Oecologia (1991) 88:317-324

Oecologia
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Diurnal variation and interrelations of ecophysiological parameters in three peatland woody species under different weather and soil moisture conditions

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Received January 31, 1991 / Accepted in revised form June 24, 1991

Summary. The diurnal patterns of twig xylem water potential, net photosynthesis rate, water use efficiency of photosynthesis, and stomatal and mesophyll conductance to CO_2 in tamarack, black spruce and swamp birch growing in a natural peatland in central Alberta, Canada, were examined. The relationships of photosynthesis to other ecophysiological parameters were investigated. Data were collected on three days with different weather and soil moisture conditions in the 1988 growing season. Day 1 was clear and warm and the ground water table was 7 cm above the average peat surface. Day 2 was clear and hot. Day 3 was cloudy but warm. On day 2 and day 3, the water tables were in the normal range for that season. Major findings were: 1) Soil flooding depressed photosynthesis in tamarack and black spruce. 2) Swamp birch was better adapted to flooding than tamarack or black spruce. 3) The trees experienced water stress in the afternoons of the two days with lower water table. 4) Changes in photosynthesis of the three species were primarily affected by changes in mesophyll conductance (g_m) and the response of photosynthesis to changes in g_m was similar for all three species.

Key words: Diurnal patterns – Photosynthesis – Water relations – Flooding stress – Peatlands

Peatlands in western Canada undergo significant variations in depth of water table during the growing season. The roots of trees on these sites are, however, generally confined to surface layers above the average water table depth, with deeper roots being pruned off by anaerobic conditions (Boggie and Miller 1976; Mannerkoski 1985; Lieffers and Rothwell 1986). When the water table rises close to the peat surface, oxygen supply to tree roots will be reduced significantly (Kozlowski 1984b; Mannerkoski 1985). This can depress the photosynthesis and productivity of trees. Dang and Lieffers (1989) found black spruce on a natural peatland had lower annual tree ring growth in extremely wet years. Presumably, these were the years when tree roots experienced floodings for longer periods of time than average or normal years. Greenhouse experiments showed soil flooding depresses the photosynthesis of tree seedlings (Kozlowski 1984b). There are, however, no field observations on the impact of flooding stress on the physiology of woody plants in natural peatlands.

Studying diurnal patterns of water relations, photosynthesis and related parameters can provide fundamental information on plant responses and adaptations to natural environments (Schulze and Hall 1982). Diurnal patterns are extensively described for agricultural crops and some woody species (Leverenz 1981; Beadle et al. 1985; Kauhanen 1986) but none of these studies report on peatland trees.

In this paper, we examined the diurnal patterns of twig xylem water potential, photosynthesis, water use efficiency of photosynthesis, mesophyll and stomatal conductance to CO_2, and the interaction among these parameters, for tamarack (*Larix laricina* (DuRoi) K. Koch), black spruce (*Picea mariana* (Mill.) B.S.P.), and swamp birch (*Betula pumila* L.), under naturally flooded and non-flooded soil conditions and different weather conditions in an Alberta peatland. We also discussed the mechanisms by which the photosynthesis in peatland trees is limited.

Materials and methods

The study site was a treed fen, located in the boreal forest east of the Saulteaux River, about 36 km south east of Slave Lake, Alberta (55° 8′ N; 114° 15′ W). The forest canopy is open and dominated by black spruce (*Picea mariana* (Mill.) B.S.P.) and tamarack (*Larix laricina* (DuRoi) K. Koch). The average ages for black spruce and tamarack were 30 and 24 years, respectively. The common shrub species are *Betula pumila* L. (swamp birch) and *Ledum groenlandicum* Oeder. The average May-to-August precipitation for the

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general area totals 275 mm and the average July to August temperature is 15° C (Monthly Record, Slave Lake Station, Climate Service, Environment Canada 1988).

Three woody species (black spruce, tamarack and swamp birch) were chosen for foliage gas exchange and twig xylem water potential (ψ_x) measurement. Three individuals of each species were selected. A branch at about breast height (tamarack and black spruce) or a terminal branch (birch) was chosen from each individual for measuring gas exchange. For black spruce, measurements were on 1-year-old needles only. For ψ_x measurement, a branch near the one for gas exchange measurement (tamarack and black spruce) or a terminal within the same clump as the one for gas exchange measurement (birch) was cut. The cut branch was inserted into a portable Scholander pressure chamber (PMS Instrument Company, Oregon, USA), with the cut end projecting through the rubber stopper. The pressure inside the chamber was increased gradually using compressed nitrogen gas. When xylem sap appeared on the cut surface of the cut branch, the reading of the pressure inside the chamber was taken immediately. This pressure is a good estimate of the xylem or foliage water potential of the twig (Ritchie and Hinckley 1975). The soil temperature in the root zone (at 15 cm depth) was also measured using a dial-thermometer.

Gas exchange was measured using an open system consisting of a portable infra-red gas analyzer (LCA-2), a leaf cuvette (PLC), and an air supply unit (all from Analytical Development Corporation, Hoddeson, England). Ambient air was drawn from 4 m height using a tower. The air was passed through a desiccator before entry into the cuvette. The air flow through the cuvette was maintained at a rate of 10 mL s^{-1}. Air within the cuvette was made turbulent with a high speed fan. An infrared filter on the cuvette shield prevented heating inside the cuvette. In addition, gas exchange measurements were taken very quickly (about 1 minute) to further reduce heating inside the cuvette. The cuvette contains sensors for measuring relative humidity, air temperature and photosynthetically active radiation. Because the leaf size was small and the air in the cuvette was highly turbulent (small boundary layer resistance), the temperature difference between leaf and air should be less than 0.7° C (Nobel 1983). So the air temperature inside the cuvette was used as an estimate of leaf temperature.

Measurements were made on three days with different weather and soil moisture conditions: a cloudless day with the soil being flooded (July 8, 1988); a clear and hot day (July 26, 1988); and an overcast but warm day (August 4, 1988). These will be referred to as "wet day", "hot day", and "cloudy day" respectively hereafter. The ground water table on the wet day was 7 cm above the average peat surface level. This was the highest water table level observed at the study site from 1984 to 1990. The soil had been flooded for 3 days prior to the sampling day. The water tables on the hot and cloudy days (respecitively, 16 and 26 cm below the average peat surface) were in the normal range for that season, those two days were used as controls in assessing flooding effect on ecophysiological parameters. The maximum temperatures in the cuvette were 26, 35 and 27° C respectively for the wet day, the hot day, and the cloudy day. The photosynthetic active photon flux densities (PAR) were above 1200 μmol m^{-2} s^{-1} during the period of gas exchange measurement on both the wet and the hot days. Since PAR was low (< 800 μmol/m^{-2} s) on the cloudy day, natural light was supplemented by a Brinkman "Q-beam" spot light which was positioned to supply light at 1600 μmol/m^2/s. The saturation PAR for photosynthesis of tamarack and black spruce was determined to be, respectively, 800 and 700 μmol m^2 s.

The ambient water vapour pressure deficit (vpd) was recorded hourly on a CR21 data-logger (Campbell Scientific Corp., Canada). But vpd data were obtained only for the hot day because of equipment failures on the other two days.

ψ_x measurements were taken at 2-h intervals during daytime and at 4h intervals at night, for a period of 24 h on the wet and hot days and from 6:00 to 21:00 on the cloudy day. Gas exchange was measured at 2 h intervals from 7:20 to 18:20 on the wet day, from 8:20 to 18:20 on the hot day, and from 6:20 to 21:20 on the cloudy day. One hour measurements were taken on the cloudy day for two time periods (i.e., 10:20 to 11:20, 19:20 to 21:20 h).

The foliage used in gas exchange measurements was collected at the end of each experiment for leaf area determination. The leaf area for black spruce and tamarack was determined from dry mass using "dry-mass vs leaf-area" equations (Macdonald and Lieffers 1990). The leaf area for birch was measured 4 times on a leaf area meter (LAMBDA Instruments Corporation LI 3100) and the average was used.

Net photosynthesis rate (P_{net}), leaf resistance to H_2O vapour (r), transpiration rate (E), and intercellular CO_2 concentration (C_i) were determined as described by Caemmerer and Farquhar (1981). Since the high speed fan in the cuvette and the design of the cuvette ensure a small boundary layer resistance (r_b) and r_b is generally very small for needles, the stomatal resistance to H_2O vapour (r_s) in tamarack and black spruce was assumed to be equal to r. The stomatal conductance was calculated as: $g_s = 1/r_s$. The stomatal conductance for birch was calculated as: $g_s = 1/(r - r_b)$, where r_b is boundary layer resistance determined as described by Coombs et al. (1985). Stomatal conductance to CO_2 (g_c) was calculated as: $g_c = g_s/1.6$ (Coombs et al. 1985). Mesophyll conductance to CO_2 (g_m) was calculated as: $g_m = P_{net}/C_i$ (Fites and Teskey 1988). The water use efficiency of photosynthesis (WUE) was determined as: $WUE = P_{net}/E$ (Larcher 1983). P_{net}, E, g_c, and g_m were all expressed on a leaf area basis.

Regression analysis was conducted on the P_{net}–g_m relationships for each species-day combination. The homogeneity of the regression coefficients (slopes) was tested (Steel and Torrie 1980). The differences in P_{net} between different species, between different days, and species-day interactions, were examined after P_{net} being adjusted to the same g_m (covariance analysis). All statistical analyses were conducted using SAS statistics package for personal computers (SAS Institute Inc. 1987). The relationship of P_{net} to ψ_x, g_c, C_i, and leaf temperature, was analyzed by examining the plots of P_{net} versus these parameters. The relationships of g_c and WUE to ambient water vapour pressure deficit were also investigated.

Results

1. Xylem water potentials (ψ_x)

In general, all three species had similar diurnal patterns of ψ on each of the three days (Figs. 1a, 2a and 3a). On the wet and hot days, ψ_x decreased rapidly before 10:00 and increased after 18:00, fluctuating at low values between the two times. Both the daily average and minimum ψ_x on the wet day were higher than on the hot day and the cloudy day. On the cloudy day, the decrease in ψ_x started later, but the decline was faster and lasted longer than on the other two days (Fig. 1a, 2a, 3a). The daily minimum ψ_x on the cloudy day was lower and delayed by 5 h compared to the wet day and the hot day. The range of the daily variation in ψ_x was the greatest on the cloudy day and smallest on the wet day. ψ_x on all sampling days generally did not return to the pre-dawn level before midnight. Among the three species, birch had the highest and tamarack had the lowest daily average and minimum ψ_x for all three days. On the wet day, the minimum ψ_x in birch occurred 4 h later than tamarack and black spruce. The daily minimum water potentials for the wet day, the hot day, and the cloudy day, were respectively, − 1.9, − 2.4, and − 2.7 Mpa for tamarack; − 1.7, − 1.9, and − 2.2 Mpa for black spruce; and − 1.2, − 1.5, and − 1.7 for birch.

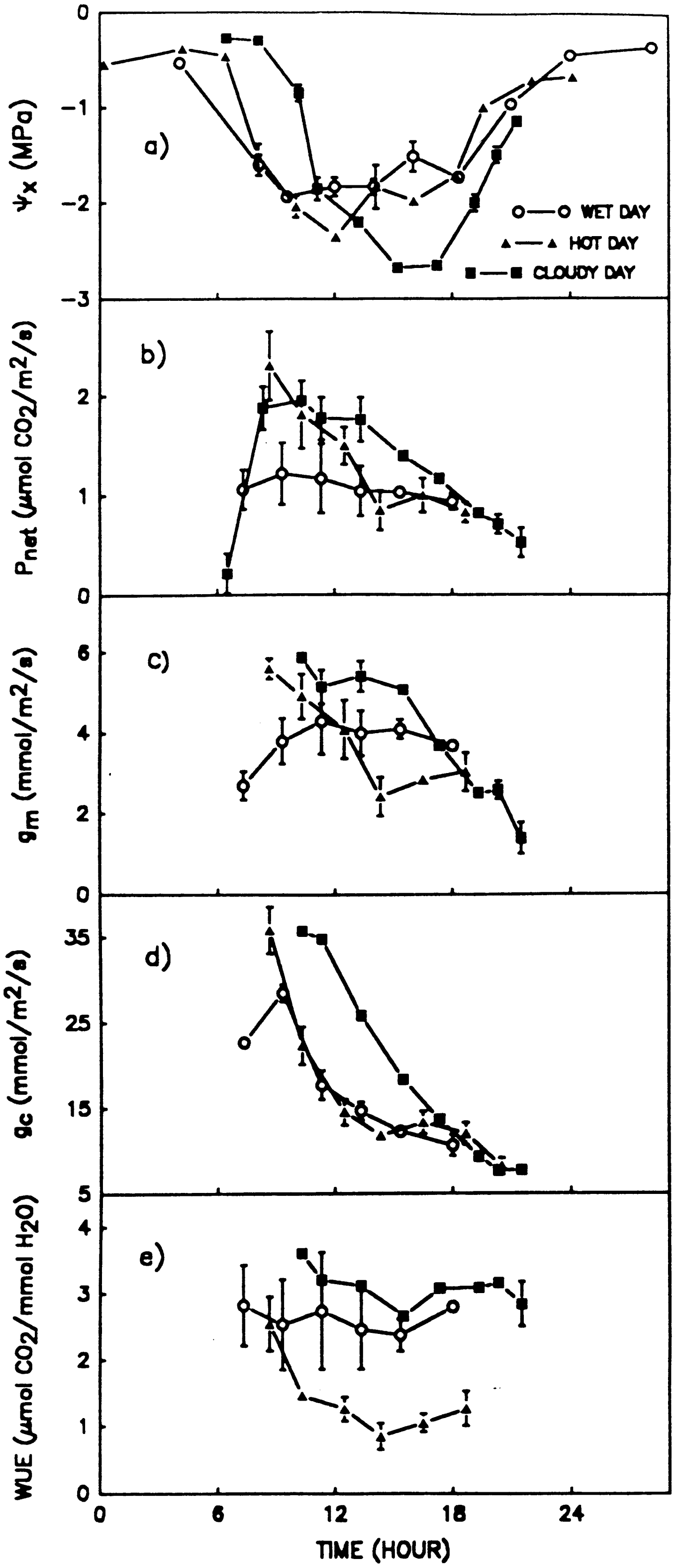

Fig. 1. Tamarack diurnal variations of: **a)** twig xylem water potential (ψ_x); **b)** net photosynthesis (P_{net}); **c)** mesophyll conductance to CO_2 (g_m); **d)** stomatal conductance to CO_2 (g_c); **e)** water use efficiency of photosynthesis (WUE) ($\bar{x} \pm$ SE.; $n = 3$). Data were collected on a clear day when soil was flooded (wet day), a clear and hot day (hot day), and a cloudy but warm day (cloudy day). The water table level on the wet day was 7 cm above the average peat surface level while it was 16 and 26 cm below the average peat surface respectively for the hot day and the cloudy day. g_m, g_c and WUE were not calculated for the first two measurements on the cloudy day because H_2O exchange measurements were not reliable due to heavy dew on the foliage early in the morning

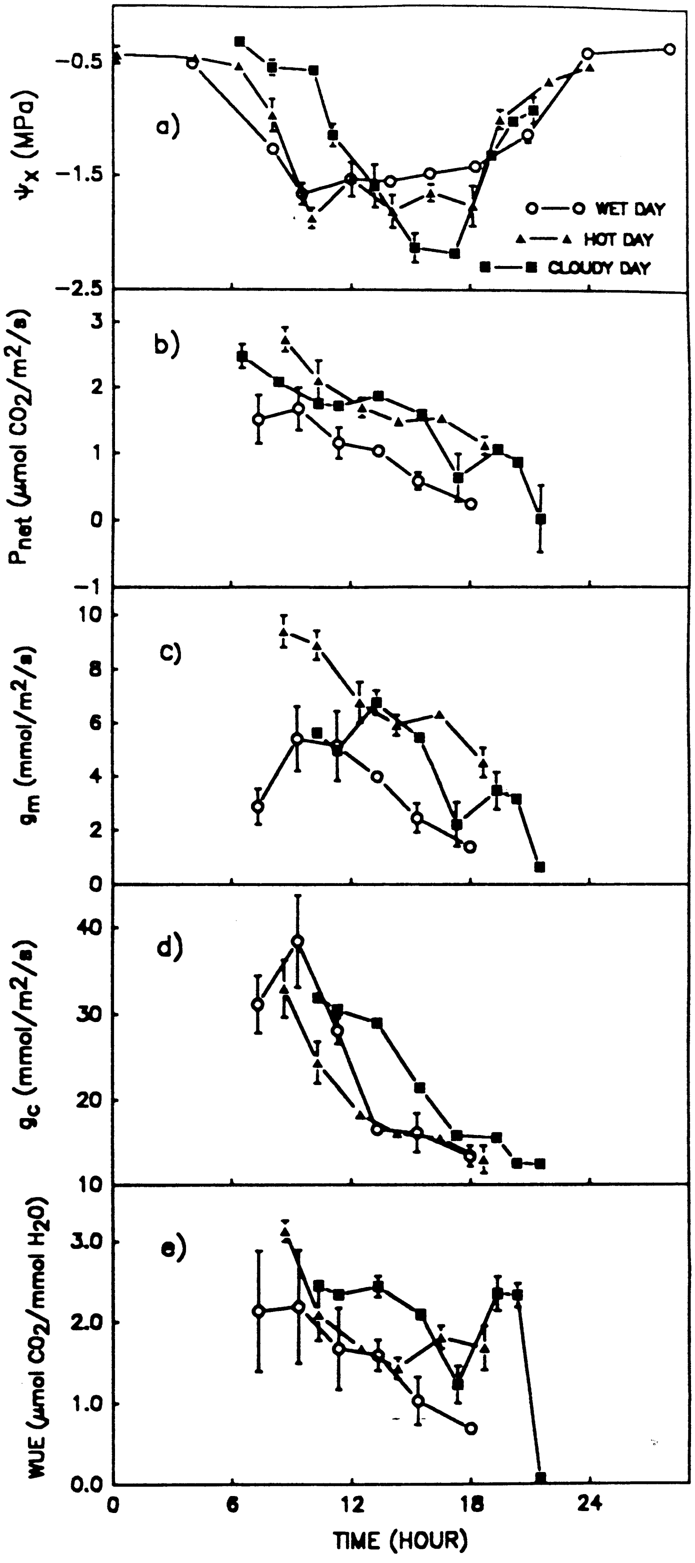

Fig. 2. Black spruce diurnal variations of: **a)** twig xylem water potential (ψ_x); **b)** net photosynthesis (P_{net}); **c)** mesophyll conductance to CO_2 (g_m); **d)** stomatal conductance to CO_2 (g_c); **e)** water use efficiency of photosynthesis (WUE) ($\bar{x} \pm$ SE.; $n = 3$). Explanations on the data are the same as Fig. 1

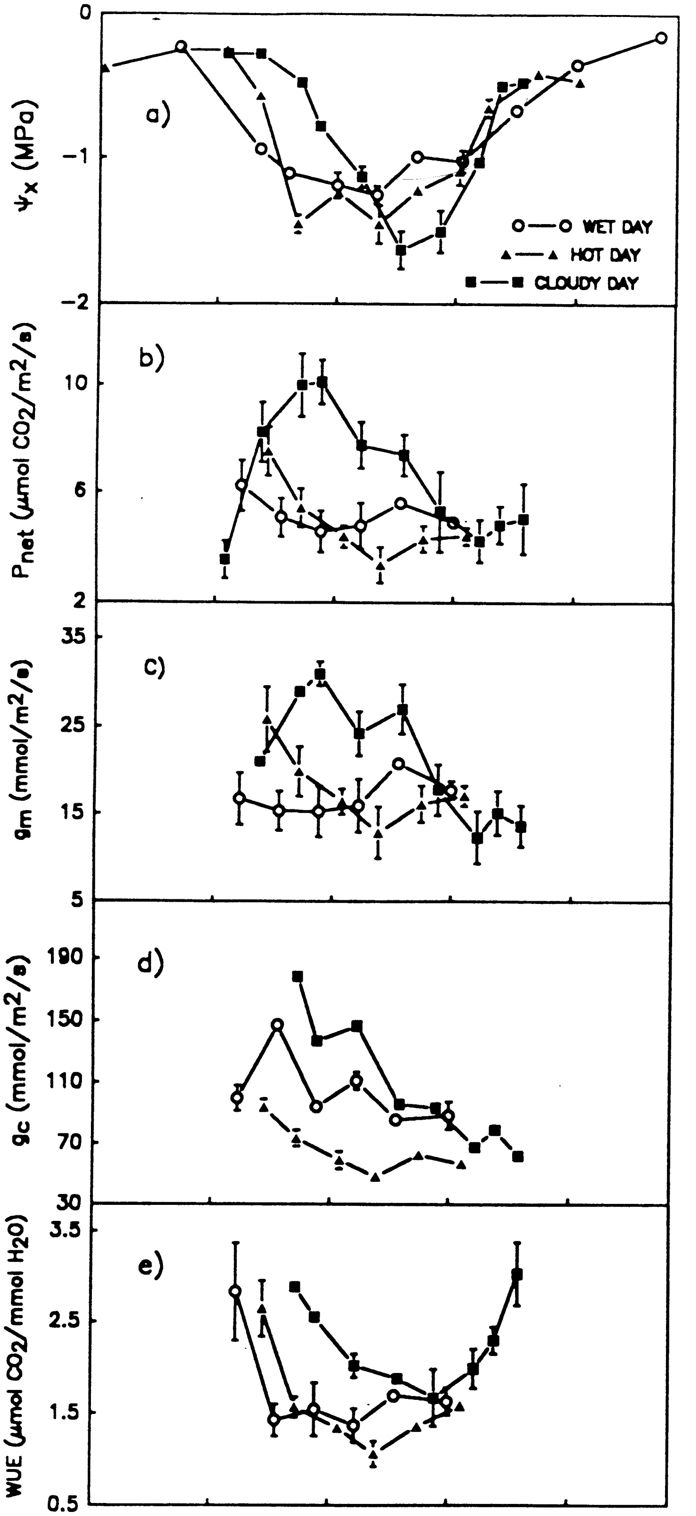

Fig. 3. Swamp birch diurnal variations of: **a)** twig xylem water potential (ψ_x); **b)** net photosynthesis (P_{net}); **c)** mesophyll conductance to CO_2; **d)** stomatal conductance to CO_2 (g_c); **e)** water use efficiency of photosynthesis (WUE) ($\bar{x} \pm$ SE.; $n = 3$). Explanations on the data are the same as Fig. 1

2. *Net photosynthesis (P_{net})*

Tamarack and birch had similar diurnal patterns of P_{net} on each sample day, but the patterns were different on different days (Figs. 1b and 3b). P_{net} for both species was relatively constant on the wet day; gererally decreased throughout the day with a small recovery after 16:20 on the hot day; and increased rapidly in the early morning and then decreased for the rest of the day on the cloudy day. The decrease in P_{net} for birch on the cloudy day started two hours later than tamarack. Black spruce, in contrast, had almost the same diurnal pattern for P_{net} on all three days (Fig. 2b). Maximum P_{net} occurred in early morning and then decreased continuously throughout the day.

On average, P_{net} for birch was usually higher than tamarack and black spruce on all three days, whereas the difference between the latter two was small. The differences in P_{net} between species, however, were not always consistant among the sample days. Tamarack and black spruce had the lowest P_{net} on the wet day, while birch had similar values on the wet and hot days. Tamarack and birch had the highest P_{net} on the cloudy day, while black spruce had similar values on the hot and cloudy days. The range of daily fluctuations in P_{net} was the smallest on the wet day and the largest on the cloudy day for all three species.

3. *Mesophyll and stomatal conductance to CO_2*

Mesophyll conductance generally had limilar diurnal patterns to photosynthesis on all three days (Figs. 1c, 2c, 3c).

In general, all three species had similar diurnal patterns of stomatal conductance (g_c) on all three days. Stomatal conductance decreased continuously throughout the day except for an increasing period before 9:20 on the wet day (Figs. 1d, 2d and 3d). Birch had greater variations on the wet and cloudy days than tamarack and black spruce. There were species-weather interactions that affected the magnitude of g_c. On average, tamarack and black spruce had the highest g_c on the cloudy day while g_c was similar on the wet and hot days (Figs. 1d and 2d). In contrast, birch had the lowest average g_c on the hot day and the highest g_c on the cloudy day (Fig. 3d).

4. *Water use efficiency of photosynthesis (WUE)*

The three species had similar diurnal patterns of WUE changes on the hot day: WUE decreased rapidly before 14:00 and recovered slightly afterwards (Fig. 4b). On the wet day and cloudy day, however, there were obvious day-species interactions. On the wet day, WUE in tamarack and birch was relatively stable for most time of the day, whereas WUE in black spruce decreased continuously throughout the day (Fig. 4a). On the cloudy day, the diurnal variation in WUE for tamarack was small while WUE in black spruce and birch generally deceased before 18:20 and recovered afterwards

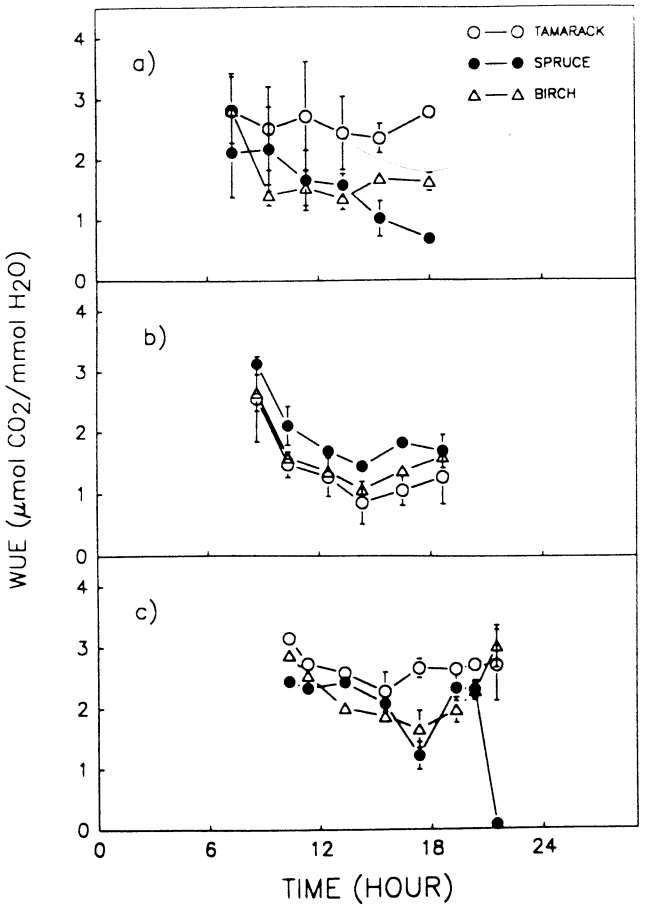

Fig. 4. Diurnal variations of water use efficiency of photosynthesis (WUE) in tamarack, black spruce and swamp birch on the wet day (**a**), the hot day (**b**), and the cloudy day (**c**)

(Fig. 4c). Interestingly, WUE in black spruce dropped almost to zero at 21:00 while WUE in the other two species was still very high (Fig. 4c).

On average, WUE was the highest on the cloudy day for all three species (Figs. 1e, 2e, 3e). In tamarack, WUE was the lowest on the hot day (Fig. 1e) while for black spruce (Fig. 2e) and birch (Fig. 3e) differences in WUE between the wet day and the hot day were generally small.

5. *Interrelations among variables*

P_{net} was positively and linearly related to g_m ($P < 0.05$) for all three species on all three days. Coefficients of determination for P_{net} regressed on g_m ranged from 0.75 to 0.97 (average = 0.90) (the plot of P_{net} on g_m for black spruce on the hot day is given in Fig. 5 as an example). Homogeneity tests of regression coefficients showed no significant differences ($P > 0.05$) in slopes of P_{net}-g_m regressions for different day-species combinations. After P_{net} being adjusted to the same g_m, there were no significant differences in P_{net} between species or significant interactions between species and day ($P > 0.05$). However, P_{net} was significantly different ($P < 0.05$) among the 3 days (highest on the wet day, lowest on the hot day). In other words, for a given day, P_{net} for all the species responded similarly to changes in g_m, but the responses of individual species were affected by the weather and soil moisture conditions experienced on different days.

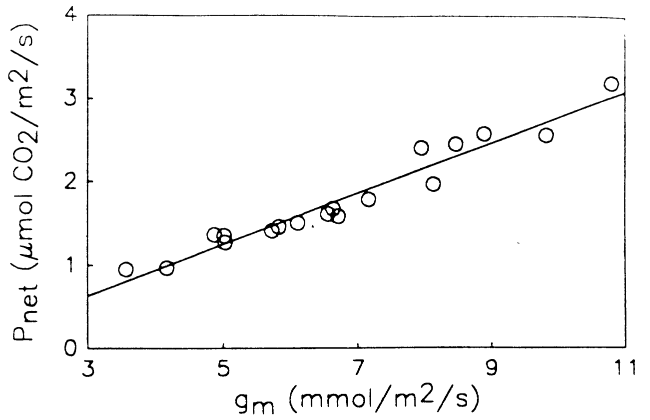

Fig. 5. Relationship between net photosynthesis (P_{net}) and mesophyll conductance to CO_2 (g_m) for black spruce on the hot day. $P_{net} = 0.31 * g_m - 0.29$, $r^2 = 0.95$, $n = 18$. This graph is typical of P_{net}-g_m relationships for tamarack, black spruce and swamp birch on the three sampling days

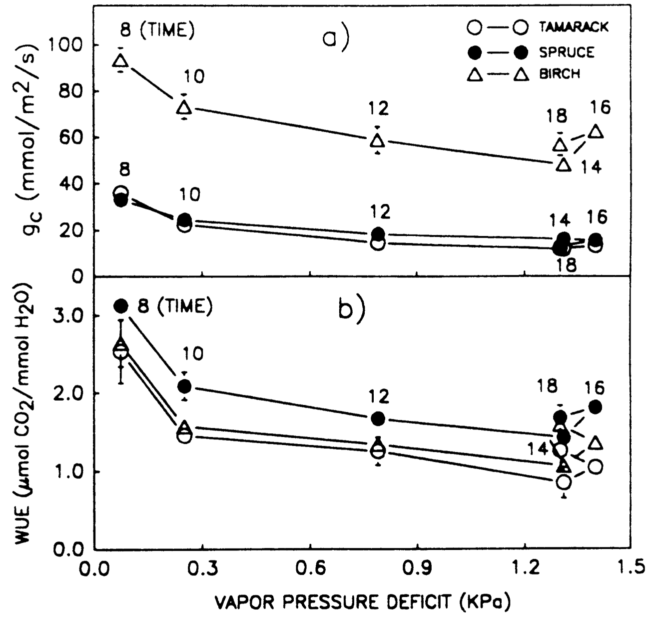

Fig. 6. Relationship of stomatal conductance to CO_2 (g_c) and water use efficiency of photosynthesis (g_m) ($\bar{x} \pm$ SE.; $n = 3$) to ambient water vapour pressure deficit for peatland tamarack, black spruce, and swamp birch on the hot day. The time of the day for each measurement is provided as numbers in the graphs

In general, g_c was 3.8 to 7.9 times greater than g_m. The g_c/g_m ratios were the highest on the wet day. There was no obvious difference in g_c/g_m between different species.

No clear relationship was found between P_{net} and ψ_x or leaf temperature for any species, or between P_{net} and Ci for black spruce or birch. In contrast, for tamarack, P_{net} was positively related to C_i on the cloudy day (data not presented).

For all three species, g_c and WUE both decreased as the ambient water vapour pressure deficit (vpd) increased on the hot day (Fig. 6). The decrease was much faster before 10:20 than after. Stomatal conductance in birch appeared to be more sensitive (steeper slope) to changes in vpd than in tamarack and black spruce (Fig. 6a).

Discussion

Our data showed that soil flooding had a negative impact on the photosynthesis of both black spruce and tamarack. P_{net} of these species on the wet day was lower than the other two days when the soil was not flooded. Depression of photosynthesis by soil flooding has also been observed in other tree species (Kozlowski 1984a; 1984b). In contrast to tamarack and black spruce, P_{net} in swamp birch on the wet day was as high as on the hot day. This indicates that swamp birch was probably better adapted to flooded soil conditions than tamarack and black spruce. Indeed, swamp birch occurs more frequently on wet peatlands than relatively drier peatland sites in central Alberta.

On the wet day, the substrate had been flooded for three days. The twig xylem water potential (ψ_x) on that day, however, was higher and more stable throughout the day for all three species than the hot and cloudy days when the soil was not flooded, while the stomatal conductance (g_c) on the wet day was similar to the other two days in both diurnal variation and magnitude. This indicates that the roots of these species probably had the capacity to absorb water from the saturated peat soil at a relatively high rate. This capacity would be an advantage for species growing on peatland sites where soil flooding occurs frequently. Conlin TS and Lieffers VJ (personal communication) found the root systems of tamarack and black spruce were able to acquire metabolic energy through anaerobic respiration when the soil was flooded. The fact that the daily minimum ψ_x on the wet day occurred four hours later in birch than tamarack and black spruce and that g_c in birch was much higher on the wet day than on the hot day could be taken as another line of evidence that swamp birch was better adapted to flooded soil conditions than the other two species.

The g_c results on the wet day were in contrast to the responses of stomata to flooding reported in the literature. Stomata generally close in response to flooding (Kozlowski 1982; 1984a; 1984b). The amplitude of diurnal fluctuations in stomatal conductance is much greater in flooded plants than non-flooded ones (Tang and Kozlowski 1982). We found the amplitudes of both stomatal conductance and its diurnal fluctuations were similar in flooded trees (on the wet day) and in non-flooded trees (on the hot and cloudy days). This discrepancy could simply reflect a difference in flood tolerance between seedings and saplings. However, since most of the reported flooding experiments were conducted in the greenhouse, it is also possible that the duration of flooding treatments in the greenhouse is not long enough or there are not enough flooding cycles to allow the seedlings to adapt.

For all species in this study, the ψ_x values early in the afternoons of the hot and cloudy days were below the recorded values for drought-stressed woody species: Buxton et al. (1985) observed that ψ_x in black spruce was -0.9 MPa after the seedlings were drought-stressed for 72 hours. Melzak et al. (1985) found that the photosynthesis in *Pinus halepensis* decreased dramatically when ψ_x was below -0.8 MPa. Similar results have been reported for birch (Osonubi and Davis 1980) and loblolly pine (Teskey et al. 1986). Kaufmann (1981) found that most plant processes (protein synthesis, enzyme activities etc.) were depressed by foliage water potentials below -1.5 MPa. In this study, the daily minimum ψ_x for black spruce and tamarack was respectively -2.2 and -2.7 MPa. Taking into account the declining trend of photosynthesis and mesophyll conductance associated with the decline of ψ_x (Figs. 1, 2 and 3), we concluded that these species were under water stress in the afternoons.

Peatlands generally have excess water in the substrate. Drought stress in peatlands is most likely due to an imbalance between the root capacity for absorbing water and the water loss from transpiration. According to the resistor-capacitor theory (Passioura 1981), transpiration early in the day is dependent mostly upon the water stored in the canopy which is recharged over night, while later in the day water uptake by roots becomes more important. The root systems of peatland trees are shallow (Lieffers and Rothwell 1986) and therefore the effective absorbing surface may be small. In addition, the peat substrate is generally cold (4 to 7° C at 15 cm for the three sampling days). Cold soil can significantly increase the root resistance to water uptake (Lopushinsky and Kaufmann 1984). Consequently the water uptake by roots was probably slow. The transpiration demand (i.e. water vapour pressure deficit), however, was generally higher in the afternoon than in the morning. Although stomatal conductance decreased in response to increases in vapour pressure deficit (Fig. 6), this decrease might not be large enough to offset the imbalance between water loss and water input in the trees. These conditions were combined to expose the trees to water stress.

For all three peatland species, it seems that mesophyll conductance to CO_2 and its responses to weather and soil moisture conditions were primarily responsible for changes in photosynthesis, whereas stomatal conductance exerted little limitation on photosynthesis. The strong linear relationship between P_{net} and g_m provided good evidence to support this conclusion. The similarity of diurnal trends in P_{net} and g_c, however, suggests that stomatal conductance might also be a major factor limiting photosynthesis. If this were the case, P_{net} would be positively related to the CO_2 concentration in the intercellular space. Our data showed this relationship was poor. The fact that g_c was much greater than g_m suggests that changes in g_c would have a trivial impact on photosynthesis. The similar diurnal trends in P_{net} and g_c could simply reflect the effect of mesophyll activities on the stoma, as suggested by Wong et al. (1979). The diurnal patterns of photosynthesis on different days showed that there were obvious species-day interactions.

However, the adjustment of P_{net} for differences in g_m between species and between days eliminated these interactions. This clearly shows that the variation in photosynthesis was caused primarily by the variation in mesophyll conductance. In addition, decreases in g_c (e.g. in response to vpd increases) should result in an increase in water use efficiency of photosynthesis (WUE) if mesophyll conductance was not limiting (Osmonubi and Davies 1980). In our data, however, g_c and WUE changed in parallel to each other (Fig. 6). This is another indication that low g_m was the major limiting factor to photosynthesis in the three peatland species. The primary role of mesophyll in limiting photosynthesis has also been observed in other species (Osonubi and Davies 1980; Farquhar and Sharkey 1982; Kozlowski 1984a; Melzack et al. 1985; Teskey et al. 1986).

The mechanisms of the mesophyll limitation to photosynthesis of the three peatland species are not well understood. Mesophyll conductance includes the diffusion of CO_2 (in aqueous phase) across the cell wall, membranes, and the cytoplasm to the carboxylation sites, and various biochemical and photochemical reactions (Bradford and Hsiao 1982; Edwards and Walker 1983). Any of these could contribute to the decrease in g_m. Decreases in g_m are often associated with mesophyll water status (Whiteman and Koller 1964). Water status change induced alteration in light harvesting, energy conversion (Bradford and Hsiao 1982), carboxylation (O'Toole 1976; Kaiser 1987), and the activity of fructose bisphosphatase (Berkowitz and Gibbs 1983) have been reported. Ögren and Öquist (1985) found that in severely drought stressed willow (leaf water potential < -1 MPa) reduction in P_{net} was solely attributed to decreased activity of ribulose bisphosphate carboxylase. Flooding reduces the activities of carboxylation enzymes and the chlorophyll content of some species (Kozlowski 1982). Flooding can also limit P_{net} through its limitation on carbohydrate translocation (Kramer and Kozlowski 1979). Also changes in plant hormones may be involved in the above or other ways (Bradford and Hsiao 1982).

Acknowledgements. The authors thank Dr. John Hoddinott for reviewing this manuscript, two anonymous referees for comments, and Dale Stelter for field assistance. Funding for this study was provided by a Natural Sciences and Engineering Research Council (Canada) Forestry Transition Grant to V.J.L.

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