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Niche partitioning and photosynthetic response of alectorioid lichens from subalpine spruce–fir forest in north-central British Columbia, Canada: the role of canopy microclimate gradients

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Abstract: The distribution of alectorioid lichens in subalpine spruce–fir forests of north-central British Columbia is strongly influenced by vertical position within the canopy; *Bryoria* dominates upper canopy exposures, while *Alectoria* dominates lower canopy positions. The hypothesis that this height-related niche partitioning reflects differential growth responses to gradients in canopy microclimate is examined. Field measurements of canopy microclimate, taken over a 2-year period, were used in conjunction with laboratory-based measurements of net photosynthesis (NP) and dark respiration to model net assimilation (NA) response of *Alectoria sarmentosa* and *Bryoria* spp. (mixed collections of *Bryoria fremontii* and *B. pseudofuscescens*) at two different heights (15 and 4 m) within the canopy. Microclimate measurements indicate that lichen thalli are regularly hydrated from snowmelt events during the winter period (October–April), totalling 26 and 29% of the time, respectively, for *Alectoria* and *Bryoria*, though most winter hydration exposure (*c.* 75%) occurred in the dark. In the summer (May–September), rainfall was the major hydration source, with *Alectoria* and *Bryoria* each hydrated *c.* 16% of the time (45% of this in the dark). The NP temperature optimum (T_{opt}) in light saturated thalli of *Alectoria* was 18·1 and 22·9°C, for winter and summer measurements, respectively. In *Bryoria* the corresponding seasonal rise in T_{opt} was smaller, from 15·9 to 16·3°C. Both species showed an increase in maximum rates of NP during the summer period, from 1·52 to 1·92 mg CO_2 g^{-1} h^{-1} for *Alectoria*, and from 1·79 to 2·33 mg CO_2 g^{-1} h^{-1} for *Bryoria*. Although lichen hydration events peaked in early winter (October and November), NA modelling predicts that maximum growth should occur during the summer period. In *Alectoria*, higher rates of NA were predicted for thalli in lower canopy positions, especially during the summer months. In *Bryoria*, no clear trends of NA uptake with canopy position were observed. Thus, while NP response to gradients of canopy microclimate may provide a basis for niche partitioning in *Alectoria*, other factors (perhaps exclusionary) may be more important for *Bryoria*. One such factor is documented, namely the greater sensitivity of *Bryoria* to extended hydration exposure and we speculate that greater rates of fragmentation in upper canopy exposures may limit upper canopy biomass accumulation in *Alectoria*. Niche partitioning in these alectorioid lichens may therefore reflect both positive (growth responses) and negative (physical and physiological limitations) responses to gradients in canopy microclimate.

Key words: alectorioid lichens, canopy microclimate, subalpine forest, lichen growth rates, *Alectoria sarmentosa*, *Bryoria*.

Introduction

The partitioning of species along environmental gradients has long been a fundamental component of our understanding of the concept of an ecological niche. In lichens, where the prevalent life-history strategy can best be characterized as

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one of stress-tolerance (Grime 1979), capture or utilization of environmental resources is often achieved by physiological adaptations (Palmqvist 2000; MacKenzie *et al.* 2001).

Within forested ecosystems a major environmental variable is that of vertical positioning within the canopy. Upper canopy exposures receive more light and have greater convective exposure, whereas lower canopy exposures are more shaded, and have higher (and more constant) levels of relative humidity. These profiles are strongly influenced by the age and structure of the forest canopy. Parker (1997) noted that in old-growth coniferous forest canopies of the Pacific Northwest, direct light transmittance penetrates more deeply into the lower canopy. This stands in contrast to younger coniferous forests, where light transmission is attenuated more rapidly in the upper canopy.

For lichen communities these vertical gradients in canopy microclimate can have a strong influence on resource availability. Harris (1971) postulated that the distribution of epiphytic lichens was primarily due to vertical gradients in two environmental parameters, water availability and light intensity. His modelling of environmental parameters suggested that changes in vertical evaporation gradients had a strong effect on net carbon assimilation in the canopy epiphyte *Parmelia caperata*.

McCune (1993) and McCune *et al.* (1997) describe vertical gradients in lichen community composition and corresponding changes in canopy structure of old-growth Douglas-fir forests in western Washington and Oregon. McCune *et al.* (1997), however, cautions that vertical gradients of lichen communities within the canopy can also represent successional gradients within these forest stands. Lichen communities from the lower canopy of young forests are often components of the upper canopy in older forests; in effect, they are vertically displaced within the canopy as forests age.

Alectorioid lichen communities growing within the canopy of subalpine old-growth forests on the windward slopes of interior mountain ranges in British Columbia show marked vertical zonation (Rominger *et al.* 1994; Campbell & Coxson 2001). Upper canopy positions are dominated by dark-coloured tufts of *Bryoria*, mainly *Bryoria pseudofuscescens* and *B. fremontii*, while lower canopy positions are dominated by the longer and more lightly coloured pendulous strands of *Alectoria sarmentosa*. Although casual observations from the ground would suggest that these two lichen communities occur in roughly equal abundance (the lower canopy *Alectoria* are visually very striking), *in situ* canopy sampling shows that over 85% of total biomass is that of *Bryoria* (Campbell & Coxson 2001).

Does this apparent preference of *Bryoria* and *Alectoria* for upper and lower canopy positions, respectively, reflect an adaptive growth response on the part of these two groups, or do physiological factors act rather in an exclusionary manner, reflecting innate tolerance limits? Previous physiological measurements on pendulous arboreal lichens (e.g. *Ramalina* spp.) have focused primarily on coastal or desert ecosystems (Lange 1980; Matthes-Sears *et al.* 1986, 1987), and to a lesser extent on maritime boreal environments (Renhorn & Essen 1995; Sundberg *et al.* 1997). It is difficult to extrapolate from these ecosystems to continental subalpine forests, where snowmelt events are a primary source of lichen hydration for over 8 months of the year (Campbell & Coxson 2001).

The question of whether vertical gradients in canopy microclimate within these relatively open subalpine forests are steep enough to provide a basis for niche partitioning between *Alectoria* and *Bryoria* is also unanswered. Measurements of canopy microclimate in the Pacific Northwest (USA and Canada) have occurred primarily in closed-canopy old-growth coniferous forests from coastal environments, such as those at the Wind River Canopy crane site (Parker 1997).

We have now profiled canopy microclimate in a subalpine spruce–fir forest in the northern Caribou Mountains of British Columbia, using a subset of the Pinkerton Mountain climate data set (Campbell &

Coxson 2001). Concurrently, we have examined seasonal patterns of net photosynthetic (NP) response in *Alectoria* and *Bryoria* using a matrix-based approach. We have also examined photosynthetic response to periods of extended hydration exposure. The response surface of NP uptake (temperature × moisture × light) has subsequently been modelled against measured field microclimatic parameters, thus facilitating the prediction of seasonal patterns of net assimilation (NA). This provides a test of whether or not lichen growth responses correlate with previously observed distributional patterns within the forest canopy.

Materials and Methods

Study site

The study area was located in the Caribou Mountains (53°37′38″N, 121°25′33″W), approximately 90 km ESE of Prince George, British Columbia, in the wet cold subzone of the Engelmann Spruce-Subalpine Fir zone (ESSFwc) (Meidinger & Pojar 1991). Climate within this part of the ESSF is characterized by long cold winters and short moist summers, with snow cover typically lasting from late October through to early June of each year (Meidinger & Pojar 1991).

The site is mesic to subhygric on a moderate, southwest facing slope at 1400 m elevation. The forest stand is composed primarily of *Abies lasiocarpa* (subalpine fir) with *Picea engelmannii* (Engelmann spruce) distributed evenly throughout the stand, although at lower abundance (*c.* one-quarter of all trees). Trees in the stand are uneven-aged, up to 350 years old, and commonly grow in clumps separated by natural gaps in the canopy. Mature trees range from 20 to 25 m in height.

Vegetation in the shrub layer is dominated by *Rhododendron albiflorum* (white-flowered rhododendron) while the herb layer is largely made up of *Valeriana sitchensis* (Sitka valerian), *Veratum viride* (Indian hellebore), *Rubus pedatus* (five-leafed bramble) and *Gymnocarpium dryopteris* (oak fern).

Canopy lichens were dominated by alectorioid species, primarily *A. sarmentosa* and *Bryoria* (including *B. capillaris*, *B. fremontii*, *B. fuscescens*, *B. glabra* and *B. pseudofuscescens*). Other lichens present within the canopy include foliose lichens such as *Cetraria platyphylla*, *Hypogymnia imshaugii*, *H. metaphysodes*, *H. occidentalis*, *H. physodes*, *H. rugosa*, *H. tubulosa*, *Parmelia sulcata*, and *Platismatia glauca*. *Bryoria* species, especially *B. fremontii* and *B. pseudofuscescens*, dominate in the upper canopy, while *Alectoria sarmentosa* is confined largely to lower canopy positions.

Sampling methods

Canopy microclimate

Canopy microclimate measurements were taken in six replicate trees from October of 1997 through to September of 1999. Instrumentation was installed on three branches at two heights (4 and 15 m) per tree, typically at the mid-point of each branch (between the trunk and branch tip). Instrumentation was distributed over all aspects at each height position. Canopy access was gained by single-rope climbing techniques (Perry 1978).

Lichen temperatures were measured using fine-wire thermocouples (Omega Engineering, Stanford, CT) held against lichen thallus surfaces (one per thallus of each species per branch). Only small differences were observed between temperatures of *Alectoria* and *Bryoria* thalli in side-by-side comparisons on the same branches, typically less than 1°C. We have therefore pooled lichen thallus temperature data at each height.

Air temperature was also measured using fine-wire thermocouples, placed at 4 and 15 m height on an instrumentation mast located in an adjacent canopy gap.

The hydration of lichen thalli was measured using an impedance technique (Coxson 1991), adapted for alectorioid lichens (Campbell & Coxson 2001), where small clips provide measurements of electrical conductivity across lichen thalli (also one per thallus of each species per branch). Using this approach, hydrated lichen thalli are readily discriminated from dry or frozen lichen thalli, which have little or no return of the impedance signal (a 10 ms duration 4 V AC pulse). Lichen clips were replaced in the spring and fall of each year to minimize experimental errors associated with any changes in thallus vitality.

Photosynthetic photon fluence rate (PPFR) over the waveband 400–700 nm was measured using Li-Cor quantum sensors (Li-Cor, Lincoln, Neb.) held level in gimbel mounts on the upper branch surface at each height location.

Precipitation was measured using a 1 mm tipping bucket rain gauge placed in an adjacent canopy gap. Snow depth was measured using a Campbell Scientific SR50 Ultrasonic Distance sensor (Campbell Scientific, Logan, UT). Snow-pack measurements were discontinued mid-winter in January 1999, after a tree fell on the sensor tower during a storm event.

Instrumentation signals were recorded using Campbell Scientific CR-7 and CR-10 dataloggers. Sampling of instrument signals was conducted at 10 s intervals, with data summaries (minimum, maximum, average, and instantaneous values) recorded every 10 min or every 3 h, using a variable rate trigger that switched to the more intensive data recording interval when lichen thalli were hydrated. This threshold for intensive data recording was set at impedance values corresponding to thallus water contents (WC) of 20% of dry weight.

We have adopted a labelling of winter and summer periods for this data set as being from October to April, and May to September, respectively. This corresponds approximately to the respective periods when most precipitation falls as snow or rain (although May and September are transitional in this regard, with precipitation events possible as either snow or rain).

Lichen physiological response

Intact pendulous mats of *Alectoria* and *Bryoria* were collected at mid-canopy heights (*c.* 6–8 m), in the zone of overlap between the distribution of these two species groups. *Alectoria* collections were composed solely of *A. sarmentosa*. *Bryoria* samples were made up of mixed collections of non-sorediate species, mainly *B. fremontii* and *B. pseudofuscescens*, which grow interwoven in mats within the mid to upper canopy. Following collection, thalli were placed under pretreatment hydration conditions in an environmental growth chamber for 24 h prior to assessment of photosynthetic activity.

Pretreatment conditions in the winter months were held at 5°C under a short day photoperiod (8 h day/16 h night) of 50 and 0 μmol m^{-2} s^{-1} PPFR. In the summer months, lichen thalli were held at 15°C under a long day photoperiod (16 h day/8 h night) of 300 and 0 μmol m^{-2} s^{-1} PPFR. Thalli were hydrated by misting with rainwater (or snowmelt in winter) solution and maintained at full thallus saturation by periodic misting. After 24 h pretreatment hydration exposure lichen clumps of *c.* 1 g wet weight were removed for subsequent photosynthetic and respiratory measurements.

Photosynthetic and respiratory responses were measured using a matrix-based approach, across two seasons (winter and summer), four temperatures (0, 5, 15, and 25°C, 0°C data in winter only), and six light intensities (0, 50, 100, 300, 600 and 1000 μmol m^{-2} s^{-1} PPFR; 1000 μmol m^{-2} s^{-1} PPFR measurements in summer only). Individual thalli were allowed to dry slowly during repeated incubations under each matrix cell temperature/light combination to obtain representation of lichen thallus hydration responses within 25% class intervals. Thallus WC was expressed as a percentage of air-dry weight. Ten replicate thalli each of *Alectoria* and *Bryoria* were used (destructive sampling) within each seasonal temperature–light matrix cell combination.

The NP response of *Alectoria* and *Bryoria* after long-term exposure to conditions of full thallus hydration was assessed in a separate set of sequential measurements taken over a 12 day period. Fresh summer-collected thalli were held under long day growth chamber conditions. Thalli were maintained at full thallus saturation during this period by misting with rainwater. Twenty replicate thalli of each of *Alectoria* and *Bryoria* were removed at regular intervals after wetting (1, 2, 4, 8, 24, 24, 72, 96, 144, 192, and 288 h) and incubated at 15°C, 300, and 0 μmol m^{-2} s^{-1} PPFR.

Gas exchange of lichen thalli was measured in 200 ml glass cuvettes, using closed cell CO_2 incubation techniques of Larson & Kershaw (1975). CO_2 concentrations were measured using a Li-Cor 6250 gas analyser (Li-Cor, Lincoln, Neb.). CO_2 drawdown during individual incubations was not greater than 40 μl l^{-1}, to minimize limitations on NP activity. Net photosynthetic rates were expressed as mg CO_2 g^{-1} h^{-1}.

Data evaluation

The temperature optimum of photosynthesis at each of 50 and 600 μmol m^{-2} s^{-1} PPFR was calculated as the point at which the deviate of a second degree polynomial regression (calculated using Sigmaplot 2001; SPSS Inc., Chicago, IL) through data points became zero (Sancho *et al.* 1997). The response of NP to PPFR was described by exponential rise equations (after Sancho *et al.* 1997), calculated separately for each temperature (at 0, 5, 15, and 25°C). *t*-Test (Bonferonni method) comparisons were made using SYSTAT 8.0 (SPSS Inc.) between rates of gas exchange (at optimal water content) in winter and summer-collected material under each measured temperature/light combination.

Assimilation potential (net CO_2 exchange) under field conditions was predicted for *Alectoria* and *Bryoria* for the period from 1 October 1997 to 30 June 1999. Estimations were obtained by using field measurements of lichen microclimate as a template upon which the laboratory-based temperature, moisture, and light response surface of NP uptake could be imposed. Where measured conditions of field temperature, moisture, and light exposure fell outside of those values defined directly by the laboratory-based physiological response matrix, an extrapolation of rates of gas exchange (at intervals of 1°C, 10 μmol m^{-2} s^{-1} PPFR, and 10% thallus WC) was obtained by use of the kriging routine in SURFER 6.0 (Golden Software, Golden, CO). Kriging is a geostatic gridding method that produces a response surface between regularly or irregularly measured points. This approach provided a 3-dimensional empirical representation of the NP response surface. These calculations were conducted on each of the 3-h climate data summaries, and summed as monthly values (expressed both as mg CO_2 g^{-1} $month^{-1}$ and mg C g^{-1} $month^{-1}$). The respiratory component of NA response was separately estimated in a simple model, where dark respiration was assumed to continue at the same rate in illuminated (hydrated) thalli.

Proportional limitations imposed on predicted NP activity by each of temperature, moisture, and light were obtained by comparing predicted rates of NA (based on field microclimate data parameters) with those that would be obtained when individual parameters of temperature, moisture, and light were set at optimal values. These results were expressed on a percent relative basis (combined limitations=100%).

Results

Climatic conditions at Pinkerton Mountain reflect the subalpine environment of the study area. Lichen thallus temperatures fell between 0 and 10°C for much of the year, briefly reaching extremes as low as −30°C during outbreaks of arctic air in mid-winter, and into the upper twenties on occasion during mid-summer (Fig. 1). Total daily PPFR shows large seasonal extremes, from less than 0·5 mol m^{-2} day^{-1} during mid-winter, to over 6 mol m^{-2} day^{-1} in early-summer. Snow remains on the forest floor

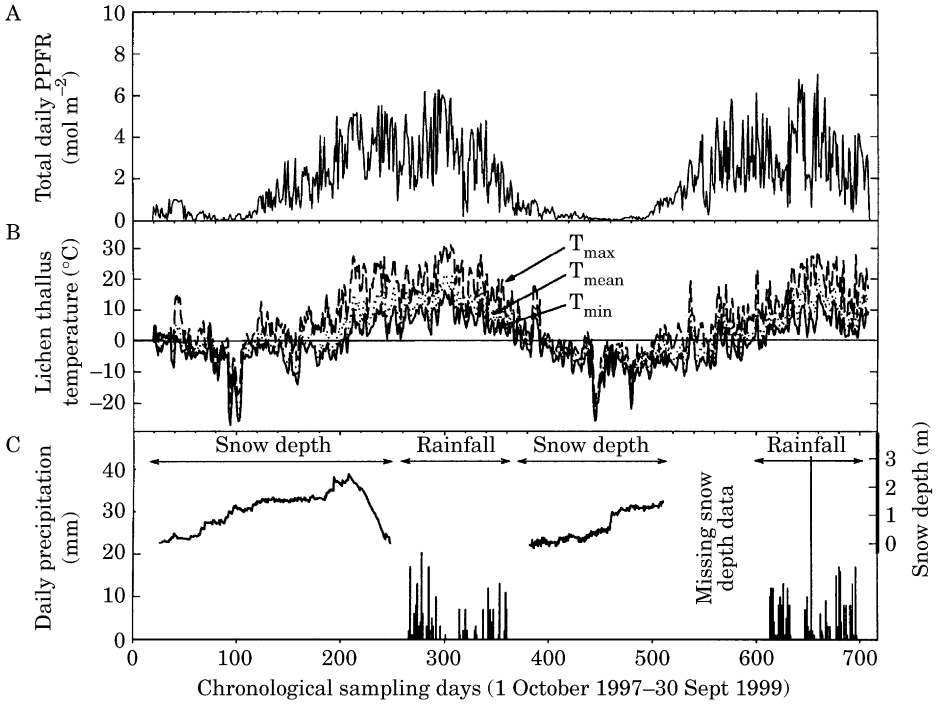

FIG. 1. Summary of canopy microclimate data for the period from October 1, 1997 to September 30, 1999 at Pinkerton Mountain, British Columbia. A, mean daily PPFR on upper branch surfaces at 15 m height within the canopy (n=18); B, minimum, mean, and maximum lichen thallus temperatures (pooled values for all thalli on all trees, both *Alectoria* and *Bryoria*) at heights of 4 and 15 m within the canopy (n=72); C, cumulative snow depth at the forest floor surface (m) and daily rates of precipitation (mm) (n=1).

surface for over 8 months of the year, typically melting in early to mid-June. The winter of 1998/1999 was a high snowfall year, with final melt at the forest floor surface delayed until after the third week in June.

Hydration of lichen thalli during much of the year (October to April) reflects snowmelt events within the canopy. A representative snowmelt event from early April 1999 (Fig. 2) shows that the onset of warmer temperatures triggers the hydration of lichen thalli, with thallus temperatures reaching 0–5°C and PPFRs up to 150 μmol m^{-2} s^{-1}. The onset of the melt event occurs slightly earlier in the upper canopy, although cessation of the period of lichen hydration occurred at close to the same time at both heights, as temperatures declined at the end of the melt period.

Lichen hydration episodes during the summer months were typically associated with major precipitation events (low pressure systems originating in the Gulf of Alaska). A representative hydration event from June 1999 (Fig. 3) shows that temperatures of lichen thalli remain low (typically under 10°C), with rapid drying of thalli evident on cessation of precipitation activity and exposure to higher PPFR. Detailed examination of a single day's precipitation event (July 23, 1999; Fig. 4) shows the characteristic attenuation of drying by lichen thalli after precipitation events, with an almost 2 h lag apparent between drying at 15 and 4 m. Conversely, the onset of lichen wetting during small precipitation events occurs first in the upper canopy, as seen on the afternoon of July 23 (Fig. 4).

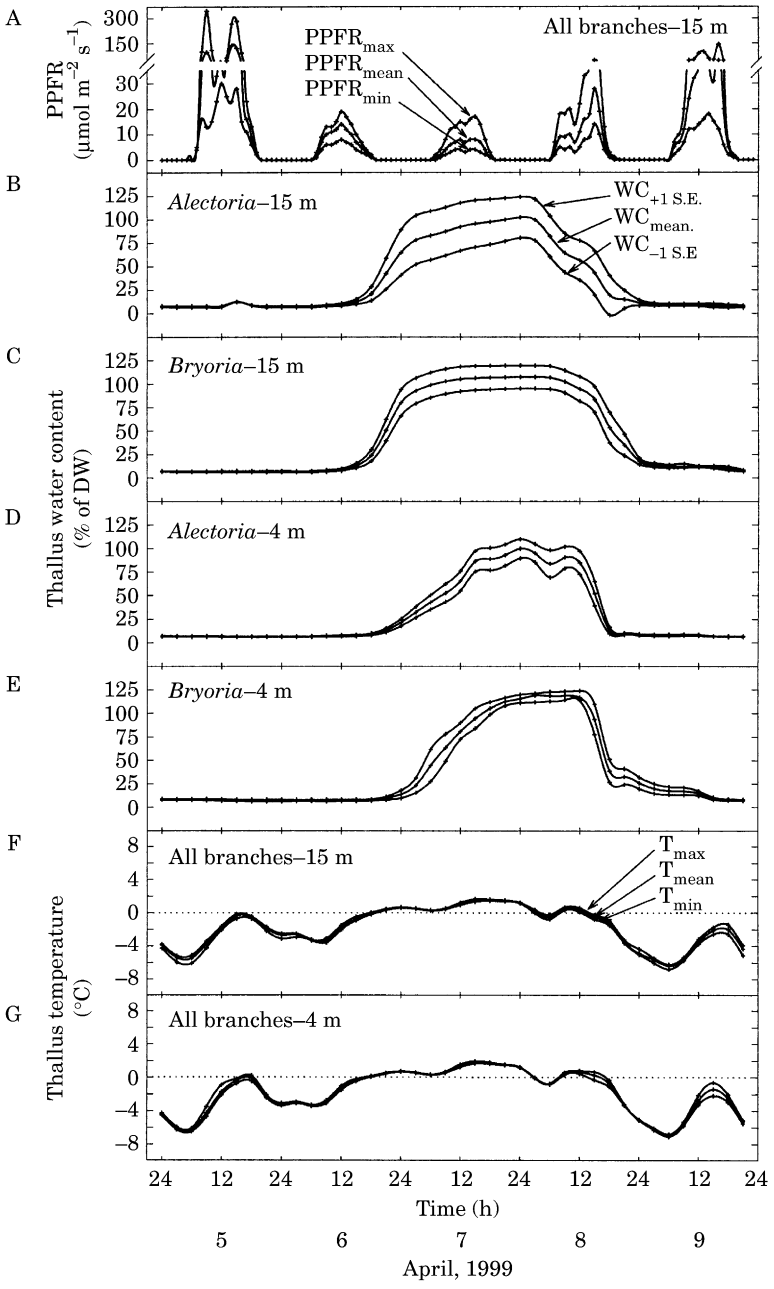

FIG. 2. A representative lichen hydration event during winter snowmelt conditions from April 5–9, 1999 (pooled data, all trees). A, minimum, mean, and maximum PPFR on upper branch surfaces at 15 m height within the canopy (n=18); B–E, mean thallus WC (± one standard error) in *Alectoria* and *Bryoria* at 15 and 4 m height within the canopy (n=18 for each species by height plot); F and G, lichen thallus temperatures (minimum, mean, and maximum) represent pooled measurements from thalli of *Alectoria* and *Bryoria*, taken at heights of both 4 and 15 m within the canopy (n=36 for each height position). Data plotted at 3 h intervals.

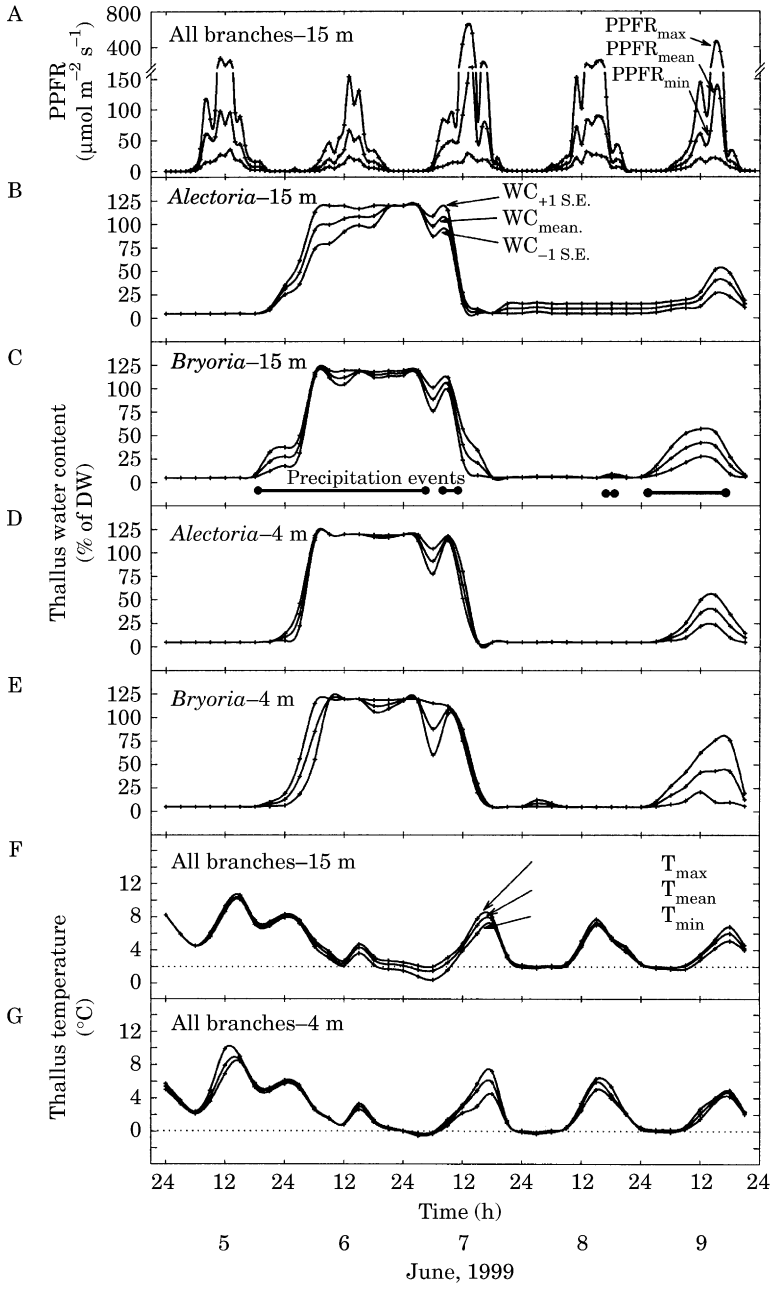

FIG. 3. A representative lichen hydration event under summer rainfall conditions from June 4 to 8, 1999 (pooled data of all trees). Duration of precipitation periods is shown by horizontal bars along the bottom of the *Bryoria* 15 m plot. For further explanation see legend to Fig. 2.

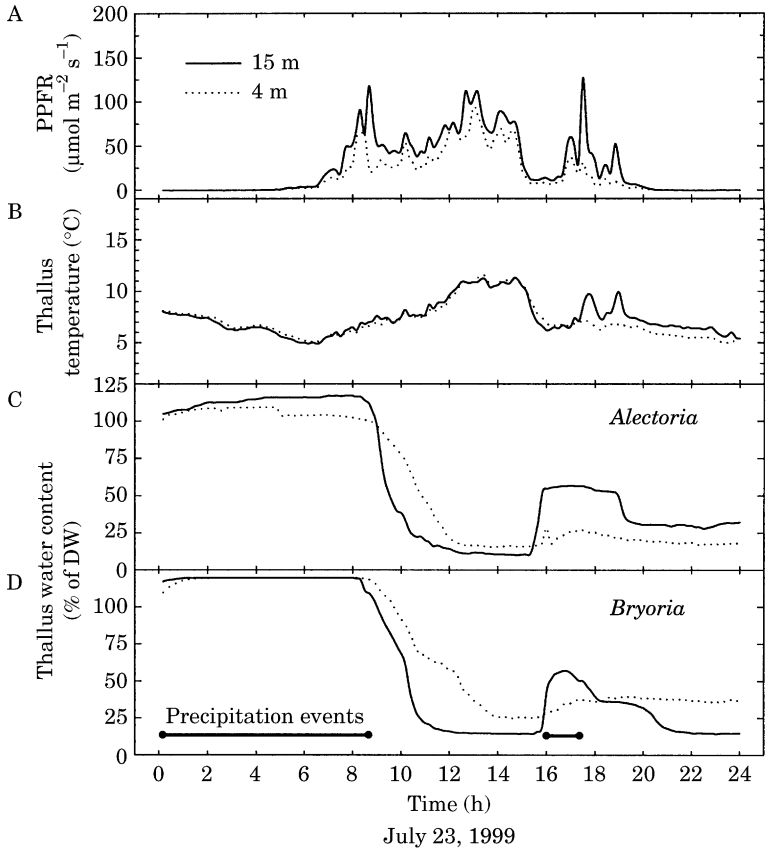

FIG. 4. A representative lichen hydration event under summer rainfall conditions on July 23, 1999 (single tree data). A, mean PPFR incident on upper branch surfaces at 15 m height within the canopy (n=3); B, mean temperature of lichen thalli (pooled data for *Alectoria* and *Bryoria*) at 15 and 4 m height within the canopy (n=3). C & D, mean thallus WC (±1 standard error) for thalli of *Alectoria* and *Bryoria* at 15 and 4 m height in the canopy (n=3 for each species by height plot). Data plotted at 10-min intervals, and duration of precipitation periods is shown by horizontal bars along the bottom of the *Bryoria* plot.

A comparison of the temperature frequency distribution of hydrated lichen thalli with that of air temperature (Fig. 5) shows a narrower range of temperatures in each case (summer and winter) is experienced by hydrated lichen thalli. During the winter months most periods of hydration fall between −5 and +5°C, whereas ambient temperatures show a greater percent frequency at temperatures below −5°C. In the summer months hydrated lichen thalli largely remain between 0 and 10°C, in comparison with ambient temperatures, which includes substantive periods up to 15°C.

Thalli of *Alectoria* show positive rates of NP uptake over a wide temperature range, from 0 to 25°C (Fig. 6). Optimal rates of thallus moisture content were between 75 and 100%, with NP uptake depressed slightly at higher thallus WC. Rates of NP uptake were generally higher in summer-collected material, although these differences were only significant at intermediate light levels (with greater variability seen in high light level measurements). Extrapolation of physiological parameters (Table 1) confirms these trends. NP_{max} was higher in summer-collected thalli of *Alectoria*. Light

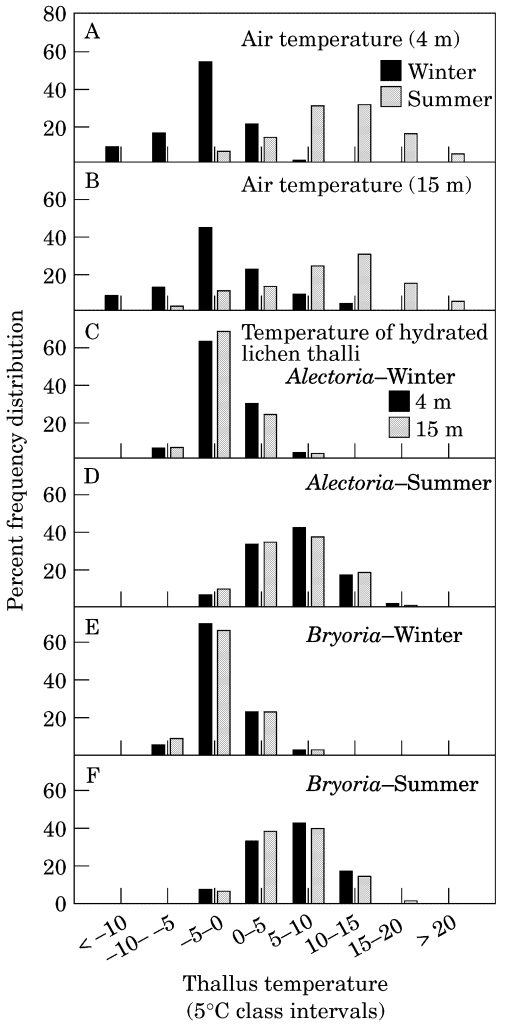

FIG. 5. Percentage frequency distribution of temperatures plotted within 5°C class intervals for winter (October–April) and summer (May–September) period measurements, taken from October 1997 to September 1999. A and B, air temperatures at 4 and 15 m (n=1); C–F, lichen thallus temperatures (hydrated lichen thalli only) of *Alectoria* and *Bryoria* at 4 and 15 m height within the canopy (n=18 for each species by height combination).

compensation points were temperature dependent, from below 10 μmol m^{-2} s^{-1} PPFR at 0°C, to near 20 μmol m^{-2} s^{-1} PPFR at 25°C. The point of light saturation at 15°C in *Alectoria* fell between 179 and 189 μmol m^{-2} s^{-1} PPFR. The temperature optimum of light saturated thalli rose from 18·1 to 22·9°C in summer versus winter-collected material.

A similar pattern of response was seen in *Bryoria* (Fig. 7). Thalli were photosynthetically active over a broad temperature range. Again, significant differences in NP response between summer and winter-collected material were confined to cells at intermediate temperature/light combinations (due to greater variability in response at higher temperature/light combinations). Rates of NP_{max} were higher than those of *Alectoria*, estimated at 2·33 mg CO_2 g^{-1} h^{-1} in the summer-collected 15°C material (Table 1). Light compensation points range from 8 to 32 μmol m^{-2} s^{-1} PPFR, at temperatures from 0 to 25°C, respectively (Table 1). NP light saturation at 15°C was near 400 μmol m^{-2} s^{-1} PPFR. At 5°C NP light saturation was near 200 μmol m^{-2} s^{-1} PPFR.

Thalli of both *Alectoria* and *Bryoria* show a rapid reactivation of NP activity on re-wetting (Fig. 8). Rates of NP were optimal in each species as measured at 1 h after wetting. Both species show a slight decline in subsequently measured rates of NP. Thereafter, NP rates remain fairly stable (declining slightly) in hydrated lichen thalli over the following week. After 6 days continuous hydration thalli of *Bryoria* show a marked decline in NP activity compared with that of *Alectoria*.

Seasonal fluctuations in the duration of lichen hydration were similar in *Alectoria* and *Bryoria*. The duration of lichen hydration peaked in October and November of both years (Figs. 9 and 10). During the remainder of the year the proportion of time lichen thalli were hydrated ranged between 10 and 30%, except during a period of prolonged high pressure (i.e. dry conditions) in February 1999. Thalli in upper canopy exposures (15 m) tended to have longer periods of hydration during the late winter. In contrast, during the mid-summer period, lower canopy lichens experienced a longer duration of lichen hydration.

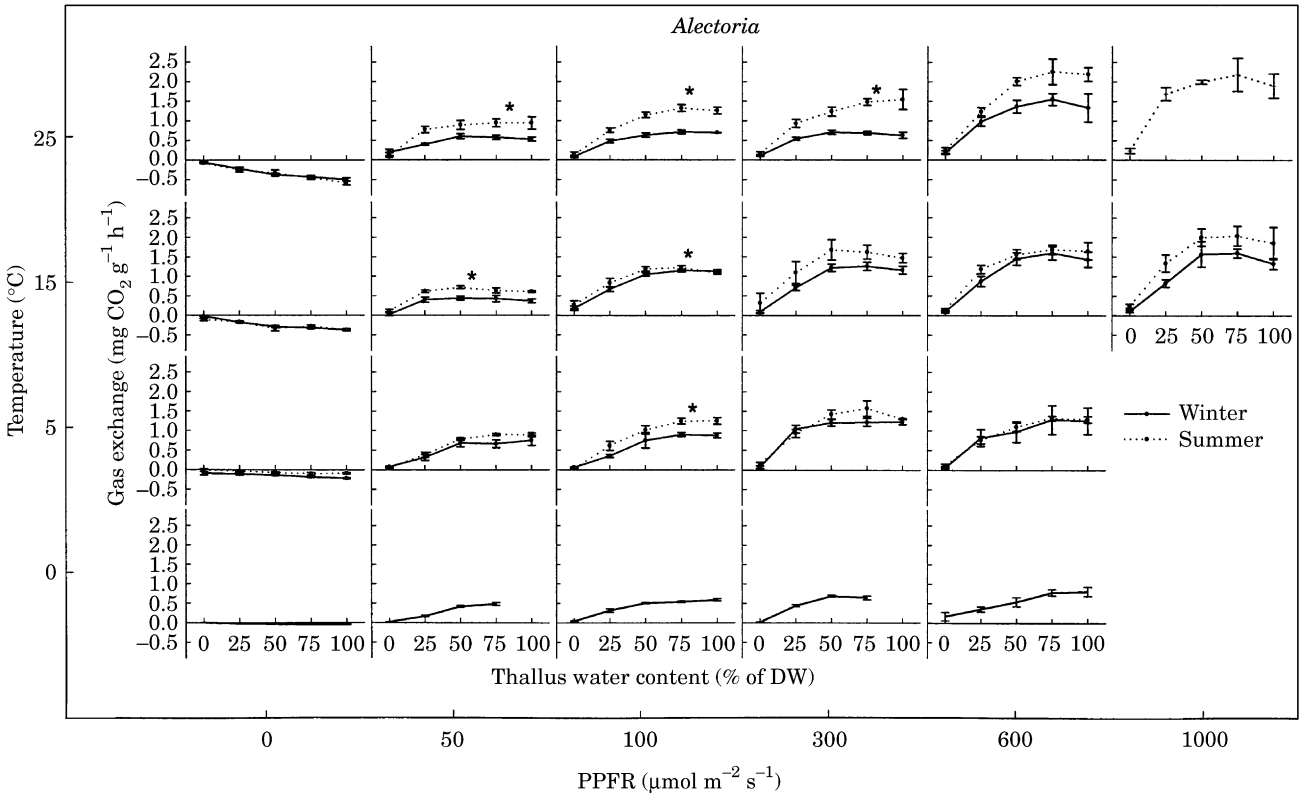

FIG. 6. Physiological response matrix (mean gas exchange, mg CO_2 g^{-1} h^{-1}) for *Alectoria*, under winter and summer conditions, measured at temperatures of 0, 5, 15, and 25°C (0°C data in winter only), PPFR of 0, 50, 100, 300, 600, and 1000 μmol m^{-2} s^{-1} (1000 μmol m^{-2} s^{-1} PPFR measurements in summer only), and at thallus WC from 0 to 100% dry weight (25% class intervals). Rates of gas exchange within each temperature/moisture/light matrix combination are plotted as mean values ± 1 standard error (n=10 for each temperature, light, and seasonal combination). Asterisk within plots denotes temperature/PPFR combinations where Bonferroni adjusted probabilities were <0·05 for comparisons of winter and summer rates of gas exchange at optimal thallus moisture content.

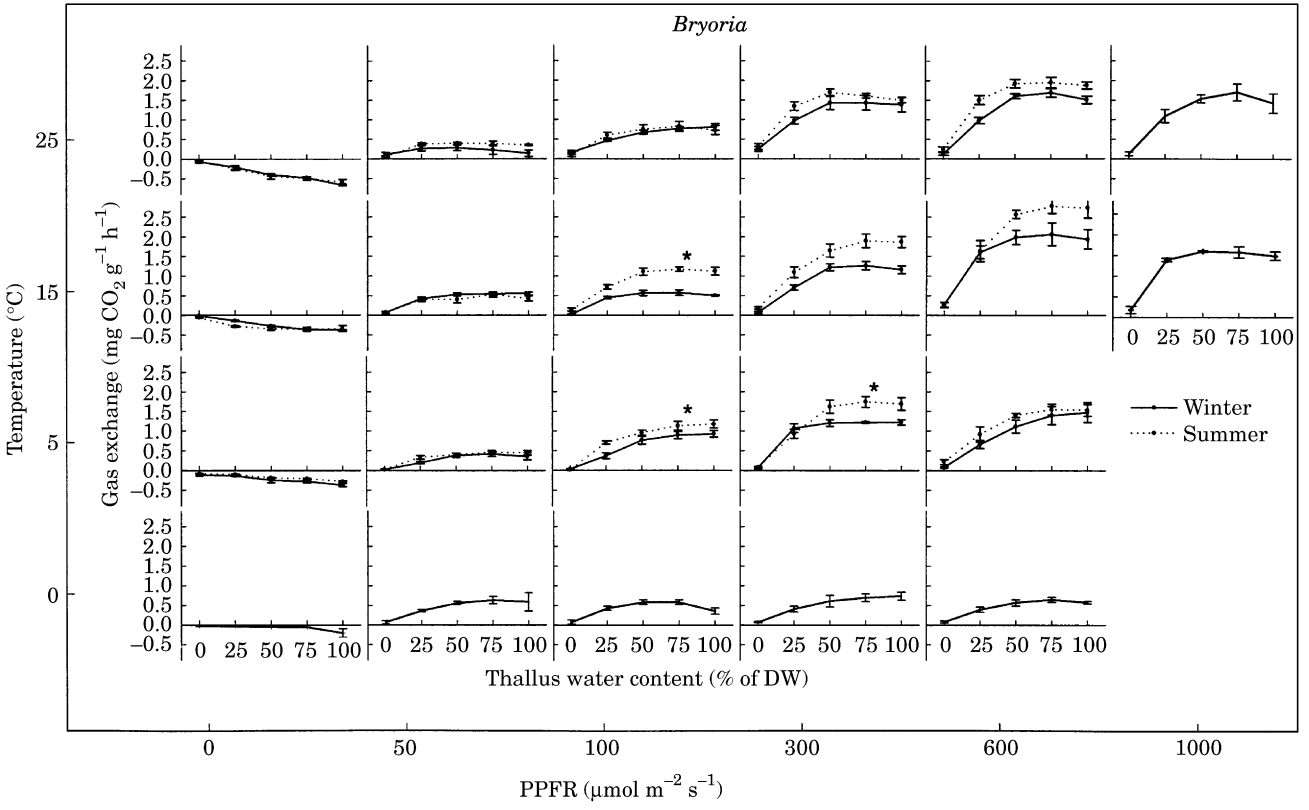

FIG. 7. Physiological response matrix (mean gas exchange, mg CO_2 g^{-1} h^{-1}) for *Bryoria*, under winter and summer conditions. For further explanation, see legend to Fig. 6.

TABLE 1. *Ecophysiological parameters in* Alectoria *and* Bryoria

Parameter*		*Alectoria*		*Bryoria*	
		Summer	Winter	Summer	Winter
	Temperature (°C)				
NP_{max} (mg CO_2 g^{-1} h^{-1})	0	–	0·70 (0·75)	–	0·68
	5	1·43 (0·91)	1·12 (0·67)	1·65 (0·94)	1·39 (0·82)
	15	1·82 (0·85)	1·52 (0·94)	2·33 (0·86)	1·79 (0·92)
	25	1·92 (0·79)	1·21 (0·86)	1·91 (0·91)	1·64 (0·92)
LCP (μmol m^{-2} s^{-1})	0	–	6 (0·82)	–	8 (0·85)
	5	9 (0·65)	7 (0·83)	17 (0·93)	20 (0·86)
	15	14 (0·86)	18 (0·91)	19 (0·88)	23 (0·94)
	25	14 (0·92)	17 (0·88)	32 (0·72)	32 (0·88)
	PPFR (μmol m^{-2} s^{-1})				
T_{opt} (°C)	50	20·6 (0·91)	14·7 (0·95)	14·4 (0·88)	10·1 (0·94)
	600	22·9 (0·90)	18·1 (0·87)	16·3 (0·86)	15·9 (0·96)

*NP_{max}, maximum rate of net photosynthesis; LCP, light compensation point; T_{opt}, temperature optimum of net photosynthesis. R^2 values for each equation are provided in parenthesis.

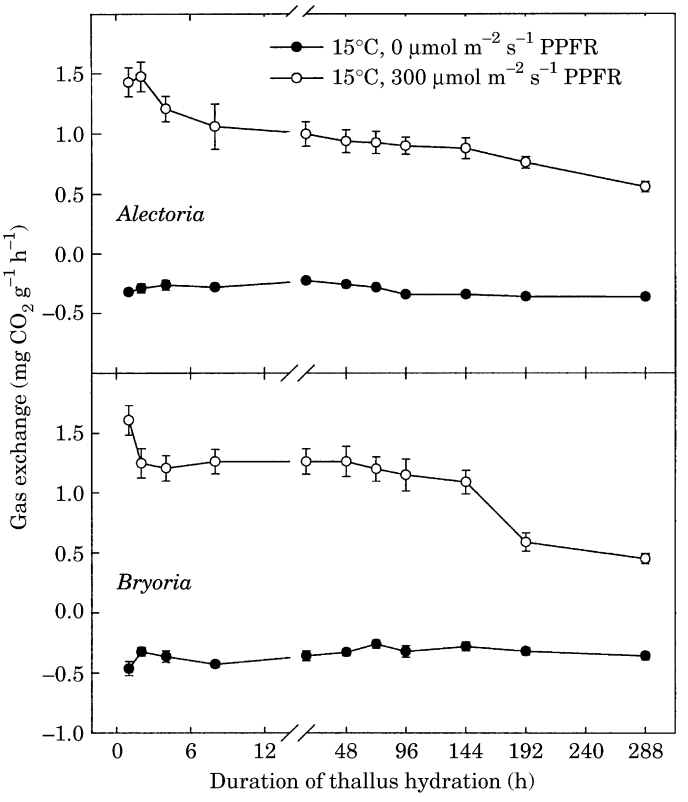

FIG. 8. Mean rates of gas exchange (mg CO_2 g^{-1} h^{-1}) in summer-collected thalli of *Alectoria* and *Bryoria* held at full thallus saturation for up to 288 h. Gas exchange measurements took place at 15°C, and for each at 0 and 300 μmol m^{-2} s^{-1} PPFR.

When examined by species (combining measurements from all lichen thalli), thalli of *Alectoria* were found to be hydrated 26% of the time during the winter months, with 75% of this hydration occurring in the dark. In the summer, *Alectoria* thalli were wet only 17% of the time, with 46% of hydration episodes occurring in the dark. The analysis for *Bryoria* shows similar results. In winter, *Bryoria* thalli were wet 26% of the time, and 77% of the hydration episodes occurred during darkness. *Bryoria* thalli in summer were wet 16% of the time, with 45% of these episodes occurring in the dark.

Predictions of NA show a marked peak in CO_2 uptake during the mid-summer period of both years (Figs 9 and 10). Predicted respiratory response (Figs 9 and 10) closely tracked availability of hydration episodes for both species groups. Although lichen thalli were hydrated more frequently during the winter period, restrictions of light availability and temperature imposed proportionally greater limitations on NA during the winter months. In both the winter and summer periods, the single largest limitation on NA in *Alectoria* and *Bryoria* was low thallus moisture content (Fig. 11). Low incident PPFR at the thallus surface was the next most important limitation on NA, particularly during the winter period. Lower canopy (4 m) *Bryoria* were restricted more by hydration status and incident PPFR than were upper canopy thalli (15 m) during winter. Thalli of *Alectoria* showed consistently higher NA rates in the lower canopy exposure (4 m). In contrast, mixed *Bryoria* collections

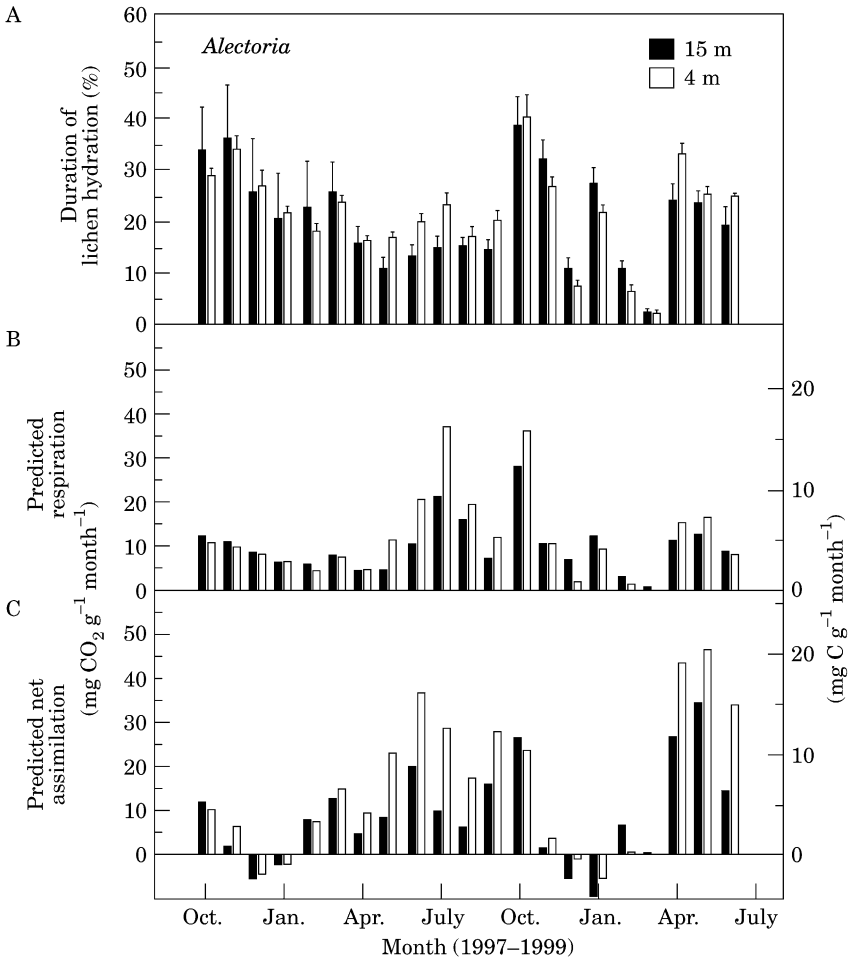

FIG. 9. A, monthly duration (% of time) of periods when lichen thalli are hydrated (>25% water content) in *Alectoria* at heights of 4 and 15 m within the canopy (mean ± 1 standard error, $n=18$); B, predicted respiration (mg CO_2 g^{-1} $month^{-1}$ and mg C g^{-1} $month^{-1}$) in *Alectoria* at heights of 4 and 15 m within the canopy; C, predicted NA (mg CO_2 g^{-1} $month^{-1}$ and mg C g^{-1} $month^{-1}$) in *Alectoria* at heights of 4 and 15 m within the canopy. Measurements are for the period from October 1997 to June 1999.

showed no clear pattern in NA response to canopy height (Figs 9 and 10).

Discussion

Alectorioid lichens in subalpine forests of the interior mountain ranges in northwestern North America (from northern Idaho to north-central British Columbia) show strong height-related preferences for positioning within the canopy (Goward 1998; Campbell & Coxson 2001), with upper canopy exposures dominated by *Bryoria* spp., while lower canopy exposures are dominated by *A. sarmentosa*. Among causal factors that can be invoked in explaining these distributional patterns are those of vertical gradients in canopy microclimate. Higher humidity and reduced convection in lower canopy environments should prolong the duration of lichen hydration, and by extension, growth potential, after wetting events. These factors may be

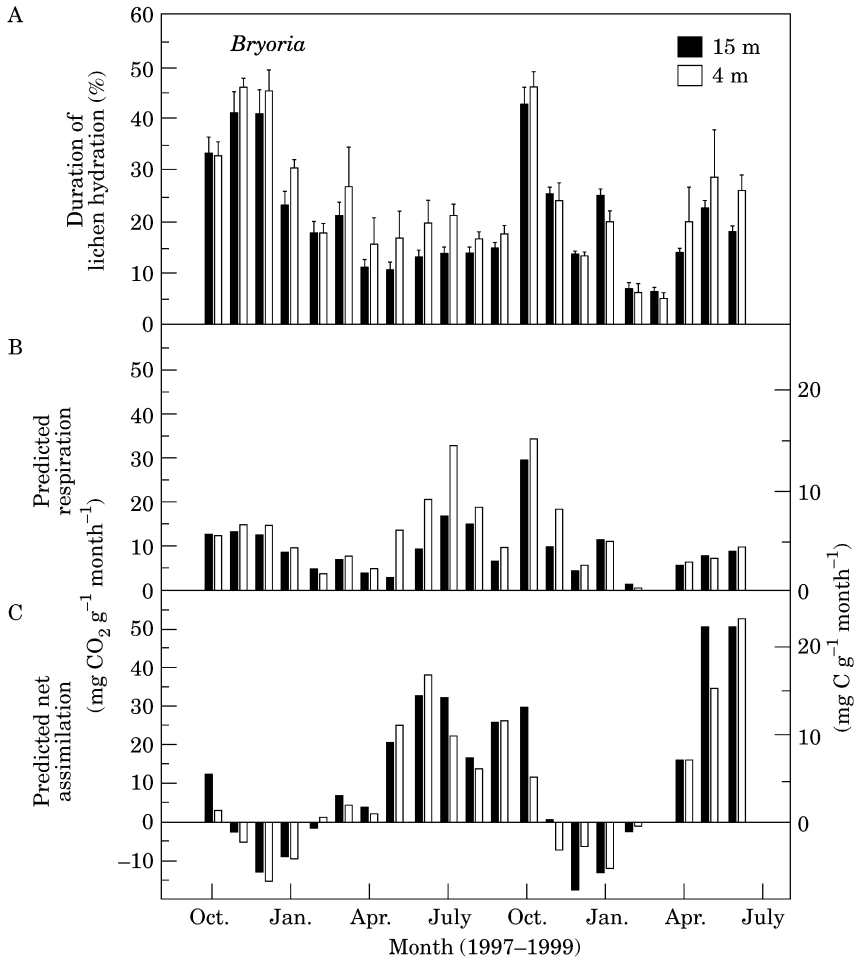

FIG. 10. A, monthly duration (% of time) of periods when lichen thalli are hydrated (>25% water content) in *Bryoria*, at heights of 4 and 15 m within the canopy (mean ± 1 standard error, n=18); B, predicted respiration (mg CO_2 g^{-1} $month^{-1}$ and mg C g^{-1} $month^{-1}$) in *Bryoria* at heights of 4 and 15 m within the canopy; C, predicted NA (mg CO_2 g^{-1} $month^{-1}$ and mg C g^{-1} $month^{-1}$) in *Bryoria* at heights of 4 and 15 m within the canopy. Measurements are for the period from October 1997 to June 1999.

counter-balanced, however, by diminishing light availability in the lower canopy. One might therefore predict that arboreal lichens will show greatest abundance at a point in the mid-canopy, where 'competing' factors reach a balance, in terms of their effect on lichen growth potential.

Our examination of lichen growth environments at Pinkerton Mountain provides some support for this hypothesis of competing factors, although gradients in canopy microclimate were strongly influenced by seasonality. During the winter months, individual snowmelt events were typically of much longer duration in the upper canopy. Measurements of canopy microclimate during snowmelt events show that the onset of lichen hydration typically occurs first in the upper canopy positions. This may reflect several factors, including reduced light availability in the lower canopy during the mid-winter period, increased

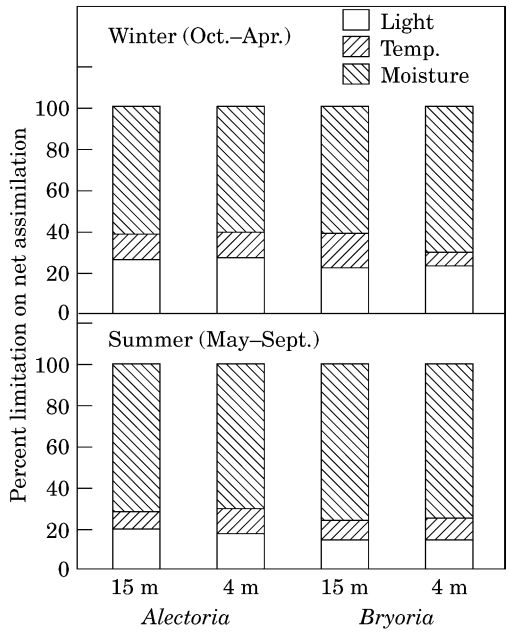

FIG. 11. Predicted relative importance (%) of major factors limiting NA (incident PPFR at lichen thallus surface, thallus temperature, and thallus WC) in *Alectoria* and *Bryoria* during the summer (May–September) and winter (October–April) periods (October 1997–September 1999).

snow-loading on lower canopy branches, and cold-air ponding at the forest floor surface. Although Kappen *et al.* (1998) and Kappen & Schroeter (1997), among others, have demonstrated the importance of snowmelt water as a hydration source for terricolous lichens, this hydration source has not previously been described for arboreal lichen communities.

During summer wetting and drying cycles, differences in the duration of lichen hydration events between upper and lower canopy positions were small, though typically showing an attenuation of lichen thallus drying in the lower canopy. Detailed plots of lichen hydration status from July 23, 1999, for instance, showed that drying of both species took longer in the lower canopy, up to 3 h after the cessation of precipitation. The balance of time spent by hydrated thalli under light versus dark conditions differed greatly by season. During the summer months, hydrated lichen thalli of both *Alectoria* and *Bryoria* were in the light *c.* 55% of the time, compared with only 25% in the winter period. In comparison, Sundberg *et al.* (1997) found that 60% of hydration episodes in the epiphytic lichens *Lobaria pulmonaria* and *Platismatia glauca* occurred in darkness.

Given this range of operating environments, do the physiological response matrices of *Alectoria* and *Bryoria* show adaptations that would allow them to persist and grow in this subalpine environment? The most striking adaptation of *Alectoria* and *Bryoria* was that each was capable of maintaining positive NP uptake over a wide temperature range, from near (and probably below) 0°C to well over 25°C. This tolerance of low temperatures parallels that of many other species. Kappen (1989), for instance, demonstrated continued NA down to −10°C in *Usnea sphacelata*.

An additional factor in the NP response of *Alectoria* was the shift in NP temperature optimum between summer- and winter-collected thalli (from 18·1 to 22·9°C) and higher rates of maximum NP during the summer months. These differences, however, were statistically significant only at intermediate light intensities, possibly due to greater variability between individual lichen thalli at high light intensities. Similar changes in seasonal NP rates were documented by Matthes-Sears *et al.* (1986), who observed higher NP rates during the winter rainy season in maritime populations of *Ramalina menziesii* in California.

Matthes-Sears *et al.* (1986) also demonstrated that the temperature optimum for NP uptake in *R. menziesii* was consistently above that of the average temperature experienced by hydrated thalli. This finding parallels our own observation that the mean temperature of hydrated thalli was below that of each species NP temperature optima. In *Alectoria*, for instance, the mean temperature of hydrated lichen thalli during summer and winter periods was 6·1 and −1·0°C, respectively (measured at 4 m). In contrast, NP_{max} at light saturation during the summer and winter periods occurred at temperatures

of 22·9 and 18·1 °C, respectively. Similar differences can be seen in *Bryoria*, where average summer and winter operating environment temperatures at 15 m were 5·6 and −1·6 °C, compared with seasonal values of NP_{max} at light saturation occurring at 16·3 and 15·9 °C, respectively. One caution that should be raised in the interpretation of our seasonal NP values is that full activation of Rubisco and other Calvin cycle enzymes may not occur during hydration events at low winter temperatures. The generally lower NP activity of our winter-collected material may therefore be one of 'dormant', rather than 'absent' photosynthetic capacity.

The light compensation points in *Alectoria* and *Bryoria* were under 10 μmol m^{-2} s^{-1} PPFR at low temperatures (<5 °C). At higher temperatures (from 5 to 15 °C) NP light compensation values generally fell between 10 and 20 μmol m^{-2} s^{-1} PPFR. The light compensation point of *Bryoria* was higher than that of *Alectoria*, possibly reflecting the dark pigmentation of this lichen species. In comparison, Sundberg *et al.* (1997) found that light compensation points in the epiphytic lichens *Lobaria pulmonaria* and *Platismatia glauca* were reached at 5–10 μmol m^{-2} s^{-1} PPFR and were saturated at 100–150 μmol m^{-2} s^{-1} PPFR. Light saturation in both *Alectoria* and *Bryoria* fell below 600 μmol m^{-2} s^{-1} PPFR.

Both *Alectoria* and *Bryoria* showed a depression of NP uptake as WC fell below 50–75% thallus WC (by weight). NP activity was also depressed at high thallus WC, in a pattern similar to that of the type 'B' response of Lange *et al.* (1993).

Our partitioning of factors limiting NA shows that limitations of thallus WC were the primary factors restricting NP, as might be expected under conditions where lichen thalli are wet less than 25% of the time. Hahn *et al.* (1993), similarly found that thallus WC was the primary limitation on NP for Alaskan tundra lichens. Smith & Gremmen (2001) note that incorporation of hydration/desiccation cycles into growth rate calculations for *Turgidosculum complicatum* substantially reduced estimates of net annual carbon gain. Surprisingly, limitations of temperature on NA in *Alectoria* and *Bryoria* were less important than limitations imposed by PPFR. This may reflect the relatively wide NP temperature range in *Alectoria* and *Bryoria*. Matthes-Sears *et al.* (1986) also found that desiccation of lichen thalli was the main limitation on growth in *R. menziesii*, followed by restrictions of light availability, and finally temperature.

Predictions of NA in *Alectoria* and *Bryoria*, using field microclimate data as a template for calculating NP response from laboratory-based physiological response matrices, showed a marked seasonality, with higher rates of NA predicted for the May through September period. Predicted rates of NA were negative for both species during the mid-winter period, although the magnitude of this carbon loss was small when compared with previous measurements on lichen species from polar environments, for instance, as reported by Schroeter *et al.* (2000). The relatively low rates of dark respiration observed in *Alectoria* and *Bryoria* may, in part, account for these differences. In this respect, our findings differ from those of many previous studies of lichens in cold-temperate and/or polar environments. Kappen (1985), for instance, found that the magnitude of dark respiration at 25 °C exceeded that of NP uptake at the same temperature for *Usnea fasciata* and *U. sulphurea* from maritime Antarctic environments.

The continued NA that we predict during the winter period for *Alectoria* and *Bryoria* clearly reflects the importance of snowmelt events. From February onwards, substantive periods of lichen hydration (at relatively high levels of PPFR) can occur during snowmelt events, particularly during inversion conditions, when warm Pacific air masses override colder continental air trapped in valley-bottom locations. Direct comparisons with seasonal patterns of lichen growth rates from other environments, particularly from polar or maritime environments (where winter PPFR levels may be much lower), should therefore be made with caution. Further confidence in our predictions of positive NA rates over the combined

winter period is provided by direct measurements of lichen growth rates (repeated biomass measurements on individual thalli held within field mesh enclosures) from the Pinkerton Mountain site, which show substantive biomass gain during the winter period (S. Stevenson & D. S. Coxson, unpublished data).

The other major finding of our NA modelling was that of differential species response to canopy position. *Alectoria* showed consistently higher NA potential in lower canopy positions, while *Bryoria* showed no clear trends in height-related NA response. Yet, for both species, hydration events lasted longer in lower canopy positions, with the exception of the mid-winter period, when greater snowmelt occurred in the upper canopy position. The similarity of the two species canopy microclimate profiles can be demonstrated by running the NA model on both species data sets (*Alectoria*'s NP results on *Bryoria* microclimate and vice-versa), which results in essentially the same data trends (data not presented). The differences in NA model predictions between *Alectoria* and *Bryoria* would therefore seem to derive more from inherent characteristics of their NP response surfaces.

The absence of clear NA response to vertical gradients in canopy microclimate for *Bryoria* poses a dilemma for the evaluation of our results. Looking at the NA model alone, *Bryoria* should occur with equal abundance in upper and lower canopy positions. In particular, we must ask what factors, if not NP response, are responsible for the exclusion of *Bryoria* from lower canopy positions. Our observation that thalli of *Bryoria* were more sensitive to extended hydration periods may be important in this regard, and supports the hypothesis of Goward (1998), that the distribution of *Bryoria* is related to the avoidance of canopy positions where thalli face prolonged hydration exposure. Although we did not observe field hydration events of sufficient duration to trigger this type of NP decline, stress physiology may nonetheless provide an important underlying response variable.

For *Alectoria* our NP assimilation model would predict a reduced biomass accumulation in upper canopy positions, though perhaps not as abrupt a decline as that actually observed under field conditions (Campbell & Coxson 2001). The observation of Renhorn & Essen (1995) that biomass accumulation in alectorioid lichens is strongly influenced by rates of thallus fragmentation, may be equally important in this regard. Given that thalli of *Alectoria* have a much longer growth form, they may be more susceptible to fragmentation and wind scouring from upper-canopy branches. Their absence from the upper canopy may therefore reflect not so much an inability to grow there, but rather physical constraints on retaining accumulated biomass (due to fragmentation) in upper canopy environments.

In summary, our data suggest that NP growth responses do not, by themselves, explain niche partitioning in alectorioid lichens from subalpine forest environments in north-central British Columbia. Rather, exclusionary factors (e.g. intolerance of desiccation and thallus fragmentation) may concurrently play an important role in determining available habitat within the canopy.

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