaucum* scale differentially with increases in canopy size. The height of cushions does not increase at the same rate as cushion diameter, resulting in flattened, less hemispherical cushions with growth. Consequently, the characteristic length (L_d) and cushion diameter are not isomorphic but are highly correlated (Fig. 1a). Surface roughness (L_r) varied between 1.0 and 2.0 mm and was positively associated

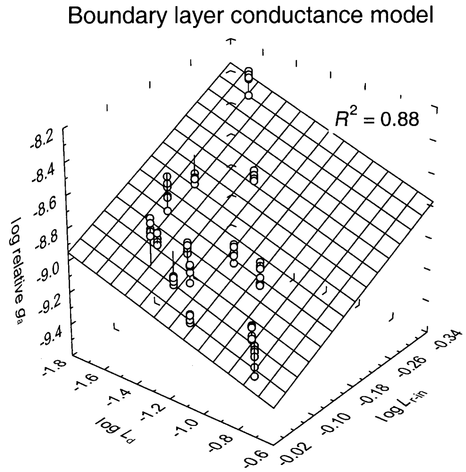

Fig. 2. Boundary layer conductance model. The relationship between boundary layer conductance to water vapor (g_a), diameter length (L_d; m) and surface roughness ($L_{r\text{-}in}$) derived from wind tunnel studies is shown. Points represent $N = 14$ cushions measured for g_a in 0.7–4.3 m/s wind speeds. The effects of wind speed have been factored out of the model by subtracting their effect from g_a (log relative $g_a = \log g_a - 1.20 \times \log[u/v]$, where u and v equal wind speed and kinematic viscosity, respectively). Consequently, multiple points with the same L_d and L_r value reflect those generated on the same cushion at different wind speeds. The surface roughness is presented in dimensionless form as an index ($L_{r\text{-}in}$) by dividing L_r of each sample by the maximal L_r in the study. Vertical lines show deviations from model. The linear model shown accounts for 88% of variation, and the slopes for both predictor variables significantly differ from zero.

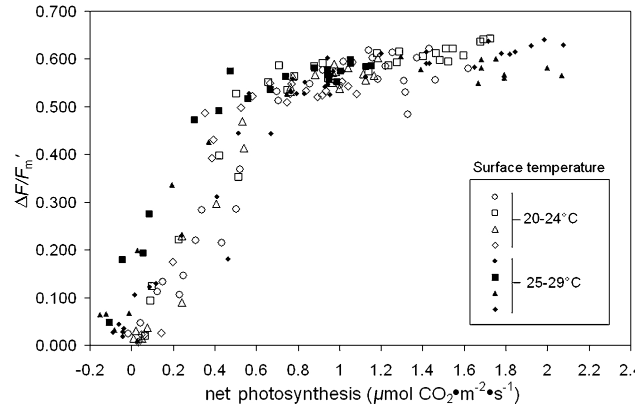

Fig. 3. Chlorophyll fluorescence. The fluorescence parameter $\Delta F/F_m'$ was measured on cushions evaluated for net CO_2 exchange during the course of a drying curve at 20°–24°C (open symbols) and 25°–29°C (closed symbols). Different symbol shapes represent individual samples. The decline in net CO_2 exchange rates below 0.7 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ is due to cushion dehydration.

with L_d ($N = 32$, $P = 0.004$, $R^2 = 0.25$; Fig. 1b). In addition, L_r and leaf area ratio were positively associated ($N = 12$, $P = 0.003$, $R^2 = 0.61$). When leaf area was estimated for all cushions from L_r, cushion leaf area increased to the 2.1 power ($\pm$0.08 for 95% confidence interval) of the L_d (Fig. 1c). This estimated area had only a slightly higher scaling function than a smooth surface (power function = 2.0), but relative to a smooth canopy surface, this area was enhanced over an order of magnitude at all cushion diameters. Cushion volume increased to the 2.8 ($\pm$0.3) power of diameter length ($P \ll 0.001$, $R^2 = 0.92$) and was not significantly different from that found in a hemisphere. The leaf area : volume ratio (LA : V) summarizes the relationship between area for evaporation and water storage volume (Fig. 1d). Given that surface roughness (L_r) increased with cushion size and that leaf area was affected by L_r, the relationship between LA : V ratio and L_d was less negative (-0.84 ± 0.10) than that expected for a hemisphere (-1).

Boundary layer conductance—For studies of boundary layer properties and water flux, cushion leaf area was used as an estimate of surface exchange area. Under wind-tunnel conditions, cushion diameter length (L_d), surface roughness ($L_{r\text{-}in}$) and wind speed interacted to control boundary layer conductance to water vapor (g_a). The model $g_a = -9.62 \times (u/v)^{1.21} \times L_d^{-0.35} \times L_{r\text{-}in}^{-1.85}$ explained 88% of the variation in the observations (Fig. 2). The significance of the exponents and their 95% confidence intervals (1.21 ± 0.09; -0.35 ± 0.11, -1.85 ± 0.39) were determined using bootstrap analysis, and all differed significantly from zero. The exponent associated with flow (1.21) was greater than the magnitude expected for flat plates or spherical shapes (0.5) and indicates turbulent flow conditions. In addition, the model predicts that evaporation will vary to the -0.35 power of differences in L_d. This value was significantly higher than that expected for hemispherical objects or flat plates (-0.5). Thus, the model indicates that g_a will vary inversely as a function of both L_d and L_r.

Physiological characteristics—Net CO_2 exchange in *L. glaucum* varied with respect to light availability, water content, and temperature. At a water content at which photosynthetic rates are maximal, *L. glaucum* reached light saturation at 550 μmol $\cdot m^{-2} \cdot s^{-1}$ ($N = 4$, data not shown). At 220 μmol $\cdot m^{-2} \cdot s^{-1}$, a light intensity comparable with the forest floor and used in field physiological studies, plants photosynthesized at 75% of their maximum rate. At this light intensity in the laboratory, net CO_2 exchange and rates of dark respiration varied as a function of water content. When maximally hydrated (16–20 g H_2O/g dry plant), plants exhibited a 30–60% reduction in net CO_2 exchange relative to their maximum. During drying, net photosynthesis increased to a mean water content of 7.8 g H_2O /g dry mass at both temperatures and then declined to zero as plants desiccated. As plants dried, it became difficult to maintain a constant cushion surface temperature and temperatures increased up to 4°C, a pattern also observed in drying plants in the field.

Rates of dark respiration decreased during drying and were elevated at higher temperatures. At maximal water contents, rates varied between a maximum of -0.33 and -0.58 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ at 22° and 27°C, respectively. These declined to -0.08 and -0.17 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ at 22° and 27°C when water content was 2 g H_2O/g dry plant, the water content at which rates of net CO_2 exchange were zero.

The effective quantum yield assessed using chlorophyll fluorescence ($\Delta F/F_m'$) was nonlinearly related to rates of net CO_2 exchange during cushion drying (Fig. 3). At maximum rates of photosynthesis, $\Delta F/F_m'$ averaged 0.570 and did not vary with temperature. This value of $\Delta F/F_m'$ was maintained as rates of net CO_2 exchange dropped to 40% of their maximum value and then declined linearly. At low rates of net CO_2 exchange, higher temperatures showed elevated $\Delta F/F_m'$, a trend that corresponded with higher rates of dark respiration at those temperatures.

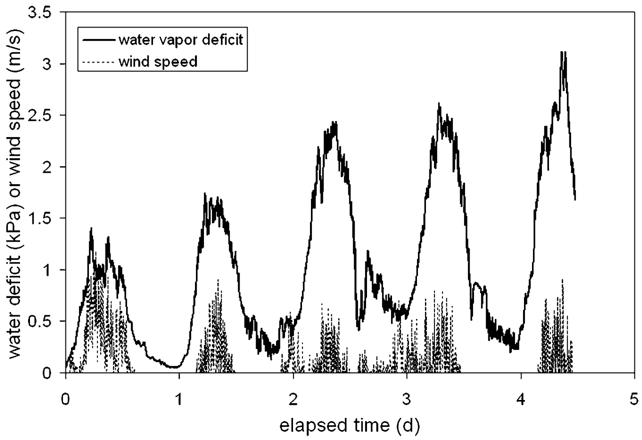

Fig. 4. Environmental conditions during the field experiment. The water vapor deficit (bold line) and wind speed (dashed line) were calculated from data collected at 2-min intervals during the course of the field drying experiment. Zero time represents 0600 hours on the first day and each day demarks the same time at each successive day.

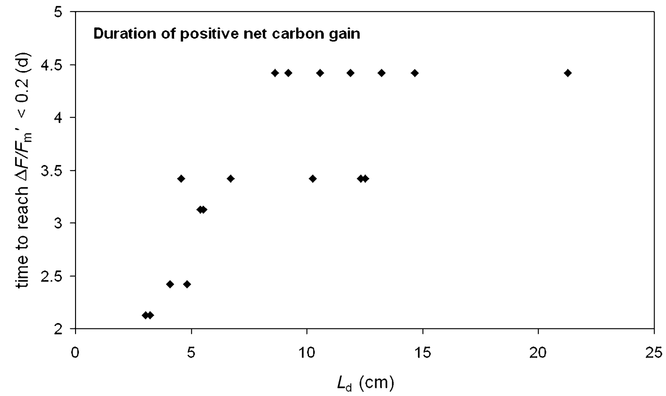

Fig. 6. Duration of positive net carbon gain. The time to reach 10% of maximal net CO_2 uptake, estimated by when $\Delta F/F_m'$ drops below 0.2 (Fig. 3), is shown relative to cushion diameter length (L_d). Fluorescence data were not collected in the morning sample on day 4, but by the afternoon, all 18 samples in the study were sufficiently desiccated to express a $\Delta F/F_m'$ below 0.2.

Field water and net CO_2 exchange—During the 5-d field experiment, skies were sunny with occasional high, thin clouds. Daytimes were windy with peak interval mean wind speeds reaching between 0.7 and 1.2 m/s at the 30-cm sampling height. Nighttime winds were below the 0.4 m/s cutoff for the cup-type anemometer. Air temperatures were higher during the day and increased during the 5-d trial (20°–27°C maximum daytime and 11°–17°C minimum nighttime temperatures). Relative humidity varied from 35 to 95% with higher values during the nighttime. Water vapor deficit also showed day–night variation and increased during the sample period (Fig. 4).

The length of the hydrated, photosynthetically active state was assessed using chlorophyll fluorescence. The dark adapted Fv/F_m parameter evaluated in fully saturated cushions at night prior to the start of the experiment averaged 0.771 ($N = 18$, 0.010 SD) and did not vary with L_d ($R^2 < 0.01$ using linear regression, $P = 0.78$). Similarly, at 220 μmol · m^{-2} · s^{-1} light intensity at the first morning measurement, $\Delta F/F_m'$ also showed no size dependency (0.401 mean and 0.068 SD; $R^2 = 0.02$, $P = 0.61$). However as cushions lost water during the experiment, $\Delta F/F_m'$ remained nearly constant or increased before declining as tissues desiccated (Fig. 5). The length of the photosynthetically active phase varied as a function of L_d. For example, the length of time during which plants went from maximal to 10% of maximal rates of net CO_2 exchange assessed using $\Delta F/F_m'$ values ($\Delta F/F_m' < 0.2$, Fig. 3) was closely associated with cushion diameter (Fig. 6). This corresponded well with differences in hydration status expressed on a water content basis (Fig. 7).

Mean daily and nightly rates of evaporation and size dependence were explored for the first four days and three nights of sampling where morning and afternoon fluorescence data were available. For this analysis, only cushions in which chlorophyll fluorescence results indicated positive rates of net CO_2 exchange ($\Delta F/F_m' > 0.2$) were used. Mean rates of evaporation calculated for all cushions were higher by a factor of three during the daytimes. The relationship between evaporation rates and the predictor variables L_d and L_r were evaluated using multiple linear regression following log transformation. For all

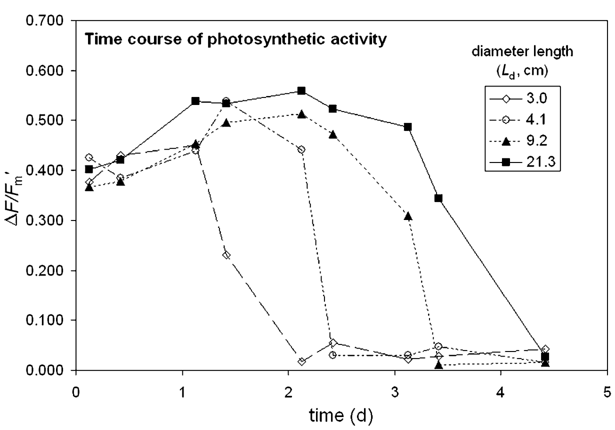

Fig. 5. Time course of photosynthetic activity. The chlorophyll fluorescence parameter $\Delta F/F_m'$ was measured at 0900 and 1600 hours daily during the course of the field drying experiment. The time course of these measurements is shown for four of the 18 samples that vary in L_d. Note that no data were taken at 0900 hours on day 4.

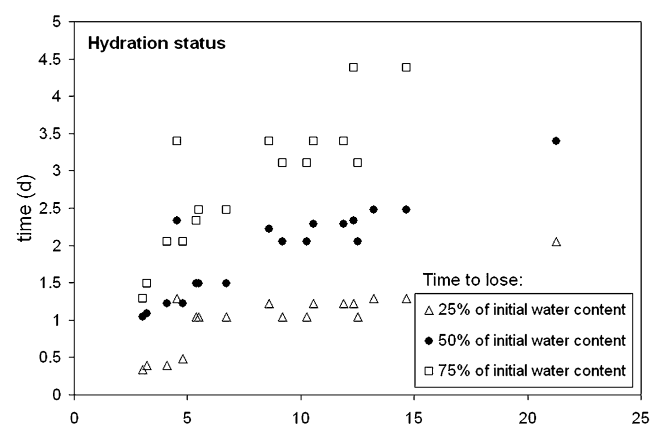

Fig. 7. Hydration status. The time to lose 25, 50, and 75% of initial water content in 18 sample cushions in the field drying experiment are shown relative to the cushion diameter length (L_d). The largest cushion had not lost 75% of its original water by the end of the last sampling period.

TABLE 1. Evaporation among cushions that vary in diameter and surface roughness under field conditions. The relationship between rates of evaporation and the morphological characteristics diameter length (L_d) and surface roughness (L_r) were evaluated using multiple regression for each day (0700–1800) and night during the field experiment. The L_d and L_r slope parameters show the slope of the rate of evaporation for all active samples following log transformation. The significance of the parameters is shown by the asterisks (*$P < 0.05$; **$P < 0.01$). Active samples were defined as ones with $\Delta F/F_m' > 0.2$.

Interval	No. of active samples	Mean rate of evaporation (mg $H_2O \cdot cm^{-2} \cdot h^{-1}$)	L_d slope parameter	L_r slope parameter
Day 1	18	0.34	−0.02	−1.17**
Day 2	18	0.35	0.11	−1.14**
Day 3	14	0.28	0.12	−0.89**
Day 4	7	0.19	0.05	−1.01
Night 1	18	0.11	−0.02	−1.05**
Night 2	16	0.12	0.29*	−0.91*
Night 3	13	0.16	0.23	−1.07**

daytime sample intervals when wind speeds were high, variation in L_d was not significantly associated with rates of evaporation (Table 1). However, during the three daytime intervals that have a sample size of at least 14, L_r was significantly and negatively associated with evaporation rates. During the fourth interval, the slope of the relationship was similar, but with only seven samples, the slope was not significant. At night, one interval showed a positive association between evaporation rate and L_d and two out of the three intervals showed an indirect relationship between L_r and rate of evaporation.

DISCUSSION

In wind-tunnel conditions, wind speed, diameter length (L_d), and surface roughness (L_r) interact to control boundary layer conductance to water vapor (g_a). Although the exponent that relates g_a to variation in wind speed (1.21) is higher than that expected in laminar flows in free air streams (0.5), its magnitude is similar to that observed for other bryophytes of similar roughness placed along wind-tunnel walls (Proctor, 1980; Rice et al., 2001). The high value of the exponent is likely caused as flow changes from dynamically smooth to transitionally rough regimes (Bandyopadhyay, 1987; Raupach et al., 1991; Krogstad and Antonia, 1999) when it encounters the moss cushion surface. Flow conditions can be approximated by calculating the roughness Reynolds number, Re_k, if the sheer stress is known (Bandyopadhyay, 1987). Rice et al. (2001) provide information to calculate this for the boundary layer adjacent to a 9.3-cm diameter *Callicladium haldanianum* (Grev.) Crum (Hypnaceae) cushion of similar roughness (2.1 mm) to the cushions in the present study. At 3.0 m/s wind speed (calculated friction velocity equals 0.81 m/s), the Re_k equals 53, which is representative of transitionally rough flow, well above the range of dynamically smooth flow (<5) and below that of fully rough flow (>70; Raupach et al., 1991). With flows adjacent to walls, the frequency of vortices shedding is approximately six times higher than in the free air stream (Bandyopadhyay, 1987). The generation of such turbulence in transitionally rough flow leads to eddy transport within the boundary layer and enhanced effective exchange area as eddies enter elements within the canopy, both of which increase the magnitude of the wind speed dependence of g_a.

Variation in both L_d and L_r also influenced g_a in the wind tunnel. Increases in L_d were associated with a −0.35 exponential decrease in g_a, which was significantly closer to zero than the value observed in flat or spherical plant organs within free airstreams (−0.5; Nobel, 1974; Schuepp, 1993). The reduced magnitude of size dependence in the present study is probably also caused by turbulence associated with the wind-tunnel wall and amplified by the roughness of the *L. glaucum* surface. Such a reduction in size dependence has not been observed in the smoother canopied moss *G. pulvinata*. In that species, samples of 3 cm diameter remain within the laminar sublayer for wind speeds from 0.2 to 4 m/s (Proctor, 1980). Consequently, that species has a magnitude of size dependence of evaporation rates similar to organs in free airstreams, at least for small cushions between 0.5 and 4.0 cm diameter (Zotz et al., 2000; measured only at approximately 1.2 m/s wind speed). In the rougher canopied *L. glaucum*, size dependence is reduced as the scale of the roughness elements approaches the thickness of the boundary layer and generates transitionally rough flow. Within these flow regimes, variation in surface roughness becomes more important in determining boundary layer properties and, thus g_a, than variation in size (Raupach et al., 1991).

Indeed, boundary layer conductance was inversely related to variation in surface roughness. Within bryophyte canopies, surface roughness elements are known to interact with wind flow generating turbulence, facilitating through-flow and enhancing conductance to water loss (Rice et al., 2001). However, in the present study increases in surface roughness caused a reduction, not an increase, in g_a. The low value and range of surface roughness in the present study may account for this difference. All *L. glaucum* cushions in the present study were smoother than those in the Rice et al. (2001) analysis (1.0–2.0 mm vs. 2.1–11.8 mm). When densely packed, plant leaves and branches cause sheltering and reduce mass transfer (Gurevitch and Schuepp, 1990; Rice and Schuepp, 1995). Although surface roughness at the scale found in *L. glaucum* appears to generate transitionally rough flow, increases in roughness may extend the laminar sublayer above the branch tips. This would create dormant air spaces within the canopy and increase mean diffusional pathlengths, thereby reducing overall rates of evaporation. In this manner, leaf tips would function similarly to hair points on leaves of *G. pulvinata* and *Tortula ruralis* (Hedw.) Gaertn., Meyer & Scherb. (Pottiaceae), which have been shown to decrease boundary layer conductance (Proctor, 1980). Thus, at the scale of bryophyte canopies, there may be a critical roughness height that determines whether increases in roughness enhance or inhibit water loss.

In contrast to the dependence of g_a on L_d and L_r in the wind-tunnel, in the field, rates of evaporation during the windy daytimes were affected only by variation in L_r. This result is further supported when evaporation periods within each day were analyzed separately (results not shown). The lack of size-dependent evaporation rate is likely caused by the additional turbulence encountered in the field. Together with turbulent eddies that propagate through forest canopies (Baldocchi and Meyers, 1988; Raupach et al., 1996), length scales associated with the forest floor and its surface roughness also generate turbulence. For example, the mulch on the forest floor has a mean roughness height at least an order of magnitude greater than the *L. glaucum* cushions (18 vs. 1–2 mm, assuming the former is the mean minimum mulch dimension). This magnitude of roughness would lead to a change from transitionally rough flow regime found in the wind tunnel to fully rough flow along the forest floor (Bandyopadhyay, 1987). Under these conditions, boundary layer properties are determined principally by the geometry and density of roughness elements and not by other length scales (Rapauch et al., 1991). Consequently, the size-dependent effects on evaporation that have been described in bryophytes and in lichens based on laboratory or wind tunnel investigations may not adequately predict water fluxes under field conditions. We encourage investigators to evaluate the range of turbulence intensities in the field and then condition flows in the laboratory to suitably match them.

This result suggests that under field conditions, surface roughness may be the best singular parameter to characterize differences in bryophyte water fluxes. In addition, differences in stem density and in the organization of bryophyte canopies that relate to light interception, photosynthesis and growth may also be well characterized by this parameter (van der Hoeven et al., 1993; Hanslin et al., 2001; Pederson et al., 2001). Given that bryophytes can account for up to 50% of gross photosynthesis and influence ecosystem hydrological budgets in many boreal systems (Van Cleve et al., 1983; Goulden and Crill, 1997; Bisbee et al., 2001), it is essential to be able to characterize functional differences of bryophyte species. Now that surface roughness can be easily determined using remote techniques employing laser scanning (S. Rice and N. Kroulicoff, Union College, unpublished data), it may allow for the development and testing of mechanistic models of bryophyte function that relate to underlying variation in their life form.

Also, the shape of *L. glaucum* cushions changes with increase in size and affects water budgets. Canopy height does not increase isometrically with diameter as cushions flatten and become less hemispherical as they grow, similar to the phenomenon observed in *Grimmia pulvinata* (Zotz et al., 2000). Under conditions where no allometric change occurs, surface area and volume are expected to scale to the second and third power of changes in cushion diameter. Because surface area represents the site of water loss from cushion surfaces and the volume serves as a water reservoir in cushion mosses, changes in the surface area : volume ratio (SA : V) will alter water budgets and the length of positive carbon uptake. In a hemisphere, increases in size cause a decrease in SA : V to the -1 power of canopy diameter. However, when leaf area (LA) is considered the LA : V ratio scales with diameter to the -0.84 power in *L. glaucum* (Fig. 1d). This relationship indicates that allometric changes associated with canopy growth increase canopy LA : V ratio relative to isomorphic growth that would result in hemispherical cushions. However, even though *L. glaucum* cushions do not decrease SA : V ratios as dramatically as hemispheres as they enlarge, larger cushions still show increased volume for water storage relative to small ones. This causes the extreme size dependence observed in the duration of favorable water status.

Consequently, the length of net carbon gain, assessed either by water loss or by chlorophyll fluorescence characteristics increased from 1.4 to 4.4 d in the smallest to the largest cushions in the sample even with no observed size-dependent differences in evaporation rate. A similar pattern is predicted for the cushion moss *Grimmia pulvinata* based on laboratory investigations of water and carbon balance (Zotz et al., 2000). However, this is the first attempt to verify these predictions in the field. Reduced lengths of favorable water status in small cushions suggests that such individuals may experience more prolonged or intense dehydration which may increase mortality in the only moderately desiccation tolerant *L. glaucum* (Takacs et al., 1999). Furthermore, slow growth and high mortality would inhibit establishment, the phase that likely limits the ecological distribution of *L. glaucum* (McAlister, 1995) as it does in *Grimmia laevigata* (Brid.) Brid. (Grimmiaceae), another cushion moss (Alpert, 1988).

In summary, surface roughness associated with bryophyte canopies and their substrates creates inherently turbulent flow conditions that affect the wind and size dependence of water fluxes. This was observed in wind-tunnel environments where transitionally rough flow regimes caused more dramatic wind dependence than has been shown in smooth cushioned mosses and in plant organs in free air streams. In the field, fully rough flows are likely to develop that eliminate the relationship between cushion size and evaporation. In contrast, variation in cushion surface roughness controls water fluxes in the field. In smooth cushions like those in *L. glaucum*, increases in surface roughness cause a decrease in boundary layer conductance. However, the duration of net carbon gain is more closely related to cushion size than to surface roughness due to a strong positive relationship between canopy size and the volume of tissue available for water storage. Consequently, even though water fluxes are not size dependent in the cushion moss *L. glaucum* in the field, there remains a strong size dependency in water balance and net carbon flux.

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