

## Carbon Gain in *Cladina mitis* from Mixed Feather Moss Mats in a Sub-Alpine Spruce-Fir Forest: The Role of Soil Respiratory Carbon Dioxide Release

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Received December 6, 2003; Accepted March 23, 2004

### Abstract

Thalli of *Cladina mitis* growing within mixed feather moss mat communities from a sub-alpine spruce-fir forest in southwestern Alberta regularly experience enhanced CO<sub>2</sub> operating environments, due to the effects of soil respired CO<sub>2</sub> trapped within the moss mat boundary layer. Measurements of *in-situ* mat profile CO<sub>2</sub> concentrations under mid-summer conditions (30 days) showed mean values of over 700  $\mu\text{l l}^{-1}$  CO<sub>2</sub> at mid-mat depth, with maximum CO<sub>2</sub> concentrations reaching 900  $\mu\text{l l}^{-1}$  CO<sub>2</sub>. Even at the mat surface, mean CO<sub>2</sub> concentrations were significantly elevated over atmospheric values, reaching 630  $\mu\text{l l}^{-1}$  CO<sub>2</sub>. These conditions of naturally enhanced CO<sub>2</sub> growth environments may potentially increase net photosynthetic (NP) response of lichens contained within the moss mat boundary layer, compensating in part for both declining light levels within mats and limitations on NP uptake at full thallus saturation. Calculations of NP assimilation, imposing a laboratory derived NP response matrix on measured field microclimatic and CO<sub>2</sub> concentration gradients, suggest that enhanced CO<sub>2</sub> concentrations at mid-mat depths could increase overall net assimilation in *C. mitis* mats by up to 40%.

Keywords: *Cladina mitis*, feather mosses, carbon dioxide enhancement, net photosynthesis, soil respiration

Presented at the 4th International Symbiosis Congress, August 17–23, 2003, Halifax, Canada

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## 1. Introduction

Feather moss mat communities, dominated by species such as *Hylocomium splendens*, *Pleurozium schreberi*, and *Ptilium crista-castrensis*, are major understory components in late-seral boreal and montane coniferous forests in Western Canada (Coxson and Marsh, 2001). These moss mats frequently contain significant lichen components, including mat forming species such as *Cladina mitis*, and foliose species such as *Peltigera aphthosa*. The relative dominance of different members of these mixed feather moss mat communities depends on local mosaics of site microtopography, substrate type (mineral soil, litter, decaying wood), canopy closure (Bisbee et al., 2001; Sulyma and Coxson, 2001), and hydrology (Gignac and Vitt, 1990).

Globally, the productivity of these forest floor non-vascular plant communities may be quite significant. Swanson and Flanagan (2001) estimated growing season (net annual) contributions of feather moss mat communities in a black-spruce boreal forest site at  $80 \text{ g C m}^{-2}$ , while other authors suggest that a greater proportion of ecosystem productivity can be attributed to forest floor non-vascular plants than to canopy dominant trees in many of these cold boreal and montane forest environments (Oechel and Van Cleve, 1986).

A major source of uncertainty in determining the significance of mosses and lichens to ecosystem productivity in boreal and montane ecosystems is the potential impact of global climate change, as expressed by changing temperature and precipitation patterns, and by increasing atmospheric carbon dioxide concentrations (Nash and Olafson, 1995; Payette et al., 2001; Potter et al., 1995).

Although the short-term response of lichen symbionts to changes in ambient atmospheric  $\text{CO}_2$  concentrations has previously been documented in laboratory studies (Coxson et al., 1983), less information is available on gradients in  $\text{CO}_2$  concentration experienced by terricolous lichen podetia under field conditions. Boundary layer conditions can impose significant barriers to gaseous diffusion, theoretically resulting in lichen thalli experiencing quite different operating environments, both from microclimate modification (Bolter et al., 1989) and from the trapping of soil derived  $\text{CO}_2$  evolution (Sommerkorn, 2000).

Sonesson et al. (1992) demonstrated this phenomenon of elevated  $\text{CO}_2$  concentration with the surface boundary layer for sub-arctic feather-moss mats, while Tarnawski et al. (1992) found elevated  $\text{CO}_2$  concentrations within Antarctic turf-forming moss mats. We have now examined gradients of ambient  $\text{CO}_2$  concentration and microclimate conditions within mixed lichen-feather-moss mat communities in a subalpine spruce-fir forest in Western Canada, where we consider potential growth responses of *Cladina mitis* to soil-derived carbon sources.

## 2. Materials and Methods

### *Study site*

Mixed feather moss-mat communities, dominated by the moss *Hylocomium splendens*, and containing both fruticose lichen thalli, such as *Cladina mitis*, and foliose lichen thalli, including *Peltigera aphthosa*, were studied in mature subalpine spruce-fir forest (*Abies lasiocarpa* and *Picea engelmannii*) on periglacial riparian terraces adjacent to Lusk Creek, near the University of Calgary Kananaskis Field Station (51°02'N, 115°03'W), as described by Wilson and Coxson (1999).

### *Field microclimate and CO<sub>2</sub> profiling*

Ambient CO<sub>2</sub> concentrations were measured at four heights; at 2 m above the forest floor surface, at the forest floor surface (moss mat surface), at 5–8 cm depth (mid-mat) within the mixed moss-lichen mats (just above the depth at which a transition from live to decaying tissue is seen); and at a depth of 15 cm (largely in decomposing podetia). CO<sub>2</sub> concentrations were sampled with a Li-Cor 6251 infra-red gas analyzer (Li-Cor, Lincoln, Neb.) connected to each sampling depth by 3 mm Tygon tubing. A datalogger (Omnidata Easylogger, Logan, UT) controlled switching system was connected to Brailsford (Model; TD-2N, Rye, NY) low-volume pumps to sample across forest floor profiles. The 2 m "atmospheric" sampling intake consisted of an open Tygon tubing end placed within a fine mesh spherical filter, this looped downwards to avoid precipitation intakes.

The moss-mat sampling intakes utilized 8 m lengths of 10 mm (internal diameter) Gore-tex tubing (W.L. Gore & Associates Inc., Newark, DE) placed on or within the moss mat at each sampling depth. Tygon tubing from the switching system was terminated 3 m inside the Gore-tex tubing sleeve, with the portion of Tygon tubing contained within the Gore-tex sleeve both open at its end and perforated (2 mm diameter openings over 50% of tube surface area) over the length of tubing held within the Gore-tex sleeve.

The ends of the Gore-tex tubing runs were separately vented to surface air intakes. Sampling of the confined space within Gore-tex tubing runs was conducted at 30 minute intervals, running sampling pumps each time until vent air (that was entering the end of the 8 m Gore-tex sleeve) had reached the sampling cell of the gas analyzer (running intake pumps for ca. 30 sec. until 1–1.2 l of air had been pulled from the buried Gore-tex tubing).

The peak CO<sub>2</sub> concentration observed at the analyzer each time air was pumped from the buried Gore-tex tubing was recorded as the profile CO<sub>2</sub>

concentration for that sampling interval. Manual evacuations of small volume gas samples from within the Gore-tex tubing, using a 10 cc syringe connected to surgical tubing that terminated within trial Gore-tex sampling sleeves showed the same CO<sub>2</sub> concentrations as were measured by the automated sampling method. This subsampling with syringes was further used to verify the time interval required for CO<sub>2</sub> concentrations within the Gore-tex tubing to return to equilibrium with the surrounding air space voids (about 10 minutes after sampling with the automated pump system).

Concurrent measurements of mixed feather moss mat microclimate included photosynthetically active radiation (PAR), measured with a Li-Cor quantum sensor mounted at 2 m height in an adjacent clearing; mat temperature, measured with fine-wire thermocouples; and thallus water content, determined indirectly from impedance clip measurements on fronds of *H. splendens* (after Coxson, 1991), where small clips were placed across the leafy portion of individual years growth fronds. Relative water content of *H. splendens* fronds was determined using calibrations on fronds of known wetness. This indirect approach to determination of *C. mitis* water content follows our observation that *H. splendens* and *C. mitis* showed very similar time course duration of individual hydration periods in mixed mat profiles (using gravimetric determinations of water content). Light attenuation in mat profiles was determined from short-term field measurements. Field measurements were taken over a 36 day period, from June 12 to July 18, 1991.

### *Lichen physiological response*

Net photosynthetic (NP) and dark respiratory (DR) responses of fresh collected mat segments of *C. mitis* were measured using a matrix-based approach, with gas exchange measured in 5 different replicates at each of three temperatures (5°, 15°, and 25°C) and six light levels (Photosynthetic Photon Flux Densities [PPFD] of 0, 25, 50, 100, 200, and 400  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). Thalli of *C. mitis* at each matrix temperature-light combination were taken from full thallus water content (WC) (with freshly saturated thalli that had been lightly blotted to remove surface water films) to dessication. Pretreatment hydration (24 h) consisted of exposure to long-day photoperiod conditions at 15°C, and 16 h day/8 h night (300 and 0  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD, respectively). Gas exchange was measured in 200 ml glass cuvettes, using closed-cell CO<sub>2</sub> incubation techniques of Larson and Kershaw (1975). CO<sub>2</sub> concentrations were measured using a Li-Cor 6250 gas analyser (Li-Cor, Lincoln, Neb.). Rates of CO<sub>2</sub> exchange were expressed as mg CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>.

The response of lichen thalli to changes in ambient CO<sub>2</sub> concentrations was assessed at 15°C and 200  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD, in sequential measurements of gas

exchange, using photosynthetic drawdown within cuvettes to obtain response curves for each thallus replicate from CO<sub>2</sub> concentrations of ca. 1,200 µl l<sup>-1</sup> down to the CO<sub>2</sub> compensation point.

Interactions effects between exposure to elevated ambient CO<sub>2</sub> concentrations and high thallus water contents were assessed in paired experiments, where NP uptake in thallus segments was sequentially measured at: 1) high thallus WC (full thallus saturation) and elevated CO<sub>2</sub> concentrations (900 µl l<sup>-1</sup> CO<sub>2</sub>); 2) high thallus WC and ambient CO<sub>2</sub> concentrations (400 µl l<sup>-1</sup> CO<sub>2</sub>); 3) optimal thallus WC (point of maximum NP uptake over drying curve) and elevated CO<sub>2</sub> concentrations; 4) optimal thallus WC and ambient CO<sub>2</sub> concentrations, 5) suboptimal (dessicating) thallus WC (between 30–40% relative water content) and elevated CO<sub>2</sub> concentrations; and 6) suboptimal thallus WC and ambient CO<sub>2</sub> concentrations.

These results were expressed as percent relative net assimilation (NA), where each replicate's NP response was plotted relative to that replicate's response at optimal thallus WC (set as 100% response rate) for either ambient or elevated CO<sub>2</sub> concentrations. This standardization against NA response at optimal thallus water content minimizes the influence of elevated CO<sub>2</sub> on plotted NP response, leaving changes in NP response to thallus water content (at different CO<sub>2</sub> concentrations) as the more likely explanation for significant differences, where observed (assessed at each WC range using Bonferonni t-tests).

#### *Data analysis*

Simple empirical predictions of NA response to measured field microclimate conditions were calculated from an interpolation between measured NP response matrix values, using a kriging routines from SURFER Ver. 6.0 (Golden Software, Golden, Col.) (taken at intervals of 1°C, 10 µmol m<sup>2</sup> s<sup>-1</sup> PPFD, and 10% thallus WC). Kriging is a geostatic gridding method that produces a response surface between regular or irregularly measured points. Response to changes in CO<sub>2</sub> concentration were subsequently imposed on interpolated matrix values, based on the CO<sub>2</sub> response curve measured at 15°C and 400 µmol m<sup>2</sup> s<sup>-1</sup> PPFD.

### **3. Results**

Mixed feather moss mat communities containing *C. mitis* were exposed to two major wetting-drying cycles during the summer monitoring period. Ambient temperature and light levels were generally lower during precipitation periods, with midday temperatures rarely exceeding 10–15°C (Figs. 1 and 2). During breaks between precipitation events, when mixed feather moss mat

communities dried out, thallus surface temperatures reached values near 35°C under full sun conditions.

CO<sub>2</sub> concentrations at each profile depth showed marked diel oscillations, typically fluctuating by over 200  $\mu\text{l l}^{-1}$  CO<sub>2</sub> each day. The absolute range of CO<sub>2</sub> concentrations to which thalli were exposed rose during the course of each hydration event, with mid-mat CO<sub>2</sub> concentrations reaching over 900  $\mu\text{l l}^{-1}$  CO<sub>2</sub>. Mean CO<sub>2</sub> concentrations within the moss-lichen mats rose sharply with depth (Fig. 3), from 430  $\mu\text{l l}^{-1}$  CO<sub>2</sub> at the mat surface to over 700  $\mu\text{l l}^{-1}$  CO<sub>2</sub> at mid-mat depths. Mean mat surface CO<sub>2</sub> concentrations were similar to those measured at 2 m above the mat surface, although maximum mat surface CO<sub>2</sub> concentrations were higher (reaching 630  $\mu\text{l l}^{-1}$  CO<sub>2</sub>).

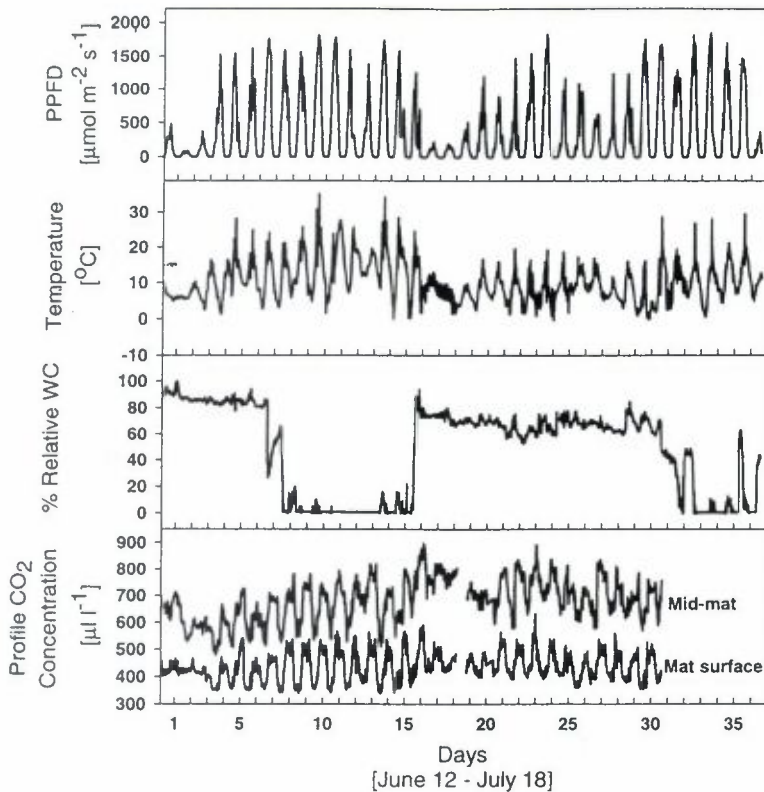


Figure 1. Summary microclimate conditions in mixed feather moss mat communities (June 12 - July 18). From top: Photosynthetic Photon Flux Density (PPFD) ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) incident above canopy, mat surface temperature ( $^{\circ}\text{C}$ ), mat surface percent relative thallus water content (WC), CO<sub>2</sub> concentration ( $\mu\text{l l}^{-1}$ ) at mat surface and mid-mat profile depths.

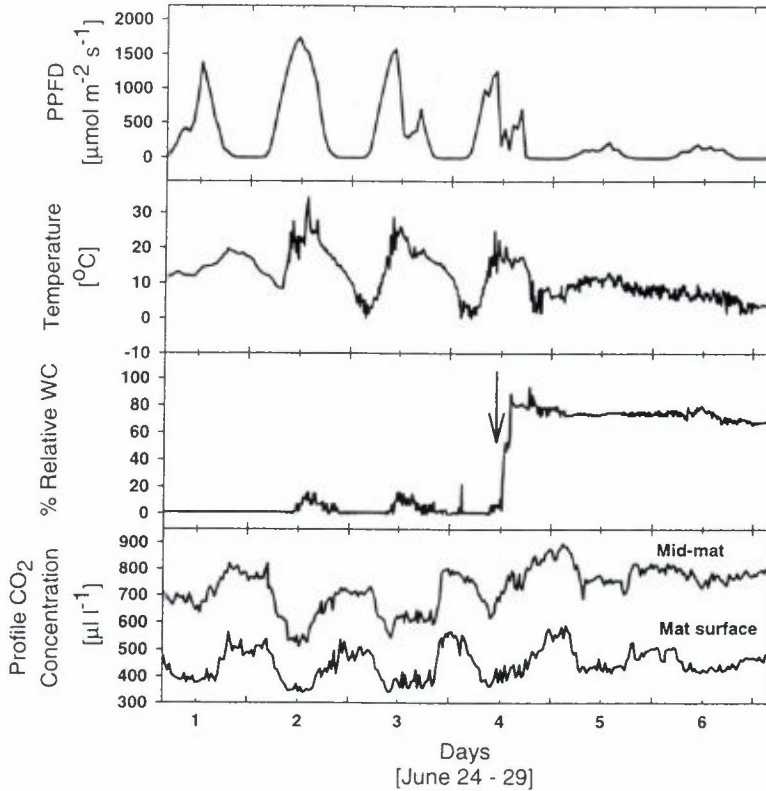


Figure 2. Detailed microclimate conditions in mixed feather moss mat communities (June 24–29). From top: Photosynthetic Photon Flux Density (PPFD) ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) incident above canopy, mat surface temperature ( $^{\circ}\text{C}$ ), mat surface percent relative thallus water content (WC) (arrow denotes start of precipitation period),  $\text{CO}_2$  concentration ( $\mu\text{l l}^{-1}$ ) at mat surface and mid-mat profile depths.

NP response was light saturated at progressively lower light intensities as temperatures fell, from near  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD at  $25^{\circ}\text{C}$ , to near  $25 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD at  $5^{\circ}\text{C}$  (Fig. 4). Measured NP uptake was highest in the  $15^{\circ}\text{C}$  incubation sets, reaching  $1.5 \text{ mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ . *C. mitis* thalli showed optimal rates of NP uptake near ca. 75% relative thallus WC, with a slight depression of NP uptake evident at full thallus WC (Fig. 5). Metabolic activity ceased when thalli fell below ca. 10% relative water content, equivalent to 15–20% thallus water content by weight. NP response to ambient  $\text{CO}_2$  concentrations showing a steep response curve, from a compensation point near  $200 \mu\text{l l}^{-1} \text{ CO}_2$ , to saturation values near  $1,200 \mu\text{l l}^{-1} \text{ CO}_2$  (Fig. 6). Laboratory tests showed that predicted rates of net assimilation were significantly higher in saturated thalli held under elevated  $\text{CO}_2$  concentrations (Fig. 7).

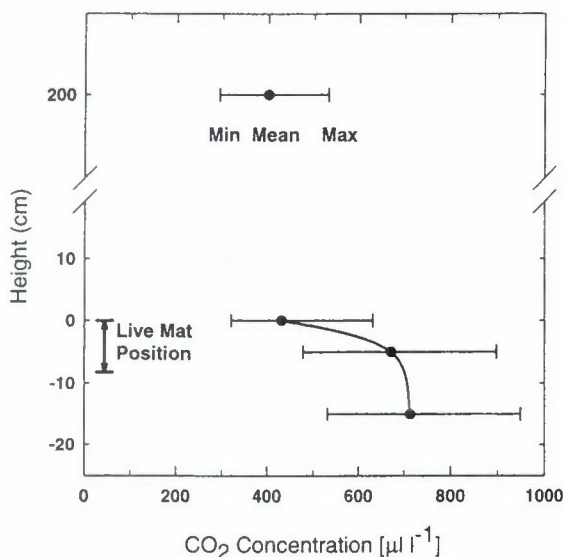


Figure 3. Profile CO<sub>2</sub> concentrations ( $\mu\text{l l}^{-1}$ ) (minimum, mean, and maximum) from June 12 – July 18 at 2 m above the forest floor surface, and at mat surface, mid-mat, and lower-mat profile positions.

Predicted rates of NA were up to 50% higher in mat-surface thalli, compared to mid-mat thalli, if analysis was confined to the influence of temperature, moisture, and light gradients (Fig. 8). When the influence of elevated CO<sub>2</sub> concentrations at mid-mat profile depths was included in calculation this pattern was reversed, with greater rates of NA assimilation predicted at mid-mat profile depths for much of the time (Fig. 8). Overall, elevated CO<sub>2</sub> concentrations within mixed moss mats were predicted to increase *C. mitis* assimilation (combined upper and lower mat results) by 40%.

#### 4. Discussion

One of the major constraints that lichens face in boreal and montane forest environments is that limitations on growth imposed by gradients of major environmental variables, e.g. temperature, moisture, and light availability, are often quite different in direction and magnitude. During periods of full sun exposure, when abundant light energy is available, thalli are typically desiccated, and incapable of active growth (Coxson and Coyle, 2003; Kershaw and Smith, 1978). In contrast, when thallus hydration status is not limiting (during precipitation events), conditions of temperature and light availability may instead be limiting (Campbell and Coxson, 2001).



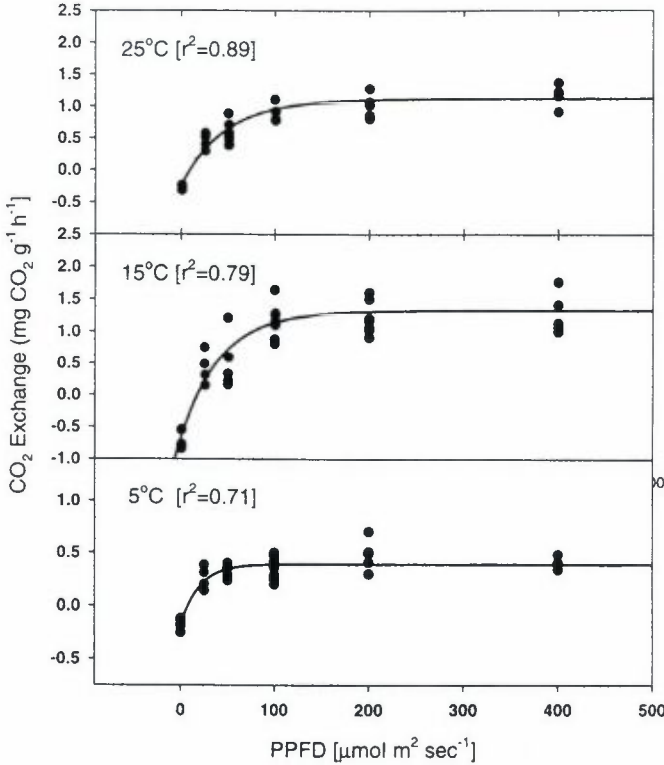


Figure 4. Scattergram of CO<sub>2</sub> exchange (mg CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>) in *C. mitis* at 5, 15 and 25°C and at Photosynthetic Photon Flux Densities (PPFD) of 0, 25, 50, 100, 200, and 400 μmol m<sup>-2</sup> s<sup>-1</sup>. Each point represents an individual replicate's response at optimal thallus water content. R<sup>2</sup> values are shown for regression lines obtained from exponential rise equations  $f=y_0+a*(1-\exp(-b*x))$ , n=5.

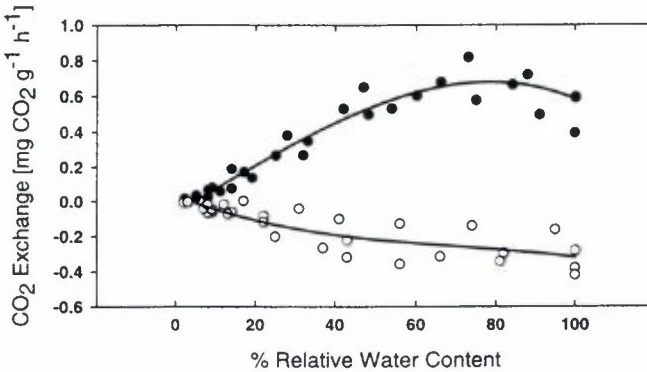


Figure 5. Representative scattergram of CO<sub>2</sub> exchange (mg CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>) during drying (from full saturation to desiccation) in *C. mitis* at 15°C, 0 (open circles) and 50 (closed circles) μmol m<sup>-2</sup> s<sup>-1</sup> PPFD. Plotted regression lines from 2nd order polynomial equations (R<sup>2</sup> values of 0.72 and 0.93, respectively under dark and light conditions).

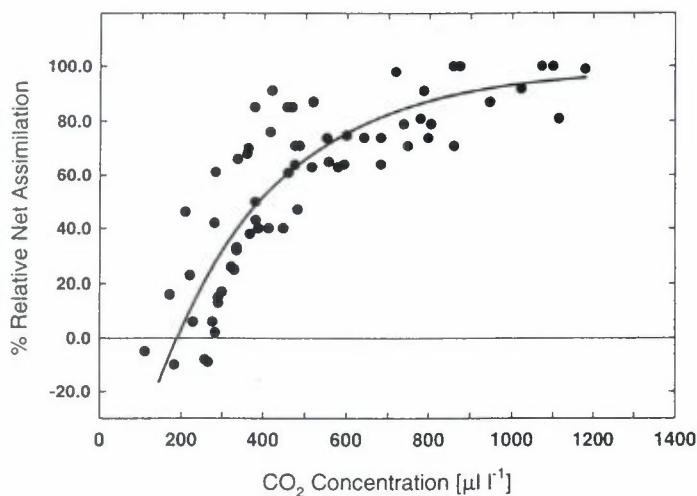


Figure 6. Scattergram of NP response (% relative net assimilation) to changes in CO<sub>2</sub> concentration in *C. mitis* at 15°C, 400 μmol m<sup>-2</sup> s<sup>-1</sup> PPFD, and optimal thallus WC. Plotted regression line from exponential rise equation  $f=y_0+a*(1-\exp(-b*x))$ ,  $R^2 = 0.69$ ,  $n=5$ .

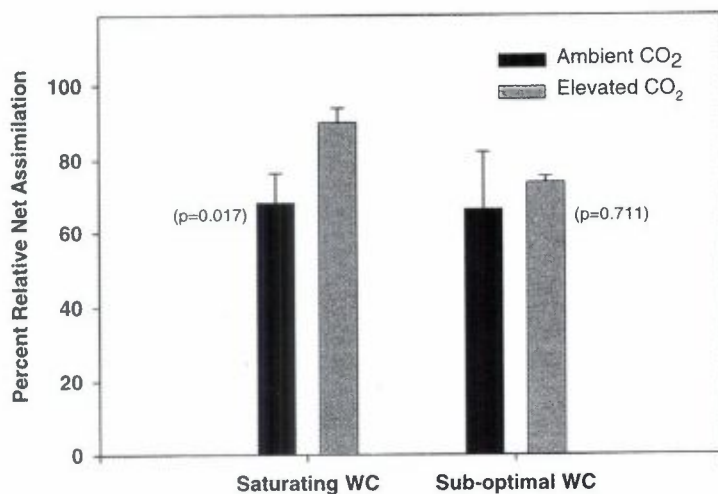


Figure 7. Comparative NP response (% relative net assimilation) in *C. mitis* to elevated and ambient CO<sub>2</sub> concentration at saturating and sub-optimal thallus WC levels. Measurements taken at 15°C and 400 μmol m<sup>-2</sup> s<sup>-1</sup> PPFD. Indicated probabilities are from Bonferonni t-tests between mean values.

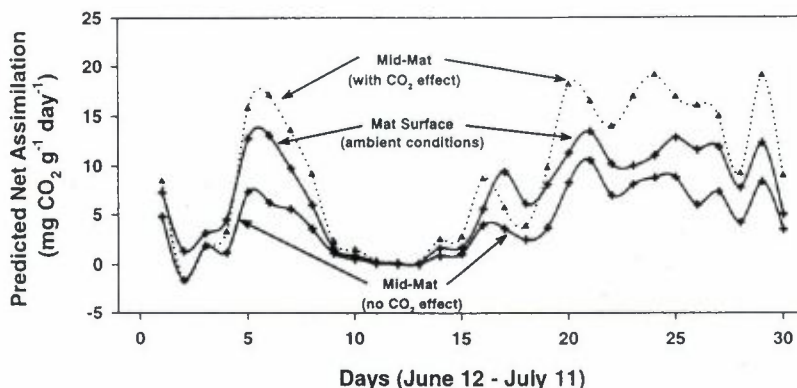


Figure 8. Predicted net assimilation ( $\text{mg CO}_2 \text{g}^{-1} \text{day}^{-1}$ ) in mat surface *C. mitis* thalli under profile conditions of temperature, moisture, light, and  $\text{CO}_2$  concentration (Mat Surface – Ambient Conditions); in mid-mat *C. mitis* thalli under profile conditions of temperature, moisture, and light, but using mat-surface  $\text{CO}_2$  concentrations in calculations (Mid-Mat, no  $\text{CO}_2$  effect); and in *C. mitis* thalli under profile conditions of temperature, moisture, light, and  $\text{CO}_2$  concentration (Mid-Mat, with  $\text{CO}_2$  effect).

Often, greatest lichen growth potential occurs during transitional periods, for instance, after precipitation events, when higher light intensities and warming of lichen thallus surfaces results in a burst of metabolic activity in the immediate period before thalli dry (Coxson, 1987), or during snowmelt events (Coxson and Coyle, 2003).

A similar pattern of contrasting resource gradients was observed in the operating environment of *C. mitis* within mixed feather moss mat communities. During major precipitation events light intensities were relatively low (under  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPF), with temperatures under  $10^\circ\text{C}$ . Predicted rates of net assimilation were highest as precipitation events waned, and lichen thalli were exposed to higher light intensities and warmer thallus temperatures. Slight increases in thallus WC that were observed during the early morning period (on otherwise dry days), were probably due to nocturnal cooling that brought thalli below dewpoint temperatures, similar to that observed by Carlton and Dunham (2003), however, the magnitude of these changes in thallus WC did not appear to be of sufficient magnitude to initiate NP responses.

Forest floor feather moss mat communities were comprised of a mosaic of lichen and moss species. However, growth form specific morphologies may have limited impact on the periodicity or duration of active response periods (i.e. duration of hydration). Not only do our own measurements of side-by-side response of intermingled moss fronds and lichen podetia (of *C. mitis*) show a

very similar duration of hydration intervals over wetting drying cycles (unpublished data), previous measurements of Hahn et al. (1993) found that physiological traits were far more important in differentiating between species specific responses than were growth-form specific morphologies in alpine tundra mats. Similarly Schroeter et al. (1999) found that physiological differentiation was more important than morphological growth form in mixed lichen and moss mat communities. The physiological response matrix of *C. mitis* in the current study was similar in pattern to those previously documented by Lechowicz and Adams (1973), and more recently by Reiter and Türk (2000), with NP temperature response optimal between 15 and 20°C, and light saturation of thalli occurring under 200  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD.

More significant was our observation that metabolically active thalli of *C. mitis* were consistently exposed to elevated  $\text{CO}_2$  concentrations (compared to atmospheric values, measured at 2 m height) at the forest floor surface, with mean  $\text{CO}_2$  concentrations at mid-mat height (over a 30 day period) of 670  $\mu\text{l l}^{-1}$   $\text{CO}_2$ . Given the steep response slope of *C. mitis* thalli to changes in ambient  $\text{CO}_2$  concentrations within the range of relevant values (from 320 up to 948  $\mu\text{l l}^{-1}$   $\text{CO}_2$ ), it was not surprising that inclusion of profile  $\text{CO}_2$  concentration in calculations of net assimilation response predicts elevated growth rates. The magnitude of this predicted increase in NA response at mid-mat profile depths was more than sufficient (over most of the modelling period) to compensate for PAR limitations.

One aspect of our results that was puzzling was the relatively high  $\text{CO}_2$  compensation point in *C. mitis* experimental material. Typically, lichen  $\text{CO}_2$  compensation points fall below 50  $\mu\text{l l}^{-1}$   $\text{CO}_2$  (Coxson et al., 1983). In contrast, the *C. mitis* material used in these experiments showed a  $\text{CO}_2$  compensation point near 200  $\mu\text{l l}^{-1}$ . One explanation may be higher rates of background (fungal) respiration in this collection, which would increase the apparent  $\text{CO}_2$  compensation point.

Other interactions that may be important in a high  $\text{CO}_2$  environment is the NP response of fully saturated lichen thalli. The depression of NP response at full thallus saturation in *C. mitis* was significantly reduced at elevated  $\text{CO}_2$  concentrations, consistent with previous observations that diffusive resistance to  $\text{CO}_2$  transport can be reduced under elevated  $\text{CO}_2$  concentrations (Lange et al., 1996). This provides a further positive feedback between NP uptake and soil  $\text{CO}_2$  pools within the moss mat boundary layer.

Although we are confident that the enhancement of  $\text{CO}_2$  concentrations within the feather moss mat boundary layer will have a major impact on NP uptake in *C. mitis*, our calculations of NA response must be regarded as preliminary in nature, as these results are based on work within one stand. However, it is clear from data of Swanson and Flanagan (2001) that soil respiratory  $\text{CO}_2$  release is a major factor in other coniferous forest ecosystems.

Swanson and Flanagan (2001) found that forest floor soils under feather moss mats released  $255 \text{ g C m}^{-2}$  during the summer period in black spruce forests of central Saskatchewan. Much of this carbon, once assimilated in mat communities, may ultimately be returned to soil pools, both through decomposition at the mat base, and from the release of carbon to throughflow solutions (Wilson and Coxson, 1999). Similarly, Sonesson et al. (1992) hypothesized that elevated within-mat  $\text{CO}_2$  concentrations (up to  $1,143 \mu\text{l l}^{-1}$ ) within *H. splendens* mats in Swedish Lapland may play a major role in "counteracting limitations in PAR supply" that would otherwise occur at the forest floor surface.

One question that remains unresolved in the present study is whether or not the observed elevation of NP response in *C. mitis* under elevated  $\text{CO}_2$  concentrations will persist after long-term exposure, recognizing that carbon availability is one of only several co-limiting variables on lichen growth rates (Palmqvist, 2000), e.g. nitrogen availability. However, studies that have examined  $\text{CO}_2$  compensation curves in lichens collected from sites with naturally (chronic) elevated ambient  $\text{CO}_2$  concentrations show that NP response curves can be stable, reflecting long-term adaptations to enhanced  $\text{CO}_2$  environments (Balaguer et al., 1999). We would anticipate that NP response to elevated  $\text{CO}_2$  concentrations might similarly be at equilibrium in *C. mitis*, given the *in-situ* nature of soil  $\text{CO}_2$  release and subsequent trapping within mat boundary layer environments.

This elevation of ambient  $\text{CO}_2$  concentrations within surface mat boundary layers may also be an important, though largely overlooked, stimulus to related physiological processes in lichens. Norby and Sigal (1989), for instance, propose that increases in atmospheric  $\text{CO}_2$  concentrations may stimulate nitrogenase activity in lichens with cyanobacterial bionts. Additionally, if lichens such as *C. mitis* respond to enhanced  $\text{CO}_2$  availability (under conditions of nitrogen limitation) by greater synthesis of phenolic compounds, the lichen communities may indeed represent an ecosystem carbon sink with relatively low turnover rates. Natural analogues to increasing atmospheric  $\text{CO}_2$  concentrations, as documented here for montane feather-moss mat communities, may therefore be important predictors of future lichen response to changes in atmospheric  $\text{CO}_2$  concentrations.

### Acknowledgements

We would like to thank J. Buchannin-Mappin (Kananaskis Field Station, University of Calgary) for assistance with climate monitoring, and Karen Stanko and Thomas Pypker (UNBC) for assistance with laboratory NP measurements. Funding support from the University of Northern BC is gratefully acknowledged.

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