The controls on net ecosystem productivity along an Arctic transect: a model comparison with flux measurements

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Abstract

Assessments of carbon (C) fluxes in the Arctic require detailed data on both how and why these fluxes vary across the landscape. Such assessments are complicated because tundra vegetation has diverse structure and function at both local and regional scales. To investigate this diversity, the Arctic Flux Study has used the eddy covariance technique to generate ecosystem CO_2-exchange data along a transect in northern Alaska. We use an extant process-based model of the soil–plant–atmosphere continuum to make independent predictions of gross photosynthesis and foliar respiration at 9 of the sites along the transect, using data on local canopy structure and meteorology. We make two key assumptions: (i) soil respiration is constant throughout the flux measurement period, so that the diurnal cycle in CO_2 exchange is driven by canopy processes only (except at two sites where a soil respiration–temperature relationship was indicated in the data); and (ii) mosses and lichens play an insignificant role in ecosystem C exchange, even though in some locations their live biomass exceeds $300 \, g \, m^{-2}$. We found that even with these assumptions the model could explain much of the dynamics of net ecosystem production (NEP) at sites with widely differing vegetation structure and moss/lichen cover. Errors were mostly associated with the predictions of maximum NEP; the likely cause of such discrepancies was (i) a mismatch between vegetation sampled for characterizing the canopy structure and that contained within the footprint of the eddy covariance flux measurements, or (ii) an increase in daytime soil and root respiration. Thus the model results tended to falsify our first assumption but not our second. We also note evidence for an actual reduction in NEP caused by water stress on warm, dry days at some sites. The model–flux comparison also suggests that photosynthesis may be less sensitive to low temperatures than leaf-level gas-exchange measurements have indicated.

Keywords: Arctic tundra, ecosystem model, productivity, respiration

Introduction

Arctic terrestrial ecosystems cover an area of more than 5.5 million km^2, and contain over 26×10^{15} g carbon (C) (Bliss & Matveyeva 1992). Future climatic warming may enhance both primary production (C accumulation) and respiration (C losses) in these ecosystems. Because the net C balance of an ecosystem is the difference between these two large fluxes, a relatively small change in either can have significant impacts on the role of the ecosystem as a sink or source of C (Shaver *et al*. 1992) and thus have important implications for the global C cycle (Oechel *et al*. 1993).

The Arctic Flux Study was set up by the Office of Polar Programs of the National Science Foundation to generate regional estimates of the present and future transfers of energy and materials between the land, atmosphere and

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ocean in the Kuparuk river basin in northern Alaska (Weller *et al.* 1995). Assessing present-day regional fluxes and predicting future net C fluxes requires measurements of the key processes, an understanding of their controlling mechanisms (Chapin *et al.* 1995), and the ability to scale this information across the landscape and over longer periods of time. To meet its goals, the Arctic Flux Study undertook direct measurements of fluxes at several scales, including a field programme of eddy covariance measurements along a 200-km transect running from the headwaters of the Kuparuk river to its mouth on the Arctic Ocean.

Scaling procedures use models and spatially referenced data to generate regional predictions of phenomena. At its simplest, a flux-scaling model can be a phenomenological system, constructed statistically from the actual flux data. However, there are practical and philosophical problems with this approach. First, the hard-won data are used to generate model parameters, and so are not available for validation. Secondly, phenomenological models lack a mechanistic basis, so their diagnostic use is limited and they cannot be used prognostically. Thus, we prefer to use a process-based model that requires a simple set of measurable parameters – completely independent of flux data – against which the model can then be compared. While our goal is to generate predictions that are in close agreement with flux measurements, the discrepancies between model and data serve as useful ecological indicators, identifying where our knowledge is most limited. The model can then be used to investigate the likely causes of such discrepancies. A successful set of tests will ultimately generate confidence in the model as a scaling tool.

In this study we use an extant model of the soil–plant–atmosphere continuum (SPA) that predicts half-hourly fluxes of C and water (transpiration) from plant stands. The model has been applied and validated in temperate and tropical ecosystems (Williams *et al.* 1996, 1997, 1998). These studies indicate that relatively simple descriptions of canopy structure, related to leaf area index (LAI) and canopy foliar N, plant and soil hydraulic parameters, and atmospheric and soil conditions, can describe and explain the majority of the variability in hourly and daily C and LE fluxes in terrestrial ecosystems.

Our approach has some important differences from other models used to study arctic ecosystem function. The GAS-FLUX model (Tenhunen *et al.* 1994) has a similar focus to the SPA model, predicting C exchange in tundra communities on a diurnal timescale. However, it uses species-level detail to describe the canopy, and requires parametrization through multiple gas exchange studies on each of the individual species or physiological types of species. Separate gas exchange studies on mosses and soils are used to derive parameters for the moss and soil

gas exchange submodels. This is a useful approach for analysing in detail a large collection of gas exchange measurements at a single site. However, such a model is difficult to apply regionally, where the species-level details are unavailable. Our goal is to develop a simple model that can be driven with a minimal set of parameters, preferably obtainable via remote sensing (e.g. NDVI seems likely to be closely related to LAI and foliar N), and this requires a different model structure.

Long-term ecological monitoring has already provided some annual estimates of net primary production (NPP) and net ecosystem production (NEP) of the major communities of northern Alaska. Rates of NPP vary from $70\,g\,C\,m^{-2}\,y^{-1}$ in heath, $100\,g\,C\,m^{-2}\,y^{-1}$ in wet sedge tundra, $215\,g\,C\,m^{-2}\,y^{-1}$ in tussock tundra, to $390\,g\,C\,m^{-2}\,y^{-1}$ in riparian shrubs (Shaver & Chapin 1991). These estimates include a fraction of production from nonvascular organisms (mosses and lichens), ranging from 4% in heath and 15% in wetlands, to 22% in shrub and 28% in tussock tundra. Vourlitis & Oechel (1997) summarize the extant estimates of seasonal NEP for wet and moist tundra ecosystems of the North Slope; in 10 studies undertaken between 1971 and 1995, tundra ecosystems were on average net sinks for CO_2 during the growing season, with a seasonal average of $22\,g\,C\,m^{-2}$, though the standard deviation was large (± 38). Over the past 25 years, Vourlitis & Oechel (1999) conclude that tundra ecosystems have alternated between net C sinks and sources.

Objectives

Our intention in this paper is to test the hypotheses embodied in our detailed model of canopy processes (Williams *et al.* 1996) against the multiple datasets collected along a transect in northern Alaskan during the Arctic Flux Study. Our goals are to use this comparison to: (i) isolate the key variables that control net C fluxes along this transect; (ii) investigate the relative contributions to ecosystem net C fluxes of mosses and lichens vs. vascular plants; (iii) investigate how these controls and contributions vary with geographical location; (iv) determine the weaknesses in our current understanding of arctic ecosystem gas exchange; and (v) develop a strategy to use our model to predict regional C exchange.

Methods

The study area

The Arctic Flux Study (AFS) undertook intensive field measurements during 1994–6 along a N–S gradient within, or near to, the $9200\,km^2$ Kuparuk river watershed that lies between latitudes 68° and 70°N in northern

Alaska (Weller *et al.* 1995). The AFS employed two mobile systems to sample fluxes over 9–14 days at each of 25 sites in a 200-km latitudinal band between the Brooks range and the coast (Eugster *et al.* 1997; McFadden *et al.* 1998). The sampled sites were chosen to reflect the range of soil moisture, climate and major vegetation types present in the study region, based on a satellite-derived vegetation classification (Muller *et al.* 1998). The main vegetation categories are tussock tundra, wetland tundra, shrub tundra, and heath (Walker & Walker 1996). Within these categories, there are subdivisions into acidic (pH < 5.0) and nonacidic (pH > 5.0) types, based on soil classification (Walker *et al.* 1998).

Flux measurements were undertaken during the growing season, which in northern Alaska lasts 70–100 days, from June to late August. Weather data collected alongside flux readings indicated that the mean daily maximum and minimum temperatures for all sites over the measurement periods were 15.8 °C and 6.4 °C, respectively. Although the maximum solar elevation at 68°N is only ~45°, the long days ensured that total daily irradiance was similar to that recorded in more temperate latitudes; the daily short-wave energy sum for all sites during flux measurements averaged 15.3 MJ m^{-2} d^{-1}.

Eddy covariance measurements and ecosystem structural data

The technique of eddy covariance determines the surface-normal flux of CO_2 by calculating the covariance between fluctuations in vertical wind velocity and CO_2 concentration (Moncrieff *et al.* 1997). The relevant instrumentation was set up on mobile towers, at a height 1.5–2.0 m above the aerodynamic displacement height (vegetation was typically < 40 cm). Each tower consisted of a foldable 3 m tall tripod, a SWS-211/3 V or SAT-211/3Vx sonic anemometer (Applied Technologies, Boulder, Colorado, USA), a Li-Cor 6262 infra-red gas analyser (Li-Cor Inc., Lincoln, NB, USA), and radiation, air and soil temperature and humidity sensors (see Eugster *et al.* 1997 for a complete description). Data were processed to remove spikes in sonic anemometer data and to correct fluxes for damping and high-frequency losses (Eugster & Senn 1995).

The two towers were run adjacent to each other to determine the relative accuracy of the equipment; on average, the differences in daily sums of fluxes must be greater than 15% for CO_2 flux to be considered true ecosystem differences rather than a difference due to measurement error. This error compares favourably with those determined for other systems (Nie *et al.* 1992; Foken & Wichura 1996). A flux source area model (Schmid & Oke 1990) estimated that 80–95% of the daytime flux footprint was within a 100 m × 100 m square area centred on the tower (Eugster *et al.* 1997).

Between 19 and 26 July 1997, we visited nine of the locations sampled by the mobile towers (Table 1). At each location we randomly selected ~7 points within a 30-m radius of the location of the eddy flux tower and sampled the vegetation within a 20 cm × 20 cm quadrat. In the laboratory, we determined the percentage cover of each quadrat by moss and lichen, using a point frame. We determined moss and lichen photosynthetic (i.e. green) biomass by coring subsamples from quadrats and scaling with cover estimates. We determined biomass and one-sided leaf area of green foliage by species (the exception being graminoids, which were sampled as a combined group) using destructive harvests. We did not collect woody material or identify moss, lichen or graminoids by species. We determined nitrogen content of foliage, mosses and lichens using a CHN analyser (Perkin Elmer,

Table 1 Vegetation characteristics of the study sites, and mean soil and air temperature during the periods when flux measurements were collected. Soil temperature is an integrated measure from 0 to 5 cm. SE=standard error

Site	Vegetation type	Total moss +lichen photosynthetic biomass (g m^{-2})	Air temperature (°C), mean (SE)	Soil temperature (°C), mean (SE)	Vascular plant one-sided LAI (m^2 m^{-2}), mean (SE)	Vascular plant foliar N (g m^{-2} ground area), mean (SE)
1	Coastal wet tundra	132	10.3 (3.9)	4.9 (1.2)	0.52 (0.06)	1.05 (0.09)
2	Coastal wet tundra	13	10.3 (3.5)	8.3 (1.5)	0.28 (0.04)	0.68 (0.10)
3	Non-acidic tussock tundra	281	7.1 (4.1)	3.3 (1.2)	0.37 (0.06)	0.60 (0.11)
4	Acidic tussock tundra	357	9.8 (5.2)	6.8 (2.9)	0.63 (0.05)	1.03 (0.10)
6	Acidic tussock tundra	126	6.9 (4.5)	3.6 (1.0)	0.70 (0.08)	1.41 (0.20)
9	Shrub (river bar)	5	15.8 (4.1)	15.3 (1.7)	1.53 (0.36)	2.25 (0.51)
13	Alder tussock tundra	93	13.4 (3.2)	9.5 (1.3)	0.81 (0.09)	1.43 (0.16)
14	Acidic tussock tundra	83	13.2 (3.2)	10.3 (2.1)	0.69 (0.10)	1.13 (0.12)
Heath	Heath	168	12.8 (2.8)	14.7 (2.0)	0.66 (0.20)	1.08 (0.27)

Norwalk, CT). Full details of the experimental methods and results are described in Williams & Rastetter (1999).

The soil–plant–atmosphere model

The soil-plant-atmosphere canopy model (SPA; see Williams et al. 1996 for a full description) is a multilayer simulator of C3 vascular plant processes. The model links leaf-level photosynthesis (Farquhar & von Caemmerer 1982) and transpiration with a model of stomatal conductance (g_s) that optimizes daily C gain per unit leaf N, within the limitations of canopy water storage and soil-to-canopy water transport. The model assumes that maximum carboxylation capacity and maximum electron transport rate are proportional to foliar N concentration, and that foliar respiration is also a function of N concentration and leaf temperature. The model does not treat each species in the ecosystem individually, but instead treats the system as a single functional type, described by vertical variations in light absorbing area (LAI), photosynthetic capacity (foliar N), and plant hydraulic properties. The model has been modified to introduce a revised radiation subroutine that calculates sun-lit and shaded fractions of the foliage in each canopy layer (Norman 1981). Sun-lit fractions are lit by both incident and diffuse radiation, while the shaded fractions receive only diffuse radiation.

We made only four changes to the original model parametrization as applied to temperate forests (Williams et al. 1996): (i) to account for acclimation to the cool arctic climate, we reset the optimum temperature for plant metabolism from ~25 °C to ~18 °C, which is close both to the mean maximum temperature for the study period and to measured optima for arctic plants (Semikhatova et al. 1992; Oberbauer et al. 1996). We ensured that photosynthetic rates at 5 °C were 60–65% of their maxima. (ii) We set the canopy minimum leaf water potential at all sites to –1.5 MPa (Oberbauer & Dawson 1992). (iii) We used our site-specific measurements of LAI and total canopy nitrogen (Williams & Rastetter 1999). Because of the small stature of tundra vegetation and relatively sparse canopies, we reduced the number of canopy layers from ten to two, dividing LAI and N equally among them. Canopy height was set to 0.3 m and the length of a typical leaf to 0.01 m. (iv) We simplified the hydraulic scheme, applying a constant soil–root–shoot hydraulic conductance to each layer. Evapotranspiration and leaf water potential data collected on *Eriophorum vaginatum* and *E.angustifolium* at Toolik Lake, Alaska (Gebauer et al. 1998) suggested that a total soil–root–shoot hydraulic conductance of $1 \, \text{mmol m}^{-2} \, \text{s}^{-1} \, \text{MPa}^{-1}$ was appropriate.

Predictions of canopy photosynthesis and respiration were compared with flux measurements of net ecosystem production. However, this comparison necessitated an estimation of the ecosystem woody material respiration and below-ground respiration, neither of which were measured at the sites.

Characterizing respiration

Eddy covariance systems provide continuous measurements of net ecosystem C exchange, the sum total of heterotrophic and autotrophic metabolisms. Because our canopy model is primarily concerned with C fixation by vascular plants, and does not simulate the activity of soil microbes, stems, and roots, the model products are not directly comparable with the ecosystem data – we require an estimate of ecosystem respiration (the major proportion of which is from belowground, arising from the respiration of roots and the soil biota). In temperate ecosystems, night-time measurements of NEP during well-mixed periods have been used to ascertain ecosystem respiration (Goulden et al. 1996). However, in the arctic summer, photosynthesis can occur 24 h per day. In such instances, minimum NEP is not determined purely by heterotrophic processes.

We used a fraction of the night-time eddy covariance data to estimate the combined respiration rate of soil, roots, stemwood, moss, and lichen (R_e). We determined on each day the mean NEP from flux data collected between 00:30 and 02:30 hours, Alaska Daylight Savings Time. In calculating this mean value, we discounted some outlying data. We then used the SPA model to estimate GPP and foliar respiration during the same period each day. At only one site (6) did the SPA model predict a complete cessation of photosynthesis (incident photosynthetically active radiation consistently dropped below $5 \, \mu\text{mol m}^{-2} \, \text{s}^{-1}$ for several hours each night). Due to their more shaded positions, we assumed that moss and lichen photosynthesis were effectively zero at all sites at this time because of low light. With these assumptions, and given that NEP is the sum of GPP and ecosystem respiration, we were then able to estimate R_e for each day at each site.

In 7 out of the 9 sites we found no relationship between the estimates of daily R_e and the minimum night-time temperature of the upper 5 cm of soil. The lack of a relationship was partly a result of the few data used (typically 4–9 points) and partly because the temperature range between successive nights was small. The two sites with statistically significant relationships were among those with the coldest soils (Tables 1 and 2; sites 3 & 6); these relationships indicated that R_e could double or triple with a rise in soil temperature of only 2 or 3 °C, suggesting Q_{10} values very much greater than typical (i.e. $\gg 2.0$). We developed linear regressions for these two sites and used them to estimate R_e (we found that

our final predictions of NEP were better with R_e determined by linear rather than exponential relationships to soil temperature). For the remaining sites we set ecosystem respiration as constant and equal to the mean of the calculated R_e values for that site (Table 2). We examined whether these constant values (and estimates of R_e at the mean minimum soil temperatures for the two temperature-responsive sites) had any relationship with measured soil characteristics. We could find no statistically significant relationship with our site-specific measurements of depth of thaw, depth to water table or depth of the organic matter layer. However, we did find statistically significant positive correlation between R_e and both vascular plant biomass ($P < 0.05$) and foliar N content ($P < 0.1$).

Previous research suggests that soil temperature, soil moisture, depth of thaw, depth of water table and nutrient status may be controlling factors for ecosystem CO_2 efflux (Oberbauer *et al*. 1991). However, soil respiration tends to show less diurnal variability than photosynthesis, even in the long days of the arctic, because microbial processes are not light-limited. The insulating properties of the dense moss layer and the presence of permafrost tend to ensure that soil temperatures in the arctic are low and less variable than air temperatures (Table 1). Furthermore, incubations of arctic soils have indicated that rates of C mineralization are insensitive to temperatures between $3°$ and $9°C$ (Nadelhoffer *et al*. 1991). Thus, the assumption of invariant R_e for the majority of sites is not unreasonable.

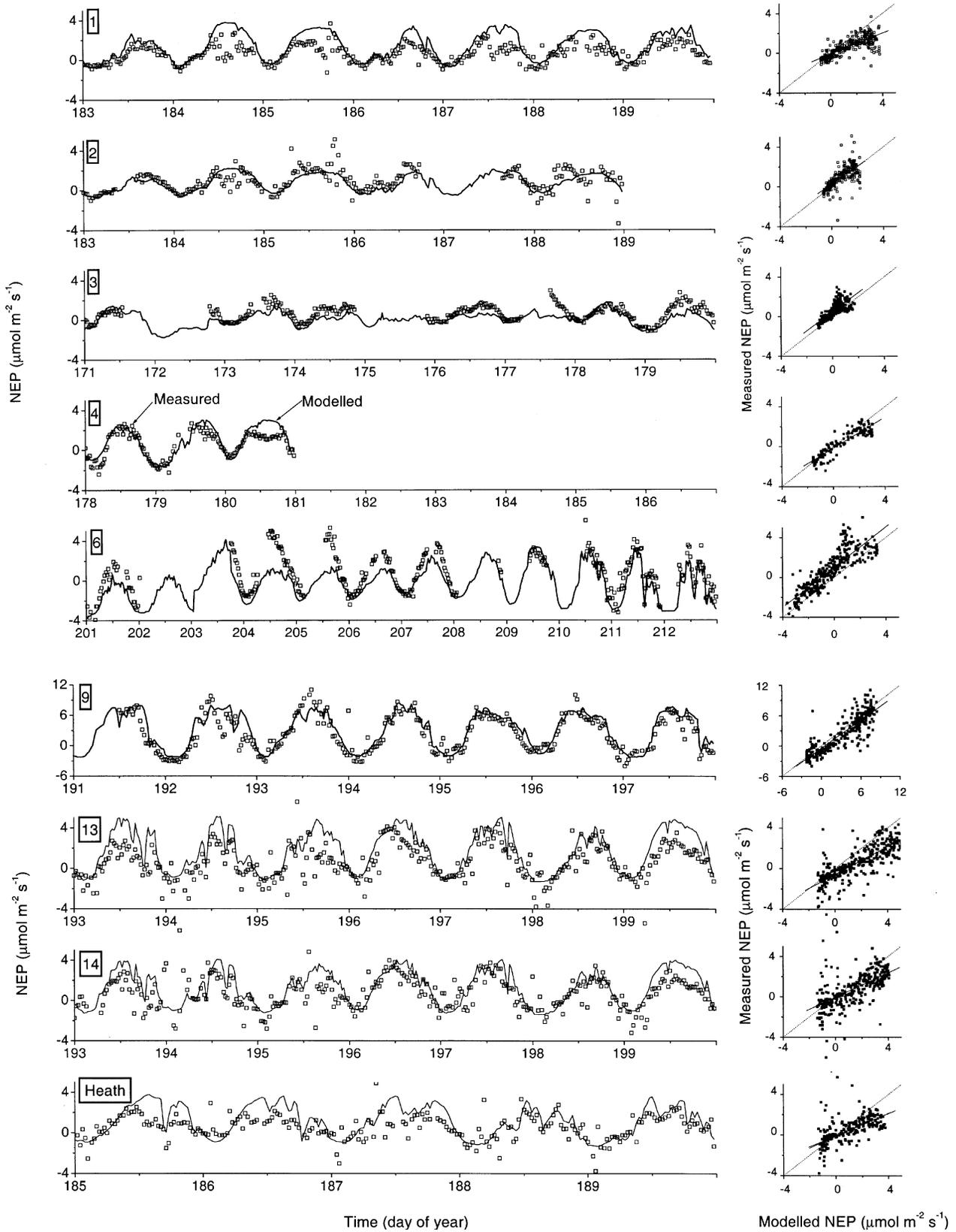## The role of moss and lichens

Arctic ecosystems often have a significant moss and/or lichen biomass (Tenhunen *et al*. 1992). The photosynthetic rates of mosses and lichens, on a dry weight or area basis, are much lower than those of C3 plants (Green & Lange 1994). In arctic ecosystems, the contribution of mosses and lichens to NPP has previously been estimated by harvest measurements. *Sphagnum* moss NPP on the North Slope ranged from $5\,g\,C\,m^{-2}\,y^{-1}$ in tussock tundra vegetation, to $82\,g\,C\,m^{-2}\,y^{-1}$ in well-shaded water tracks (Murray *et al*. 1989b); both the sites in the Murray *et al*. study had a moss biomass $> 300\,g\,m^{-2}$. Chapin *et al*. (1995) estimated that nonvascular NPP in tussock tundra at Toolik Lake was $35–40\,g\,C\,m^{-2}\,y^{-1}$. The large differences in productivity seem to arise because mosses tend to be strongly photoinhibited and are sensitive to water availability (Murray *et al*. 1989a). At the 9 sites we measured, moss biomass ranged from 10 to $327\,g\,m^{-2}$ or from 4 to 81% of the total photosynthesizing biomass (Table 1). Lichen biomass ranged from 0 to $149\,g\,m^{-2}$, or from 0 to 59% of the total photosynthesizing biomass (Table 1).

Our model of vascular plant processes is not an effective predictor of the metabolic activity of poikilohydric organisms like mosses and lichens, because our scheme of stomatal control linked to plant hydraulics is not applicable to nonvascular organisms. An effective model would have to determine the energy balance and dynamic water status of the organism, and resultant effects on photosynthesis. To be broadly applicable, the

Table 2 Estimated mean soil, woody & nonvascular biomass respiration (R_e, $\mu mol\ m^{-2}\ s^{-1}$) over the measurement period at each site, and the linear regression statistics for measured vs. modelled net ecosystem productivity at each site. Standard errors of slope and intercepts are shown in parentheses. T_s is soil temperature

| Site | Estimated R_e | Measured vs. modelled NEP | | |
		r^2	Slope (SE)	Intercept (SE)
1	0.94	0.60	0.53 (0.02)	−0.09 (0.05)
2	0.75	0.49	0.90 (0.06)	0.26 (0.07)
3	$-0.24 + 0.42 \times T_s$	0.59	0.97 (0.05)	0.5 (0.03)
4	1.60	0.80	0.78 (0.03)	−0.16 (0.06)
6	$0.35 + 0.74 \times T_s$	0.73	1.00 (0.03)	1.00 (0.06)
9	2.00	0.78	0.92 (0.03)	−0.47 (0.13)
13	1.17	0.62	0.69 (0.03)	−0.58 (0.08)
14	1.28	0.22	0.60 (0.06)	−0.03 (0.13)
Heath	1.37	0.42	0.55 (0.04)	−0.08 (0.08)

Fig. 1. Left-hand panels show time-course of predicted (solid lines) and observed (□) net ecosystem productivity (NEP) at the 9 tundra sites. Sites are identified by number (see Table 1). Time is given in day of year (day 171 = 20 June), Alaska Daylight Savings Time. Right-hand panels shows the direct comparison of measured vs. modelled NEP, with both the regression line (solid) and the 1 : 1 line (dotted) also plotted. Regression statistics are listed in Table 2. Note different scale for site 9.

NEP (μmol m^{-2} s^{-1})

Measured NEP (μmol m^{-2} s^{-1})

Measured NEP (μmol m^{-2} s^{-1})

Time (day of year)

Modelled NEP (μmol m^{-2} s^{-1})

model would require a few simple, mechanistically sound and validated parameters to describe moss function, in the way that LAI and foliar N concentration provide very workable descriptions of canopy light absorption and metabolic capacity in vascular plants. While we do not present such a model, our goal in this analysis was to generate insights into succeeding at this task. Our intention in this paper was to make predictions of C exchange using the SPA model of vascular plant processes and our empirical estimate of R_e. Discrepancies between predictions and measurements were then investigated in the light of information concerning moss and lichen components of each community.

Results

Coastal wet tundra

In arctic coastal tundra (sites 1 and 2) net ecosystem production ranged between –1 and 3 µmol C m^{-2} s^{-1} (a positive flux indicates a net uptake of C by the ecosystem; as a rule of thumb, a flux of 1 µmol C m^{-2} s^{-1} would scale to ~1 g C m^{-2} d^{-1}). Even though these data were gathered shortly after the summer solstice (day of year 172), a period of 24 h daylight, we still observed a strong diurnal cycle in fluxes. Our flux predictions capture both the form and the magnitude of the diurnal cycle (Fig. 1) and could explain 60% and 49% of the variance in fluxes (Table 2). A regression analysis of modelled vs. measured NEP showed that the model tended to overestimate maximum NEP at site 1 (Fig. 1).

Tussock Tundra

Carbon fluxes in nonacidic tussock tundra (site 3) varied between –2 and 2 µmol m^{-2} s^{-1}. In acidic tussock tundra (sites 4, 6, 13 and 14), NEP varied diurnally between –2.5 and 4 µmol m^{-2} s^{-1}, although site 4 was less productive and respiration at site 6 was sensitive to temperature. Our predictions at sites 4 and 6 were among the best, explaining >73% of variance in the data (Fig. 1 and Table 2). The poorest fit was at site 14; early in the measurement period there were highly intermittent night-time fluxes (Fig. 1), which are thought to be caused by meteorological conditions that are outside the scope of our SPA model, which assumes continuous (not intermittent) turbulence in the atmosphere; when data from midnight to 06:00 hours were removed at site 14, the model could explain 52% of measured variance.

At site 6 the model captures the impact of variable cloudiness on productivity on days 211 and 212, though it underestimates the maximum NEP on a number of days (204–207). These days were cold, with freezing nights. Sites 13 and 14 are colocated on a tussock tundra hillside with similar vegetation – apart from the presence of alder at site 13 – and flux measurements were collected at these sites contemporaneously. The measured and predicted fluxes are slightly greater at site 13, the more densely vegetated of the two, and there is greater scatter among the data at site 14. The regression statistics at both sites show slopes < 0.70, which suggests a tendency for maximum predicted NEP to be greater than measured values; the figures show that much of this trend can be traced to a large over-estimation of NEP at both sites on day 199. This was a bright, warm day with a large vapour pressure deficit (VPD > 1.5 kPa in the afternoon).

Heath tundra

At the heath site, diurnal NEP varied between –2 and 2.7 µmol m^{-2} s^{-1}. The heath site was sampled contemporaneously by two separate towers; the flux data presented here are the mean of these two datasets. The flux amplitudes at the heath site were among the lowest, and the data were often scattered, so that the model could only explain 42% of the observed variance. The model tended to over-predict maximum NEP during the sunny conditions of the first two days, whereas predictions during the overcast conditions at the end of the measurement period are in much closer agreement with the data (Fig. 1).

Riparian shrub tundra

The shrub tundra site (9) had the greatest diurnal amplitude in fluxes, with NEP ranging between –3 and 9 µmol m^{-2} s^{-1}. This site had the highest LAI, a large depth of thaw and unrestricted water availability in a sandy soil. The model effectively tracks the dynamics of net C fluxes (Fig. 1), and the slope of the regression line is among the closest to unity (Table 2).

To summarize, the statistical analysis (Table 2) shows that the closest agreements between model and data occur in tussock tundra and shrub tundra communities, followed by wetland tundras, with the poorest fit in heath tundra. In sites 1, 4, 13, 14 and heath, there was a tendency to over-predict maximum NEP.

Discussion

The discrepancy between the measured values and the model reflect potential errors and biases in both the measurements and the model. For example, low windspeed and low turbulence that frequently occur at night can lead to a systematic underestimate of

night respiration (i.e. an overestimate of minimal daily values of NEP). Thus, our estimates of R_e are potentially too small, which might reduce the discrepancy between the model and midday measurements of NEP.

Discrepancies between predictions and measurements are mostly associated with some poor predictions of maximum productivity and ecosystem respiration. However, the dynamics of C exchange – the timings of variability – are well explained – and plots of measured vs. modelled NEP (Fig. 1) do not suggest curvature in their relationships. Because the diurnal cycle in C exchange is governed primarily by variation in photosynthesis linked to changes in irradiance, the generally close dynamical correspondence between our model and data suggests that our two-layer radiation model is sufficient to capture the basic light response of photosynthesis in arctic conditions of low sun angle and sparse canopies. It also suggests that our simple representation of arctic canopy light interception, using LAI measurements and the assumption of a spherical leaf angle distribution, is adequate. We have made no attempt to parametrize our model for different growth forms (e.g. graminoids vs. shrubs). Thus, our results suggest that that the important differences in the photosynthetic capacity of the species that occur in each vegetation type can be simply summarized in terms of LAI and total foliar N. This result is consistent with comparisons across biomes in which there is a common regression line between absorbed photosynthetically active radiation (closely related to LAI) and NPP; i.e. ratios of dry matter production to integrated energy absorbed are similar across many different ecosystem types (Field 1991).

The observed trends in NEP are largely explained within the SPA model by simple descriptions of canopy N and LAI. Because the proportional differences in LAI and total canopy N between arctic ecosystems are large (up to an order of magnitude), and because the model is so sensitive to variation in these parameters at the relatively low levels at which they occur in the arctic (Williams & Rastetter 1999), precisely determining the correct and representative LAI and N data is critical for accurate NEP predictions. While the direct measurement techniques that we employed are accurate, our sampling may not be representative of the much larger and more directional 'footprint' that the eddy covariance system samples. There is also significant vegetation heterogeneity at fine scales that our sampling of 5–10 quadrats may have failed to capture. For example, on the coastal tundra our measurement of LAI at site 1 was significantly greater ($P < 0.01$) than at nearby site 2. Yet the fluxes at the two sites were not noticeably different (Fig. 1). Vegetation heterogeneity may be responsible for our overestimation of LAI and, thus, C uptake at site 1. (It is also possible that

the different moisture conditions at the two sites may affect gas exchange; site 1 had high-centred ice polygons with dry centres, while site 2 had low-centred polygons with moist centres.) The sampled vegetation quadrats at the Heath site had the highest coefficient of variation in LAI among all sites. The structure of the heath vegetation tends to correlate with the micro topography, with denser vegetation in sheltered hollows, and sparser canopies on hummocks. Because of this heterogeneity and our small sample size, we think it probable that at this site our vegetation sample is not representative of the vegetation within the footprint. However, it is unlikely that a sampling problem can explain the tendency of the model to slightly overestimate NEP at a number of the sites – such an error should be unbiased.

There are several possible explanations for the tendency to overestimate NEP at a number of the sites.

1 A diurnal variation in soil and root respiration (the main components of R_e) results in higher soil CO_2 effluxes during warmer midday periods; this would systematically reduce our estimates of NEP. There is supporting evidence for this hypothesis; field studies have measured diurnal cycles in soil CO_2 effluxes, linked to variations in soil temperature (Oberbauer *et al*. 1991). A simple model that can explain the magnitude and cycles of ecosystem respiration is clearly a priority for effective scaling of C exchange.

2 The relationships between foliar N content and the photosynthetic parameters originally parametrized from temperate vegetation (Williams *et al*. 1996), may differ for arctic vegetation. If these parameters were lower for a given N content, our predictions of maximum photosynthetic rates (and thus NEP) would be reduced. Leaf level gas exchange studies to relate foliar N content to the key photosynthetic parameters in arctic plants would test our assumption that these relationships are globally conservative.

3 Water stress may reduce productivity on warm, dry days at some sites. For example, in the sunny conditions on day 199 at sites 13 and 14, and on day 180 at site 4, the model predicts that high insolation should result in a broad peak of NEP during several hours at mid-day. The data show that fluxes fail to reach these peaks (Fig. 1). A sensitivity analysis with SPA shows that C fixation on these days would have been restricted by a lower soil–plant hydraulic conductance ($0.25 \, \mathrm{mmol \, m^{-2} \, s^{-1} \, MPa^{-1}}$). When atmospheric demand for water exceeds the capacity of the plant–soil system to supply water, because of reduced hydraulic conductance or lower soil water potential, stomata close to constrain water loss to the atmosphere, thus inhibiting C uptake and reducing NEP. The mismatch on days 180 and 199 suggests that hydraulic conductance at these sites may be lower than we parametrized.

While the SPA model did not identify stress at sites 4, 13 and 14, it did so successfully at the shrub site (9). During the final three days of flux measurements, conditions were very warm, cloudless and dry (VPD > 1.7 kPa), and afternoon fluxes declined slightly from morning peaks. In the SPA model, stomata close due to hydraulic stress at high VPD, photosynthesis is reduced, and modelled NEP tracks the measured fluxes. Thus, the hydraulic parametrization is valid at this site. Why are NEP responses to high VPD different between site 9 and sites 4, 13 and 14? Site 9 is located on a river bar over deeply thawed soils (> 0.9 m), while sites 4, 13 and 14 are underlain by permafrost at 0.33–0.45 m. A shallow thawed layer may explain why vegetation at sites 4, 13 and 14 is more vulnerable to soil drying.

At two sites (3 and 6) modelled NEP underestimates measured fluxes during periods of low temperatures and relatively low irradiance: days 176–177 at site 3 (maximum temperatures of 6 °C) and days 204–208 at site 6 (maximum temperatures of 4–9 °C). Predicted leaf level temperatures are no more than 1 °C warmer than air temperature at these times. The underestimate suggests that photosynthesis may not be as constrained by low temperatures as the observations in leaf-level studies at Imnavait creek by Oberbauer *et al.* (1996) suggest, even though site 6 and Imnavait creek are only 10 km apart. However, a sensitivity test with SPA shows that keeping photosynthetic rates at 95% of their maxima at 5 °C reduced, but did not remove, the modelled underestimate. This suggests that variations in ecosystem respiration at these sites are not properly accounted for. Sites 3 and 6 are the only sites where a diurnal variation in R_e, based on temperature, is modelled. We found that fluxes during these cold periods could be matched only if R_e was held constant and photosynthetic rates were set to 95% of their maxima at 5 °C. These results suggest that temperature sensitivity of both plants and soils needs to be examined in more detail.

The multisite comparison has ignored the contribution of mosses and lichens to C exchange. The excellent NEP predictions at site 9, the site with the least moss and lichen biomass, indicate that the SPA model accounts for the behaviour of arctic vascular plants satisfactorily. If nonvascular plants played a significant role in ecosystem productivity, we would expect that, in those sites where they formed a large proportion of the photosynthetic biomass, our predictions of NEP would be clear underestimates of the observed fluxes. However, the statistical analysis (Table 2) indicates that the common tendency is for the model to slightly overestimate NEP. Some of the highest moss biomasses were observed at sites 3 and 4, yet the daily amplitude of NEP at these sites is relatively low and can be explained purely by the interaction of local meteorological variability and the characteristics of the vascular plant community.

Thus, our model results suggest that mosses and lichens play a minor role in determining the diurnal character of NEP during the measurement periods; i.e. moss and lichen photosynthetic rates make up a much smaller fraction of gross ecosystem productivity than do those of vascular plants. However, some previous studies have ascribed a significant proportion of ecosystem productivity to nonvascular plants (see above: The role of moss and lichens). There are several possible explanations for the apparent discrepancy between our conclusions and these other data. (i) Mosses and lichens are most active early and late in the growing season (i.e. outside the period when the flux measurements were made); moisture conditions may be more favourable at these times and photoinhibition may be less severe. However, this is unlikely to be a complete explanation because the flux measurements spanned a fair part of the season, and included moist conditions when mosses should be active. (ii) Harvest measurements used in previous studies might have overestimated moss production – which is likely as there are very few direct measurements of moss production in Alaska, and the methods used are imprecise. (iii) The diurnal pattern of moss photosynthesis might differ from that of vascular plants, because mosses light-saturate at low light, have a low light compensation point, and their photosynthesis is reduced by high light or moss drying (Harley *et al.* 1989). If mosses had close-to-constant photosynthesis through the diurnal cycle, then we may have inadvertently incorporated moss carbon exchange into the R_e term, in which case we would not expect to see any effect of mosses on the diurnal pattern of NEP. Further studies to determine the dynamics of moss and lichen NEP across arctic ecosystems are required.

We conclude that species level details are not required to explain landscape variations in short-term C fluxes. Instead, LAI and foliar N differences explain much of the intersite variability. Our field studies have also demonstrated a strong relationship between LAI and total canopy N (Williams & Rastetter 1999), which simplifies the information required to generate landscape-level predictions of canopy productivity, because it suggests that we can use LAI data to infer canopy foliar N. This assumption greatly simplifies the task of generating a regional C budget, because it removes the need for species level data and for chemical analyses of foliage. Instead, remote sensing studies can focus on describing the landscape variation in LAI (e.g. using NDVI), and total canopy N can be predicted empirically, though this assumes that foliar N concentrations do not change over the growing season (Chapin & Shaver 1996). However, over longer timescales, species effects will be more

important, because of their control on seasonality of growth, allocation and litter quality. In a warmer, high CO_2 world, the relationship between LAI and foliar N may alter. Manipulation experiments (Chapin *et al.* 1995) coupled with biogeochemical ecosystem models (McKane *et al.* 1997) will provide insights into these issues.

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