Photosynthesis and productivity in heterogeneous arctic tundra: consequences for ecosystem function of mixing vegetation types at stand edges.

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Summary

1. Arctic vegetation tends to be spatially heterogeneous and can have large areas of mixed 'transition zone' vegetation between stands dominated by a single or few species. If plant photosynthesis and growth within these transition zones differs significantly from main vegetation stands, and if transition zones are not considered when extrapolating stand-level findings to larger scales in space, then transition zones will provide considerable error to landscape-level estimates of gross primary productivity (GPP).

2. In a heterogeneous sub-Arctic tundra landscape, we undertook a detailed assessment of plant and ecosystem photosynthesis and plant growth in stands dominated by the short-stature evergreen dwarf shrub Empetrum hermaphroditum, the deciduous dwarf shrub Betula nana, the taller deciduous shrub Salix glauca and also the transition zones between them.

3. Our findings show that plants in transition zones towards taller and more productive vegetation types frequently showed reduced shoot growth, equal or reduced light-saturated photosynthesis (Pmax) and other typical shade responses (e.g. increased leaf chlorophyll and leaf area per mass) when compared with conspecific plants in main stands where the species is dominant. Critically, whole-ecosystem GPP per leaf area was 20–40% lower in transition zones than in main vegetation

stands as a consequence. A modelling analysis suggests that the under-productivity of some transition zones results from the lack of a clear 'winner' in the competition for light, such that active leaves of some species are shaded by relatively inactive leaves of others.

4. These findings highlight how biotic interactions can considerably influence plant performance to the extent that productivity of mixed vegetation (transition zones) cannot be predicted from their main stands either side. How the consequences of mixing vegetation relate to mechanisms in biodiversity-function theory is discussed.

5. Synthesis: Our work shows that the productivity of transition zones of arctic vegetation is considerably lower than may be estimated from the main stands on either side. This reduced GPP in transition zones, therefore, must be considered when modelling carbon fluxes at the landscape scale and suggests that the impact of transition zones on ecosystem function needs further investigation in heterogeneous landscapes, where they make up a significant proportion of the land cover.

Introduction:

Climate change has impacted high-latitude areas earliest and most strongly, and considerable climate feedback effects will result if there is a net release of carbon (C) in response to warming (ACIA, 2004). Measurements of whole-vegetation photosynthesis are critical for developing the process-based understanding required to quantify the Arctic carbon cycle, but integrating small-scale measurements into landscape-level C fluxes has proved challenging due to the highly heterogeneous nature of Arctic vegetation (Oechel et al. 1998; Soegaard et al. 2000; Asner, Scurlock & Hicke 2003; Williams et al. 2006; Shaver et al. 2007).

Arctic vegetation commonly consists of stands of one vegetation type, merging through a transition zone of mixed vegetation into stands of another vegetation type, on a scale of just metres to tens of metres (Walker, Walker & Auerbach 1994). This pronounced spatial heterogeneity is often cited as the primary reason why 'upscaled' estimates from patch-level studies do not agree with flux measurements at larger spatial scales from flux towers and aircraft (Oechel et al. 1998; Fox et al. 2008). Critically, measurements of C uptake are usually made in well-defined vegetation stands. However, where (i) a large proportion of the landscape consists of mixed vegetation in the transition zones between stands, and (ii) C dynamics differ in these transition zones compared with the main stands around them, then transition zones must be quantified and integrated into upscaled (e.g. landscape) carbon flux estimates. Indeed, if changes in plant growth (rather than other ecological factors such as reproductive success or herbivory) cause the changes in species abundance from one stand to another (McGill et al. 2006), then individual plants in transition zones are likely to be more or less productive than in the stands in which they are most abundant. The predictive relationships between leaf area, ecosystem photosynthesis and plant productivity seen previously in main vegetation stands may therefore not hold true for transition zones (Shaver et al. 2007; Street et al.

2007), and these differences must be determined to improve our quantification and understanding of the arctic C cycle.

Furthermore, transition vegetation may also provide ecological insight into how mixing of vegetation types may impact ecosystem function in ways that have previously only been considered at the species- or functional-type level. For instance, mixing of vegetation types could provide benefit to ecosystem function analogous to heightened function when increasing the mix (diversity) of functional types (and possibly species) in plant communities (Hooper et al. 2005). Similarly, function may be mediated by competitive or facilitative interactions that occur when vegetation types mix (Brooker et al. 2008).

How might transition-zone vegetation CO_2 fluxes differ from the main vegetation stands? If all plant species are best-suited to the environmental conditions in the stands in which they are most abundant, and perform poorly elsewhere, then transition zones will have lower net productivity. However, previous studies have shown that performance of common arctic species does not necessarily decline in proportion to abundance (Fletcher et al. 2010), because optimum physiological conditions may be found in areas where that species is less abundant and are instead dominated by another more competitive species. Therefore, along a gradient of increasing stature, through stands of increasingly competitive species, a species may be expected to be more productive in the transition zone towards more competitive species than its own stand and less productive in the transition zone to more stress-tolerant/smaller-stature species (Wisheu 1998; McGill et al. 2006). When the responses of all species within a transition zone are integrated, with some species in more 'favourable' microclimatic or edaphic conditions than their own stands where they are most abundant, and others in harsher conditions, these processes may potentially balance out. This would be the best-case scenario for estimating landscape C fluxes (or more broadly, predicting ecosystem function), as transition zones would effectively be an average of the stands either side and so could be ignored. Support for this approximation can be found from measurements made in stands of different vegetation types that included many of the same species but at different abundances, and from which have been found to have relatively constant primary productivity per leaf area (Williams & Rastetter 1999; Shaver et al. 2007; Street et al. 2007).

To quantify the role of transition zones on arctic plant function and vegetation productivity, we combined detailed species-level and whole-vegetation-level studies in an area of heterogeneous tundra in northern Sweden, which was largely dominated by three species: the short and evergreen dwarf shrub Empetrum hermaphroditum Hagerup on exposed terraces and ridges; the deciduous dwarf shrub Betula nana L. in less exposed areas and the taller deciduous shrub Salix glauca L. in more sheltered snow beds and hollows. Along this exposure gradient, in the principal types of vegetation that were dominated by one of the three species ('stands'), and mixed vegetation in the

transition zones in between those stands ('transition zones'), we made measurements of soil moisture and fertility, light availability through the canopy and its effect on each species' potential photosynthetic rates. We then measured the growth of apical shoots, light-saturated rates of photosynthesis of apical leaves of each species and other responses to shading (leaf thickness, chlorophyll content and leaf mass per shoot length) to quantify the impact of stand location on shoot growth of each species. To quantify the effects of transition zones on ecosystem carbon flux, we measured whole-ecosystem CO_2 fluxes per leaf area of the stands and transition zones using 1-m^2 vegetation cuvettes. Finally, in a smaller supporting study, we also compared stand- and transition-zone productivity using this approach in similar vegetation near Kevo, Finland (see Appendix S1 in Supporting Information), to test whether findings here are consistent with the larger Swedish study.

We hypothesised that (H1a) greatest shoot growth and photosynthesis of *E. hermaphroditum* and *B. nana* would be found not in their own stands, but in stands dominated by taller and more competitive species, whereas greatest growth and photosynthesis of the tallest statured species S. glauca would be found in its own stand (presumably also the most productive and competitive vegetation). We also hypothesised (H1b), more specifically, that for each species, there would be fewer individual shoots (compared with that species' stand centre) each growing faster in transition zones towards taller (presumably more productive) vegetation and fewer, more slowly growing shoots in the transition zone to shorter vegetation. In a transition zone, therefore, species from neighbouring taller stature vegetation will grow less, because the transition zone represents a move towards less favourable (more stressful) abiotic conditions, while species from neighbouring shorter stature vegetation will grow more, because for them, the transition zone represents a move towards more favourable conditions. Ultimately, this would mean that (H1c) when effects on both sets of species were averaged, there would be no net change in mean species growth and photosynthesis in the intermediate environmental conditions in transition zones. As, by definition, transition zones have an intermediate species composition, and we expected no net change in species' responses, we hypothesised (H2a) that this would lead to a relationship between gross primary productivity (GPP) and leaf area that was constant across stands and transition zones. More specifically, we hypothesised (H2b) that the increased potential rates of photosynthesis per leaf area resulting from the presence of faster photosynthesising species in taller vegetation would be balanced by increased shading due to the greater total leaf area.

Materials and Methods:

Study site

Eight transects were established in a *c.* 15 000 m^2 area of heterogeneous tundra vegetation, 6 km south of the Abisko Scientific Research Station, northern Sweden (68.3°N, 18.8°E, 747–756 m a.s.l; see Fox *et al.* (2008) for additional information). Transects were *c.* 70 m long and ran from bare, rocky ground to stands of tall shrubs. In each transect, six plots (1 × 1 m) representing three main

vegetation types ('stands') and three transition zones were established. These were (i) in the shortest, sparse vegetation with partial coverage of *E. hermaphroditum* and other dwarf shrub species in the transition zones between rocky areas and stands of *E. hermaphroditum*-dominated vegetation ('Rocky–*Empetrum* transition zones'), (ii) in the homogeneous stands of *E. hermaphroditum*-dominated vegetation ('*Empetrum* stands'), (iii) in the mixed *E. hermaphroditum–B. nana* vegetation ('*Empetrum–Betula* transition zones'), (iv) in the homogeneous *B. nana*-dominated vegetation ('*Betula* stands'), (v) in the mixed *B. nana–S. glauca* vegetation ('*Betula–Salix* transition zones'), and finally, (vi) in the homogeneous stands of *S. glauca*-dominated vegetation ('*Salix* stands'), the tallest vegetation at the site. Shoot growth was measured in all eight transects, biomass harvest and whole-vegetation CO_2 flux measurements were made in five transects, and leaf-level photosynthesis and chlorophyll content in 3–4 transects (due to time constraints). The proportion of the study area occupied by each stand and transition zone vegetation type was estimated by analysis of six evenly spaced line transects across a high-resolution aerial photograph.

Plant cover and growth

Above-ground biomass was harvested at peak season (late July–early August) from a representative 20×20 cm area of each 1-m^2 plot. One-sided projected leaf area of each species was measured using a Delta-T digital image analysis system 1.10 (Delta-T, Burwell, UK) to calculate leaf area index (LAI, m^2 leaves per m^{-2} ground) for each species and overall. Leaves were weighed after drying for 2 days at 65 °C, to determine leaf area per mass (specific leaf area, SLA). The absolute aerial percentage cover occupied by each vascular plant species in the 20×20 cm harvest area, as well as the whole 1-m^2 plot, on which vegetation CO_2 fluxes were to be measured, was assessed by eye prior to harvesting, in late July. We used this estimate-by-eye, as we found that total cover in the 20×20 cm harvest area was a good predictor of LAI ($r^2 = 0.68$, all vegetation types combines) and performed better than alternative NDVI measurements. The LAI of the larger 1-m^2 area was calculated by multiplying the LAI of the smaller harvested area by the 1-m^2 plot/harvest plot cover ratio.

Photosynthetically active radiation (PAR) was measured at 10-cm height intervals through the canopy (SKP 2200 PAR sensor; Skye Instruments, Llandrindod Wells, UK) above five points within each 1-m^2 plot. Measurements were made within three hours of mid-day on a sunny day. To assess the distribution of leaf area through the canopy, the cumulative LAI above each height interval was estimated from the Beer–Lambert law, with a light extinction coefficient (k) of 0.6 (Jones 1992). The leaf area within each 10-cm height class was then calculated by subtracting the cumulative LAI at the interval above from the cumulative LAI at the interval below. Measurements of the upper and lower height of each species' leaves within the canopy were then used to assign this estimated leaf area to one or more species.

After harvests were completed (mid-August), soil moisture was determined gravimetrically on samples from the top 5 cm of soil. Plant available inorganic nitrogen was assessed by shaking 5-g dry

weight equivalent of the soil in 50 mL of 2 mol L^{-1} KCl for 30 min. Samples were filtered through Whatman No. 42 ashless filter paper, and the ammonium (NH_4^+) and nitrate (NO_3^-) contents were determined colorimetrically using an automated flow injection analyser (FIAflow2; Burkard Scientific, Uxbridge, UK).

Photosynthetic light response of key species

Photosynthetic light response curves were measured in July using a LI-COR 6400 portable photosynthesis system with leaf cuvette (LI-COR Inc., Lincoln, NE, USA). Measurements were made on representative, fully expanded apical leaves of *S. glauca* and *B. nana* and apical current-year shoots of *E. hermaphroditum* from within the vegetation stands dominated by that species and within transition zones. Initial measurements were taken after 2 min acclimation at 2000 μmol m^{-2} s^{-1} PAR and then after *c.* 35 s at 1500, 1000, 800, 500, 250, 100, 50 and 0 μmol m^{-2} s^{-1} PAR, with a cuvette CO_2 concentration of 375 ± 5 p.p.m.v., and ambient temperatures (19 ± 2°C) and humidity (65 ± 10% RH). A nonlinear hyperbola (Lambers, Chapin & Pons 1998) was fitted to the curves using a least-squares fitting procedure. Light-saturated photosynthesis rates (P_{max}) of the three study species were measured in July. P_{max} was taken as the mean of measurements made after 5 and 15 min acclimation time, using a Ciras-1 IRGA with a PLC4(N) leaf cuvette, supplied with 720 μmol m^{-2} PAR from a TPS-2 LED Light Unit (PP Systems, Hitchin, UK), 385 ± 15 p.p.m.v. CO_2, and ambient temperatures of 20 ± 2 °C. In addition, the mean photosynthetic rate at saturating irradiances (1500, 1000 and 800 μmol m^{-2} s^{-1} PAR) from three light response curves (see 'Photosynthetic light response of key species', above) of *S. glauca* in *Salix* stands, *B. nana* in *Betula* and *Salix* stands, and *E. hermaphroditum* in *Empetrum* and *Betula* stands were included in the analyses.

Estimating photosynthesis under canopy light conditions

Net photosynthesis of the three study species in each plot was modelled by using each species' photosynthetic light response curves and the irradiance available at each height increment to calculate photosynthesis per leaf area at each height. Total net photosynthesis for each species was calculated by multiplying photosynthetic rate at each height by the species' leaf area in that height section and summing for all heights. The mean photosynthetic rate per species was then obtained by dividing by the total leaf area of that species. This approach may overestimate rather than underestimate photosynthesis, due to possible physiological adaptation to lower light in the lower canopy. Light interception by leaves was calculated using leaves with a random facing and a leaf zenith angle of 52 − 5° for every 10 cm below the top of the canopy (from a linear regression fitted to measurements of Stoner, Miller & Miller 1978) and a solar elevation of 45° using the equations of Jones (1992). This calculation, therefore, allowed the effects of shading and the relative contributions of each species to canopy photosynthesis to be assessed.

Whole-canopy gross primary production per leaf area (GPP/LA) was calculated by summing the net photosynthesis and dark respiration of all the study species' leaves and dividing by their leaf area.

Gross photosynthesis of all species combined required estimates of photosynthesis for the non-study species of low abundance, for which light response curves were not available. Inclusion of these species was therefore estimated by taking graminoids to have the same photosynthetic light response as *S. glauca*, other deciduous species as *B. nana* and other evergreen species as *E. hermaphroditum*, as these species have similar maximum rates of assimilation on a leaf area basis (Oberbauer & Oechel 1989).

Change in dominant species' growth and leaf traits along transects

Buds of six shoots per 1-m^2 plot of *S. glauca*, *B. nana* and *E. hermaphroditum* were tagged before budburst, and these shoots were harvested after shoot extension was completed, just before senescence (mid-August). Current year's growth was determined from the stem scar left by the new season's bud (Phoenix *et al.* 2001). Leaf and stem mass of the current-year growth was determined after drying for 2 days at 65 °C, and total shoot mass and leaf mass per shoot length were calculated. The total number of shoots of each of the three study species in the 1-m^2 plot was approximated by dividing the harvested leaf mass per m^2 by the mean leaf mass per shoot.

Leaf chlorophyll was extracted in July by immersion of leaf punches, or whole leaves, whose area was first measured as described earlier, in Dimethylformamide for 48 h at 4 °C (Moran & Porath 1980). Extracts were analysed with a UV-160A spectrophotometer (Shimadzu, Kyoto, Japan), and chlorophyll content was calculated using the absorption coefficients of Wellburn (1994).

Vegetation CO_2 flux measurements

Light response curves of whole-vegetation plot CO_2 flux measurements were made *in situ* (in stands and transition zones) using the LI-COR 6400 connected to a 1 × 1×0.25 m plexiglass chamber with 0–0.75 m high side skirts adjustable for height of the vegetation (previously described in Williams *et al.* 2006; Street *et al.* 2007 and Shaver *et al.* 2007). Each curve was then used to determine photosynthesis at a moderately sunny 600 µmol PAR m^{-2} s^{-1}, which was divided by the leaf area inside the chamber to produce photosynthesis per leaf area ($GPP_{600/LA}$). To compare with measured values, expected $GPP_{600/LA}$ values for the transition zone plots were calculated from the mean of the measured values of stands on either side, weighted by the leaf area of the study species (as the transition plots were not necessarily exactly intermediate in species composition to main stands). Therefore, expected $GPP_{600/LA}$ values were as follows:*Betula*–*Salix*$_{expected}$ = 0.52 *Betula* + 0.48 *Salix*, *Empetrum*–*Betula*$_{expected}$ = 0.36 *Empetrum* + 0.64 *Betula*. The expected values were then compared with measured transition zone $GPP_{600/LA}$. Expected values were not calculated for Rocky–*Empetrum* transition zones, as no measurements were made in the rocky areas due to their negligible LAI.

Statistical analysis

Individual species' growth, P_{max} and shade responses were analysed by one-way ANOVA with plot type (i.e. vegetation) as the main factor. Differences between each plot type were determined with post hoc Tukey's tests. The relationship between GPP_{600} and LAI was analysed using linear regression. Differences between measured and expected $GPP_{600/LA}$ values were analysed by two-way ANOVA with

plot type and estimated vs. measured as the main factors. All tests were performed using Minitab version 13.31 (Minitab Inc., State College, PA, USA).

Results

Vegetation composition and canopy structure

The six stands and transition zones were estimated to occupy 84% of the landscape. This was in good agreement with a previous gridded ground survey (Fox *et al.* 2008), with a mean difference in cover of each vegetation type of 3% compared with Fox *et al.* (2008) (Table S1).

Leaf area index increased as vegetation became taller. LAI increased from 0.7 m^2 m^{-2} in the rocky–*Empetrum* plots to 1.8 m^2 m^{-2} in *Empetrum* and *Betula* plots and 3.1 m^2 m^{-2} in *Salix* plots (Fig. 1). Overall, the plots were dominated by these three study species, which between them comprised 72% of the total leaf area. *Empetrum hermaphroditum* made up 65% of the total leaf area of rocky–*Empetrum* plots and 72% of *Empetrum* plots, where it was most dominant (Fig. 1). The contribution of *E. hermaphroditum* to total leaf area fell as LAI rose, falling to 7% in *Betula–Salix* plots, and was absent from *Salix* plots. *Betula nana* was absent from rocky plots, increasing to 46% in *Betula* plots, where it was dominant before falling to 13% of LAI in *Salix* plots. *Salix glauca* was absent from plots with lower LAI, made up only 1% of the total leaf area of *Betula* plots, rising to 26% in *Betula–Salix* plots and 55% in *Salix* plots, where it was dominant.

The three study species were increasingly tall in the sequence *E. hermaphroditum* < *B. nana* < *S. glauca* and gradually overtopped one another as vegetation became taller. Rocky–*Empetrum* and *Empetrum* plots had a low canopy with little or no shading of one species by another (Fig 2a,b,g,h,m,n respectively). In *Empetrum–Betula* plots, *B. nana* began to grow above *E. hermaphroditum*, reducing irradiance for the majority of *E. hermaphroditum* leaves by *c.* 30%, but was itself also partly shaded by *E. hermaphroditum* Fig. 2c,i,o). However, in *Betula* plots, *B. nana* almost completely overtopped *E. hermaphroditum,* meaning that approximately 89% of *E. hermaphroditum* leaves received only *c.* 30–60% of incident irradiance (Fig. 2d,j,p). In *Betula–Salix* plots, *S. glauca* began to grow above *B. nana*, reducing irradiance for the majority (*c.* 89%) of *B. nana* leaves by *c.* 25–45%, but was itself also partly shaded by its own leaves as well as those of *B. nana* (Fig. 2e,k,q). Because of decreasing irradiance through the canopy, *E. hermaphroditum* received only *c.* 25–45% of incident irradiance in these *Betula–Salix* plots. However, in *Salix* plots, *S. glauca* leaves were almost unshaded by *B. nana* (Fig. 2f,l,r). *Salix* leaves formed a dense canopy between 60 and 90 cm above the ground, intercepting *c.* 60% of all irradiance. Below this height, irradiance fell gradually, with *B. nana* leaves intercepting another *c.* 10% of incident irradiance, leaving *c.* 30% available for *E. hermaphroditum* and other low-statured species.

Light limitation of photosynthesis

The taller vegetation with higher LAI was dominated by species with greater rates of light-saturated photosynthesis and an increase in the irradiance at which photosynthesis was light-saturated (Fig. 3): P_{max} was at 6.5 μmol m^{-2} s^{-1} in *E. hermaphroditum*, 11.4 μmol m^{-2} s^{-1} in *B. nana* and 15.8 μmol m^{-2} s^{-1} in *S. glauca*. Photosynthesis rates reached 75% of P_{max} at 330 μmol PAR m^{-2} s^{-1} in *E. hermaphroditum*, at 450 μmol PAR m^{-2} s^{-1} in *B. nana*, and not until 500 μmol PAR m^{-2} s^{-1} in *S. glauca* (Fig. 3).

As vegetation became taller and total LAI increased, the irradiance available for each species' leaves tended to decrease (Fig. 4a). An average leaf of each species did not receive the greatest amount of irradiance in the stand in which that species was dominant. Instead, leaves received more irradiance on average when mixed in with other species in lower LAI vegetation. This was because shading by other species in shorter, mixed vegetation was lower than self-shading in the species' own stand (Fig 4a). The increase in shading as vegetation became taller resulted in a steady reduction in leaf photosynthetic rates achievable, given 600 μmol m^{-2} s^{-1} incident irradiance (Fig. 4b). Summing these leaf photosynthetic rates (after weighting by the relative LAI of each species) produced an estimated whole-vegetation GPP$_{600/LA}$ of *c.* 7–10 μmol m^{-2} s^{-1} (Fig. 4c). The potential photosynthetic rates in taller vegetation with greater LAI were much higher, because species with much greater rates of photosynthesis were more abundant there. However, the actual estimated rise in GPP$_{600/LA}$ was relatively small, because shading was greatly increased. Modelled GPP$_{600/LA}$ in transition zones was within 5% of values estimated by taking the mean GPP$_{600/LA}$ of the main vegetation stands on either side.

Soil moisture and nitrogen

Gravimetric soil moisture increased from 66% in rocky–*Empetrum* vegetation to 73–76% in *Empetrum*, *Betula* and *Salix* vegetation and the transition zones between them (Fig. 4d). Soil ammonium increased through the main vegetation types, as they became taller, by *c.* 60% from *Empetrum* to *Betula* stands and *c.* 80% from *Betula* to *Salix* stands. Soil ammonium in transition zones tended to be greater (although not significantly so), by *c.* 60–180%, compared with the main vegetation stands on either side (Fig. 4e). Little or no nitrate was detected.

Relationship between vegetation type, shoot numbers and shoot growth

Empetrum hermaphroditum shoot numbers fell sharply by *c.* 50% from *Empetrum* stands to transition zones either side (Fig. 5a). Compared with growth in *Empetrum* stands, growth was significantly greater (+85%) in the *Empetrum*–*Betula* transition zone (Fig. 5b). In the taller *Betula* and *Betula*–*Salix* vegetation, very few shoots were found, but these grew marginally more than in *Empetrum* stands (i.e. growth was non-significantly greater by 17%, Fig. 5a,b). Summing these leaf photosynthetic rates (after weighting by the relative LAI of each species) produced an estimated whole-vegetation GPP$_{600/LA}$ of *c.* 7–10 μmol m^{-2} s^{-1} (Fig. 4c). The potential

photosynthetic rates in taller vegetation with greater LAI were much higher, because species with much greater rates of photosynthesis were more abundant there. However, the actual estimated rise in $GPP_{600/LA}$ was relatively small, because shading was greatly increased. Modelled $GPP_{600/LA}$ in transition zones was within 5% of values estimated by taking the mean $GPP_{600/LA}$ of the main vegetation stands on either side.

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Betula nana shoot numbers remained fairly constant across *Betula* stands and *Empetrum–Betula* and *Betula–Salix* transition zones (Fig. 5g). However, shoot mass tended to be lower (but not significantly so) in transition zones than in the *Betula* stand. Shoot mass was 21% lower in*Empetrum–Betula* transition zones and 15% lower in the taller *Betula–Salix* transition zones (Fig. 5h). Beyond these immediate transition zones, many fewer shoots were found, but shoot growth increased significantly. Shoot mass was 56% higher in the tallest *Salix* stands and 12–34% higher in the shortest *Empetrum* and rocky–*Empetrum* vegetation (Fig. 5h).
Salix glauca shoot growth was greatest in the *Salix* stands. Shoot numbers fell by 64% in the shorter *Betula–Salix* transition zone, and shoot mass was significantly lower (−35%, Fig. 5m,n). There was not a consistent, simple relationship between individual species' shoot growth and either shoot numbers or the height (and hence relative productivity) of the vegetation, but some trends were found. *Empetrum hermaphroditum* and *B. nana* shoot growth tended to be greater in taller vegetation, despite having fewer shoots compared with their own stands where they dominated. *Salix glauca* shoot growth was also greatest in the tallest and most productive vegetation – its own stand. Furthermore, when comparing growth between stands and transition zones, all species tended to have lower shoot growth in the transition zones towards shorter vegetation, although this trend was not always statistically significant.

Relationship between vegetation type, P_{max} and leaf traits

Empetrum hermaphroditum and *B. nana* leaves responded in a generally consistent way as LAI increased in taller vegetation. P_{max} decreased, SLA increased, leaf chlorophyll increased and leaf mass per shoot length tended to decrease as vegetation became taller (Fig. 5c–f,i–l). Shoot growth was consequently unrelated to P_{max}.

However, against this general trend, there was a tendency for decreased P_{max}, increased SLA, increased leaf chlorophyll and decreased leaf mass per shoot length in the shorter transition zones with lower LAI than a species' own patch (Fig. 5, grey shaded areas). For example,*E. hermaphroditum* SLA was slightly higher (i.e. a response typical of taller plots with higher LAI) in the rocky–*Empetrum* transition zones compared with *Empetrum* stands, and *S. glauca* SLA was marginally higher in the *Betula–Salix* transition zones compared with *Salix* stands.*Betula nana* leaf chlorophyll was marginally higher in *Empetrum–Betula* transition zones compared with *Empetrum* stands, and *S. glauca* leaf chlorophyll was higher in the *Betula–Salix* transition zones compared with *Salix* stands. Also, *S. glauca* leaf mass per shoot length was lower in the *Betula–Salix* transition zones compared with *Salix* stands. Importantly, while these responses were often subtle in individual cases, overall, in transition zones, shade responses (including reduced shoot growth) were shown by the shorter statured species 80% of the time, but also by the taller species 53% of the time. This propensity for shade adaptation suggests a degree of 'sub-optimality' in canopy photosynthesis in transition zones.

Gross primary productivity

GPP_{600} was significantly correlated with leaf area across the vegetation types ($r^2 = 0.72$, $P < 0.05$), increasing from 3.2 µmol m^{-2} s^{-1} in Rocky–*Empetrum* vegetation to 9.6 µmol m^{-2} s^{-1} in *Salix* vegetation (Fig. 6a). Main vegetation type stands tended to fall above the regression line ($GPP_{600} = 2.28$ LAI + 1.36), and transition zones below the regression line, with $GPP_{600/LA}$ 28% and 45% lower in the*Betula–Salix* and *Empetrum–Betula* transition zones, respectively, than would be predicted by taking the study species leaf area–weighted average of the stands on either side (Fig. 6b). The rocky–*Empetrum* vegetation was not significantly different from the regression line.

Here, we have reported the most detailed assessment to date on changes in plant productivity in main stands and the transition zones between them in a heterogeneous landscape. The responses of the individual species reveal large changes in plant growth over small spatial scales and show the considerable influence of local biotic and abiotic interactions such that transition zone productivity cannot be predicted from productivity of the main stands either side. Importantly, these interactions result in considerable under-productivity of transition zones that would account for error in upscaling studies that have previously only considered main stands.

Shoot growth and photosynthesis in transition zones and their relation to productivity

The gradient of increased LAI in vegetation dominated by *E. hermaphroditum*, *B. nana* and *S. glauca* occurred along a gradient of marginally increasing soil moisture and nitrogen, which probably in combination with deeper-winter snow insulation in the taller vegetation (R. Baxter & B. Huntley, unpubl. data) lead to a general increase in shoot growth in these more favourable conditions. Along the transects, first *B. nana* and then *S. glauca*, assisted by their greater rates of photosynthesis, shoot growth and height, were able to overtop and out-compete the other, shorter species, reducing those species' shoot numbers. Overall, shoot growth of *E. hermaphroditum* and *B. nana* was not greatest, where those species made up the majority of the leaf area (their own stands), but in each case was greatest in more productive and taller vegetation, where they were less abundant, consistent with previous observations in the area (Fletcher *et al.* 2010). In comparison, *S. glauca* had the greatest shoot growth where it was most abundant (its own stands) in the tallest and most productive vegetation, consistent with hypothesis H1a. This overall pattern is consistent with the displacement of stress-tolerant species from more amenable habitats by a series of increasingly competitive species, where all species have a shared preference for the more favourable end of a gradient, termed 'centrifugal organisation' (Wisheu & Keddy 1992; McGill *et al.* 2006). It may also reflect a degree of facilitation, with the taller species protecting the smaller species (Brooker *et al.* 2008). Similarly, should species adapted to the more productive (and benign) end of the gradient be facilitated by shorter species allowing penetration deeper into the harsher end of the gradient, this would provide an example of where facilitation promotes diversity at moderate-to high-environmental stress levels, by expanding the realised niche of more competitive species into harsher conditions (*c.f.* the Michalet *et al.* (2006) re-assessment of Grime's humped back relationship between species richness and community biomass). This would also be an example of the expanded niche concept (i.e. where the realised niche is larger than the fundamental niche; Bruno, Stachowicz & Bertness 2003) and could also effectively widen the transition zone. Given the importance of transition zones to landscape GPP (see 'reduced GPP in transition zones' below), the mechanisms driving the size of these zones warrants further investigation.

There was inconsistent support for our hypothesis (H1b) that growth would be greater in the transition zone to taller and more productive vegetation and lower in the transition zone to shorter vegetation. For instance, *B. nana* did not show greater growth in its taller *Betula–Salix* transition zone and also grew well in the shorter rocky–*Empetrum* and *Empetrum* vegetation. In that case, the pattern is consistent with an increase in light availability for *B. nana* in this shorter vegetation (Fig. 1), enabling increased photosynthesis and growth and possibly enhanced by earlier initiation of growth in spring in this vegetation (data not shown) as a result of earlier snowmelt from these exposed ridges (Aerts, Cornelissen & Dorrepaal 2006).

All three species showed changes in leaf traits as vegetation became taller and LAI increased that were consistent with typical shade responses. With the increase in height and LAI came generally larger, thinner leaves that were more spread out along stems, had lower P_{max} and greater chlorophyll

content. These are responses that maximise light capture when that is a limiting factor (e.g. Anten 2005) and occurred alongside a reduction in light available for typically positioned leaves of each species. However, this trend was not universal in the study. Shoot growth and P_{max} were sometimes lower than expected in transition zones, and other shade responses were sometimes shown, even when an increase in light availability was predicted from the species' canopy position. This was particularly notable for *S. glauca* in *Betula–Salix* transition zones. These findings are not consistent with our hypothesis (H1c) that growth and photosynthetic responses in transition zones would behave as a simple average of the stands on either side. Confirmation of this is seen in the reduced GPP in transition zones (see next).

Reduced GPP in transition zones

Gross primary productivity was strongly related to leaf area across stands of different vegetation types, as seen previously in tundra vegetation (Fig. 6) (Williams *et al.* 2006; Street *et al.* 2007) (and despite the potential error introduced when upscaling LAI measurements to the 1-m^2 plot). However, in previous tundra productivity studies (Williams *et al.* 2006; Street *et al.* 2007), GPP was not measured in transition zones but only in the main vegetation types. Here, we show for the first time that transition zones, contrary to our hypothesis (H2a), have significantly lower GPP/LA than would be expected from measurements made in main vegetation stands alone. A similar under-productivity (−20%) of transition zones compared with main stands was also seen in the supplementary study at Kevo, Finland (Appendix S1), indicating the broader applicability of this phenomenon in Arctic vegetation. As GPP$_{600/LA}$ was lower by 20–40% in the Abisko transition zones, and we estimate transition zones to occupy approximately half the study area, upscaling C flux measurements made only in main stands to the landscape level could lead to a nontrivial *c.* 10–20% overestimation of GPP (e.g. Fox *et al.* 2008). Clearly, transition zones need to be considered when upscaling vegetation productivity to the landscape.

Further, given the considerable impact of mixing vegetation types on ecosystem function (i.e. transition zone under-productivity), the consequences of mixing vegetation (equivalent to increasing the 'diversity of vegetation types') warrants further investigation analogous to that seen at the species and functional type level in the biodiversity-function literature (Hooper *et al.* 2005). The under-productivity of transition zones highlights that biotic interactions can have such substantial impacts on ecosystem properties such that emergent community properties cannot simply be predicted from the summation of component vegetation types (*c.f.* the mass ratio theory; Grime 1998). Furthermore, in transition zone productivity, there is no evidence, for instance, of what might be the equivalent to overyielding (Hooper *et al.* 2005– which in this case would mean overproductivity of the transition zones) and also no evidence of transition zone productivity being that of the most productive species from a neighbouring main stand (essentially functioning provided by the best performer: Cardinale *et al.* 2006; Phoenix *et al.* 2008). Clearly, in landscapes where transition zones are abundant and may play a strong mediating role in ecosystem function, there is need for new theoretical (as well as empirical) understanding.

The reduction in $GPP_{600/LA}$ in transition zones was not due to the presence or absence of certain species in transition zones, as the abundances of all species in transition zones were intermediate between their abundance in the main vegetation stands on either side. In addition, there was no evidence of lower soil moisture or N in transition zones (in fact, soil N was generally higher in transition zones). Although the soil data are from only one point in time, they indicate that the reduction in $GPP_{600/LA}$ in transition zones was probably not due to photosynthesis being limited by stomatal closure due to water stress, or lack of N availability.

Alternatively, our data suggest that light utilisation may not have been as efficient in transition zones. Competing individuals do not behave in a way that would maximise whole-canopy productivity, but to maximise their own returns, particularly where shading of plants by other individuals increases relative to self-shading. This reduces productivity per leaf area (Monsi, Uchijima & Oikawa 1973; Shieving & Poorter 1999; Anten 2005). In transition zones, there appeared to be less separation of sun- and shade-adapted species into the upper and lower canopy, so a less efficient canopy may exist if, with competition for light between more, smaller, intermixed plants, there is greater shading between individuals (Anten 2005) (see Appendix S2). Therefore, our hypothesis that there was no difference between shading in main stands and transition zones (H2b) would not hold true. In supporting modelling analyses, where one species was allowed to dominate the sunlit fraction of the canopy and was never overtopped by shade species (i.e. improving the efficiency of the canopy structure; Appendix S2), GPP/LA increased in *Betula–Salix* transition zones and so brought that transition zone GPP/LA in line with what would be predicted from the main stands either side (although this did not work for *Empetrum–Betula* transition zones). The mechanism for under-productivity of transition zones suggested here, therefore, is that active leaves of some species are shaded by relatively inactive leaves of others. Other analyses that either altered the shade response of *all* species in the transition zones or altered transition zone composition explained transition zone under-productivity less well (Appendix S2), again suggesting inefficient canopy structure may be the best explanation.

In fact, inefficiency of canopy architecture can be seen in cases rather different to tundra transition zones. For example, in intercropping, while studies frequently show increased productivity when two species are grown together, this tends to result from even greater increases in leaf area (Harris, Natarajan & Willey 1987; Barnes *et al.* 1990; Kropff & Lotz 1992; Baumann *et al.* 2002; Awal, Koshi & Ikeda 2006). Indeed, a simple analysis of these intercropping data suggests that productivity *per leaf area* decreases by 5–20% in intercrops. Similar ideas have been raised regarding monoculture forest systems, where, for instance, greater variation in stand structure and dominance (*c.f.* this study's transition zones) reduces stand productivity due to lower light use efficiency of subordinates without benefit to dominants (Binkley *et al.* 2010). Overall, although, while it is clear from our study that there is a reduction in productivity in transition zones, the mechanistic explanation for this phenomena warrants further investigation.

Conclusion

Arctic ecosystems are an important component of the global carbon cycle, yet quantification of plant community contribution to carbon uptake is challenging due to the often highly heterogeneous nature of the vegetation. Our work shows that contrary to expectations, taller transition zones (towards more productive vegetation) frequently showed reduced shoot growth and other shade responses. This resulted in a lower productivity per leaf area in transition zones than main stands of vegetation, which at our study site may account for a non-trivial 10–20% error, if not considered in upscaling efforts. If productivity of arctic landscapes is to be accurately quantified across space, the considerable proportion of the landscape that comprises transition zone vegetation must be accounted for. Furthermore, should transition zones be equally abundant in other heterogeneous landscapes, this work suggests greater ecological understanding of these is needed, not just in terms of upscaling of carbon balance, but also to seek ecological theory to allow understanding of how mixing of vegetation types alters ecosystem function.

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Figure legends:

Figure 1: Ground coverage and leaf area index of the study vegetation stands (bold) and transition zones. For each vegetation type, the height of the bar represents the leaf area of each species, stacking up to the total leaf area ± SE. The width represents the proportion of the study area covered by that vegetation type.

Figure 2: Light attenuation through the canopy, (a–f) and mean of presence or absence (1 or 0) of each species' leaves at different heights through the canopy (g–l). The light attenuation data were used to calculate the total leaf area at each height (line and point plot, m–r). The harvested total leaf area of each species (Fig. 1) was assigned to different heights through the canopy (bars, m–r) consistently with each species' mean presence/absence score and the calculated total leaf area at each height. For m–r, note that discrepancies between estimated leaf area index (LAI) (dots) and accumulated species LAI (stacked bars) increase at lower heights, suggesting a change in light extinction coefficient.

Figure 3: Leaf-level photosynthetic light response curves of the three study species. Error bars show SE.

Figure 4: Environmental conditions in the study vegetation stands and transition zones. The mean fraction of the incident irradiance received by each species (a), from Fig. 2, was used to calculated mean leaf-level photosynthesis per second (P_{600}, b), and whole ecosystem GPP per leaf area ($GPP_{600/LA}$, c) with an incident irradiance of 600 µmol m^{-2}. Whole-ecosystem $GPP_{600/LA}$ was calculated twice: first assuming only the study species were present and secondly including all other species, by assuming that their photosynthetic response was the same as the most similar study species (see Materials and methods). Soil moisture (d) and soil-extractable ammonium (e) are shown ± SE; for plot-type abbreviations, seeFig. 1.

Figure 5: Shoot growth, light-saturated photosynthesis (P_{max}) and leaf traits. Typical direction of response to increased shading is shown by arrows on right. For each species, the stand where it was most abundant is indicated with a dark grey column and black-filled symbol, and its transition zones with a light grey column and grey-filled symbol. Error bars show SE; P-values from ANOVA comparison of all stands and transition zones, with significant differences at $P < 0.05$ from Tukey's test denoted, where lower case letters are not shared. Note that y-axes vary between species. For plot-type abbreviations, see Fig. 1.

Figure 6: Whole-ecosystem gross photosynthesis measured directly with a 1-m^2 flux chamber. Total (a) and per-leaf-area (b) gross photosynthesis at 600 µmol PAR m^{-2} s^{-1}, in stands (black-

filled symbols and bars) and transition zones (white-filled symbols and bars). Transition zone photosynthesis per leaf area estimated from stands on either side shown with grey-filled bars; *P*-values from ANOVA comparison of observed and estimated transition zone values. For plot-type abbreviations, see Fig. 1. Error bars show SE. PAR, Photosynthetically active radiation.

Figures:

Figure1:

Figure 2:

Height (cm)

Irradiance
(proportion incident PAR)

Leaf height
(presence/absence)

LAI (m² m⁻²)

S. glauca
B. nana
E. hermaphroditum
Other deciduous
Graminoids
Evergreens
Estimated LAI

S. glauca
B. nana
E. hermaphroditum

Rocky-*Empetrum* (a) (g) (m)
Empetrum (b) (h) (n)
Empetrum-Betula (c) (i) (o)
Betula (d) (j) (p)
Betula-Salix (e) (k) (q)
Salix (f) (l) (r)

Figure 3:

Figure 4:

Figure 5:

Empetrum hermaphroditum   *Betula nana*   *Salix glauca*   Typical shade response

Figure 6:

Panel (a): Plot of GPP_{600} ($\mu mol\ m^{-2}\ s^{-1}$) versus LAI ($m^2\ m^{-2}$).

Legend:
- ○ R-E
- ● **E**
- □ E-B
- ■ **B**
- △ B-S
- ▲ **S**

$$GPP_{600} = 2.28 \times LAI + 1.36$$
$$r^2 = 0.72,\ P = 0.033$$

Panel (b): Bar chart of $GPP_{600/LA}$ ($\mu mol\ m^{-2}\ s^{-1}$) by Vegetation type (**stand** or transition zone).

Legend:
- ■ Stand
- □ Transition zone (measured)
- ▨ Transition zone (estimated)

*$P = 0.034$

−45%*

−28%*

R-E **E** E-B **B** B-S **S**
Vegetation type
(**stand** or transition zone)