

What is the relationship between changes in canopy leaf area and changes in photosynthetic CO₂ flux in arctic ecosystems?

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Summary

1 The arctic environment is highly heterogeneous in terms of plant distribution and productivity. If we are to make regional scale predictions of carbon exchange it is necessary to find robust relationships that can simplify this variability. One such potential relationship is that of leaf area to photosynthetic CO₂ flux at the canopy scale.

2 In this paper we assess the effectiveness of canopy leaf area in explaining variation in gross primary productivity (GPP): (i) across different vegetation types; (ii) at various stages of leaf development; and (iii) under enhanced nutrient availability. To do this we measure net CO₂ flux light response curves with a 1 × 1 m chamber, and calculate GPP at a photosynthetic photon flux density (PPFD) of 600 μmol m⁻² s⁻¹.

3 At a subarctic site in Sweden, we report 10-fold variation in GPP among natural vegetation types with leaf area index (LAI) values of 0.05–2.31 m² m⁻². At a site of similar latitude in Alaska we document substantially elevated rates of GPP in fertilized vegetation.

4 We can explain 80% of the observed variation in GPP in natural vegetation (including vegetation measured before deciduous leaf bud burst) by leaf area alone, when leaf area is predicted from measurements of normalized difference vegetation index (NDVI).

5 In fertilized vegetation the relative increase in leaf area between control and fertilized treatments exceeds the relative increase in GPP. This suggests that higher leaf area causes increased self-shading, or that lower leaf nitrogen per unit leaf area causes a reduction in the rate of photosynthesis.

6 The results of this study indicate that canopy leaf area is an excellent predictor of GPP in diverse low arctic tundra, across a wide range of plant functional types.

Key-words: Alaska, Arctic tundra, carbon balance, CO₂ flux, gross primary productivity, landscape heterogeneity, leaf area index, light response, normalized difference vegetation index, Sweden

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Introduction

Climate change is predicted to affect high latitudes both sooner and more intensely than the rest of the globe. Significant warming has already been observed in arctic regions, together with increased precipitation, thawing of permafrost and earlier snow melt; in Alaska, for example, winter temperatures have increased by up to 3–4 °C in the past 50 years (ACIA 2004). Regional arctic warming will feed back on the global climate

system if large amounts of carbon presently stored in terrestrial ecosystems are released in to the atmosphere (Oechel *et al.* 1993). This release may result from enhanced soil microbial activity due to higher temperatures or a lowering of the water table (Oechel & Billings 1992; McGuire *et al.* 2000). The concurrent increase in nitrogen mineralization, however, may stimulate plant growth in what are generally nutrient-limited systems (Shaver & Chapin 1980, 1986; Chapin *et al.* 1995). Combined with warmer, longer growing seasons, enhanced plant carbon sequestration may offset losses of carbon from the soil. Studies have already indicated that the composition of arctic vegetation is changing

(Myneni *et al.* 1997; Sturm *et al.* 2001), so it is important to understand how structural and compositional differences in vegetation will affect ecosystem processes. Quantification of the balance between plant productivity and ecosystem respiration in the arctic is critical to accurate forecasting of future climate scenarios.

Predicting plant productivity in the arctic is difficult due to the highly heterogeneous nature of tundra vegetation; within a single small catchment communities may range from unproductive dry heath on exposed hillcrests to dense, highly productive woody shrubs near water tracks (Walker *et al.* 1994). These communities differ markedly in biomass, leaf area and functional type composition (systems dominated by graminoids, deciduous and evergreen shrubs, are all common). It is well established that leaf level photosynthetic characteristics vary within and between individuals, species and functional types (Oberbauer & Oechel 1989; Shaver & Chapin 1995), so in order to make landscape-scale carbon budgeting feasible it is necessary to find simplifying relationships that hold for whole ecosystems. One useful emergent ecosystem property is the tight relationship between leaf area and total canopy nitrogen that exists in low arctic vegetation regardless of species composition (Williams & Rastetter 1999; van Wijk *et al.* 2005). This relationship suggests that the environment imposes strict controls on plant canopy development, such that, on average throughout the canopy at peak season, nitrogen per unit leaf area remains constant despite considerable differences within and among species (Stoner *et al.* 1982). Canopy nitrogen and leaf area have been shown to be major long-term controls on arctic plant productivity (Williams & Rastetter 1999), so it follows that if a tightly constrained leaf area index (LAI)–N relationship exists across communities, a similar universal relationship may exist for leaf area and gross primary productivity (GPP) itself.

In this paper we assess the importance of leaf area in controlling carbon uptake through time and space and in a scenario of enhanced nutrient availability. We ask whether the relationship between leaf area and GPP is the same, regardless of vegetation type, leaf developmental stage, or increased nutrient availability. To answer these questions, we describe the results of a uniquely detailed CO₂ flux survey covering a wide range of vegetation types, at two low arctic sites on opposite sides of the globe. Previous studies using similar chamber measurement techniques have focused on fluxes during peak season (Boelman *et al.* 2003; Williams *et al.* 2006) or in just one vegetation type (Shaver *et al.* 1998; Johnson *et al.* 2000). For the first time, we present data from northern Sweden that covers the period from leaf bud burst and expansion, through peak season to early senescence. In northern Alaska we compare five distinct tundra types with and without 15+ years of N and P fertilization. We hypothesize that: (i) total canopy leaf area explains variation in GPP between vegetation types; (ii) total canopy leaf area explains seasonal increases in GPP; and (iii) leaf area explains increases in GPP as

a result of fertilization. Alternative scenarios are: (i) GPP of whole canopies is determined solely by species or growth form level differences in photosynthesis; at the canopy scale light penetration through differently structured canopies (i.e. shrub vs. graminoid) could also influence GPP; (ii) changes in photosynthetic capacity *per unit leaf area* or increases in self-shading within canopies also affect the relationship between leaf area and GPP; and (iii) differences in GPP between control and fertilized vegetation are at least in part due to changes in light environment, species composition or photosynthetic capacity per unit leaf area.

Materials and methods

THE STUDY AREAS

Flux measurements in Sweden were conducted at the STEPPS site (68°18' N, 18°51' E, elevation 710 m) (<http://www.dur.ac.uk/stepps.project/>) near the Abisko Scientific Research Station on the southern shore of Lake Torneträsk, about 200 km north of the arctic circle. Annual precipitation at the site is 225–475 mm, average annual temperature –1 °C and average July temperature 11 °C (van Wijk *et al.* 2005). The STEPPS site is located approximately 7 km due south of the research station on a north-facing slope above the tree line. Soils are typically well drained without continuous permafrost. We measured ecosystem CO₂ flux in 15 × 1 m plots in five vegetation types classified by the dominant vascular plant species (Table 1). 'Betula' and 'Salix' vegetation types grew close together on a sheltered bank and both had ericaceous understory vegetation. Maximum canopy height reached approximately 0.8 m. The 'dry heath' was on an exposed ridge and consisted of sparse patches of prostrate ericaceous shrubs and scattered forbs between cryptogamic crust and rock. 'Empetrum heath' was situated below the shrub sites and was less well drained, with almost continuous cover of *Empetrum hermaphroditum* Hagerup. The 'wet sedge' vegetation was still further down the slope and dominated by *Carex* species. All plots were within 100 m of each other.

In Alaska we made flux measurements within the long-term Ecological Research Site at Toolik Lake, in the northern foothills of the Brooks Range (68°38' N, 149°34' W, elevation 760 m). Annual precipitation at Toolik is 200–400 mm, Annual temperature –10 °C, and average July temperature 14 °C (van Wijk *et al.* 2005). Fertilization experiments have been running at Toolik for more than 15 years; site and methodological descriptions can be found in Hobbie *et al.* (2005). We made measurements in control and fertilized treatments of moist acidic tussock (MAT), non-acidic tussock (NAT), non-acidic non-tussock (NANT), wet sedge, and heath vegetation (Walker *et al.* 1994; Hobbie *et al.* 2002; Gough & Hobbie 2003; Hobbie *et al.* 2005). All sites were within *c.* 2 km of each other. MAT has soil pH around 4 and overlies surfaces that

Table 1 Average aerial percentage cover of the dominant plant species, lichen and moss in 1 × 1 m flux plots in each vegetation type at Toolik in 2004 and Abisko in 2005

| Site | Vegetation | Treatment | No. flux plots | Dominant vascular plant species (average percentage cover in August) |
|----------------|-----------------------|-----------|----------------|---|
| Toolik, Alaska | MAT | Control | 4 | <i>Eriophorum</i> and <i>Carex</i> species (25), <i>Rubus chamaemorus</i> (15), <i>Betula nana</i> (14), <i>Vaccinium vitis-idaea</i> (6), <i>Ledum palustre</i> (8), moss (10), lichen (6) |
| | | Fert | 4 | <i>B. nana</i> (55), <i>R. chamaemorus</i> (48), moss (3), lichen (< 1) |
| | NAT | Control | 4 | <i>Eriophorum</i> and <i>Carex</i> spp. (21), <i>Cassiope tetragona</i> (14), <i>Salix reticulata</i> (12), <i>Dryas octopetala</i> (5), moss (37), lichen (7) |
| | | Fert | 4 | <i>Eriophorum</i> and <i>Carex</i> spp. (48), <i>Salix reticulata</i> (6), <i>Draba</i> spp. (8), <i>Dryas octopetala</i> (5), moss (11), lichen (< 1) |
| | NANT | Control | 4 | <i>Eriophorum</i> & <i>Carex</i> spp. (19), <i>Cassiope tetragona</i> (14), <i>Dryas octopetala</i> (21), <i>Salix</i> spp. (7), moss (26), lichen (10) |
| | | Fert | 4 | Grass (75), <i>Salix</i> spp. (15), <i>Equisetum</i> spp. (8), moss (< 1), lichen (< 1) |
| | Sedge | Control | 4 | <i>Eriophorum</i> and <i>Carex</i> spp. (53), moss (15), lichen (< 1) |
| | | Fert | 4 | <i>Eriophorum</i> and <i>Carex</i> spp. (40), grass (23), moss (17), lichen (< 1) |
| | Heath | Control | 4 | <i>Arctostaphylos alpina</i> (19), <i>Ledum palustre</i> (14), <i>V. vitis-idaea</i> (16), <i>E. nigrum</i> (10), moss (< 1), lichen (18) |
| | | Fert | 4 | <i>Hierochloe alpina</i> (44), <i>B. nana</i> (49), moss (2), lichen (2) |
| Abisko, Sweden | <i>Betula</i> | – | 3 | <i>B. nana</i> (63), <i>E. hermaphroditum</i> (19), <i>V. vitis-idaea</i> (9), <i>Lycopodium</i> spp. (9), <i>V. uliginosum</i> (9), moss (17), lichen (< 1) |
| | <i>Salix</i> | – | 3 | <i>Salix glauca</i> (43), <i>E. hermaphroditum</i> (56), <i>V. vitis-idaea</i> (15), <i>B. nana</i> (19), <i>Juniperus communis</i> (18), <i>V. myrtilus</i> (18), moss (18), lichen (< 1) |
| | <i>Empetrum</i> heath | – | 3 | <i>E. nigrum</i> (73), <i>V. uliginosum</i> (10), <i>B. nana</i> (12), <i>R. chamaemorus</i> (5), moss (15), lichen (< 1) |
| | Sedge | – | 3 | <i>Carex</i> spp. (50), <i>E. nigrum</i> (37), <i>Andromeda polifolia</i> (10), moss (37), lichen (< 1) |
| | Dry heath | – | 3 | <i>E. nigrum</i> (22), <i>B. nana</i> (5), <i>V. uliginosum</i> (8), cryptogamic crust (45), moss (4) |

are 50 000–120 000 years old. The dominant species are the tussock-forming sedge, *Eriophorum vaginatum* L., with ericaceous shrubs such as *Betula nana* L., *Ledum palustre* L. and *Vaccinium vitis-idaea* L. Fertilization of MAT doubled leaf area, with *B. nana* becoming dominant. Moss cover decreased (Shaver *et al.* 2001). NAT and NANT sites overlie glacial surfaces aged 11 500–20 000 years, with soil pH of 5.5–7. Non-acidic sites have lower plant biomass but greater species richness, and *B. nana* is absent (Hobbie *et al.* 2002). Fertilization of NAT resulted in increased biomass without loss of species richness (Gough *et al.* 2002; Hobbie *et al.* 2005). Wet sedge vegetation is dominated by rhizomatous sedges, mostly *Carex* and *Eriophorum* species. Five years of fertilization increased wet sedge above ground biomass two- to fourfold (Shaver *et al.* 1998; Boelman *et al.* 2005). Heath vegetation is characterized by ericaceous shrubs such as *Vaccinium uliginosum* L. and *Loiseleuria procumbens* L. Soils are well drained, with an upper organic mat 0–0.05 m thick and annual thaw depth > 1 m. Annual net primary productivity increased with fertilization; a tussock forming grass, *Hierochloe alpina* Sw. ex Willd, replaced prostrate shrubs (Gough *et al.* 2002).

during four rounds of field measurements (7–11 June, 16–17 June, 26–30 June and 10–15 August), the first of which was before leaf bud break. In Alaska during 2004 we measured 20 plots in control and fertilized treatments of five vegetation types, one to two times between 26 June and 8 July and 22 July and 4 August (Table 1).

To measure CO₂ fluxes we used a LI-COR 6400 portable photosynthesis system (LI-COR Inc., Lincoln, Nebraska, USA) connected to a 1 × 1 × 0.25 m Plexiglas chamber (Williams *et al.* 2006). In late season 2004 we used a LI-COR 6200 and corrected CO₂ fluxes for the effects of water vapour flux according to the methods of Hooper *et al.* (2002). We placed the chamber on top of a 1-m² aluminium frame base, with a rubber gasket on both surfaces to ensure an airtight seal. The base was supported approximately 0.05–0.20 m above the ground by steel legs driven down to the permafrost. We attached a plastic skirt to the bottom of the base to enclose the volume between the base and the ground surface; at the ground surface we weighted the skirt with heavy chains pushed down onto the moss layer. This method enabled us to move the chamber from site to site with minimal disturbance to the surface of the organic mat. The air inside the chamber was mixed using four small fans, which we ran for 30–60 s before taking the first measurement. To provide an estimate of total chamber volume we measured the height of the chamber base above the ground in a grid of 36 points. We then added the volume of the air space within the base to that of the chamber itself.

CO₂ FLUX MEASUREMENT

We measured the response of net ecosystem CO₂ exchange to manipulated light on 1 × 1 m plots. In Sweden in 2005 we measured 15 plots in five vegetation types

To create a light response curve we took two to three net CO₂ flux measurements at full light, followed by one to two measurements at several (usually three) successive levels of shading, followed by three measurements in full darkness. We shaded the chamber using one to three layers of plastic window screening or mosquito netting and used an opaque tarpaulin to block all light from the chamber. We assumed the mosquito netting was not selective in its transmission of the different wavelengths of PAR. Flux measurements under complete darkness represent ecosystem respiration. Each flux measurement lasted 45–60 s, the LI-COR 6400 recording CO₂ and H₂O concentrations every 1–2 s. We lifted the chamber between flux measurements to allow internal conditions to return to ambient. The LI-COR 6400 also recorded photosynthetic photon flux density (PPFD) inside the chamber, as well as air temperature and pressure. After completing the light response curve we took five regularly spaced measurements of soil temperature at 5 cm depth. We also measured soil volumetric water content at five points using a Hydrosense handheld soil moisture probe (Campbell Scientific, Logan, Utah, USA) inserted where possible to the maximum depth of 20 cm. We adjusted the soil moisture data using a calibration developed across a wide range of soil types found near Toolik Lake (J. Powers, unpublished data).

VEGETATION CHARACTERIZATION

At each plot we took measurements of canopy reflectance and calculated a normalized difference vegetation index (NDVI) using the formula:

$$\text{NDVI} = (R_{\text{nir}} - R_{\text{vis}}) / (R_{\text{nir}} + R_{\text{vis}}) \quad \text{eqn 1}$$

where R_{NIR} is reflectance at a wavelength of 0.725–1.0 μm and R_{VIS} is reflectance at 0.56–0.68 μm (Boelman *et al.* 2003). At Toolik in 2004 we used a Skye portable field sensor (Skye Instruments Ltd, Llandrindod Wells, UK), which measures total reflected light in the wavebands specified in equation 1. At Abisko in 2005 we used a Unispec spectral analyser (PP systems, Haverhill, Massachusetts, USA), which records complete reflectance spectra from 0.3 mm to 1.0 mm, but used only the reflectance in the appropriate wavebands. We took measurements in a regular grid of nine points with both instruments, holding each sensor at a vertical height such that the field of view was approximately 0.04 m². The two instruments agreed well in cross-calibration. The relationship between Skye sensor NDVI and Unispec NDVI, both measured on 89 1 × 1 m flux plots, was Skye NDVI = 0.92 × Unispec NDVI + 0.051, $R^2 = 0.94$.

To use NDVI to predict LAI of the flux plots we destructively measured the leaf area of 81 independent 0.04 m² plots and developed an NDVI-LAI calibration curve. After taking an NDVI measurement we removed all the leaf material from the plot and then sorted by species in the laboratory. We measured leaf area of each

species using a scanner and WinRhizo/WinFolia software (Regent Instruments Inc, Ste-Foy, Canada). At Abisko in 2005 we took a total of 40 harvests, approximately one-third of which were taken in mid-June, in late June and in August. At Toolik in 2004 we took 18 harvests in fertilized plots. We used data from 23 harvests from 2003 in unfertilized vegetation at Toolik, using the same methods (the same data used by Williams *et al.* 2006). We estimated absolute aerial cover in each flux plot by species for all vascular plants (i.e. total cover can be > 100%). We did this by placing a 5 × 5 string grid (each square = 0.04 m²) over the plot, and visually estimating cover. In 2004 we estimated cover by species in each square, then calculated an average species cover for the entire plot. In 2005 we estimated cover for each species in turn, counting a running total of percentage cover (¹/₄ of a square = 1% of total plot) in squares 1 through to 25. We also noted bryophyte cover, bare ground, cryptogamic crust, rock and standing water. At Toolik in 2004 we estimated cover in each flux plot once, while at Abisko we estimated cover each time a light response curve was measured.

DATA ANALYSIS

CO₂ fluxes are calculated from the change in chamber CO₂ concentration through time according to the formula:

$$F_c = \frac{\rho \cdot V \cdot dC/dt}{A} \quad \text{eqn 2}$$

where F_c is net CO₂ flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$), ρ is air density (mol m^{-3}), V is the chamber CO₂ volume (m³), dC/dt is the slope of chamber CO₂ concentration against time ($\mu\text{mol mol}^{-1} \text{s}^{-1}$) and A is the chamber surface area (m²). The light response of net CO₂ exchange, or net ecosystem productivity (NEP), is modelled as a rectangular hyperbola with a term for ecosystem respiration:

$$\text{NEP} = \text{ER} - \frac{P_{\text{max}} \cdot I}{k + I} \quad \text{eqn 3}$$

where P_{max} is the rate of light saturated photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), k is the half-saturation constant of photosynthesis ($\mu\text{mol PAR m}^{-2} \text{ s}^{-1}$), I is the incident PPFD ($\mu\text{mol PAR m}^{-2} \text{ s}^{-1}$) and ER is ecosystem respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Ecosystem respiration can then be subtracted to produce a light response curve of gross primary productivity (GPP):

$$\text{GPP} = \frac{P_{\text{max}} \cdot I}{k + I} \quad \text{eqn 4}$$

E_0 , the initial slope of the light response curve or quantum efficiency ($\mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ PAR}$), and LCP, the light compensation point ($\mu\text{mol PAR m}^{-2} \text{ s}^{-1}$) are calculated as:

$$E_0 = \frac{P_{\text{max}}}{k} \quad \text{eqn 5}$$

$$\text{LCP} = \frac{\text{ER} \cdot k}{P_{\text{max}} - \text{ER}} \quad \text{eqn 6}$$

Table 2 Best-fit exponential regression parameters and root mean squared errors of prediction (RMSE) for the LAI-NDVI relationships used to predict LAI (equation 7). The regressions were calculated using data from 81 0.2 × 0.2 m harvests, classified according to species composition

| Vegetation type | <i>a</i> | <i>b</i> | <i>n</i> | <i>R</i> ² | RMSE |
|-----------------------|----------|----------|----------|-----------------------|------|
| <i>Betula</i> | 0.0132 | 6.271 | 22 | 0.79 | 0.58 |
| <i>Salix glauca</i> | 0.0323 | 5.625 | 11 | 0.89 | 0.26 |
| <i>Empetrum</i> heath | 0.0259 | 5.087 | 7 | 0.48 | 0.26 |
| Dry heath | 0.0137 | 5.446 | 8 | 0.43 | 0.11 |
| Tussock | 0.0064 | 7.210 | 10 | 0.85 | 0.27 |
| Sedge | 0.1516 | 2.663 | 18 | 0.50 | 0.22 |
| Grass | – | – | 5 | – | – |
| All data | 0.0148 | 6.192 | 81 | 0.75 | 0.36 |

To make comparisons of photosynthetic activity between plots it is necessary to take account of the large differences in GPP that occur under changing light. To do this each light curve was used to predict photosynthesis at 600 μmol m⁻² s⁻¹ PPFD (GPP₆₀₀). GPP₆₀₀ values were also normalized by predicted leaf area for each flux plot to give GPP per unit leaf area at 600 μmol m⁻² s⁻¹ PPFD (GPP_{600L}).

The LAI of each flux plot was predicted from NDVI using the equation:

$$\text{LAI} = a \cdot e^{(b \cdot \text{NDVI})} \quad \text{eqn 7}$$

where *a* and *b* are parameters specific to each vegetation type (Table 2).

STATISTICAL ANALYSIS

For the Abisko data, we analysed seasonal changes in LAI, GPP₆₀₀ and GPP_{600L} using repeated measures ANOVA in SYSTAT 11.0, with vegetation type as the between-

subject factor and date of measurement as the within-subject factor. The average date of each measurement round is used to account for irregularity of spacing between dates. Univariate results are presented. We analysed LAI, GPP₆₀₀ and GPP_{600L} at Toolik using two-way ANOVA in SYSTAT 11.0, with vegetation type and treatment as factors. Data were natural log transformed prior to each ANOVA analysis. Simple contrasts between treatments within each vegetation type were used to examine interaction effects in more detail.

Results

LEAF AREA AND NDVI

NDVI and leaf area were strongly correlated overall with an *R*² of 0.75. As expected, NDVI saturated at high LAI, reaching a maximum value of approximately 0.86. As a result, the exponential model tended to underestimate leaf area at high NDVI, though only two plots (both in fertilized MAT) had NDVI greater than 0.85. Combining all the harvest data and using a single exponential regression led to biased estimates of leaf area due to differences in the LAI-NDVI relationship between vegetation types (Fig. 1a). Sedge plots, for example, generally had higher leaf area than dry heath plots at a given NDVI. This may have been due to the presence of sedge leaf litter, which obscured live green material or moss cover, which contributed to the NDVI signal. Harvests dominated by *Salix glauca* L. also had consistently higher LAI than *Betula* plots at the same NDVI; this was caused by a covering of pale hairs on *S. glauca* leaves, which made them appear grey-green. Harvests were therefore grouped by vegetation type (*Betula*, *Salix glauca*, sedge, dry heath, *Empetrum* heath, tussock or grass, based on dominant species and harvest location) in order to predict leaf area. Table 2 gives

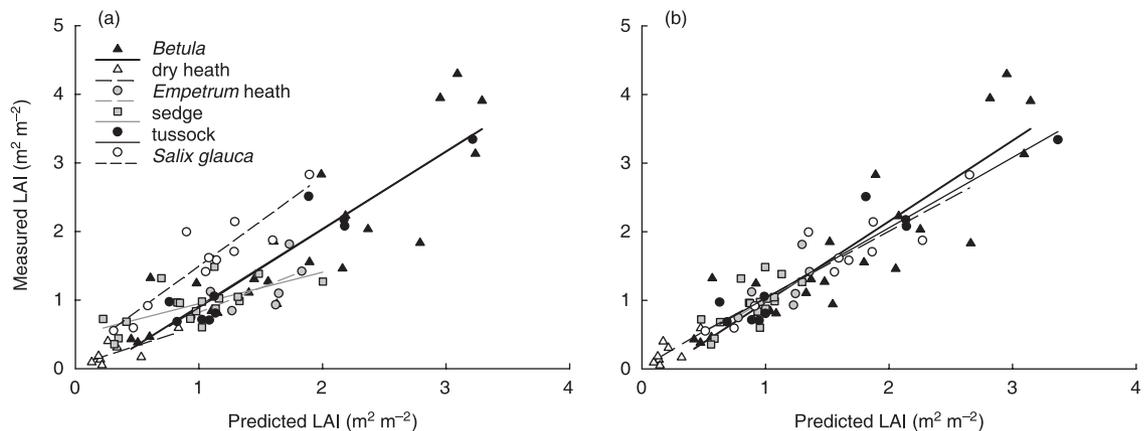


Fig. 1 Predicted LAI vs. measured LAI for 81 0.20 × 0.20 m harvests from Abisko & Toolik in 2003–05. Each panel shows the same data. In (a) the overall best-fit exponential relationship between LAI and NDVI (equation 7, Table 2) for all 81 harvests is used to predict LAI (*x*-axis). In (b) separate exponential relationships between LAI and NDVI for each vegetation type (Table 2) are used to predict LAI (*x*-axis). In both panels the best-fit linear regression of predicted vs. measured LAI is plotted for each of the six vegetation types. *R*² of predicted vs. measured LAI for all 81 harvest data points in (a) = 0.74 and (b) = 0.84 (overall regression lines are not shown). Harvests were classified as representative of ‘*Betula*’, ‘*Salix*’, ‘sedge’, ‘dry heath’, ‘*Empetrum* heath’, ‘*Salix glauca*’ or ‘tussock’ vegetation depending on species composition and harvest location.

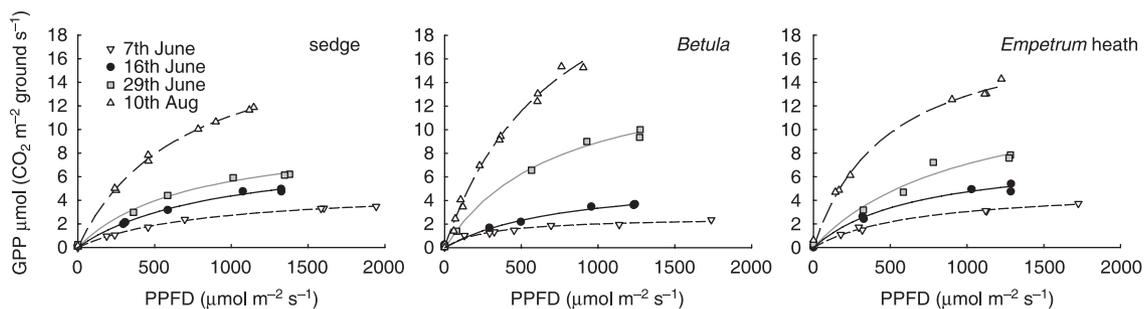


Fig. 2 Response of GPP to photosynthetic photon flux density (PPFD) for three flux plots dominated by sedge, *Betula nana* and *Empetrum* heath vegetation at Abisko in 2005. Light response curves were measured on each plot four times during the growing season.

best-fit parameters, R^2 and RMSE values for equation 7 for each vegetation type individually and for all data combined. Using vegetation-specific regression relationships to predict LAI explains 10% more of the total variation in LAI (Fig. 1b). Separating LAI-NDVI data by site or date (early or late season) of harvest did not result in similar improvements in precision. Grass harvests covered only a very small range in LAI so it was not possible to fit a useful regression equation. Instead, the overall regression was used to predict LAI and the result multiplied by a factor of 1.6; on average, grass-dominated harvests had 1.6 times more leaf area than predicted by the overall model.

SEASONAL PATTERNS AT ABISKO

GPP showed a clear saturating response to light at all sites and time periods, with the average RMSE

of prediction for all light curves = $0.20 \mu\text{mol C m}^{-2} \text{ ground s}^{-1}$ (Fig. 2). Ecosystem respiration (ER) and air temperature were exponentially related ($R^2 = 0.35$), but there was no relationship between air temperature and GPP_{600} , LCP or E_0 . Plots with high LAI and GPP also had the highest ER. Multiple regression of air temperature and LAI against ER explains 52% of the variation across all vegetation types and time periods (see Appendix S1 in Supplementary Material). There were significant differences in GPP_{600} between vegetation types ($P < 0.0005$) and dates of measurement ($P < 0.005$; Fig. 3a). In early June before leaf break GPP_{600} was low for all vegetation, between 0.4 and $2.9 \mu\text{mol C m}^{-2} \text{ ground s}^{-1}$. By August GPP_{600} had increased in all plots, but those dominated by *Betula* and *Salix* increased the most, to 10.6–14.8 $\mu\text{mol C m}^{-2} \text{ ground s}^{-1}$. This led to a strong interaction between date and vegetation type ($P < 0.0005$; Fig. 3a).

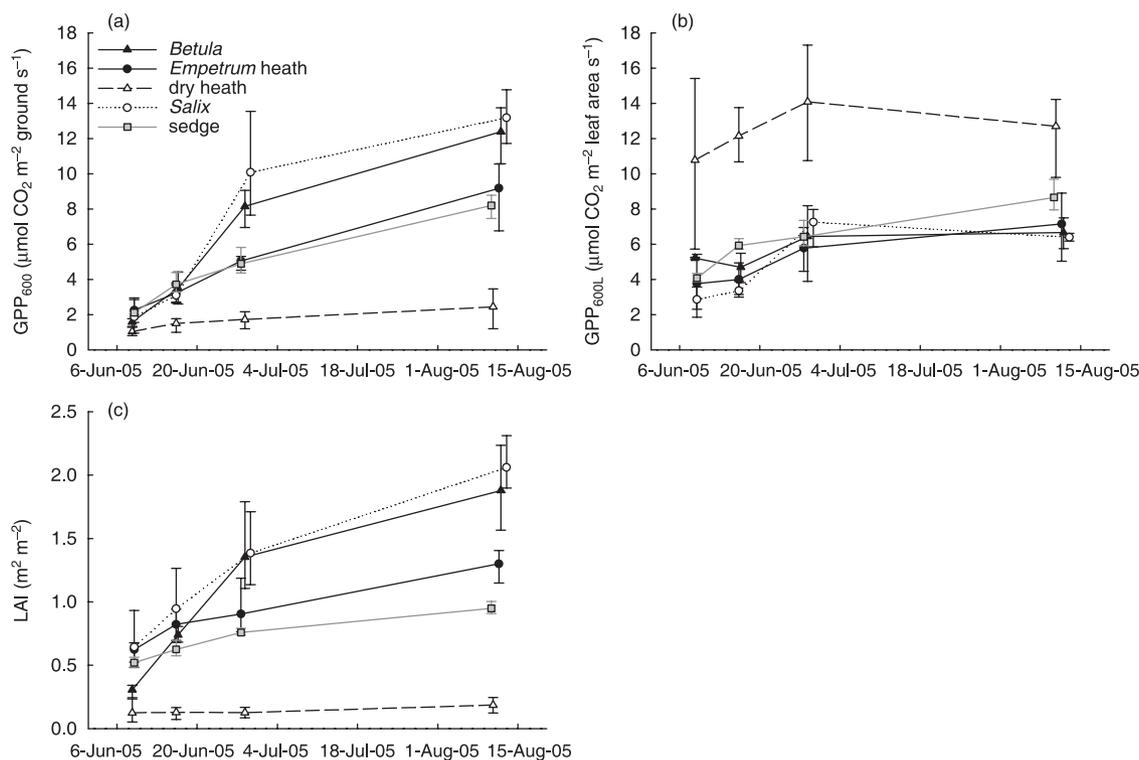


Fig. 3 (a) Estimated GPP_{600} , (b) estimated GPP_{600L} and (c) predicted leaf area, measured in five vegetation types, four times through the growing season at Abisko. Bars show ranges for each vegetation type.

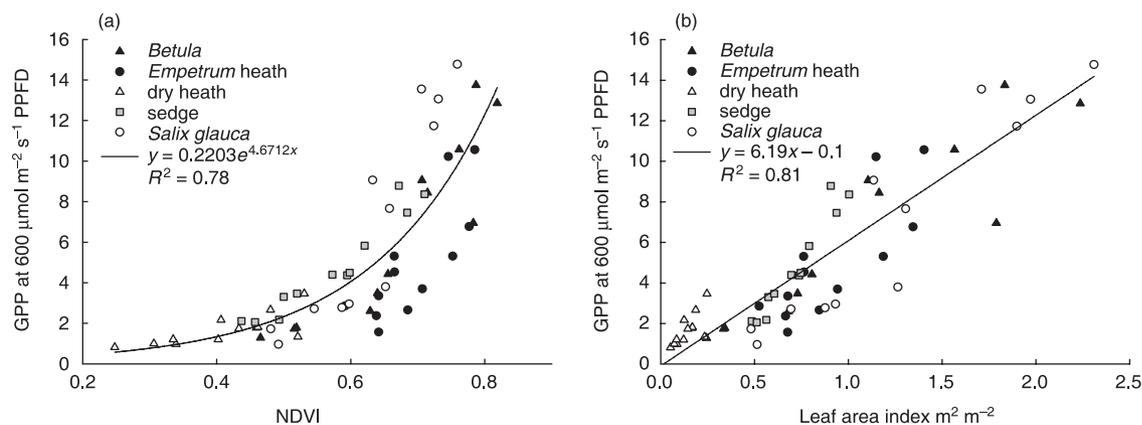


Fig. 4 The relationship between GPP_{600} and (a) NDVI and (b) predicted LAI for all flux plots at Abisko. Each point represents one measurement made on one plot; 15 plots were each measured four times between early June and mid-August ($n = 60$).

Leaf area index varied 30-fold across plots and sampling dates, from a minimum of 0.07 in dry heath vegetation in early season to 2.31 in *Salix* plots in August (Fig. 3c). Before leaf bud break, *Empetrum* heath, sedge and *Salix* plots all had leaf area index above 0.5 due to the presence of evergreen species (all *Salix* plots had *E. nigrum* and *V. vitis-idaea* in the understory; one had *Juniperus communis* L.). Leaf area increased in all vegetation types through the season, with the greatest increase in deciduous shrub plots; on average LAI in *Betula* and *Salix* plots increased three- to fivefold by August (Fig. 3c). Dry heath vegetation had very low LAI, which increased by less than 0.1 $m^2 m^{-2}$. Across all plots and time periods 75% of the variation in GPP_{600} was explained by NDVI (Fig. 4a), translating to a strong linear relationship between leaf area and GPP_{600} . After leaf development in August LAI explained 90% of the variation in GPP_{600} across vegetation types. Across all vegetation types and measurement periods, LAI explained 81% of the variation in GPP_{600} (Fig. 4b).

Average GPP_{600} per unit leaf area (GPP_{600L}) showed a statistically significant change through time ($P < 0.0005$), but there appears to be only a slight overall increase in GPP_{600L} through the season (Fig. 3b). GPP_{600L} values for the dry heath plots are obvious outliers. This could be due to the presence of cryptogamic crust and lichen, which covered around 45% of the surface of these plots. Cryptogamic crusts are very dark green or black in colour, and lichens are often almost white, yet both are still potentially photosynthetically active. If NDVI (greenness) is used to predict leaf area but the carbon uptake by non-vascular plants is not accounted for, then GPP per unit leaf area will be overestimated. Although photosynthesis by crust and lichens is presumably low, vascular leaf area was also very low in the dry heath plots. The reflective properties of the 'background', including exposed soil and rock, will also influence the NDVI signal, particularly in very open canopies. Large standard errors for dry heath plots reflect the greater sensitivity of GPP_{600L} to errors in LAI prediction at very low values. GPP_{600L} is the same between vegetation types

if dry heath plots are excluded from analysis ($P > 0.20$). At peak season in August the coefficient of variation in GPP_{600} across all 15 plots was 47%, but in GPP_{600L} was only 19% (excluding dry heath). Spatial heterogeneity in carbon uptake is therefore substantially reduced if expressed per unit canopy leaf area. The relative importance of canopy leaf area vs. GPP_{600L} in seasonal changes in GPP_{600} can also be compared. For example, in *Betula* plot 1, GPP_{600L} increased by 11% between June and August, while LAI increased by 600%; leaf area explains six times more of the increase in carbon uptake than GPP_{600L} . On average for deciduous shrub plots, the contribution of leaf area is 3.2 times that of GPP_{600L} . In evergreen-dominated communities the contribution of the two factors is approximately equal, on average (see Appendix S1).

FERTILIZER ADDITION AT TOOLIK

The leaf area of flux plots in fertilized treatments was greater than that of control treatments in all vegetation types ($P < 0.0005$; Fig. 5c). LAI in control plots ranged from 0.27 $m^2 m^{-2}$ in NANT to 1.41 $m^2 m^{-2}$ in MAT and in fertilized flux plots from 0.92 $m^2 m^{-2}$ in wet sedge to 2.82 $m^2 m^{-2}$ in MAT. The largest differences in LAI between control and fertilized treatments corresponded to dramatic shifts in species composition and dominance; in MAT vegetation *B. nana* replaced a mix of functional types (graminoid, deciduous and evergreen shrubs and forbs), while in NANT tall stands of grasses dominated almost exclusively compared with diverse short-stature vegetation in control plots. Sedge and NAT vegetation, by contrast, had more similar LAI and more similar species composition between treatments (Table 1).

There was no significant response of GPP_{600} to air or soil temperature at Toolik. ER was exponentially related to air temperature in fertilized plots but not in control plots ($R^2 = 0.53$ and $R^2 = 0.06$, respectively) and ER rates were higher in fertilized plots (see Appendix S2). GPP_{600} was also greater in fertilized plots ($P < 0.0005$), with a highly significant interaction between treatment and vegetation type ($P < 0.0005$; Fig. 5a). NANT vegetation had both the highest and lowest GPP_{600} ,

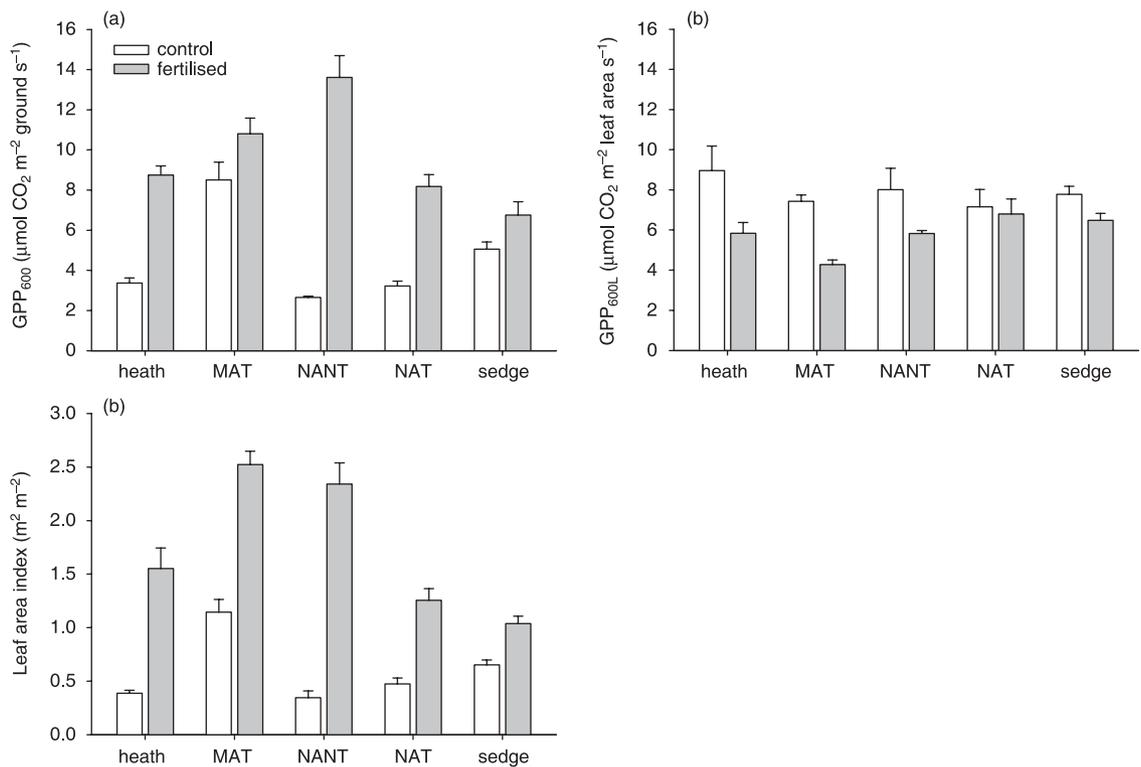


Fig. 5 (a) GPP₆₀₀, (b) GPP_{600L} and (c) leaf area index for control and fertilized treatments at Toolik 2004, averaged across measurement rounds. MAT = moist acidic tussock, NANT = non-acidic non-tussock, NAT = non-acidic tussock. Bars show standard errors.

with averages of 13.6 μmol C m⁻² s⁻¹ and 2.6 μmol C m⁻² s⁻¹ in the fertilized and control treatments, respectively. GPP_{600L} in fertilized treatments of heath, MAT and NANT vegetation was significantly lower than control plots, i.e. the relative increase in leaf area as a result of fertilization exceeded the relative increase in photosynthesis. GPP_{600L} in sedge and NAT fertilized vegetation was also lower than control treatments, but not significantly so (Fig. 5b, Table 3).

GPP₆₀₀ and NDVI show a very similar relationship at Toolik and Abisko, though NANT plots consistently had higher GPP₆₀₀ relative to NDVI (Fig. 6a). These were

Table 3 Results of simple contrasts between control and fertilized plots (control minus fertilized) within each vegetation type at Toolik Lake in 2004. ****P* < 0.005, ***P* < 0.05, **P* < 0.1, NS = non-significant

| Vegetation type | LAI (m ² m ⁻²) | GPP ₆₀₀ (μmol CO ₂ m ⁻² ground s ⁻¹) | GPP _{600L} (μmol CO ₂ m ⁻² LA s ⁻¹) |
|-----------------|---------------------------------------|---|--|
| Heath | *** | *** | *** |
| Mat | *** | ** | *** |
| Nant | *** | *** | * |
| Nat | *** | *** | NS |
| Sedge | *** | ** | NS |

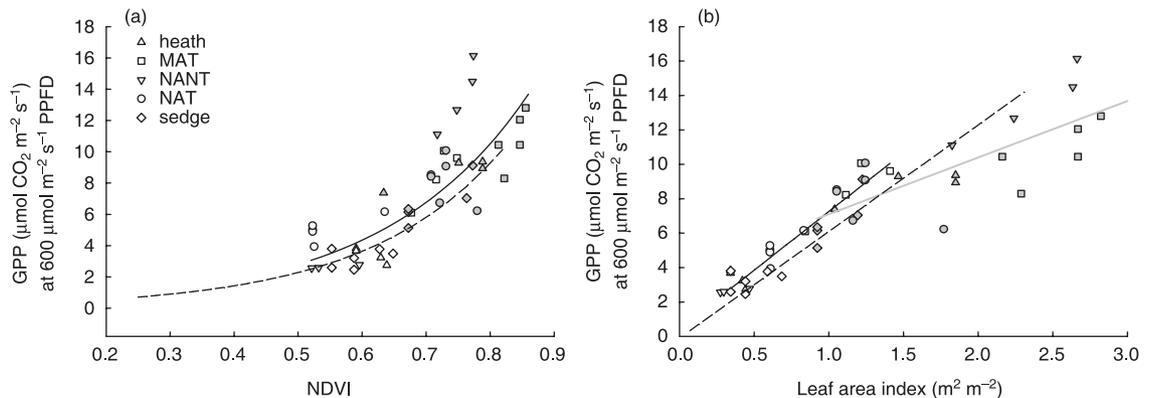


Fig. 6 (a) Relationship between GPP₆₀₀ and NDVI for control and fertilized flux plots at Toolik 2004. Dashed line shows the same relationship for Abisko 2005. Filled symbols are fertilized plots. (b) Relationship between GPP₆₀₀ and LAI for control and fertilized flux plots at Toolik 2004. Filled symbols are fertilized plots. Grey line is the best-fit linear regression for Toolik 2004 fertilized plots only (*R*² = 0.63), solid line is for Toolik 2004 control plots only (*R*² = 0.89). Dashed line is for Abisko 2005.

graminoid-dominated plots, which had lower NDVI at high given leaf area, presumably due to very different canopy level properties (Steltzer & Welker 2006). This was accounted for in the calculation of leaf area (see methods section). Up to LAI of 1.5 m² m⁻² the slope of the linear relationship between GPP₆₀₀ and LAI for control plots at Toolik and all plots at Abisko (over the whole season) is not significantly different ($P = 0.38$), though GPP₆₀₀ is slightly greater at Toolik than at Abisko ($P = 0.02$; Fig. 6b). Average GPP_{600L} after full leaf expansion had occurred is not significantly different between sites (at Toolik in July, and at Abisko in August, GPP_{600L} was 7.8 ± 0.36 and 7.2 ± 0.39 $\mu\text{mol C m}^{-2} \text{LA s}^{-1}$, respectively). However, above leaf area index of 1.5 m² m⁻² the relationship between GPP₆₀₀ and LAI in fertilized plots at Toolik begins to deviate from linear (Fig. 6b); this is reflected in lower GPP_{600L} in fertilized plots (Fig. 5b).

Discussion

LEAF AREA CONTROLS CO₂ UPTAKE

By fitting CO₂ flux light response curves and estimating GPP at constant irradiance, we were able to investigate seasonal and spatial patterns in GPP. The results highlight the importance of leaf area as the primary driver of photosynthesis in arctic systems. At peak leaf area in August, 90% of the variation in GPP across five vegetation types was explained by leaf area alone. This correlation is remarkable considering clear differences in community composition (Table 1) and the range in leaf-level photosynthetic activity between individual species; P_{max} values near Toolik Lake range from 6 to 20 $\mu\text{mol CO}_2 \text{m}^{-2} \text{leaf s}^{-1}$ in common tundra species (Oberbauer & Oechel 1989). At the canopy level, differences between species become unimportant because communities are assembled in such a way that GPP at a given canopy leaf area is tightly constrained (Fig. 3b). The underlying mechanism may be strict environmental controls over canopy nitrogen allocation. Van Wijk *et al.* (2005) found a constant ratio of 1.9 g N m⁻² leaf across a wide range of vegetation types at peak season at Toolik and Abisko. Leaf area and N are key biotic controls on photosynthesis (Williams & Rastetter 1999), so coupling between them would constrain ecosystem photosynthesis in relation to canopy leaf area as demonstrated (Fig. 4b).

GPP at Abisko increased by an order of magnitude between early June and mid-August in deciduous shrub-dominated plots, the most rapid increase coinciding with early season leaf expansion. GPP in graminoid and evergreen-dominated communities increased more gradually; both vegetation types were photosynthetically active before deciduous leaves emerged but did not attain such high rates of GPP by August. Where leaf area was very low on dry, exposed ridges GPP was also very low and only increased slightly (Fig. 3a). Spatial patterns in ecosystem carbon uptake are there-

fore community dependent and change over time such that heterogeneity between 'patches' in the landscape increases as canopies develop. Not all of the increase in GPP through time is attributable to increases in leaf area, however; we have shown that average GPP *per unit leaf area* increases up to two- to threefold by peak season (Fig. 3c). There are currently no data available on the LAI-N relationship during canopy development. Do canopies converge on the optimum 1.9 g N m⁻² LA at peak season and is early season canopy N less than 1.9 g N m⁻² LA? If not, what is the explanation for increases in average canopy GPP per unit leaf area through the season?

In evergreen-dominated communities we show that increases in GPP_{600L} and increases in LAI contribute equally to seasonal increases in GPP₆₀₀. This is because throughout the growing season evergreen canopy development involves both new leaf production, 're-activation' of previous year's leaves, and leaf senescence. *E. hermaphroditum* leaves at Abisko, for example, survive over three seasons and are then shed (Kudo *et al.* 2001). On average, evergreen leaf photosynthetic capability increases slightly through the season, but the increase in leaf area is less dramatic than in deciduous species, where canopy development is characterized by the emergence and expansion of a single leaf cohort. Despite these differences in leaf life span, the average increase in GPP_{600L} is very similar across vegetation types (Fig. 3b). Leaf area is a more important factor in determining GPP, explaining 80% of observed variation through space and time (Fig. 4b).

LEAF AREA AND GPP RESPONSE TO FERTILIZATION

Unexpectedly, rates of photosynthesis per unit leaf area were lower in fertilized treatments (Fig. 5b), i.e. relative increases in leaf area *exceeded* relative increases in GPP. Harvest results by Shaver *et al.* (2001) suggest that canopy nitrogen per unit leaf area is lower in fertilized MAT plots than control plots, despite an increase in tissue nitrogen concentration by mass. The decrease in N per unit leaf area is mostly the result of increased dominance by *Betula nana*, which has much higher specific leaf area (leaf area per unit mass). If the ratio of leaf area to canopy nitrogen optimizes productivity in natural vegetation, then this would suggest that MAT has not (yet) reached an optimum canopy structure in response to fertilizer addition. Detailed investigation of the LAI-N relationship in treatment plots of different ages would provide insight into whether vegetation is converging to some optimal N:LA ratio, and the speed of that response. Self-shading may also explain some or all of the observed depression in GPP per unit leaf area. Although lower GPP_{600L} rates were not evident at Abisko at comparably high LAI (Fig. 6b), the loss of species diversity associated with fertilization may affect canopy structure such that light capture becomes limiting only at Toolik.

GPP in fertilized vegetation was higher than in controls (Fig. 5a) but the more productive plots also tended to have greater ecosystem respiration, offsetting some of the increase in plant carbon uptake. Although the data presented here are insufficient to provide an annual carbon budget, it is known that 20 years of fertilization of MAT vegetation at Toolik Lake has resulted in substantial net carbon *loss*, despite a doubling of above-ground net primary production. This net loss is caused by stimulation of decomposition in organic and mineral soils below 5 cm depth (Mack *et al.* 2004). Enhanced respiration in long-term fertilizer experiments in wet sedge vegetation may be due to the combination of increased litter input, increased root biomass, or thicker soil organic mats (Shaver *et al.* 1998; Johnson *et al.* 2000; Boelman *et al.* 2003).

THE ROLE OF MOSSES

Throughout this study we have effectively assumed that the contribution of mosses to both NDVI and ecosystem CO₂ fluxes is zero. In reality, they are a significant part of tundra plant communities. Moss biomass can contribute up to 35% of total above-ground biomass in tussock and shrub tundra, and 50% in wet sedge tundra (Shaver & Chapin 1991). It is possible that the loss of moss cover as a result of nutrient addition leads to the apparently lower GPP per unit leaf area in fertilized plots, as mosses were included in the flux measurements but not in the estimation of leaf area. The largest change in moss cover between treatments at Toolik was in NANT vegetation, where moss cover decreased from an average of 26% to < 1% with fertilization (Table 1).

At Abisko in 2005, J. C. Douma (unpublished data) found a strong negative linear relationship between the contribution of mosses to total system GPP and the LAI of vascular plants, across a variety of tundra types. Control NANT vegetation also had the lowest leaf area index (0.35 m² m⁻²; Fig. 5c), so the change in moss cover is likely to have the biggest impact in this vegetation type. In the study by Douma, at vascular LAI of 0.4 m² m⁻² and moss cover of 100% beneath the vascular canopy, mosses contributed around 60% of the total GPP measured. At LAI of 1.0 m² m⁻² and moss cover of 100%, mosses contributed around 25% of GPP. If the same relationship applies to NANT control plots, as a rough estimate with only 26% moss cover, moss GPP₆₀₀ might account for 15% of total system GPP₆₀₀. Without mosses, the GPP_{600L} value would then decrease from 8.0 to 6.6 μmol C m⁻² LA s⁻¹. This is still higher than the average GPP_{600L} in fertilized NANT plots, but clearly mosses can be important when leaf area is low. In control MAT vegetation where LAI values are above 1.0 m² m⁻², moss photosynthesis is much less important and cannot fully explain the reduction in GPP_{600L} with fertilization.

The role of mosses will be particularly important in early season when shading by vascular plants is at a

minimum. Applying J.C. Douma's results to our data at Abisko suggests that in early June the contribution of mosses would be highest in *Betula* (lowest leaf area) and wet sedge vegetation (highest moss cover). For *Betula* plots with average LAI of 0.3 m² m⁻² and moss cover of 17%, accounting for moss photosynthesis reduces average GPP_{600L} by about 10%. In wet sedge vegetation, with LAI of 0.5 m² m⁻² and moss cover of 37%, the reduction in GPP_{600L} would be approximately 15%; 3.9 μmol C m⁻² LA s⁻¹ including mosses, and 3.3 μmol C m⁻² LA s⁻¹ without mosses. This is still well within the range of GPP_{600L} values measured across all vegetation types during early season, although moss productivity could account for some of the unexplained variation in GPP_{600L} between vegetation types.

NDVI AND LEAF AREA

NDVI has been used extensively in production models as a measure of leaf area. We have shown, however, that when using NDVI data measured on scales that match the spatial scale of variation in vegetation type, 'calibrating' NDVI to leaf area in each vegetation type separately increases precision (Fig. 1a,b). This is due to differences in leaf colour and canopy structure between vegetation types dominated by different species or growth forms (Steltzer & Welker 2006). The presence of moss also represents a potential source of error in the NDVI-LAI relationship as mosses contribute to the NDVI signal but were not quantified as a part of vascular leaf area. It was necessary in this study to account for as much noise in the LAI-NDVI relationship as possible, in order to understand differences in LAI *between* vegetation types. For scaling up and averaging *across* vegetation types it has been shown that a single LAI-NDVI relationship can be acceptable (van Wijk & Williams 2005). For example, in this study if a single LAI-NDVI relationship is used to predict LAI at Abisko, there is still a strong positive relationship between GPP₆₀₀ and LAI (GPP₆₀₀ = 5.45 × LAI + 0.47) but the R² value falls to 0.69.

We have shown that leaf area is an excellent predictor of ecosystem photosynthesis in the low arctic, regardless of vegetation type. This simplifies the task of regional carbon budgeting as it removes the need for detailed ground surveys and aggregation of species level data into ecosystem models. Expressing GPP per unit leaf area substantially reduces spatial heterogeneity in ecosystem photosynthesis. We conclude that leaf area is a good predictor of GPP (i) across different vegetation types and (ii) through the stages of leaf development. Differences between species are unimportant, though there is evidence for increases in per unit leaf area photosynthesis through the season. However, vegetation that is responding to manipulated nutrient conditions does not follow the same rules as natural vegetation. Under enhanced nutrients, leaf area is still related to GPP but the relationship differs from that in 'normal' vegetation. The LAI-GPP relationship for fertilized plots at

Toolik Lake and control plots at Abisko diverges above 1.5 m² m⁻². The cause could be self-shading within the canopy, fertilization affecting canopy structure such that self-shading occurs at Toolik Lake but not at Abisko. The divergence in LAI-GPP could also be related to the divergence of LAI-N relationships between Swedish and Alaskan vegetation at high leaf area, as demonstrated by van Wijk *et al.* (2005). The cause and generality of this phenomenon needs further research; if a warmer climate results in increases in soil fertility then adapting vegetation may also have lower rates of photosynthesis per unit canopy leaf area.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1 Table of best fit parameters, NDVI, leaf area and environmental conditions for each NEP light response curve measured at Abisko in 2005.

Appendix S2 Table of best fit parameters, NDVI, leaf area and environmental conditions for each NEP light response curve measured at Toolik Lake in 2004.

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