Seasonal controls on net branch CO_2 assimilation in sub-Arctic Mountain Birch (*Betula pubescens* ssp. *czerepanovii* (Orlova) Hamet-Ahti).

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Highlights:

We measured growing season branch-level CO_2 fluxes in sub-Arctic Mountain Birch. Photosynthetic parameters dynamically acclimated to temperature within 5–7 days. Whole-branch respiration was higher during shoot growth and leaf expansion. Cumulative CO_2 fluxes averaged 640 g CO_2 m^{-2} across the two measured sites.

Abstract:

Forests at northern high latitudes are experiencing climate-induced changes in growth and productivity, but our knowledge on the underlying mechanisms driving seasonal CO_2 fluxes in northern boreal trees comes almost exclusively from ecosystem-level studies on evergreen conifers. In this study, we measured growing season whole-branch CO_2 exchange in a deciduous tree species of the tundra-taiga ecotone, Mountain Birch (*Betula pubescens* ssp. *czerepanovii* (Orlova) Hamet-Ahti), at two locations in northern Fennoscandia: Abisko (Sweden) and Kevo (Finland). We identified strong seasonal and environmental controls on both photosynthesis and respiration by analysing the parameters of light response curves. Branch-level photosynthetic parameters showed a delayed response to temperature, and, at Kevo, they were well described by sigmoid functions of the state of acclimation (*S*). Temperature acclimation was slower (time constant, τ = 7 days) for maximum photosynthesis (βbr) than for quantum efficiency (αbr) (τ = 5 days). High temperature-independent values of the respiration parameter (γbr) during leaf and shoot expansion were consistent with associated higher growth respiration rates. The ratio $\gamma br/\beta br$ was positively related to temperature, a result consistent with substrate-induced variations in leaf respiration rates at the branch level. Differences in stand structure and within-site variation in the active period of C uptake determined the spatiotemporal patterns in net assimilation amongst branches. Growing season CO_2 uptake of individual branches on a leaf area basis did not show a significant relationship with total incident photosynthetically active radiation, and did not differ across sites, averaging *ca.* 640 g CO_2 m^{-2}.

Introduction:

Growth and productivity of northern boreal trees are highly sensitive to climatic changes. Earth observation, atmospheric inversions and tree-ring studies have shown both positive (Juday et al., 2005 and Nemani et al., 2003) and negative (Angert et al., 2005 and Zhang et al., 2008) trends in growth and productivity of northern boreal forests associated with increased temperatures. This variety of responses is likely due to site-specific variables, such as species composition, tree density (Bunn and Goetz, 2006) or climate continentality (Beck et al., 2011). In order to understand the key mechanisms underlying these patterns and to be able to anticipate the effects on terrestrial carbon balance at high latitudes under a warmer climate (Christensen et al., 2007), we need a better knowledge of the seasonality in plant and environmental controls on plant CO_2 fluxes (McGuire et al., 2009).

Our understanding of the main mechanisms controlling seasonal forest-atmosphere CO_2 exchange at northern boreal latitudes is incomplete because it largely stems from ecosystem-level studies (i.e. based on fluxes estimated from eddy covariance data) on evergreen (e.g. Thum et al., 2008) and deciduous (e.g.Nakai et al., 2008) conifers. Deciduous broadleaved species of cold-limited environments may differ from conifers in their seasonal regulation of CO_2 fluxes, and may also respond differently to climatic changes (Welp et al., 2007). Moreover, the study of detailed plant controls on CO_2 fluxes from eddy covariance data might be hampered by the confounding signal of CO_2 exchange from other components of the ecosystem, the uncertainties in delimiting the flux footprint or the unreliability of night-time data. The only studies to date analysing seasonal and environmental drivers on CO_2 fluxes from branches or shoots have, to the best of our knowledge, been carried out on evergreen conifers (Kolari et al., 2007 and Rayment et al., 2002).

Light is the main meteorological driver of photosynthesis, and, at high latitudes, the marked variability in photoperiod leads to a high seasonal variation in the diurnal course of CO_2 uptake. In these cold-limited environments, temperature strongly influences the annual cycle of photosynthetic potential in evergreen conifers (Mäkelä et al., 2004) and growing season duration through the influence on bud-burst and leaf expansion in deciduous trees (Karlsson et al., 2003). Variation in leaf nitrogen content and drought (Wilson et al., 2000) have been identified as the main drivers of seasonal changes in photosynthetic parameters in deciduous trees but the role of temperature has been frequently overlooked. With regard to respiration, Arctic plants show a marked seasonal pattern, with maximum rates occurring at the beginning of the growing season, coinciding with leaf expansion and shoot extension (Semikhatova et al., 1996). This has also been observed for boreal evergreen conifers (Hollinger et al., 1999 and Rayment et al., 2002).

The taiga-tundra ecotone in north-western Eurasia is dominated by Mountain Birch woodland, occupying a total extent of 600,000 ha in northern Fennoscandia (Haapanala et al., 2009). Mountain Birch (*Betula pubescens* ssp. *czerepanovii* (Orlova) Hamet-Ahti) is currently expanding both elevationally and latitudinally into the tundra zone (Kullman and Öberg, 2009) and responding to recent warming by advancing bud burst (Karlsen et al., 2007), hence increasing the potential period for C uptake. Photosynthetic parameters of Mountain Birch derived from ecosystem-level studies display a marked seasonal variation (Aurela et al., 2001 and Lindroth et al., 2008), but, we are not aware of any study attempting to disentangle the effects of microclimate, leaf area and inherent photosynthetic and respiratory parameters.

In this study, we used an automated branch bag system (Dufrêne et al., 1993 and Rayment and Jarvis, 1999) to measure growing season branch-level CO_2 fluxes at two Mountain Birch forests, representing denser (Abisko, Sweden) and sparser (Kevo, Finland) canopy covers typical across northern Fennoscandia. Photosynthetic light response curves were fitted in order to obtain the

seasonal course of photosynthetic parameters and to obtain gap-filled CO_2 cumulative fluxes for the entire growing season. We hypothesised that the sparser canopy in Kevo would result in less within-site variability in photosynthetic parameters and growing season cumulative CO_2 fluxes. With regard to the drivers of seasonality in net CO_2 fluxes, we expected that endogenous controls on leaf phenology would determine the photosynthetic light response and branch-level leaf respiration rates in Mountain Birch branches just after leaf emergence and during senescence. Finally, we hypothesised that, over the central part of the growing season, temperature would directly control respiration rates whereas photosynthetic parameters would dynamically acclimate to temperature, following a state of acclimation response (Mäkelä et al., 2008), as it has previously been reported for boreal evergreen conifers.

Methods:

Study sites and Mountain Birch stands

Field measurements were undertaken at two Mountain Birch forest sites in northern Fennoscandia during two consecutive growing seasons. In 2007, measurements were performed *ca.* 5 km south-east of the Abisko Research Station (northern Sweden) whereas in 2008, the field site was located *ca.* 40 km south of the Kevo Subarctic Research Institute (northern Finland). Mean annual temperature in Abisko is −0.8 °C and annual precipitation is only 304 mm (both averaged over the period 1961–1990) (Johanson et al., 1995). Mean annual temperature is −2.0 °C in Kevo, with 395 mm of annual precipitation (1962–1990, Kevo Subarctic Research Institute). Abisko and Kevo are situated within the northern Fennoscandian sub-Arctic vegetation belt, in a landscape dominated by Mountain Birch woodland. Mountain Birch stands in the Abisko region are included in the oceanic-continental transition type, whereas those in the Kevo area are classified as slightly oceanic (Wielgolaski, 2001).

The study stand in Abisko (Abisko Birch, AB) was located near the tree line (68°19′29″N, 18°49′ 51″E, 564 m.a.s.l.), on a micro-podzol on coarse glacial till (Hartley et al., 2010). The understorey was largely composed by *Empetrum nigrum* ssp. *hermaphroditum* (Lange ex Hagerup) Böcher and various ericaceous dwarf shrubs. The Kevo stand (Kevo Birch, KB) was located near Petsikko (69°29′30.6″N, 27°13′52.45″E, 275 m.a.s.l.), also on a glacial till substrate. Understorey vegetation around the birch stems was dominated by *E. nigrum*, with lichens (*Cladonia* spp.) and dwarf birch (*Betula nana* L.) shrubs in more open areas.

Automated measurements of branch CO_2 fluxes using the branch bag technique

At both field sites, we measured hourly branch-level CO_2 fluxes of eight representative branches in low and mid-canopy conditions (cf. Appendix A), using a multiplexed branch bag device based on the closed system approach (Rayment and Jarvis, 1999 and Wingate et al., 2007). Details on the design and operation of the branch bags system can be found in Appendix A.

In Abisko, branches were enclosed in the bags with leaves already unfolded (bud burst was on DOY 141) and the system operated from DOY 153 (2nd of June) until DOY 241 (29th of August), when leaves began to senesce. In Kevo, branch bags were already deployed on DOY 152 (30th of May), well before bud-break (DOY 163) but the system was not fully operative until DOY 171 (19th of June), just when leaves were unfolding; flux measurements stopped on DOY 257 (13th of September) with most of the leaves on the sampled branches senescing.

We considered CO_2 uptake by vegetation as positive, and therefore calculated net branch CO_2 assimilation ($Abag,net$, µmol CO_2 s^{-1}) as:

equation(1)

$$A_{bag,net} = \frac{P_{bag}V_{bag}}{RT_{bag,0}} \frac{d}{dt}[CO_2]_{dry,bag}$$

where *Pbag* is air pressure, *Vbag* is bag volume, *R* is the ideal gas constant, *Tbag,0* is absolute temperature inside the bag and $d[CO_2]dry,bag/dt$ is the rate of change in CO_2 concentration during each observation, corrected for water vapour dilution. We preferably estimated $d[CO_2]dry,bag/dt$ from the first order term of a quadratic fit between CO_2 concentration and time since chamber closure, following the recommendations by Kutzbach et al. (2007) (cf. Appendix A).

Gaps in net assimilation data were due mainly to power failures or depletion of reference gas for the IRGA. At Abisko, the solenoid valve failed to operate correctly for most of the measurement period (until 17th August); as a result, reliable CO_2 flux data were available for the whole growing season from four of the eight original branch bags. Overall, hourly CO_2 fluxes were obtained for 55–69% and 48–63% (across-bags range) of hourly intervals at Abisko and Kevo, respectively.

Leaf area-based fluxes

The seasonal course of leaf area was monitored by counting of the number of leaves inside the bags, multiplied by an estimation of their average leaf area obtained from a sample of leaves ($N = 10$) close to the measured branch. After the end of the measurement period, we measured average leaf area inside and outside the bags to correct for the differences in size between leaves inside and outside the bags.

A combination of two sigmoid curves was used to describe leaf area as a function of day of year (Fisher et al., 2006), minimising root mean squared error (RMSE) using Microsoft Excel 2007 Solver. Leaf senescence inside each bag was assessed visually in Kevo, assigning a score from 1 (green leaves) to 8 (yellow leaves), and then expressed as a relative value from 0 (green) to 1 (yellow).

We used flux data measured during a period before bud-burst in Kevo to obtain linear relationships between woody tissue respiration (*Rw*) and temperature for six branches. These linear fits performed better than more commonly used exponential relationships, but still, the fits were poor (maximum $R^2 = 0.26$). To generalise these relationships to other branches, the intercept from these linear fits was predicted from branch woody biomass, based on the relatively good fit found between these two variables ($R^2 = 0.78$, $N = 6$, $p = 0.021$); the slope was considered equal to the average slope among the six branches. We subtracted the calculated *Rw* from *Abag,net*, and then standardised fluxes by leaf area inside the branch bags (*Abr,net*, µmol CO_2 m^{-2} s^{-1}).

Seasonal course of branch-level photosynthetic parameters

For each individual branch, we used flux and PAR data binned into 3-day classes to fit a phenomenological light response curve (Lindroth et al., 2008):

equation(2)

$$A_{br,net} = (A_{br,sat} + \gamma_{br})\left[1 - \exp\left(\frac{\alpha_{br}PAR}{\alpha_{br} + \gamma_{br}}\right)\right] - \gamma_{br}$$

where *αbr* is the initial slope of the light response curve (quantum efficiency, mol CO_2 mol PAR^{-1}), *Abr,sat* is maximum net photosynthesis, *γbr* is the respiration parameter, and *βbr* is the light-saturated gross assimilation (µmol CO_2 m^{-2} s^{-1}), calculated

as *Abr,sat* + *γbr* (Lindroth et al., 2008). The model was fitted using the Gauss–Newton algorithm in R, version 2.9.2 (R Development Core Team, 2009). Other possible formulations were discarded because they either overestimated parameter values (rectangular hyperbola) or had an extra parameter to fit (non-rectangular hyperbola) (cf. Appendix A).

2.5. Temperature controls on photosynthetic and respiratory parameters

The state of acclimation concept (Mäkelä et al., 2004) was used to investigate the relationships between the photosynthetic parameters and the seasonal course of air temperature. Based on mean daily air temperature (*Tk*, °C), the state of acclimation was calculated as a function of *Xk* (Mäkelä et al., 2008), where:

equation(3)

$$X_k = X_{k-1} + \frac{1}{\tau}(T_k - X_{k-1})$$

$$S_k = \max\{X_k - X_0, 0\}$$

where *τ* (days) is the time constant and X_0 a threshold value of the delayed temperature; we set X_0 = 0 °C and $X_1 = T_1$. In this study, we calculated different values of *S* using time constants of *τ* = 3, 5, 7 and 10 days, based on previously reported ranges (Mäkelä et al., 2004). Then, maximum photosynthesis and quantum efficiency parameters were fitted (minimising RMSE, Microsoft Excel 2007 Solver) to sigmoid functions, in which *S*, calculated using the different time constants stated above, was the explanatory variable (Kolari et al., 2007).

The temperature response of respiration fluxes was assessed in three different ways: (1) relating the value of the respiration parameter *γbr* to temperature, (2) examining the temperature responses of night-time fluxes and (3) analysing the temperature responses obtained in a shading experiment. At Abisko, each branch bag was shaded completely during a measurement cycle and hourly respiration rates were recorded on two days (DOY 161, 10th June and DOY 204, 23rd July) of the 2007 growing season. Temperature responses were assessed using exponential fits, yielding respiration at a reference temperature of 0 °C (R_0) and temperature sensitivity (Q_{10}) (Atkin et al., 2005).

2.6. Growing season CO_2 balance at the branch level

We interpolated linearly the seasonal course of light response parameters when these were missing, obtaining a light response curve for each individual day that was used to gap-fill the daytime CO_2 fluxes. At Abisko, we assumed the late-season decline in photosynthetic parameters was similar to that observed in Kevo, since senescence dates for Mountain Birch do not show much climate-induced variability (Heino, 1995). Night-time fluxes at both sites were gap-filled using the site- and branch-specific temperature responses described in the previous section.

A previous study using the branch bag system in a boreal forest reported small temperature increases inside the cuvettes due to radiative warming, although with negligible effects on seasonal C uptake (Rayment and Jarvis, 1999). Radiative warming may, however, be greater in Mountain Birch stands due to their relatively sparse canopy. To quantify any effect of this, we used branch-specific temperature responses of net assimilation measured at Kevo to correct net CO_2 fluxes at that site (cf. Appendix A).

Results

Site meteorology and within-bag temperature conditions

During the measurement period, air temperatures at Abisko were only slightly higher than at Kevo; comparing a common period (DOY 180–240), mean minimum daily temperatures were 7.6 °C and 6.6 °C and mean maximum daily temperatures 13.9 °C and 13.4 °C for Abisko and Kevo, respectively. Over the same common period, above-canopy cumulative PAR flux was higher at Abisko (1908 mol m^{-2}) than at Kevo (1460 mol m^{-2}).

Daytime air temperatures inside the branch bags were generally higher than those measured at the site, the difference being significantly positively correlated with PAR flux (Abisko, $R^2 = 0.55$; Kevo $R^2 = 0.59$). However, warming was less at Abisko (median difference between air temperature inside the bag and ambient air was 0.47 °C), than at Kevo (median difference of 1.98 °C), as the denser forest structure (Table 1) led to reduced radiation transmission through the canopy. During the peak growing season, the fraction of above-canopy PAR measured in the bags was much lower in Abisko (32%) than in Kevo (51%). Air temperature inside the bags was 8.47 °C (Abisko) and 11.43 °C (Kevo) above ambient temperature for 5% of daytime intervals. In contrast, the denser stand at Abisko resulted in branch bags there cooling down less at night (median bag to ambient temperature *difference ca.* −0.4 °C) than did those at Kevo (*ca.*−0.6 °C).

Seasonal dynamics of leaf area and net branch assimilation

Leaf expansion started earlier at Abisko than at Kevo, although 90% of maximum leaf area had been achieved by DOY 190 at both sites. Our visual estimates of senescence showed that leaves in Kevo kept, on average, only 20% of their greenness by the end of the study period. Leaf abscission was not generally observed, except for branch KB1 (Fig. 1a and b). At Kevo, leaves inside the branch bags grew larger (60% greater mean leaf area) than those outside the bags because bags were installed for some time before leaf unfolding, raising the temperature during the period of leaf expansion. This did not happen in Abisko, as branch bags were installed just after bud-burst (cf. Section 2).

Wood respiration, as measured prior to leaf emergence in Kevo, showed maximum rates of 0.25 ± 0.07 µmol CO_2 (expressed per branch surface area), equivalent to dry mass-based rates of 0.20 ± 0.03 mg CO_2 g^{-1} h^{-1} (across-bags mean $\pm$ SE). The complete seasonal dynamics of leaf area-based fluxes was better captured at Kevo (Fig. 1f and h) than at Abisko (Fig. 1e and g). Typical maximum net assimilation rates, expressed as the 95th percentile of the hourly CO_2 uptake rates, were 6.7 ± 1.03 µmol CO_2 m^{-2} s^{-1} at Abisko and 6.6 ± 0.18 µmol CO_2 m^{-2} s^{-1} at Kevo (across-bags mean $\pm$ SE) (Fig. 1e and f). Maximum night-time fluxes (95th percentiles) were more than four times higher at Abisko (1.43 ± 0.07 µmol CO_2 m^{-2} s^{-1}) than at Kevo (0.29 ± 0.03 µmol CO_2 m^{-2} s^{-1}).

Diurnal patterns of CO_2 assimilation varied seasonally in response to photoperiod (Fig. 2). At the peak of the growing season, the coefficient of variation of maximum CO_2 uptake rates amongst branches was *ca.*25% in Abisko and only *ca.* 10% in Kevo. Although no significant decline in CO_2 uptake rates was observed at the end of August at Abisko (Fig. 2), by mid-September all branches at Kevo except KB6 showed near-zero fluxes (Fig. 2). Leaves on KB6 showed a 50% level of senescence, whereas leaves on the other branches were already 75–100% yellow.

Seasonal course of photosynthetic parameters

The simple light response model provided satisfactory descriptions of net branch assimilation, as shown by model performance results (cf. Appendices B and C) and the lack of consistent patterns between model residuals and other variables (air temperature, vapour pressure deficit and time of day) (cf. Appendix A).

Maximum values of individual branch light-saturated gross photosynthesis (βbr) reached about 11 μmol CO_2 m^{-2} s^{-1} at both sites; mean values across branches had maxima of 7.3 and 8.5 μmol CO_2 m^{-2} s^{-1} at Abisko and Kevo, respectively (Fig. 3). Quantum efficiency (αbr) peaked at 0.12 mol CO_2 mol PAR^{-1} at Abisko and 0.07 mol CO_2 mol PAR^{-1} at Kevo. Both parameters showed a clear seasonal pattern of increase, plateau and decrease at Kevo, but not at Abisko (Fig. 3). At Kevo, the respiration parameter (γbr) peaked at a mean value of *ca.* 1.5 μmol CO_2 m^{-2} s^{-1} during the period of leaf expansion, declining rapidly thereafter to <0.5 μmol CO_2 m^{-2} s^{-1}. At Abisko, values of $\gamma br > 0.5$ μmol CO_2 m^{-2} s^{-1} were observed frequently throughout the season, no seasonal trend being detected (Fig. 3).

Temperature controls on photosynthetic parameters

For both sites, the state of acclimation, S, better described the seasonal dynamics of βbr than of αbr (Fig. 4). However, discrepancies were evident between S and the photosynthetic parameters during the senescence process; at Kevo, S increased whereas βbr continued declining after the 80th day since bud-burst (Fig. 4). At Kevo, sigmoid curves relating S calculated with time constants of $\tau = 7$ days and $\tau = 5$ days adequately described the seasonal variation of αbr and βbr, respectively. (Table 2, Fig. 5); model performance at Abisko was comparatively worse (Table 2, Fig. 5).

Respiration responses to temperature

Considering only values after leaf expansion was complete (DOY 190) to avoid phenological effects, at Kevo, the respiration parameter was related to air temperature, following an exponential response ($R_0 = 0.08$, $p = 0.036$; $Q_{10} = 2.26$, $p = 0.014$); at Abisko, the same model gave non-significant results ($R_0 = 0.18$, $p = 0.398$; $Q_{10} = 1.89$, $p = 0.470$). The ratio between the respiration parameter and gross photosynthesis ($\gamma br / \beta br$) was also positively and significantly related to air temperature inside the bag across all branches at Kevo (linear function, $R^2 = 0.13$, $N = 60$, $p = 0.006$) but was only marginally related at Abisko (power function, $R^2 = 0.14$, $N = 20$, $p = 0.082$).

Whereas early season data recording the instantaneous response of branch respiration to temperature, measured in the Abisko shading experiment, was described adequately by an exponential model (DOY 161; $R_0 = 0.16$, $p = 0.009$; $Q_{10} = 3.67$, $p < 0.001$), the fit was only marginally significant for peak season data (DOY 204; $R_0 = 0.26$, $p = 0.083$; $Q_{10} = 1.62$, $p = 0.086$) (Fig. 6a).

As a result of their high latitudes, dark night conditions only occurred at the sites after the end of July; night-time fluxes plotted in Fig. 6b and c thus are representative of mid- to late-season. Whereas physically reasonable values of R_0 and Q_{10} were obtained for all eight branches at Kevo, only four branches from Abisko yielded realistic fits (cf. Appendix D). In summary, mean values (±SE) of R_0 and Q_{10} across branches were $R_0 = 0.21 \pm 0.03$ and $Q_{10} = 3.11 \pm 0.49$ for Abisko and $R_0 = 0.09 \pm 0.01$ and $Q_{10} = 2.91 \pm 0.28$ for Kevo. The temperature responses of night-time fluxes

did not depart significantly from the shading experiment data obtained in Abisko at peak season (Fig. 6b and c).

Growing season CO_2 balance at the branch level

Growing season, gap-filled, CO_2 net assimilation per unit leaf area of individual branches ranged between 492 and 884 g CO_2 m^{-2} at Abisko (mean ± SE: 685 ± 85 g CO_2 m^{-2}) and between 559 and 665 g CO_2 m^{-2} (mean ± SE: 618 ± 12 g CO_2 m^{-2}) at Kevo (Fig. 7a). Cumulative CO_2 net assimilation did not differ across sites (two-tailed t-test, $p = 0.49$), and showed no relationship to total incident PAR (Fig. 7b) when all branches from Abisko and Kevo were considered ($R = 0.02$, $p = 0.67$). The estimated cumulative wood respiration in Abisko was only 0.12 ± 0.03 g CO_2 g^{-1} of dry wood and 0.096 ± 0.01 g CO_2 g^{-1} in Kevo; depending on the branch, these values represented 1.4–5.2% of the total leaf net assimilation at the branch level.

If the sigmoid responses based on the state of acclimation, rather than linear interpolation, were used to estimate the seasonal course of photosynthetic parameters, growing season CO_2 uptake at Kevo yielded slightly higher values (mean ± SE: 667 ± 13 g CO_2 m^{-2}). Finally, correcting our estimates of seasonal CO_2 fluxes at Kevo for the differences between inside-bag and ambient air temperature (cf. Appendix A) yielded cumulative fluxes that were, on average, 8% higher than those computed from the uncorrected fluxes (across-branches range 1.5–13%). This overestimation would be less at Abisko where cuvette warming was less important.

Discussion

Performance of the branch bag technique to measure CO_2 canopy fluxes in sub-Arctic Mountain Birch

To our knowledge, the present study is the first to describe and analyse the seasonal course of branch-level net CO_2 uptake of a deciduous broadleaf species. The automated branch bag system enabled us to obtain hourly CO_2 exchange rates covering 50–70% of the entire measurement period (depending on the branch), a temporal coverage comparable to that obtained with eddy covariance techniques (Moffat et al., 2007). However, we could not avoid the radiative warming of the branch bags as also occurred in previous studies using the same system (e.g. Rayment and Jarvis, 1999). Warmer conditions inside the bags led to overestimation of growing season CO_2 uptake by <10% for the worst case scenario at Kevo, where radiation-induced bag warming was greater due to the sparse canopy. We also observed increased individual leaf areas inside the branch bags due to this warming effect during early phases of leaf expansion, as reported for related *Betula* species (Mäenpää et al., 2011 and Xu et al., in press). Bag warming, however, is inevitable in closed systems unless more efficient, but also more power-demanding, temperature-regulation mechanisms are employed (Hunt, 2003). Currently, this is not practicable in the remote sites where data needs to be collected. Nevertheless, the potential of the branch bag technique to measure exclusively plant CO_2 exchange and to identify its controlling processes in remote high-latitude environments considerably outweighs these quantifiable and attributable measurement artefacts.

Maximum instantaneous rates of net CO_2 uptake measured in the branch bags were lower than those of about 15–17 µmol CO_2 m^{-2} s^{-1} reported on the basis of leaf-level measurements (Karlsson, 1991, Karlsson and Nordell, 1988 and Sveinbjörnsson, 2001). These results agree with the reported decrease in photosynthetic capacity with increasing organisational scale (i.e. from leaf to branch) due to mutual shading (Rayment et al., 2002).

With regard to respiration, only stem respiration has been measured previously in Mountain Birch, showing a typical maximum value of *ca.* 1.0 mg CO_2 g^{-1} h^{-1} (Sveinbjörnsson et al., 1996). We found maximum values of mass-based wood respiration in branches which were five times lower than these reported measurements taken on the main stem, but comparable to branch respiration rates measured in a related*Betula* species (Künstle and Mitscherlich, 1976, as cited in Gansert et al., 2002). When comparing night-time data, foliage respiration rates were, on average, five times higher than wood respiration as found elsewhere (e.g. Ryan et al., 1994).

Within- and across-site variability in instantaneous CO_2 fluxes

Mountain Birch bud-burst is highly sensitive to late-spring temperatures (Karlsson et al., 2003); accordingly, bud-burst dates differed by *ca*. 20 days between Abisko (April–May 2007 mean temperature at Abisko Research Station: 1.55 °C) and Kevo (April–May 2008 mean temperature at Kevo Subarctic Research Institute: −0.55 °C). The active CO_2 uptake period lasted 85–90 days at Kevo, consistent with similar values to those reported in eddy flux (Aurela et al., 2001) and remote sensing (Shutova et al., 2006) studies. Some branches continued assimilating CO_2 for longer than others, related to differential senescence across branches and consistent with substantial variability in leaf traits reported for Mountain Birch individuals (Karlsson and Nordell, 1988 and Senn et al., 1992). The denser canopy structure at Abisko led to greater variability in instantaneous PAR fluxes and, therefore, to higher between-branch variability in instantaneous CO_2 exchange compared to Kevo, as we hypothesised. The across-branch coefficient of variation of maximum CO_2 uptake rates at Abisko was more comparable to the value of 18% reported for a closed Black Spruce (*Picea mariana* (Miller) Britton, E.E. Sterns & Poggenb.) stand (Rayment and Jarvis, 1999) than to the one observed in Kevo.

Light response curves: model performance and parameter seasonality

Marked seasonal patterns in photosynthetic parameters, regardless of the model employed, have been reported for northern boreal conifers at the shoot (Kolari et al., 2007 and Rayment et al., 2002) and ecosystem (Lindroth et al., 2008 and Thum et al., 2008) scales, and also for Mountain Birch at the ecosystem scale (Aurela et al., 2001 and Lindroth et al., 2008). However, these latter studies analysed ground-based parameters that did not enable the separate contributions of the intrinsic parameter values and of leaf area dynamics to be elucidated. Here, we have shown that leaf area-based parameters of photosynthetic light response curves followed a clear seasonal pattern in Kevo, where data spanned the entire growing season from bud-burst to senescence. Early and late season dynamics of light response parameters at Abisko were not well described, though, because of lack of data during these periods. In Kevo, light-saturating photosynthesis and quantum efficiency increased, stabilised and then decreased as the season progressed, although both began declining before signs of senescence were observed. These findings could explain previous ecosystem-level observations at the same site (Aurela et al., 2001). Whereas Aurela et al. (2001) attributed the decrease in photosynthetic capacity of Mountain Birch at the beginning of August to reduced water availability, we have shown a decline in intrinsic photosynthetic potential in August taking place without the occurrence of any drought period.

Temperature modulates photosynthetic light response

Several studies have shown that the state of acclimation approach presents a useful framework to describe photosynthetic dynamic acclimation to temperature in boreal vegetation at the shoot

(Kolari et al., 2007 and Mäkelä et al., 2004), patch (Kulmala et al., 2009) and canopy (Gea-Izquierdo et al., 2010) scales. A delayed effect of temperature on photosynthetic light response parameters could also be inferred in some ecosystem level studies (e.g. Hollinger et al., 1999). However, all these studies were mainly focused on evergreen species.

Here, we have shown that, in its first application on a deciduous broadleaf tree, the state of acclimation approach has performed satisfactorily when parameterised with data spanning the entire growing season (i.e. in Kevo). The time constant that optimally described the dynamics of maximum gross photosynthesis of Mountain Birch ($\tau = 7$ days) fell within the inter-annual range (4.2–11.4 days) observed for northern boreal Scots Pine (*Pinus sylvestris* L.) at the shoot scale (Kolari et al., 2007). Our results are also consistent with those of controlled-environment studies, which show that photosynthesis acclimates to prevailing temperature conditions within 2–6 days (Gunderson et al., 2010). Further studies should investigate the mechanisms behind these responses. A possible explanation is that higher prevailing temperatures may lead to a faster respiratory-driven depletion of leaf carbohydrates, which, in turn, enhance photosynthetic capacity (Turnbull et al., 2002).

Seasonality and temperature controls on respiration

Our results show a strong seasonality in branch-level respiration and its temperature response, which was related to leaf phenological stage. At Kevo, we observed disproportionately high values of the respiration parameter in light response curves for Mountain Birch during the early growing season, consistent with the observed seasonality of foliar respiration in other deciduous trees (Collier and Thibodeau, 1995, Ow et al., 2009 and Xu and Baldocchi, 2003). The temperature response of whole-branch respiration measured at Abisko also varied seasonally, indicating higher temperature sensitivity during the early season. Assuming that growth respiration would dominate over maintenance respiration during the early growing season, as a result of leaf and shoot expansion, these results appear to contradict observations showing that growth respiration is relatively insensitive to temperature (Penning De Vries et al., 1974). However, factors other than temperature may be influencing diel courses of respiration (Bruhn et al., 2008), for example, the availability of photosynthetic substrate (Whitehead et al., 2004). Indeed, respiration as a fraction of maximum gross photosynthesis, as indicated by the ratio $\gamma br/\beta br$, increased with temperature; this is consistent with substrate-mediated short-term responses to temperature of the respiration/photosynthesis ratio (Dewar et al., 1999).

Growing season CO_2 fluxes

There were no site-specific differences in the cumulative CO_2 fluxes, although, as hypothesised, the denser stand structure at Abisko may have induced more between-branch variability, as compared to the sparser stand at Kevo. Interestingly, the branch with a higher net C uptake in Kevo (KB6), was the one which showed the longest active period (Fig. 3), suggesting that leaf traits varying at the branch scale can determine growing season length and branch-level net assimilation in Mountain Birch.

There are very few published studies reporting growing season CO_2 fluxes at the branch or shoot levels, and most of them have been carried out on evergreen conifers. For example, growing season net CO_2 uptake values of about 600–800 g CO_2 m^{-2} have been reported for Scots pine in Finland (Sevanto et al., 2003). In a study using a similar branch-bags system in a boreal Black Spruce forest, total annual CO_2 uptake of four branches ranged between 498 and 937 g CO_2 m^{-2}, giving a mean (±SE)

of 657 ± 96 g CO_2 m^{-2} (Rayment and Jarvis, 1999). For both studies, the reported values are remarkably similar to those we observed in Mountain Birch. For the Black Spruce study, the annual net CO_2 uptake was unrelated to total incident PAR, as we have also found for Mountain Birch over the growing season. This is probably a result of the saturating relationship of net photosynthesis with incident PAR and the relatively open canopy of Mountain Birch woodland.

Concluding remarks

Branch-level measurements of gas exchange are unique in the sense that they provide valuable information about plant controls on net CO_2 fluxes in forests. Indeed, we have found evidence consistent with leaf phenology and temperature history controlling the seasonal variation of photosynthetic parameters in Mountain Birch. Warmer springs in sub-Arctic Fennoscandia (Callaghan et al., 2010 and Virtanen et al., 2010) might thus enhance C uptake due to both longer growing seasons and increased photosynthetic potential. Photosynthetic parameters derived from models using the state of acclimation approach agree well with remotely sensed NDVI (Gea-Izquierdo et al., 2010), meaning that seasonal estimates of productivity could be obtained at both landscape and regional scales. The similarity in growing season CO_2 balance per unit leaf area between Abisko and Kevo, gives us further confidence that models based on light and temperature only could well describe Mountain Birch net CO_2 uptake across more extensive areas. Furthermore, the relatively oceanic climate of northern Fennoscandia, and the projected increase in precipitation (Christensen et al., 2007) likely mean that sub-Arctic Mountain Birch forests are less prone to suffer the drought-induced declines in productivity observed in other northern boreal forests (Angert et al., 2005). Indeed, remotely sensed productivity of deciduous broadleaved forests above 50°N showed moderate increases between 1982 and 2003 (Bunn and Goetz, 2006). Finally, the strong phenological influences on respiration rates and the likely feedbacks between photosynthesis and respiration require further investigation using a combination of observational and experimental studies with mechanistic models.

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Figure legends:

Figure 1. Seasonal course of relative leaf area (a, b), above-canopy daily-integrated PAR (c, d) and net branch CO_2 assimilation per unit leaf area measured at Abisko (e, g) and Kevo (f, h), respectively. Mid panels (e, f) show the across-branches mean of the hourly values, whereas lower panels (g, h) display daily box and whisker plots (minimum, maximum, median and quartiles), of hourly net assimilation rates, illustrating the seasonal course in net assimilation due to changes in photoperiod and the variability amongst branches. In lower panels (g, h), only data for even days are shown, for better clarity. Leaf area relative to seasonal maximum is only shown for two branches with distinct seasonal patterns. For Kevo (b), the average relative senescence is also shown (cf. Section 2.3).

Figure 2. Seasonal variation in the diurnal patterns of net branch assimilation at Abisko (AB, top row) and Kevo (KB, bottom row). The panels show three sunny days selected from early, peak and late seasons. The selected days were DOY 158 (a), 198 (b), and 240 (c) for Abisko (2007), and DOY 172 (d), 190 (e), and 255 (f) for Kevo (2008). Note that for Abisko, panel (c) shows all eight branch bags, after the solenoid valve in the measuring system returned to proper operation. Photoperiod is shown by the shaded area above the x-axis.

Figure 3. Box plots showing the seasonal course of the parameters obtained from exponential-based light response curves, fitted every three-day interval at Abisko (left) and Kevo (right). The parameters are shown in different panels: (a, b) maximum net photosynthesis, *Abr,sat*; (c, d) quantum efficiency, *αbr*; (e, f) maximum gross photosynthesis, *βbr*; and (g, h) dark respiration parameter, *γbr*. Lines represent median values, boxes define the inter-quartile range and outliers are represented by individual points. Mean air temperature inside the bags is also shown (i, j).

Figure 4. Seasonal course (described by the number of days since bud-burst) of the state of acclimation (*S*) (open symbols), and across-branches mean values of *βbr* (maximum net photosynthesis; a, b), and *αbr* (quantum efficiency; c, d) (closed symbols) obtained from exponential-based light response curves at Abisko (a, c) and Kevo (b, d).

Figure 5. Relationships between the state of acclimation (*S*) and the across-branches mean of the parameters *βbr,EXP* (light-saturated photosynthesis; a, b) and *αbr,EXP* (quantum efficiency; c, d) obtained from exponential-based light response curves at Abisko (a, c) and Kevo (b, d). Sigmoid curves of parameter values as a function of *S* (Table 2) are also shown.

Figure 6. Branch respiration responses to temperature during two shading experiments carried out at Abisko, early (DOY 161; 10th June) (diamonds) and later (DOY 204; 23rd July) (inverted triangles) in the 2007 growing season. Lower panels depict hourly night-time fluxes (dots) measured in all branch bags at Abisko (b) and Kevo (c) plotted against air temperature, together with data from the experimental respiration response to temperature measured at mid-season in Abisko (inverted triangles). The exponential functions in both lower panels were fitted pooling data from all branch bags (night-time and shading experiment fluxes).

Figure 7. Cumulative CO_2 fluxes (a, b) and PAR (c, d) for the branch bags with data available for the entire measurement period at Abisko (left panels) and all eight branches at Kevo (right panels).

Tables:

Table 1. Stand characteristics from tree inventories at the Abisko and Kevo field sites. Data show mean ± SE for 30 m × 30 m plots measured in 2007 (Abisko) and 2008 (Kevo). Data from the closest plot (within plot mean ± SE) to the actual site where the branch bags system was installed are also shown. Mountain Birch trees in the studied sites are typically polycormic; therefore, apart from tree density, the number of stems per tree was also measured. Leaf area index was calculated using stand inventory data (A. Prieto-Blanco, unpublished data) and site-specific allometric equations for Abisko (Dahlberg et al., 2004) and Kevo (R. Poyatos, unpublished data).

Site	Tree density (trees ha^{-1})	Stems per tree	DBH (mm)	Height (m)	LAI (m^2 m^{-2})
Abisko					
Mean (*N* = 5)	1300 ± 155	4.6 ± 0.5	38.3 ± 1.7	4.0 ± 0.20	1.05 ± 0.15
Closest plot	2222	2.4 ± 0.2	38.1 ± 0.9	4.1 ± 0.10	2.28
Kevo					
Mean (*N* = 8)	876 ± 85	3.3 ± 0.2	37. 2 ± 2.0	3.76 ± 0.01	0.61 ± 0.06
Closest plot	833	3.8 ± 0.3	30.6 ± 7.2	3.78 ± 0.30	0.53

Table 2.Parameter values and fit statistics for the sigmoid curves describing the relationship between parameters of the photosynthetic light response curves *(Abr,sat,max, αbr, ƃbr,EXP)* and state of acclimation *(S)* calculated for different time constants (τ = 3,5,7 and 10 days). Sigmoid curves (Kolari et al., 2007) followed the same formulation for all parameters, for example, $\beta = \beta_{max}/(1 + e^{b(S - T_{s,\beta})})$. The model for *Abr,sat,max* at Abisko could not be fitted.

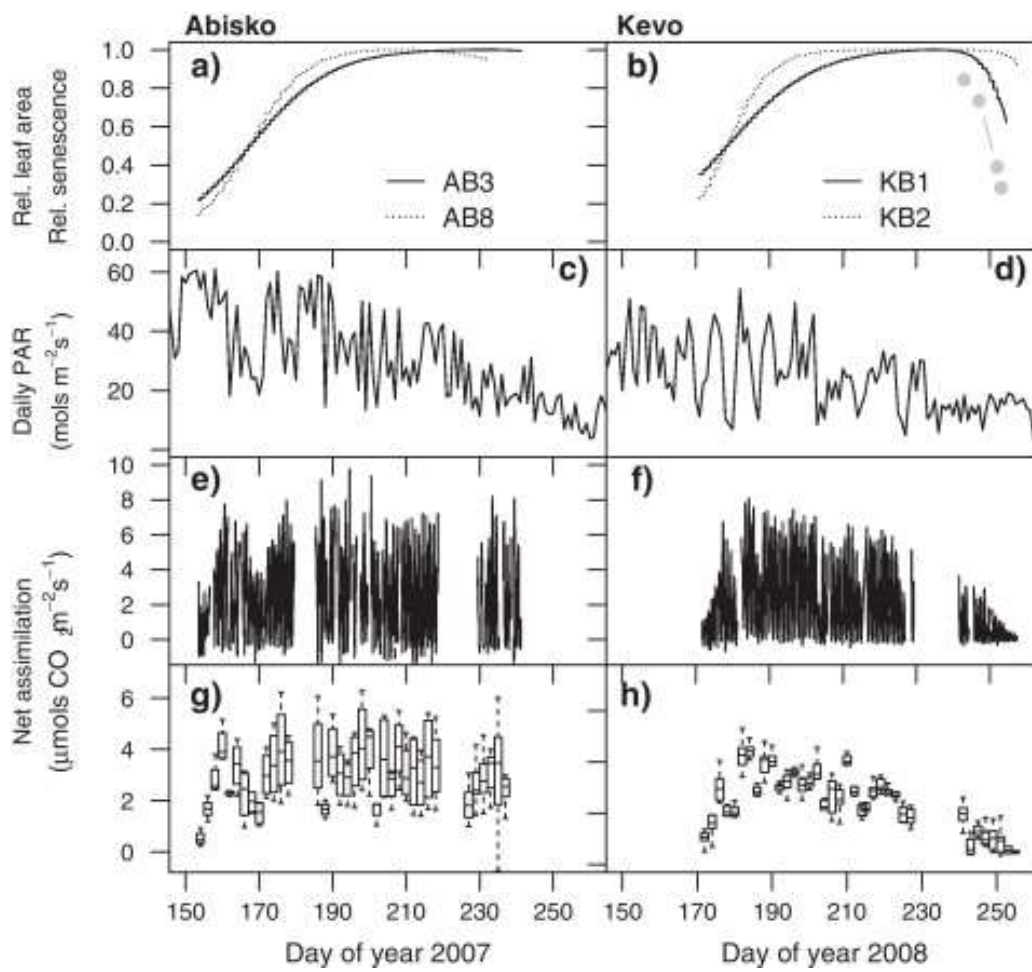|	Abisko				Kevo			
	$\tau = 3$	$\tau = 5$	$\tau = 7$	$\tau = 10$	$\tau = 3$	$\tau = 5$	$\tau = 7$	$\tau = 10$
Abr,sat,max				7.74	8.21	7.17	7.21	**7.24**
b				−0.127	−0.289	−0.710	−0.904	**−1.032**
Ts,A				9.5	9.1	9.1	9.4	**9.5**
RMSE				2.24	1.84	1.49	1.20	**1.17**
R^2				0.34	0.60	0.76	0.85	**0.86**
αbr,max	**0.065**	0.068	0.073	0.360	0.045	**0.042**	0.040	0.041
b	**−0.18**	−0.17	−0.14	−0.06	−0.38	**−0.78**	−0.91	−0.62
Ts,β	**2.11**	2.96	4.04	40.83	8.05	**8.49**	8.34	7.94
RMSE	**0.0071**	0.0074	0.0076	0.0077	0.0088	**0.0077**	0.0078	0.0093
R^2	**0.60**	0.56	0.53	0.51	0.66	**0.75**	0.74	0.60
ƃbr,max	**9.7**	8.9	8.5	8.2	8.1	7.4	**7.5**	7.6
b	**−0.068**	−0.097	−0.114	−0.127	−0.350	−0.766	**−0.890**	−0.928
Ts,β	**9.1**	9.1	9.4	9.5	8.8	9.1	**9.3**	9.4
RMSE	**1.87**	2.14	2.34	2.48	1.79	1.43	**1.20**	1.29
R^2	**0.33**	0.36	0.34	0.32	0.64	0.79	**0.86**	0.83

Parameters for the models with lowest RMSE values are shown in bold.
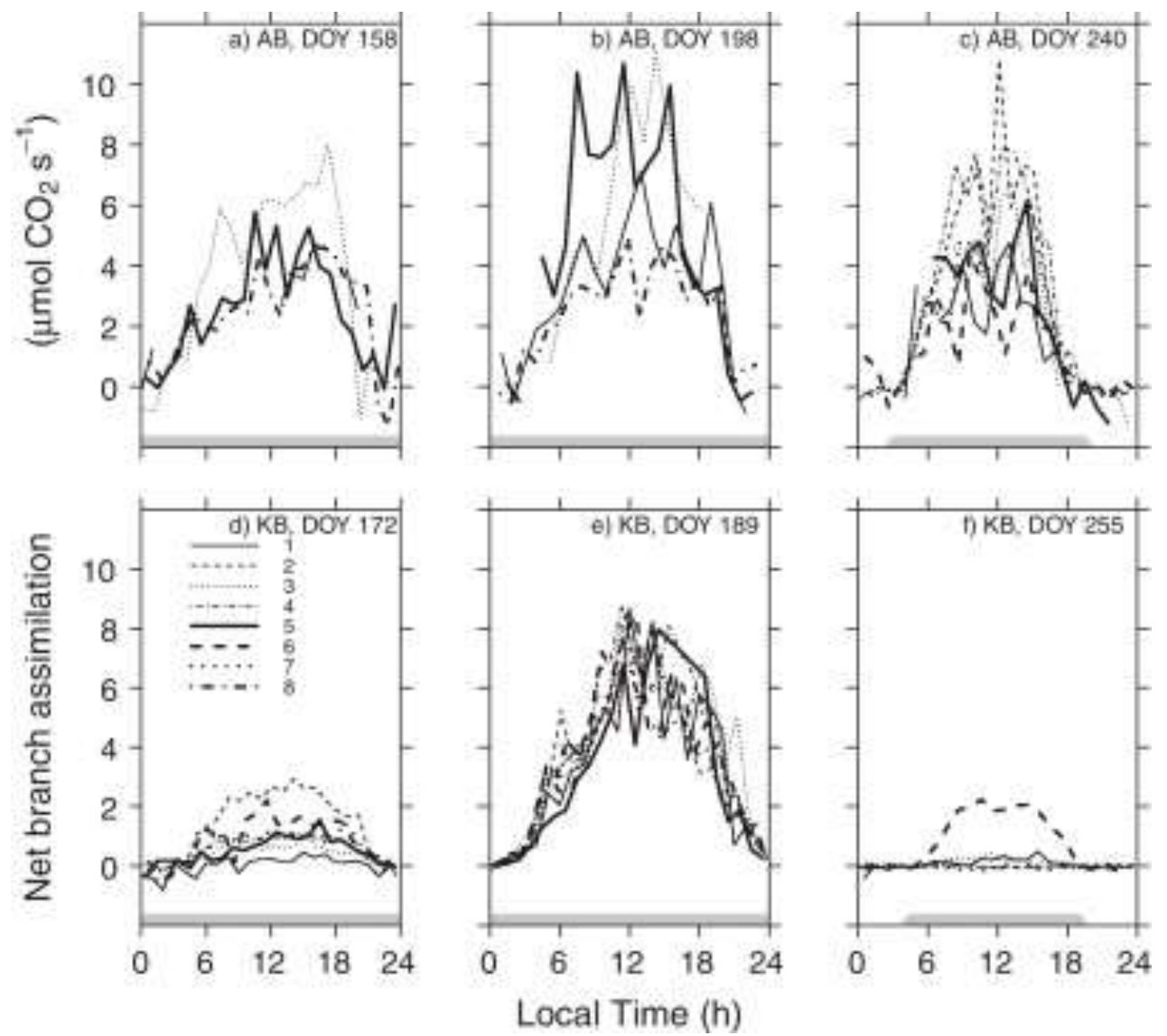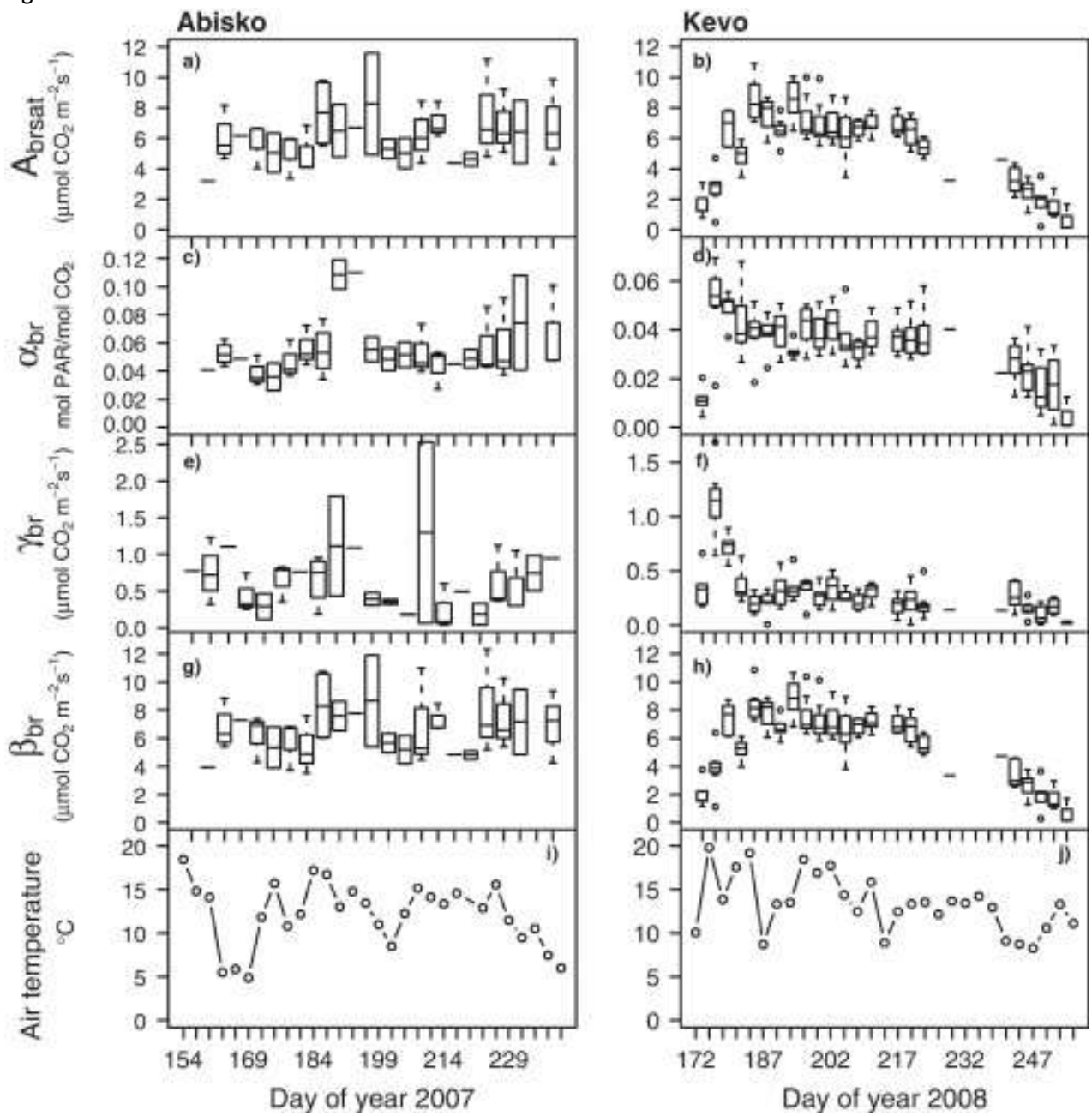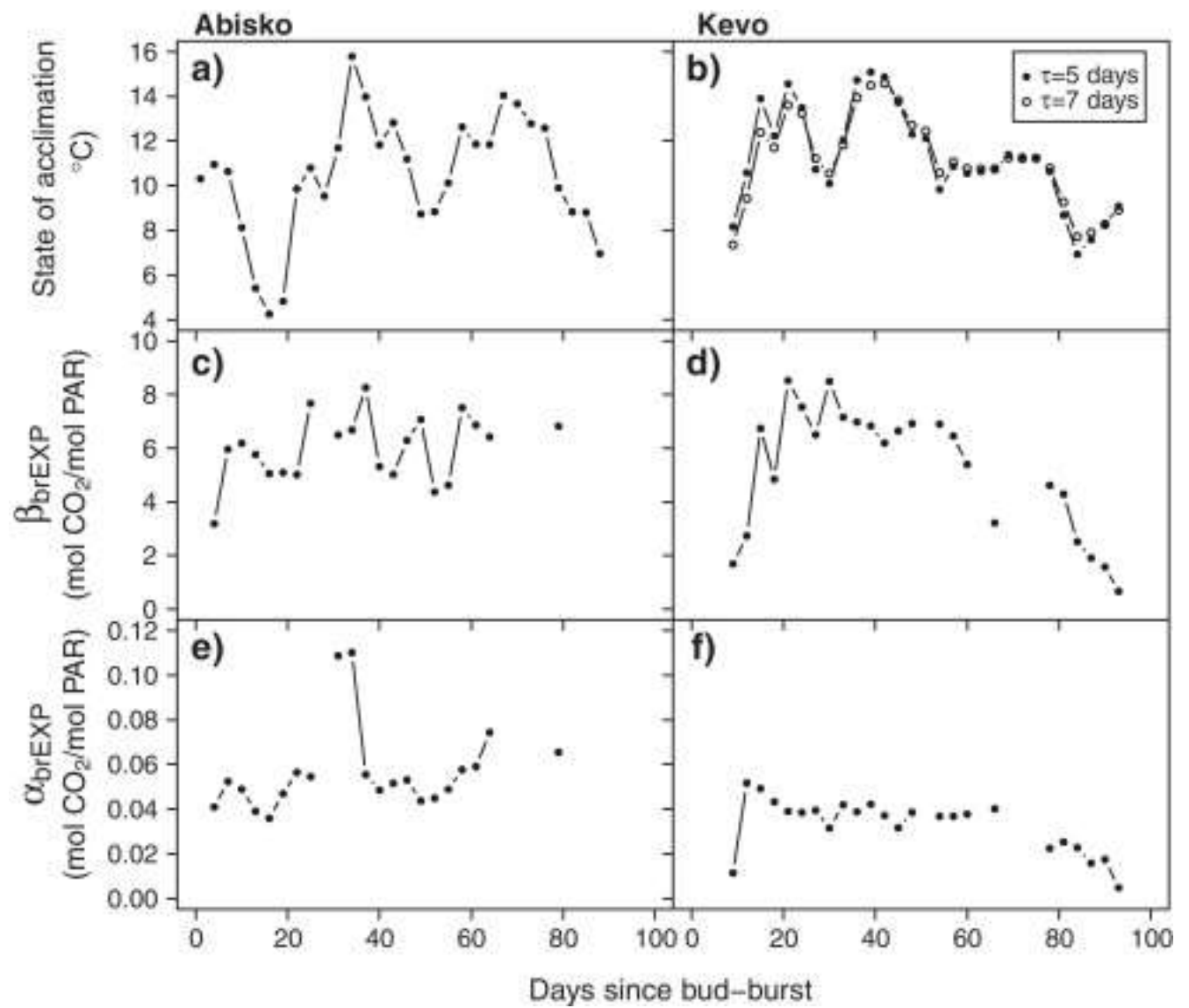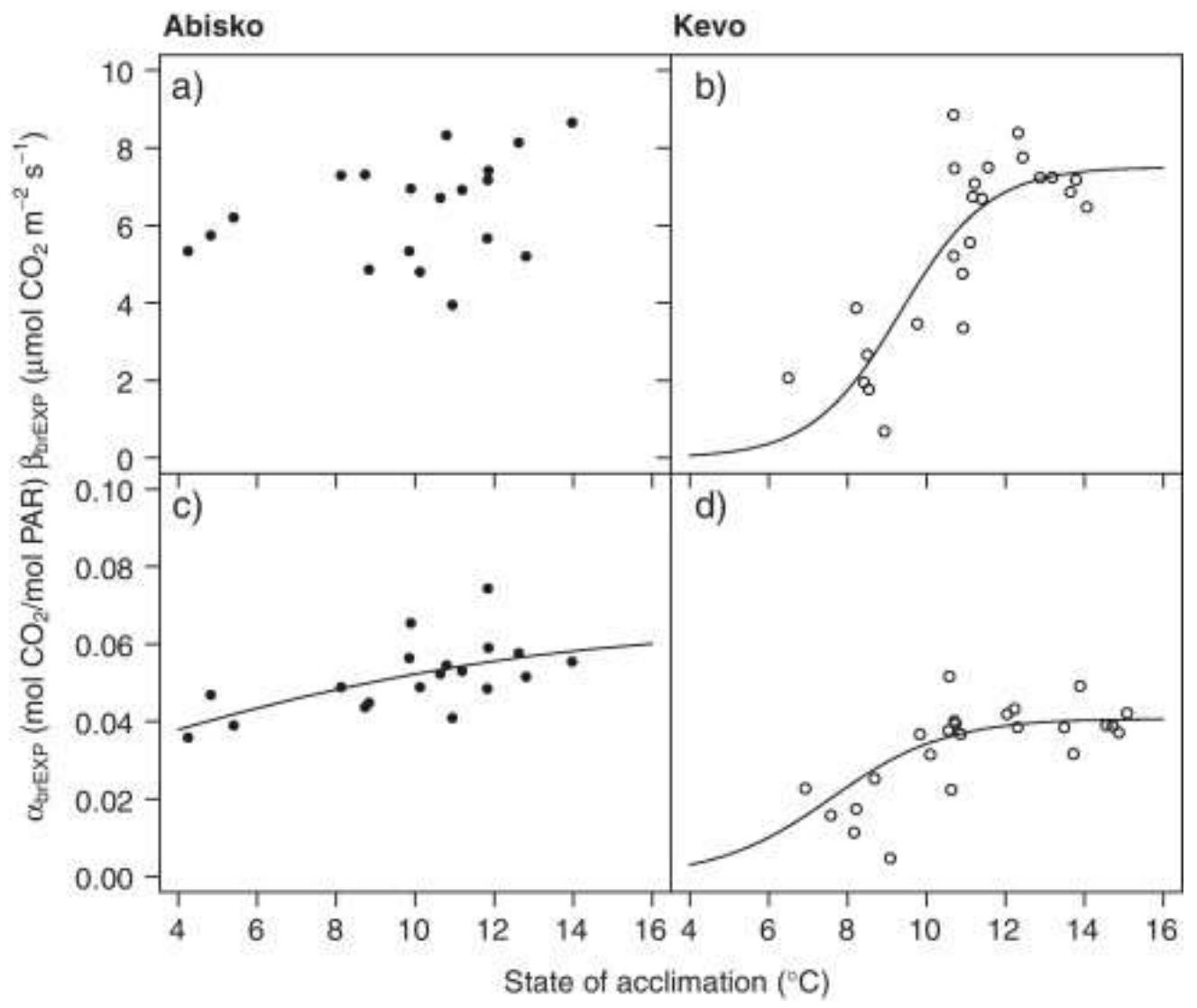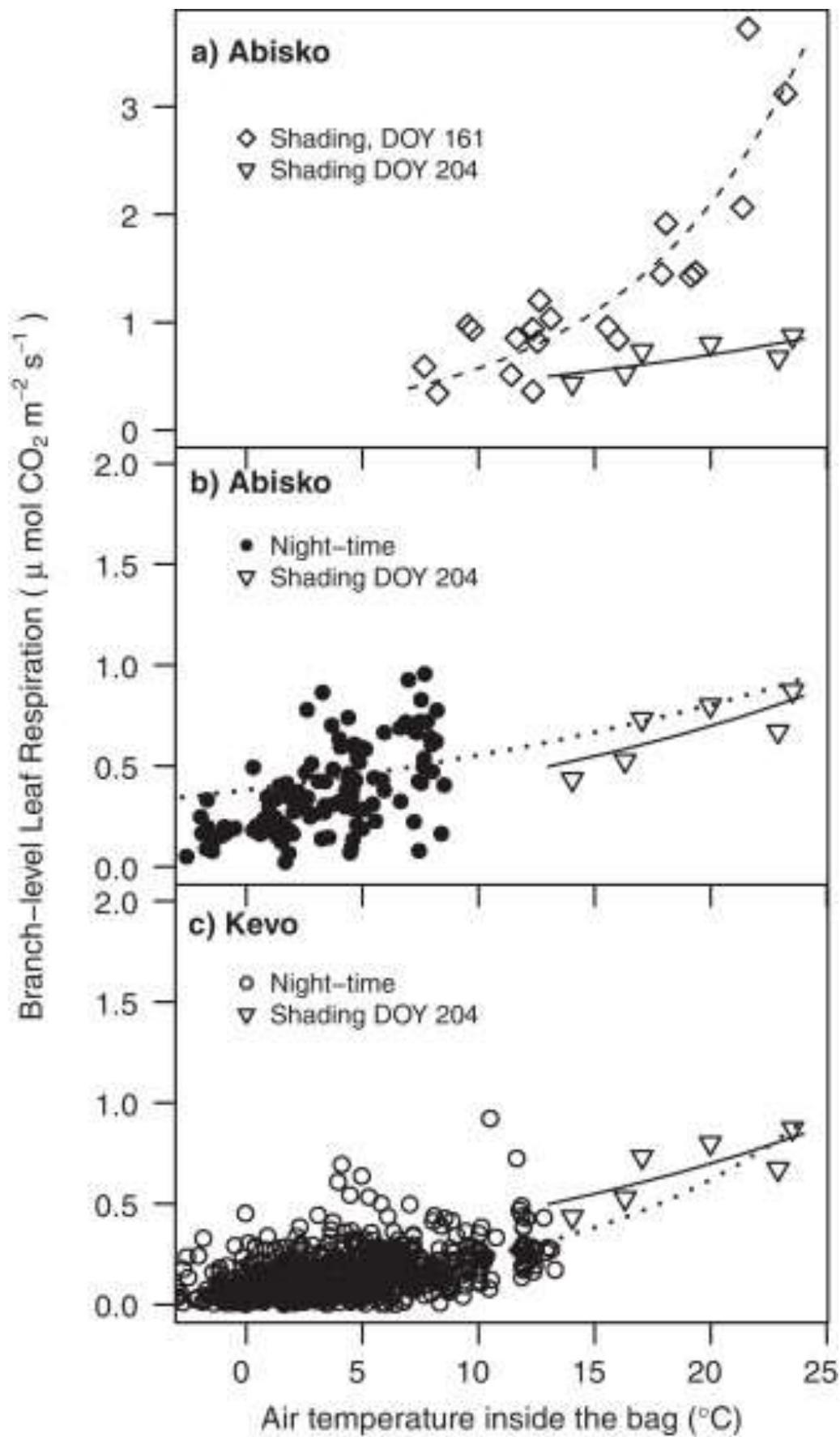
Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.

Abisko   **Kevo**

State of acclimation (°C)

Figure 6.

Figure 7.