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Foliar maintenance respiration of subalpine and boreal trees and shrubs in relation to nitrogen content

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ABSTRACT

A nitrogen-based model of maintenance respiration (R_m) would link R_m with nitrogen-based photosynthesis models and enable simpler estimation of dark respiration flux from forest canopies. To test whether an N-based model of R_m would apply generally to foliage of boreal and subalpine woody plants, I measured R_m (CO_2 efflux at night from fully expanded foliage) for foliage of seven species of trees and shrubs in the northern boreal forest (near Thompson, Manitoba, Canada) and seven species in the subalpine montane forest (near Fraser, Colorado, USA). At 10 °C, average R_m for boreal foliage ranged from 0·94 to 6·8 μmol kg^{-1} s^{-1} (0·18–0·58 μmol m^{-2} s^{-1}) and for subalpine foliage it ranged from 0·99 to 7·6 μmol kg^{-1} s^{-1} (0·28–0·64 μmol m^{-2} s^{-1}). CO_2 efflux at 10 °C for the samples was only weakly correlated with sample weight ($r = 0{\cdot}11$) and leaf area ($r = 0{\cdot}58$). However, CO_2 efflux per unit foliage weight was highly correlated with foliage N concentration [$r = 0{\cdot}83$, CO_2 flux at 10 °C (mol kg^{-1} s^{-1}) = 2·62 × foliage N (mol kg^{-1})], and slopes were statistically similar for the boreal and subalpine sites ($P = 0{\cdot}28$). CO_2 efflux per unit of foliar N was 1·8 times that reported for a variety of crop and wildland species growing in warmer climates.

Key-words: boreal; dark respiration; maintenance respiration; nitrogen; subalpine.

INTRODUCTION

Dark respiration of foliage consumes carbon fixed in photosynthesis for the construction of new tissue and the maintenance of existing tissue. For forests, the annual cost of foliage dark respiration can be considerable, particularly in conifer stands, where large leaf areas are maintained throughout the year. For example, foliage dark respiration as a fraction of annual assimilation was 9% for a 20-year-old Scots pine (*Pinus sylvestris* L.) stand (Linder & Axelsson 1982; Linder 1985), 11% for a second-growth mixed temperate hardwood stand (Harris *et al.* 1975), 12% for a 16-year-old slash pine (*P. elliottii* Engelm.) stand (Gholz *et al.* 1991; Cropper & Gholz 1993), 16% for a 16-year-old loblolly pine (*P. taeda* L.) stand (Kinerson, Ralston & Wells 1977), and 21% for a subalpine lodgepole pine (*P. contorta* Dougl.) stand in New Zealand (Benecke & Nordmeyer 1982). Complete carbon budgets for these stands are given in Ryan *et al.* (1994).

While well-established models exist that explain the variability in photosynthesis with respect to environment and leaf composition (e.g. Farquhar, von Caemmerer & Berry 1980), variability in dark respiration is not as well understood. The functional model of plant respiration (McCree 1970) has been useful for interpreting plant respiration, and further understanding is likely to build on this construct. The functional model states that the energy generated through respiration is used either for growth of new tissue or for maintenance of existing biomass (Amthor 1984, 1986). Construction respiration varies with the amount of new tissue built and its chemical nature. Good models exist to predict variability in construction respiration from elemental analysis (McDermitt & Loomis 1981), heat of combustion, ash, and organic N content (Williams *et al.* 1987), or carbon and ash content (Vertregt & Penning de Vries 1987). Maintenance processes, such as the replacement or repair of proteins and the maintenance of ion gradients, also require energy. While maintenance respiration has been reported to vary with temperature, protein content, atmospheric CO_2 concentration, pollutants and general physiological activity (Amthor 1989, 1991; Ryan 1991), no general model for estimating maintenance requirements has been established.

A general model estimating maintenance respiration (R_m) from temperature and tissue N content has been proposed (Ryan 1991), but not widely tested for different species and ecosystems. In this model, N is used as an easily measured surrogate for protein concentration because, typically, most of the nitrogen in plant cells is associated with protein (Lexander *et al.* 1970). The relationship between R_m and protein content exists because maintenance respiration supports protein repair and replacement, and because other maintenance processes may be correlated with cellular activity. Estimates of the fraction of R_m used for protein repair and replacement vary from small (17–21%; Bouma *et al.* 1994) to moderate (27–36%; Barneix *et al.* 1988) to large (50–60%; Penning de Vries 1975).

For individual species, R_m has been shown to increase with increasing tissue N content (Kawahara *et al.* 1976;

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Jones *et al.* 1978; Merino, Field & Mooney 1982; McCree 1983; Waring *et al.* 1985; Irving & Silsbury 1987), but some exceptions have been noted (e.g. Byrd, Sage & Brown 1992). Another complication is that maintenance respiration per unit of plant nitrogen can vary with growth rate (McCree 1982), species (McCree 1983) and tissue type (Szaniawski & Kielkiewicz 1982), perhaps because protein content and protein turnover are not strictly related. However, variability in maintenance rates per unit tissue nitrogen is often small when compared to the range of respiration rates expressed per unit dry weight.

Use of a nitrogen-based model of R_m would link respiration with other processes, such as photosynthesis, carbon allocation, litter decomposition and nutrient release. Because of the close relationship between N, Rubisco and chlorophyll content, N content serves as a useful surrogate for photosynthetic capacity in foliage, and a strong relationship between N and photosynthetic capacity has been documented (Field & Mooney 1986). Litter decomposition and release and immobilization of nutrients are also strongly related to litter N content (Melillo, Aber & Muratore 1982), because N to support microbial populations is partly derived from the substrate. Nitrogen can also control allocation, although mechanisms are not well understood (cf. Thornley 1972).

To test the hypotheses (1) that R_m is generally related to tissue N content and (2) that R_m per unit N is similar among species growing at two different sites, I compared R_m rates for foliage of seven boreal and seven subalpine trees and shrubs. The trees included deciduous angiosperms, and deciduous and evergreen gymnosperms; shrubs were all deciduous angiosperms.

MATERIALS AND METHODS

Study areas

This study compared foliage respiration rates from trees and shrubs growing in a Rocky Mountain subalpine forest with similar species growing in the boreal forest. Samples in the Rocky Mountain subalpine forest were taken at Fraser Experimental Forest near Winter Park, CO, USA (39° 54'N 105° 52'W). The subalpine forests at Fraser experience short growing seasons and cool night temperatures, and have abundant moisture throughout the growing season; about two-thirds of the precipitation falls as snow (Alexander et al. 1985). Frost limits photosynthetic activity during the spring and autumn, but summer rain storms keep soil moisture high during the growing season so that stomatal closure associated with drought is rare (Kaufmann 1982). Nitrogen levels in the soil are low for these forests (Ryan & Waring 1992) and poor nitrogen availability may limit photosynthetic capacity and growth. Trees and shrubs measured for this study were at an elevation of 2800 m.

Subalpine species sampled for foliar dark respiration were alder (*Alnus tenuifolia* Nutt.), aspen (*Populus tremuloides* Michx.), Engelmann spruce [*Picea engelmannii* (Parry) Engelm.], subalpine fir [*Abies lasiocarpa* (Hook) Nutt.], lodgepole pine [*Pinus contorta* ssp. *latifolia* (Engelm.) Critchfield], buffalo-berry [*Shepherdia canadensis* (L.) Nutt.] and willow (*Salix planifolia* Pursh). Aspen, spruce, subalpine fir, lodgepole pine and buffaloberry occurred in a mixed-age, mixed-species stand on an upland site. Alder and willow occurred in a riparian zone near a small stream about 300 m from the upland site. Trees and shrubs were less than 70 years old.

Boreal trees and shrubs were sampled at the Northern Study Area of the Boreal Ecosystem–Atmosphere Study (BOREAS) near Thompson, Manitoba, Canada (55° 48'N 97° 52'W). The boreal forest west of Thompson is close to the northern limit of the closed-crown boreal forest. Terrain is flat to broadly rolling, and soils are predominantly derived from sediments from glacial Lake Agassiz. The site experiences marked seasonal variation in solar radiation, with cool summers and extremely cold winters; about 40% of the precipitation falls as snow (NASA 1993).

Boreal species sampled for foliar dark respiration were alder (*Alnus crispa*), aspen (*Populus tremuloides* Michx.), black spruce [*Picea mariana* (Mill.) B.S.P], larch [*Larix laricina* (Du Roi) K. Koch], balsam poplar (*Populus balsamifera* L.), paper birch (*Betula papyrifera* Marsh.) and jack pine (*Pinus banksiana* Lamb.). All species were sampled from a young (approximately 20-year-old) mixed-species stand about 4 km from Thompson at an approximate elevation of 220 m.

Climate data for 13 years at Thompson and 10 years at Fraser are summarized in Fig. 1. The two sites have similar total precipitation and summer temperatures, but winter temperatures are much colder in the boreal forest than in the Rocky Mountain subalpine forest, yielding a much lower mean annual temperature. Because the boreal site receives more precipitation in the summer, potential evapotranspiration is lower relative to precipitation compared with the subalpine site. The boreal site also experiences much longer summer days, lower sun angles, and less diurnal variation in temperature in the summer.

Gas exchange measurements

Respiration from fully expanded foliage represents maintenance respiration (R_m) only, because growth (and construction respiration) does not occur. R_m was estimated from CO_2 efflux measured at night (2300–0300 h) from fully expanded foliage 16–19 August 1993 at the Thompson site and August 31–September 2 1993 at the Fraser site. For each species, CO_2 efflux was measured on 3–10 shoots, and each shoot came from a different tree. For those species with distinct sun and shade foliage (determined by inspection), half of the samples were measured for each foliage type. For all species except spruce, pine and fir, foliage was initiated in 1993. For spruce, pine and fir, between 0 and 60% of the foliage was initiated before 1993 (i.e. needles were > 1 year old).

Foliage was enclosed in a 10 cm × 15 cm lexan chamber, and CO_2 efflux was measured using an open system infrared gas analyser (LCA3, Analytical Development

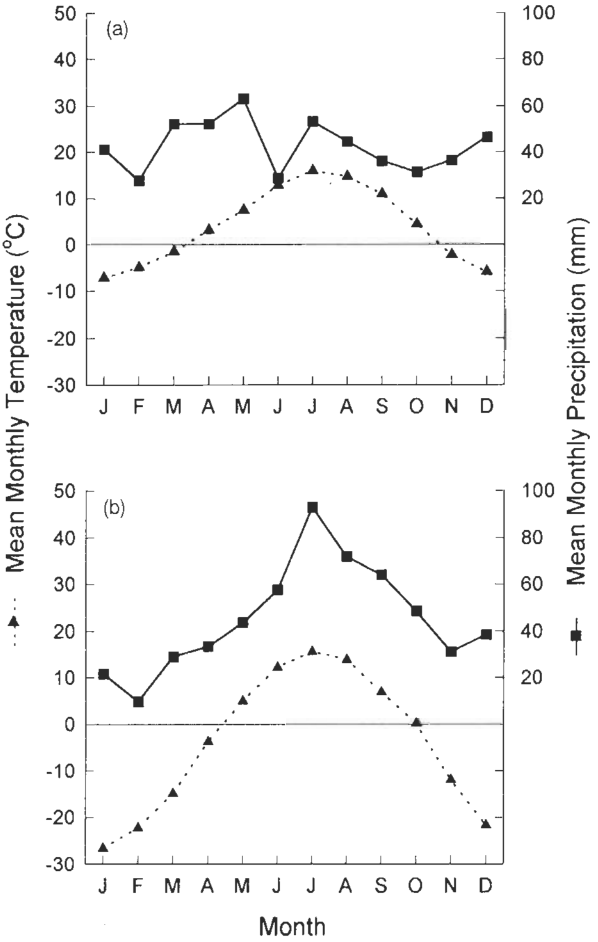

Figure 1. Climates of (a) Fraser Experimental Forest Headquarters, near Fraser, CO (2750 m), and (b) Thompson, Manitoba. Climate diagrams follow the usual convention of 10 °C/20 mm precipitation; mean total precipitations were (a) 513 and (b) 542 mm, and mean average temperatures were (a) 4·0 and (b) –3·9 °C. Data for Fraser were from 1976 to 1985; much of the experimental forest is at a greater elevation, and precipitation for the forest as a whole averages 740 mm. Data for Thompson were from 1979 to 1991, summarized in NASA (1993).

Company or CI-301, CID, Inc.), with flow rates through the chamber of 140–300 μmol s^{-1}. The internal volume of the foliage chamber was about 200 cm^3; air inside the chamber was stirred by a small fan. For all measurements, reference air was drawn through a 20 dm^3 mixing chamber to maintain a stable CO_2 concentration. Flux data were recorded after the difference in CO_2 concentration between reference and chamber was stable for 3 min. Air and foliage temperatures were 12–13 °C at the Thompson site and 1–7 °C at the Fraser site during sampling. Flux rates were adjusted to 10 °C for comparison, using a Q_{10} of 2.

Foliage was dried at 65 °C for 24 h, separated from twigs (for the conifers) and weighed to 0·01 g. Samples were ground in a Wiley mill to pass a 20-mesh screen and analysed for N and P content by autoanalysis of Kjeldahl digests (Anonymous 1992a,b). Conifer twigs were pooled by species and site and also analysed for N and P content. Leaf area was estimated from leaf weight using published relationships: relationships for aspen, lodgepole pine, subalpine fir and Engelmann spruce were obtained from Kaufmann, Edminster & Troendle (1982); the relationship for larch was obtained from Gower *et al.* (1987), and alder, birch values for and black spruce were calculated from the stand-level leaf mass:leaf area ratio given in Cannell (1982). The relationship for jack pine was assumed to be the same as that for lodgepole pine, and the relationships for balsam poplar, willow and buffalo brush were assumed to be the same as that for aspen.

Statistical analysis

Statistical analysis tested whether R_m at 10 °C (1) varied with foliar N between sites and for each species within a site, (2) differed among species and between the two sites, and (3) was influenced by foliar P. Correlations of R_m on a leaf mass basis ($R_{m,m}$, μmol kg^{-1} s^{-1}) and foliar N concentration (mol kg^{-1}) were compared with correlations of R_m on a raw-flux basis (nmol s^{-1}) and leaf area, leaf mass, leaf+twig mass, leaf N, leaf+twig N, leaf P, and leaf+twig P. Differences between sites and among species in $R_{m,m}$, R_m per unit leaf area ($R_{m,a}$, μmol m^{-2} s^{-1}), and R_m per unit leaf N ($R_{m,N}$, μmol mol^{-1} s^{-1}) were assessed with analysis of variance using the MANOVA procedure of SPSS/PC (Norusis 1988). Regression slopes for the relationship between R_m at 10 °C and leaf area and leaf mass, and between $R_{m,m}$ and foliar N concentration were also compared between sites using the MANOVA procedure in SPSS/PC. If the intercept in a linear regression was not significant, I estimated a zero-intercept slope and calculated R^2 as

$$1 - [\Sigma(Y_i - \bar{Y}_i)^2 / \Sigma(Y_i - \bar{Y})^2]$$

(Kvalseth 1985).

RESULTS

Average maintenance respiration at 10 °C varied from 0·94 to 6·8 µmol kg^{-1} s^{-1} (0·18–0·58 µmol m^{-2} s^{-1}) for foliage from boreal species and from 0·99 to 7·6 µmol kg^{-1} s^{-1} (0·28–0·64 µmol m^{-2} s^{-1}) for foliage from subalpine species (Table 1). Average $R_{m,m}$ was 3·26 µmol kg^{-1} s^{-1} for the selected boreal species and 3·50 µmol kg^{-1} s^{-1} for the selected subalpine species; these means are not significantly different ($P = 0·61$). CO_2 efflux at 10 °C was weakly correlated with sample leaf mass ($r = 0·33$, $P < 0·01$, $n = 82$) and leaf+stem mass ($r = 0·27$, $P = 0·01$) for data from both locations combined (Fig. 2). CO_2 efflux was also correlated with estimated sample leaf area ($r = 0·58$, $P < 0·01$), but two samples with large leaf areas strongly influenced the results (exclusion of these samples gave a correlation of 0·34, $P < 0·01$, $n = 80$). For both leaf weight and leaf area, correlations were not substantially different between

Table 1. Maintenance respiration (CO_2 efflux) corrected to 10 °C and foliage N and P contents for boreal and subalpine trees and shrubs. Respiration rates are given per unit (1) foliage dry mass ($R_{m,m}$, μmol kg^{-1} s^{-1}), (2) estimated foliage leaf area ($R_{m,a}$, μmol m^{-2} s^{-1}), and (3) foliage N amount ($R_{m,N}$, μmol mol^{-1} s^{-1}). Values in parentheses are standard errors. Correlation coefficients are given for the correlation between $R_{m,m}$ and % Kjeldahl N (r_N) and % Kjeldahl P (r_P)

Location	Species	n	$R_{m,m}$ (μmol kg^{-1} s^{-1})	$R_{m,a}$ (μmol m^{-2} s^{-1})	$R_{m,N}$ (μmol mol^{-1} s^{-1})	N (%)	P (%)	Correlation Coefficient r_N	Correlation Coefficient r_P
Manitoba	*Alnus crispa*	6	6·8 (0·78)	0·58 (0·66)	3·0 (0·25)	3·2 (0·14)	0·21 (0·02)	0·80	–0·42
	Populus tremuloides	4	3·0 (0·38)	0·28 (0·36)	2·4 (0·29)	1·9 (0·02)	0·22 (0·02)	–0·43	–0·95
	Populus balsamifera	10	3·6 (0·45)	0·33 (0·41)	2·9 (0·34)	1·7 (0·06)	0·33 (0·03)	0·45	0·24
	Betula papyrifera	6	3·6 (0·20)	0·27 (0·15)	3·1 (0·20)	1·6 (0·05)	0·29 (0·03)	–0·01	–0·53
	Picea mariana	6	0·94 (0·15)	0·18 (0·29)	2·1 (0·24)	0·6 (0·06)	0·10 (0·01)	0·65	0·81
	Pinus banksiana	7	1·7 (0·33)	0·45 (0·87)	2·0 (0·31)	1·2 (0·10)	0·13 (0·02)	0·62	0·83
	Larix laricina	6	3·2 (0·30)	0·38 (0·35)	2·2 (0·21)	2·1 (0·07)	0·21 (0·01)	0·09	0·61
Colorado	*Alnus tenuifolia*	6	7·6 (0·49)	0·64 (0·41)	3·4 (0·21)	3·1 (0·12)	0·20 (0·01)	0·32	–0·48
	Populus tremuloides	6	3·5 (0·49)	0·32 (0·45)	2·1 (0·35)	2·3 (0·07)	0·24 (0·02)	–0·35	0·00
	Picea engelmannii	3	1·3 (0·06)	0·33 (0·14)	2·0 (0·07)	0·9 (0·02)	0·16 (0·02)	0·79	0·71
	Pinus contorta var. *latifolia*	6	2·1 (0·33)	0·56 (0·86)	2·8 (0·35)	1·0 (0·08)	0·12 (0·02)	0·77	0·40
	Abies lasiocarpa	6	0·99 (0·13)	0·28 (0·35)	1·5 (0·13)	0·9 (0·06)	0·15 (0·01)	0·77	0·63
	Shepherdia canadensis	6	4·1 (0·41)	0·37 (0·38)	2·2 (0·43)	2·7 (0·2)	0·17 (0·02)	–0·74	0·28
	Salix planifolia	4	4·0 (0·58)	0·37 (0·53)	2·1 (0·18)	2·7 (0·16)	0·25 (0·02)	0·97	0·88

sites. Species differed significantly in respiration rates per unit dry mass or estimated leaf area (Table 1); alder had the highest $R_{m,m}$ and $R_{m,a}$ at both sites.

For all species combined, $R_{m,m}$ was strongly correlated with foliar N concentration for both sites (Fig. 3). Slopes for a linear regression of $R_{m,m}$ and foliar N concentration were similar between sites ($P = 0{\cdot}28$), and the intercept term was not statistically significant at either site. Fitting of a zero-intercept linear regression to data from both sites gave the following equation ($r^2 = 0{\cdot}68$, $P < 0{\cdot}01$, $n = 82$):

$$R_{m,m} = 2{\cdot}62\,N, \tag{1}$$

where $R_{m,m}$ is CO_2 efflux from foliar maintenance respiration at 10 °C (μmol kg^{-1} s^{-1}) and N is foliar N concentration (mol kg^{-1}). When $R_{m,m}$ is expressed per unit *shoot* mass (shoots with twigs were enclosed in the chamber for

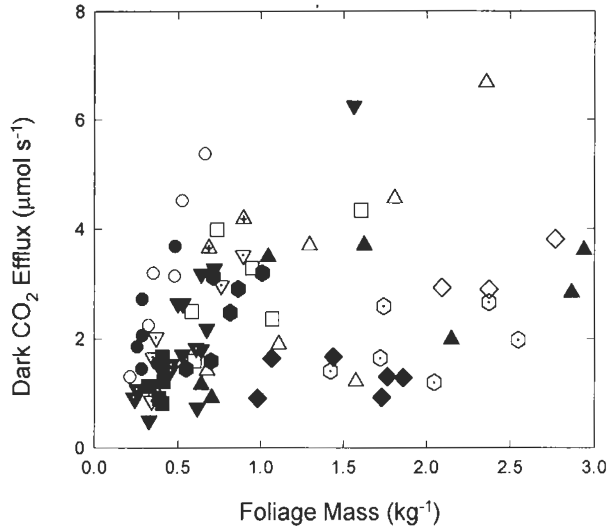

Figure 2. Estimated maintenance respiration (CO_2 efflux at night, corrected to 10 °C) versus dry mass of foliage in sample ($r=0\cdot34$, $p=0\cdot02$ for boreal species; $r=0\cdot27$, $p=0\cdot11$ for subalpine species). Filled symbols are boreal species (■, *Populus tremuloides*; ▼, *Populus balsamifera*; ▼, *Betula papyrifera*; ◆, *Picea mariana*; ▲, *Pinus banksiana*; ⬢, *Larix laricina*; ●, *Alnus crispa*); hollow symbols are subalpine species (□, *Populus tremuloides*; ◇, *Picea engelmannii*; △, *Pinus contorta* var. *latifolia*; ⊙, *Abies lasiocarpa*; ▽, *Shepherdia canadensis*; △, *Salix planifolia*; ○, *Alnus tenuifolia*).

conifers), the correlation between respiration and *shoot* N concentration was slightly greater than that for foliage alone ($r^2=0\cdot72$). Equation 1 is also appropriate for estimating foliar R_m directly from foliar N *content*, because leaf mass occurs on both sides of the equation and can be factored out (i.e. $R_{m,N}=2\cdot62\,\mu mol\ mol^{-1}\ s^{-1}$). Foliar P concentration was only weakly correlated with foliar N concentration ($r=0\cdot34$, $P>0\cdot05$, $n=82$) but did not explain significant additional variation in $R_{m,m}$.

Within a species, $R_{m,m}$ was correlated with foliar N concentration for many, but not all, species (Table 1). In two species (*Populus tremuloides*, *Shepherdia canadensis*), $R_{m,m}$ was negatively correlated with foliar N concentration. Correlations of $R_{m,m}$ and foliar N concentration were similar for deciduous ($r=0\cdot66$, $p<0\cdot01$, $n=54$) and evergreen ($r=0\cdot71$, $P<0\cdot01$, $n=28$) species, but differed strongly between species grouped by whether foliage differentiated into sun and shade morphology (all conifers except larch plus alder and willow: $r=0\cdot94$, $P<0\cdot01$, $n=44$) or did not ($r=0\cdot05$, $P<0\cdot77$, $n=38$).

Species differed in $R_{m,N}$, but the differences were not large (Table 1). For example, using the conservative Tukey's means comparison test, the only significant differences in $R_{m,N}$ were between species with high N (alder, birch and balsam poplar) and subalpine fir. $R_{m,N}$ was lower for shade leaves ($2\cdot17\,\mu mol\ mol^{-1}\ s^{-1}$) than for sun leaves ($2\cdot58\,\mu mol\ mol^{-1}\ s^{-1}$), but the difference was not statistically significant ($P=0\cdot07$). Using the least conservative means-comparison test (least significant difference at $\alpha=0\cdot05$), there were no significant differences in $R_{m,N}$ between pairs of similar species between the boreal and subalpine sites (e.g. Engelmann spruce and black spruce, jack pine and lodgepole pine). $R_{m,N}$ did not vary with foliar N or P concentration (Fig. 4).

DISCUSSION

For individual species, much support exists for the hypothesis that $R_{m,m}$ increases linearly with tissue N content (Kawahara *et al.* 1976; Jones *et al.* 1978; Merino, Field & Mooney 1982; McCree 1983; Waring *et al.* 1985; Irving & Silsbury 1987). This is not surprising, given that an estimated 50–60% of maintenance respiration supports protein turnover (Penning de Vries 1975). Results from this study suggest that maintenance respiration is related to foliar N for a wide variety of species growing in the same environment, and that maintenance respiration per unit N is fairly conservative because $R_{m,N}$ did not differ between the boreal and subalpine sites and the variability in $R_{m,N}$ among species and between leaf types was not large.

However, several species showed no relationship between $R_{m,m}$ and foliar N concentration or a highly variable $R_{m,N}$. For *Populus tremuloides*, *Betula papyrifera*, *Shepherdia canadensis* and *Larix laricina* there were low or negative correlations of R_m and foliar N concentration, even though the relationship between R_m and N for these species fitted the overall pattern (Fig. 3). For these species (but not necessarily for an ecosystem as a whole), the N-

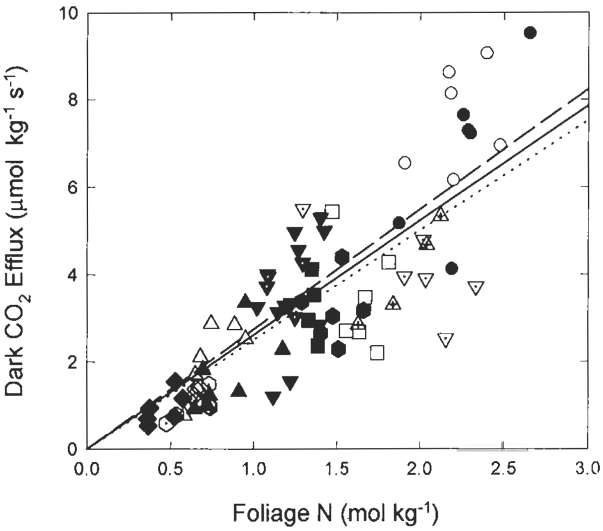

Figure 3. Estimated maintenance respiration corrected to 10 °C per unit leaf mass ($R_{m,m}$, $\mu mol\ kg^{-1}\ s^{-1}$) versus foliage N concentration (N, mol kg^{-1}); $r=0\cdot87$ for boreal species and $r=0\cdot80$ for subalpine species; $P<0\cdot01$. Symbols are as in Fig. 2. The dashed line is for boreal species, the dotted line for subalpine species, and the solid line for all species. A zero-intercept linear regression gave the following equation for data combined from both sites: $R_{m,m}=2\cdot62\times N$ ($r^2=0\cdot68$, $p<0\cdot01$, $n=82$).

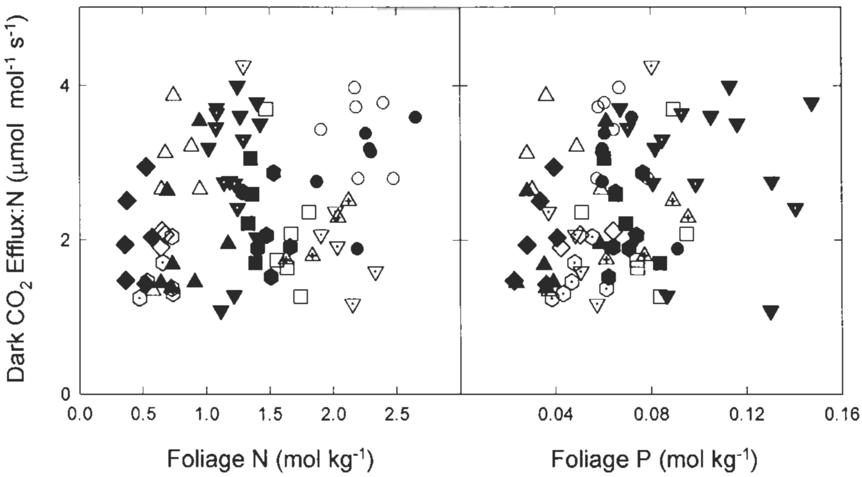

Figure 4. Maintenance respiration per unit foliar N ($R_{m,N}$, mol mol^{-1} s^{-1}) plotted against foliar N and P concentrations (mol kg^{-1}). Symbols are as in Fig. 2.

based respiration model may not be suitable. Interestingly, these species did not appear to form shade foliage in lower light environments (or in the case of *Shepherdia*, only grew in a shady environment). With the exception of *Shepherdia*, the range of foliar N concentration within a species was much lower for those species that showed no relationship between R_m and N (Fig. 3), suggesting that the leaves developed in a similar light environment. Other studies have found a poor or non-existent relationship between R_m and N for individual species (e.g. Byrd *et al.* 1992), and between total respiration and N (Wilson 1975; Woledge & Pearse 1985).

Differences in $R_{m,N}$ could arise from differences in the fraction of N in protein. Foliar protein content is often assumed to be a constant fraction of foliar N, but the protein fraction can vary with season and decrease dramatically under fertilization (Nasholm & Ericsson 1990; Billow, Matson & Yoder 1994). Additionally, the fraction of N in Rubisco can vary markedly among species (cf. Evans 1989). The fact that $R_{m,N}$ differed among species, but was not related to foliage N concentration, suggests that the protein fraction of N may be more variable for these species than the almost uniform 90% reported by Lexander *et al.* (1970). Also, differences in protein composition can affect R_m (Penning de Vries 1975) and perhaps $R_{m,N}$.

Differences in photosynthesis and carbohydrate production could also explain the differences in $R_{m,N}$ between sun and shade foliage and among species. Other studies have shown that bulk respiration varies with photosynthesis (McCree 1982; Azcon-Bieto & Osmond 1983) because carbohydrate concentrations increase with photosynthetic activity. Most of the variability in respiration with carbohydrate levels can be partitioned to growth respiration, but differences in respiration rate related to carbohydrate concentration have been observed in mature wheat leaves (Azcon-Bieto & Osmond 1983) and when carbohydrate export was suppressed (Ho 1979). Also, McCree (1982) found differences in R_m for plants with similar protein contents but different daily assimilation rates. However, even though photosynthetic capacity increases with foliar N (Evans 1989), $R_{m,N}$ in this study did not vary with foliar N concentration (Fig. 4). These results are an interesting contrast to those of Reich & Schoettle (1988), who show that maximum *assimilation* rates per unit foliar N decline with increasing N and increase with increasing P. Also, while the carbohydrate contents of these samples were not measured, starch contents are known to be low at the end of the growing season (Cranswick, Rook & Zabkiewicz 1987; Gholz & Cropper 1991; Billow, Matson & Yoder 1994), when these samples were measured.

$R_{m,N}$ for the foliage of boreal and subalpine trees and shrubs in this study (2·62 μmol mol^{-1} s^{-1} at 10 °C) was 1·8 times the $R_{m,N}$ for a variety of crop and wildland tissues (1·48 μmol mol^{-1} s^{-1} at 10 °C; Ryan 1991) and for perennial ryegrass (1·42 μmol mol^{-1} s^{-1} at 10 °C; Jones *et al.* 1978). The higher $R_{m,N}$ for boreal species is consistent with generally higher respiration rates found for cold-adapted species at a given temperature (Lechowicz, Hellens & Simon 1980; Earnshaw 1981) but suggests that $R_{m,N}$ may vary with growing season temperature. However, because a Q_{10} of 2 was used to adjust respiration estimates from Ryan (1991) and Jones *et al.* (1978) to 10 °C, the use of a different Q_{10} to adjust respiration rates to a common temperature would alter the relative differences among studies.

Despite the general appeal of a nitrogen-based model of maintenance respiration, its use may be limited to ecosystems, such as the boreal and subalpine forests studied here, where N limits plant growth. Currently, however, most temperate and boreal ecosystems are limited by N (Schlesinger 1991). In systems where N is in excess, R_m may poorly match N (M.G. Ryan and R.M. Hubbard, unpublished results) perhaps because protein represents a smaller fraction of foliar N (Waring *et al.* 1985; Nasholm & Ericsson 1990). In white pine (*P. strobus* L.), the proportion of N and P was important for predicting maximum assimilation rates (Reich & Schoettle 1988); perhaps the same applies to R_{m}. The nitrogen-based model for maintenance respiration may not therefore apply to heavily fertilized stands or be useful for estimating forest carbon budgets under heavy atmospheric deposition of N.

CONCLUSION

Foliar maintenance respiration was linearly related to foliar N concentration for a variety of boreal and subalpine trees and shrubs, and $R_{\mathrm{m,N}}$ was the same between sites. For individual species, $R_{\mathrm{m,m}}$ was related to N concentration if foliage showed differentiation into sun and shade foliage and had a large range in foliar N concentration. $R_{\mathrm{m,N}}$ varied somewhat among species, perhaps because N is only a surrogate for protein concentration or photosynthetic activity. Despite the limitations of an N-based model of R_{m}, N content appears to be a more reliable predictor of R_{m} than the traditional tissue-specific rates based on biomass or leaf area. Use of an N-based model of R_{m} would connect R_{m} with the photosynthesis models that link photosynthesis to nitrogen and with models of other ecosystem processes.

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