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Seasonal Variation in Gross Ecosystem Production, Plant Biomass, and Carbon and Nitrogen Pools in Five High Arctic Vegetation Types

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Abstract

The Arctic is extremely vulnerable to projected climate change, and global warming may result in major community reorganizations. The aim of this study was a thorough investigation of plant biomass production throughout an entire growing season in five different high arctic vegetation types: *Cassiope*, *Dryas*, and *Salix* heath, grassland, and fen. The main focus was on the gross ecosystem production (GEP), and the biotic and abiotic factors which may influence GEP. Photosynthesis, aboveground biomass, and carbon, nitrogen, and chlorophyll content were measured weekly during nine weeks.

There were large differences in seasonal growth and production within and among vegetation types. Mosses contributed considerably to the total C and N pool in grassland, fen, and *Salix* heath. Fen, which had the highest pool of leaf N, leaf chlorophyll, and moss N, was the most productive vegetation type in terms of GEP, despite the lowest total biomass. Across vegetation types, leaf biomass, leaf N, and moss N pool size influenced GEP. Within most vegetation types GEP correlated with leaf N, in correspondence with the notion that N may limit plant production in many high arctic ecosystems. The timing of the peaks in C and N pools in leaves did not coincide with that in the mosses and in woody tissues. This emphasizes the importance of sampling throughout the growing season, when using field data from the Arctic to estimate plant biomasses and modeling C and N fluxes and pool sizes.

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Introduction

The Arctic is extremely vulnerable to climate change, and the effects of global warming are expected to be most pronounced at the poles (IPCC, 2001, 2007; ACIA, 2004). Fossil records provide evidence that large-scale climate changes may result in major community reorganizations and new types of dominant ecosystems (Brubaker et al., 1995). Approximately 14% of the world soil carbon (C) pool is stored in the tundra (Post et al., 1982), and changes of the C balance are of great interest because release of CO_2 from these large C stocks into the atmosphere potentially could create positive feedbacks to global warming. If the heterotrophic respiration is higher than net primary production, the Arctic will act as a C source in which C is lost to the atmosphere, while if the reverse occurs the tundra will act as a C sink (Shaver et al., 1992; McKane et al., 1997). Photosynthetic capacities of different plant communities are therefore important. A number of experimental studies in a limited number of ecosystem types in the Arctic have until now provided evidence that an ecosystem shift from a C sink to a source or vice versa may depend on soil moisture, temperature, and soil nutrient (mainly nitrogen) availability (Nadelhoffer et al., 1992; Oechel et al., 1993, 1995; Illeris et al., 2004). Such environmental factors may differ strongly among ecosystems and may influence the relative abundance of major plant growth forms such as mosses, graminoids, and dwarf shrubs and their contribution to ecosystem C accumulation. However, until we have a clearer picture of C and nitrogen (N) pool sizes and seasonal variation in gross ecosystem production in dominant arctic vegetation types under present conditions, we cannot foresee how these ecosystems will react to future changes.

There are few studies of the variation in net photosynthesis in high arctic vegetation types in general (but see Welker et al., 2004) and to our knowledge there are no simultaneous investigations of the variation in net photosynthesis, chlorophyll, and C and N pool sizes of different ecosystem components in a range of different vegetation types with high temporal resolution throughout an entire growing season. For instance, in one of the most comprehensive studies comprising four different tundra vegetation types in the Low Arctic, most of the data on primary production, biomass and element content were derived from only three harvests throughout the growing season (Shaver and Chapin, 1991). Furthermore, although of high importance for estimation of C stocks and C cycling, timing of ''peak biomass'' may depend upon vegetation type.

We investigated five major vegetation types through one growing season, i.e. nine weeks, with weekly measurements of daytime gross ecosystem production (GEP), aboveground biomass, C, N, and chlorophyll content, in order to establish the timing of aboveground peak biomass and C and N pools, which could be used to provide some general recommendations for biomass sampling strategies in arctic settings. The five selected

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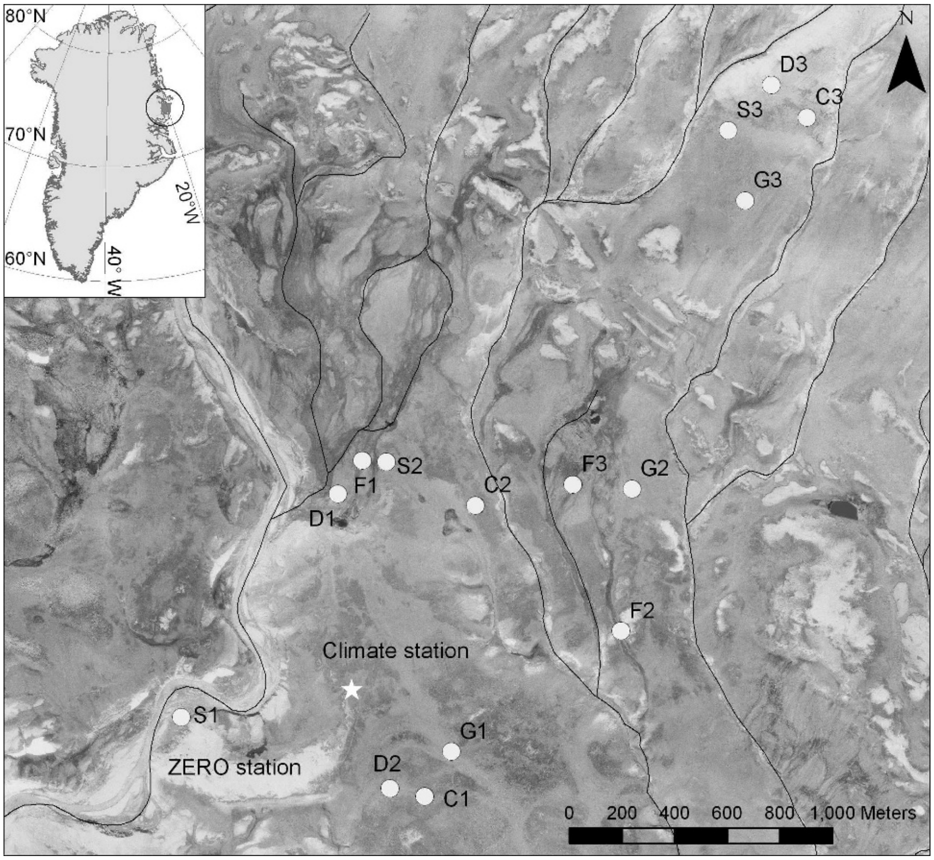

FIGURE 1. Map depicting the Zackenberg Valley with field plots marked as follows: C1–C3, *Cassiope tetragona* heath plots 1–3; D1–D3, *Dryas integrifolia x octopetala* heath plots 1–3; S1–S3, *Salix arctica* heath 1–3; G1–G3, grassland 1–3; F1–F3, fen 1–3. Inserted: map showing the location of Zackenberg in Northeast Greenland.

vegetation types, *Cassiope*, *Dryas*, and *Salix* heaths, and grassland and fen, are widespread in the High Arctic.

We expected the evergreen vegetation types to have similar, low production in terms of GEP and biomass increase throughout the growing season, compared to the deciduous vegetation types. We also expected grassland and fen to be the most productive in terms of GEP and biomass increase during the growing season due to higher N contents of photosynthetic tissues. Also, we expected the grassland, the fen, and the *Salix* heath to show greater seasonality, with earlier timing of peak leaf biomass but, due to continued moss growth, later timing of peak total plant biomass than the vegetation types dominated by evergreen and wintergreen plants.

Methods

SITE DESCRIPTION

The study took place in Northeast Greenland (74°28′N; 20°34′W) close to the Zackenberg Research Station. In Zackenberg the yearly mean air temperature 2 m above terrain is approximately −8.3°C and the total precipitation is 261 mm (Hansen et al., 2008), which makes growth limited to little more than 2 months, i.e. mid June till late August. The main study area is the Zackenberg Valley that is situated next to Young Sound, approximately 30 km from the outer coast (Fig. 1). The area was deglaciated about 10,000 years ago. The valley is flat, dominated by non-calcareous sandy fluvial sediments with the eastern part of the sloping hillsides originating from sedimentary and basaltic bedrock. Further details on the environmental conditions can be found in Elberling et al. (2008).

The five most dominant vegetation types in the Zackenberg area as defined by Bay (1998) were selected for this study. The vegetation types on moist soils are classified as belonging to the prostate dwarf-shrub, herb tundra (P1), and the fen and grassland types on wet to moist soils are referred to the graminoid, prostrate dwarf-shrub, forb tundra (G2) according to the CAVM mapping (CAVM Team, 2003). The *Cassiope tetragona* heaths cover 6% of the vegetated area of the Zackenberg valley below 200 m a.s.l. and are dominated by *Cassiope tetragona*. Other dwarf shrubs (*Vaccinium uliginosum*, *Dryas* sp.), graminoids, and mosses are also present. The *Dryas* heaths cover 9% and are dominated by *Dryas* sp. and a hybrid between the eastern species *Dryas octopetela* and the western *Dryas integrifolia* (Bay, 1998). This species will be referred to as *Dryas* sp. further on in this paper. The *Dryas* heaths occur with *Salix arctica* and *Polygonum viviparum* as subdominants. The *Salix arctica* snowbeds cover 11% and are found on sloping terrain where the snow cover is prolonged compared to the other four vegetation types. The deciduous dwarf shrub *Salix arctica* is the dominant species, but also other dwarf shrubs and graminoids are present. The grasslands cover 30% and are found on mesic-wet soils where the soil dries out during summer (Fredskild and Mogensen, 1997; Bay, 1992). The grasslands are dominated by the graminoids *Arctagrostis latifolia*, *Eriophorum triste*, *Alopecurus alpinus*, and *Carex bigelowii* and there is a dense moss cover. The fens cover 4% and the type is located in lowland areas, and the soil is water-saturated throughout the growing season. The vegetation is dominated by the graminoids *Dupontia psilosantha* and *Eriophorum scheuchzeri* with a dense, almost complete moss cover underneath.

EXPERIMENTAL SETUP

Fifteen field sites covering the phenological gradients of the five major vegetation types in the area were established, i.e. three replicate sites of each vegetation type. These three replicate sites were not chosen in order to be homogeneous among sites but to

TABLE 1

Dates of measurements, and numbering of weeks in 2004.

Week number	Period of measurements
1	23 June–26 June
2	28 June–4 July
3	5 July–8 July
4	12 July–17 July
5	18 July–25 July
6	29 July–2 August
7	3 August–8 August
8	9 August–13 August
9	16 August–19 August

represent the ecological amplitude of variation within the specific vegetation type. That is, the specific field site was homogenous within the site but varied from the two other sites of the specific vegetation type. Each field site within a vegetation type consisted of nine separate homogeneously vegetated squares (19.5 × 19.5 cm) at least 1 m apart, eight for weekly biomass harvests and one for weekly CO_2 measurements.

The squares were selected to represent the vegetation within the site, but did not contain completely non-vegetated areas as such are very rare within the five selected vegetation types.

The CO_2 plot was harvested at the end of the study after the final CO_2 measurements. The nine plots enabled sequential sampling of biomass and measuring of CO_2 flux in similar and representative plots within each vegetation type throughout the growing season. All 15 field sites were measured once per week. This period was named "week 1" and during the next 7 days another 15 sites were measured, named "week 2," etc. Usually the 15 sites were measured within 3 days (±1–3 days due to occasionally bad weather). Data collection lasted from 23 June 2004 (DOY 175) till 19 August 2004 (DOY 232), enabling us to measure for 9 consecutive weeks, covering the growing season (see Table 1 for exact dates).

All field work and measurements were performed between 10:00 a.m. and 4:00 p.m. to exploit the highest Photosynthetically Active Radiation (PAR) conditions on dry, mostly clear days with stable weather.

PLANT BIOMASS AND CARBON, NITROGEN, AND CHLOROPHYLL CONTENT

Aboveground biomass was harvested once a week in one of the plots per site, i.e. biomass was collected in 9 consecutive weeks producing a measure of change throughout the growing season. Prior to harvest the plant cover in percentage of the ground area covered by leaves and mosses was estimated visually. Vascular plants were sorted to species level and separated into five fractions: flower, leaf, stem, litter, and standing litter. In the *Cassiope* and the *Dryas* heaths the stem fraction had standing litter included, as dead leaves could not be separated from the stems due to practical reasons. Mosses and lichens were also harvested but not identified to species level.

Fresh and dry biomass was weighed (dried at 70°C); all samples >0.1 g were ground in a mill and total C and N content were determined with a CN elemental analyzer (LECO Truespec^{TM} CN, St. Joseph, Michigan, U.S.A.). A few leaves of the most dominant species from each site were harvested just outside the plot for chlorophyll analysis. Leaves were kept cool in dark boxes until returning to the laboratory. Samples were then ground and extracted in 96% ethanol and placed in a freezer until the fraction was scanned with a spectrophotometer (U-2010, Hitachi, Tokyo, Japan). The pigment concentration of chlorophyll *a*, chlorophyll *b*, and carotenoids were obtained by insertion of the measured absorbance in the equation according to (Lichtenthaler, 1987). The collected species were *Cassiope tetragona*, *Dryas* sp., *Salix arctica*, *Eriophorum triste*, *Eriophorum scheuchzeri*, *Dupontia psilosantha*, *Vaccinium uliginosum*, *Arctagrostis latifolia*, *Polygonum viviparum*, and *Carex bigelowii*.

CARBON EXCHANGE

One aluminum chamber base of 19.5 × 19.5 cm was inserted into the soil in each of the 15 sites in mid June 2004. CO_2 fluxes were measured once a week at each site using a portable Infra Red Gas Analyzer (EGM 4, Hitchin, Herts., U.K.) connected to a transparent chamber. The chamber, with a volume of 13.5 L, was placed in the chamber base and sealed air-tight with water during measurements. The EGM logged the CO_2 concentration every 20 s during a period of 3 min and 20 s (11 measurements in total). Net Ecosystem Production (NEP) was first determined with the chamber uncovered. After a short removal of the chamber to restore CO_2 concentration to ambient, the chamber was replaced and covered with a dark cloth to exclude light; soil and plant respiration (Ecosystem Respiration, ER) were determined. The difference between NEP and ER yielded Gross Ecosystem Production (GEP), which was used for further analysis. By convention the carbon flux into the system was set positive, i.e. GEP is positive. A linear relation between time and CO_2 concentration in the chamber was expected. A few records not fulfilling the linear relation were deleted. The regression coefficient from this linear relationship was used for calculating CO_2 flux using the ideal gas law (Sjögersten et al., 2006; Tiiva et al., 2008).

Along with CO_2 measurements, air temperature and incoming photosynthetic active radiation (PAR) in the chamber were registered by the EGM-4 system. Soil temperature was recorded at 2 cm depth inside the chamber base immediately after flux measurements. Soil moisture was measured with a Theta Probe (Delta-T Devices, U.K.) at five different positions outside the chamber base.

DATA ANALYSIS

All statistical analyses were conducted using the GLM (General Linear Model) in the SAS v. 9 package (SAS Institute, 2003). To meet the assumptions of homogenous variances, Levene's test was used. If necessary, data were transformed. Only significant differences ($P < 0.05$) or tendencies ($0.05 < P < 0.10$) are reported; all means are averages of three replicate plots.

Measured CO_2-fluxes for each vegetation type were examined by repeated measurements analysis of variance (RM ANOVA) using PROC GLM to assess the variation among the five vegetation types. With vegetation type as factor and week as "repeated" within each plot, the differences among the vegetation types were evaluated. Pearson product moment correlation between gross ecosystem production (mg CO_2 m^{-2} h^{-1}) and leaf and moss nitrogen (g m^{-2}), chlorophyll *a* (g m^{-2}), leaf and moss biomass (g m^{-2}), and soil moisture (m^3 m^{-3}) were carried out to identify the environmental and biotic factors that may influence GEP, for all vegetation types and for each type separately. Mean values ($n = 9$) across growing season for each vegetation type are used in this analysis.

Biomass, C, N, and chlorophyll data across vegetation types were all analyzed with two-way ANOVA with vegetation type and

TABLE 2

Soil water content and soil temperature (depth 2 cm) in the five vegetation types (means ± SE). Means with different letters are significantly different (Tukey's test; $P < 0.05$).

Vegetation type	Soil water ($m^3 m^{-3}$)	Soil temperature (°C)
Cassiope heath	0.345 ± 0.015 d	11.8 ± 0.51 b
Dryas heath	0.270 ± 0.018 e	15.2 ± 0.96 a
Grassland	0.519 ± 0.013 b	10.6 ± 0.53 b
Fen	0.600 ± 0.0 a	10.0 ± 0.50 b
Salix heath	0.408 ±0.019 c	11.8 ± 0.44 b

week as factor in the model and their interaction. In cases of significance the differences were found using Tukey's test. The seasonal variation (time effect) within a vegetation type was additionally analyzed using one-way ANOVA with week as factor, followed by Tukey's test.

Results

ENVIRONMENTAL CONDITIONS

The annual mean temperature for 2004 in Zackenberg was −8.5°C (2 m above terrain) and the annual precipitation was 253 mm in total. The total precipitation during 2004 in June, July, and August was 17 mm, and the mean air temperature during these three months was 2.5, 7.2 and 5.6°C, respectively.

Soil water content was significantly different (ANOVA, $P < 0.0001$) among the five vegetation types (Table 2), while there was no seasonal variation in any of the vegetation types. The water content was highest in the fen with standing water throughout the growing season, with wet soil also in the grassland, mesic conditions in the *Salix* heath, and drier soils in the evergreen and wintergreen vegetation types. Soil temperature in the five vegetation types was also significantly different (vegetation type, $P < 0.0001$; week, $P < 0.0001$) and inversely related to the soil water content, with the *Dryas* heath being warmer than the other vegetation types (Table 2).

PLANT BIOMASS AND C, N, AND CHLOROPHYLL CONTENT

The total leaf cover differed significantly among samplings ($P < 0.0001$) and among vegetation types ($P < 0.0039$), with significantly higher leaf cover in *Salix* heath and *Dryas* heath than in the grassland across the growing season, and with *Cassiope* heath and the fen with intermediate cover (Fig. 2). The moss cover also differed among vegetation types ($P < 0.0001$), with highest cover in the fen and grassland, intermediate cover in the *Cassiope* and the *Salix* heath, and very little moss in the *Dryas* heath (Fig. 2). The leaf biomass is the sum of all leaves in a vegetation type (Fig. 3). Even though the dominant species made up the largest leaf biomass fraction, a range of other species contributed to leaf biomass. Seasonal mean leaf biomass was significantly different among the vegetation types ($P < 0.0001$) and was highest in the *Cassiope* heath, intermediate in the *Dryas* heath and the fen, and lowest in the *Salix* heath and the grassland. In the fen the leaf biomass increased from 12 g m^{-2} in the first week to 110 g m^{-2} in the sixth week. This ninefold increase in leaf biomass from early to late growing season was the most pronounced among the five vegetation types.

The moss biomass was significantly different among the vegetation types ($P < 0.0001$) and with highest biomass in the grassland and lowest in the *Dryas* heath (Fig. 4). The fen was the only vegetation type with significantly increasing moss biomass throughout the season, although all vegetation types showed a trend of two- or threefold higher moss biomass in late than early growing season.

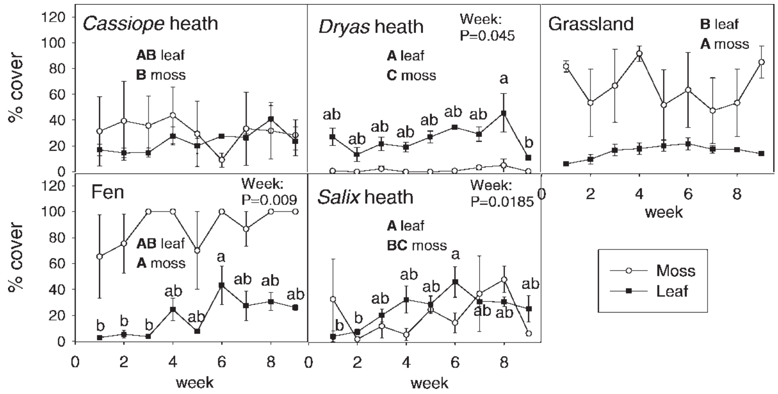

FIGURE 2. Leaf and moss cover in the five vegetation types in NE Greenland. Different capital letters indicate significant differences among vegetation types whereas different lowercase letters indicate differences among the weeks within the vegetation types as analyzed with the Tukey's test ($P < 0.05$; means ± SE). Results of ANOVA shown for effect of week, if significant.

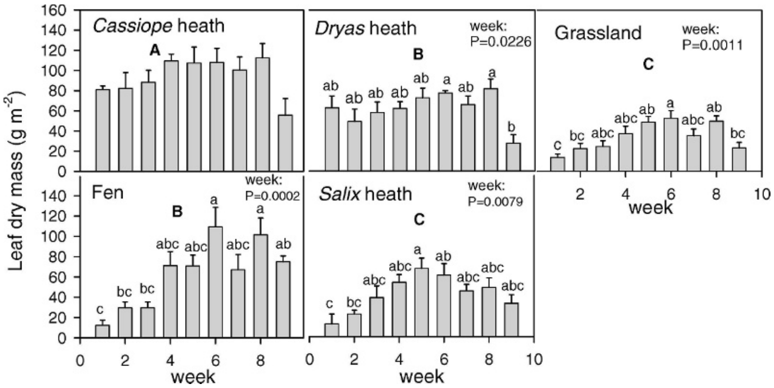

FIGURE 3. Leaf biomass in the five vegetation types in NE Greenland. Different capital letters indicate significant differences among vegetation types whereas different lowercase letters indicate differences among the weeks within the vegetation types as analyzed with the Tukey's test ($P < 0.05$; means ± SE). Results of ANOVA shown for effect of week, if significant.

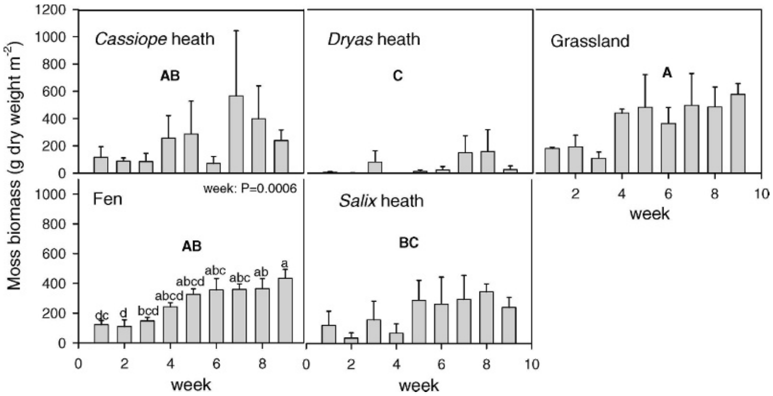

FIGURE 4. Total moss biomass in the five arctic vegetation types. Different capital letters indicate significant difference among vegetation types whereas different lowercase letters indicate differences among the weeks within the vegetation type as analyzed with the Tukey's test ($P < 0.05$; means ± SE). Results of ANOVA shown for effect of week, if significant.

The total C pool per unit area in the five vegetation types (Fig. 5) was derived from total biomass of the different plant pools multiplied by their C concentration. There were significant differences in pool size among the five vegetation types ($P < 0.0001$) with the *Cassiope* and the *Dryas* heaths having the significantly highest C pools because of high stem biomass. The total C pool of the grassland, the fen, and the *Salix* heath was dominated by mosses, which often made up more than 50% of the total C pool. The only vegetation type that showed a significant seasonal variation was the fen (ANOVA, $P < 0.0001$).

The C concentration (not shown) of the moss biomass was significantly higher in the grassland and the fen (means of 349 and 400 mg C g^{-1} dry weight) compared to the *Salix* and *Cassiope* heaths (251 and 305 mg g^{-1}). None of the vegetation types showed any seasonal variation in moss C concentration.

The total N pool size per unit area (Fig. 6) also resembled the C pool and biomass pattern during the growing season. There were significant differences in total N pool size among the five vegetation types ($P < 0.0001$) with highest pool size in the *Cassiope* and the *Dryas* heaths and lowest in the *Salix* heath. The sole significant seasonal variation was found in the fen with increasing N pool size throughout the growing season (Tukey's test, $P < 0.05$). There were also significant differences in leaf N pool among the five vegetation types (Fig. 7). The fen had higher seasonal mean leaf N per unit ground area than the other vegetation types (Tukey's test, $P < 0.05$) while the grassland had the lowest leaf N pool size. Both graminoid-dominated types showed significant seasonal variation of leaf N, with a peak in week 6 (one-way ANOVA and Tukey's test, $P < 0.05$).

The moss N concentration (not shown) was significantly different among the vegetation types. The grassland and the fen showed the highest concentrations of 10.6–11.7 mg g^{-1} while the *Cassiope* and the *Salix* heaths had means of 6.9–7.0 mg g^{-1}, stable through the growing season.

The chlorophyll *a* content in leaves per unit ground area (not shown) closely matched the leaf biomass during the growing season. The fen chlorophyll *a* was higher than in the other four vegetation types, and varied significantly through the growing season. In the species *C. tetragona* and *Dryas* sp. the chlorophyll

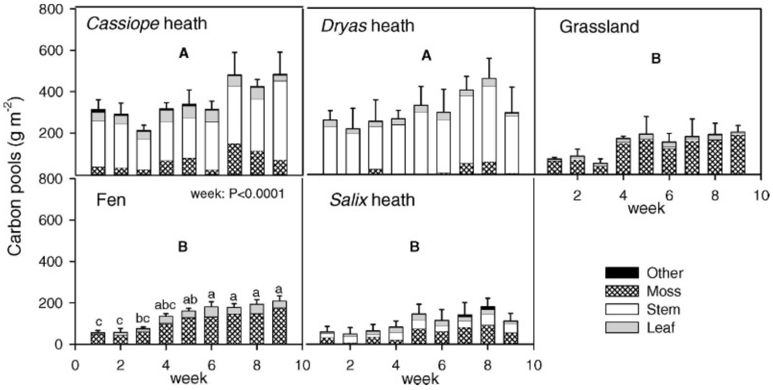

FIGURE 5. Total carbon in the five arctic vegetation types. Different capital letters indicate significant difference among vegetation types, whereas different lowercase letters indicate differences among the weeks within the vegetation type as analyzed with the Tukey's test ($P < 0.05$; means ± SE). Results of ANOVA shown for effect of week, if significant.

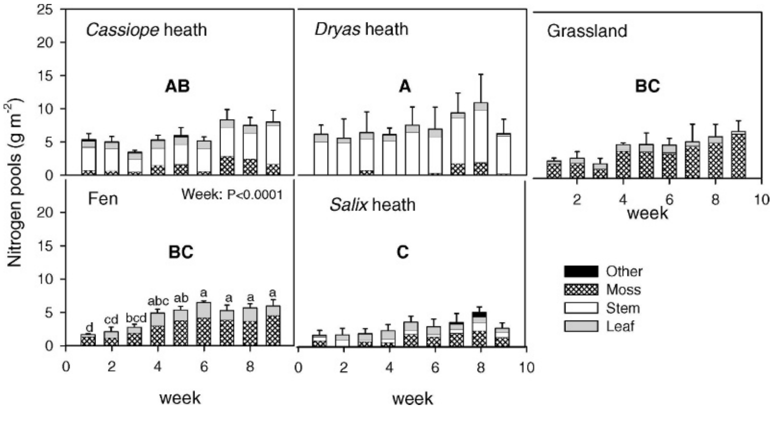

FIGURE 6. Total nitrogen in the five arctic vegetation types. Different capital letters indicate significant difference among vegetation types, whereas different lowercase letters indicate differences among the weeks within the vegetation type as analyzed with the Tukey's test ($P < 0.05$; means ±SE).

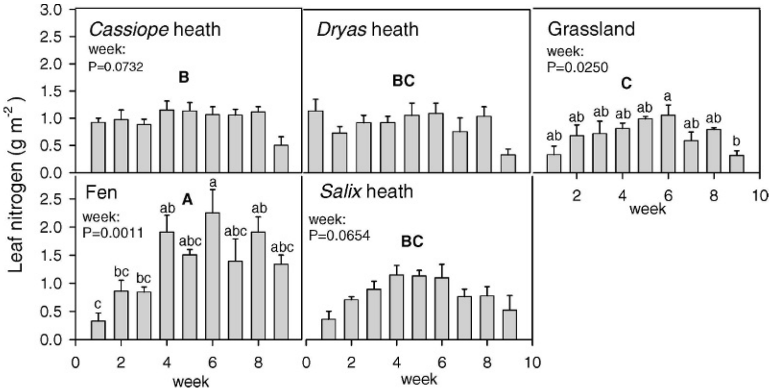

FIGURE 7. Leaf nitrogen in the five vegetation types in NE Greenland. Different uppercase letters indicate significant difference among vegetation types, whereas different lowercase letters indicate differences among the weeks within the vegetation type as analyzed with the Tukey's test ($P < 0.05$; means ±SE).

concentrations (mg g^{-1}) were lower than in the other species and declined throughout the growing season. None of the other dominant species showed any seasonal pattern in the chlorophyll concentration.

GROSS ECOSYSTEM PRODUCTION

Gross Ecosystem Production (GEP) differed significantly among vegetation types (RM ANOVA, $P = 0.0009$) and tended to change through the season across vegetation types (Fig. 8; $P = 0.057$). GEP did not correlate with PAR in any vegetation type or across all vegetation types (Pearson Product Moment Correlation Analysis). The GEP was significantly higher in the fen than in any other vegetation types across the season (Tukey's test, $P < 0.05$). The other vegetation types were not significantly different but the grassland had the second highest total GEP (mean) and the *Salix* heath was almost identical to the grassland, with a similar seasonal pattern. The *Dryas* and *Cassiope* heaths showed the lowest mean GEP. All vegetation types showed mid-season peaks in GEP, significantly so in the grassland and the fen.

GEP correlated positively with leaf N ($r = 0.54$, $P < 0.0001$) (Fig. 9), moss N ($r = 0.24$, $P < 0.0006$), and leaf chlorophyll ($r = 0.58$, $P < 0.0001$) across vegetation types, and these variables also correlated with GEP in analyses separate for each vegetation type; for leaf N in the *Cassiope* ($r = 0.45$, $P = 0.047$) and *Salix* heath ($r = 0.78$, $P = 0.0016$) and the grassland ($r = 0.51$, $P = 0.0310$) and

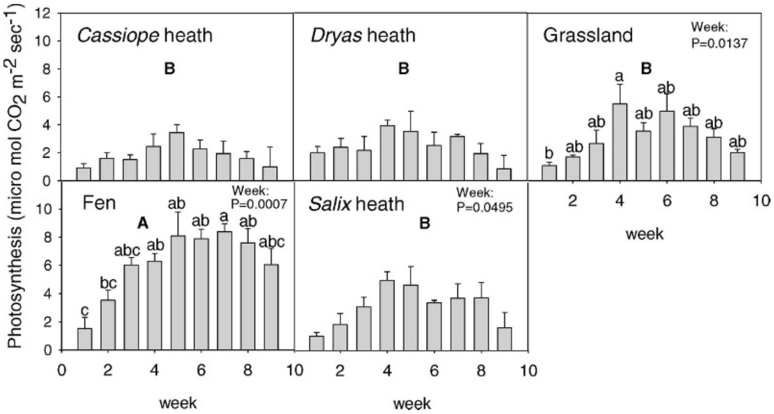

FIGURE 8. Photosynthesis in the five vegetation types in NE Greenland. Different uppercase letters indicate significant difference among vegetation types from repeated measurements analysis, while different lowercase letters indicate differences between week 1 and the following weeks within the vegetation type from analysis of variance of contrast variables ($P < 0.05$; means ±SE).

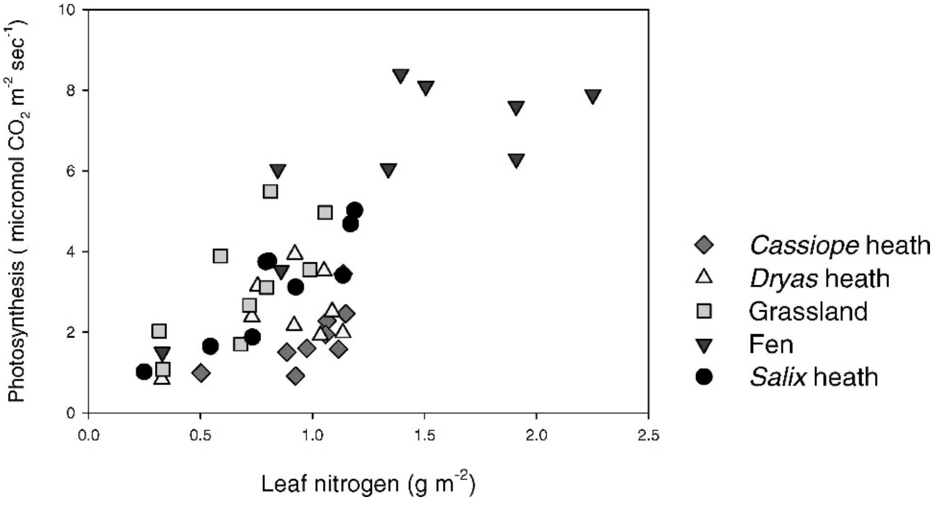

FIGURE 9. Gross ecosystem production plotted against the leaf nitrogen. Note that within-site gross ecosystem production data are not statistically independent across dates.

fen ($r = 0.63$, $P = 0.0108$), for moss N ($r = 0.65$, $P = 0.0079$) in the fen, and for chlorophyll in the *Salix* heath ($r = 0.57$, $P = 0.0193$), the grassland ($r = 0.69$, $P = 0.0058$), and the fen ($r = 0.52$, $P = 0.0291$). GEP was positively related to leaf biomass in the *Cassiope* heath ($r = 0.4049$, $P = 0.0358$), the *Salix* heath ($r = 0.78$, $P = 0.0015$), the grassland ($r = 0.57$, $P = 0.0183$), and the fen ($r = 0.64$, $P = 0.0093$).

Discussion

VASCULAR PLANT BIOMASS

The pattern of a rapidly increasing leaf biomass in deciduous vegetation types at the beginning of the growth season and a decreasing biomass within the last weeks of the season (Fig. 3) is due to a rapid expansion of preformed tissue followed by a period of new tissue production and maturation, and a phase of stable biomass and finally leaf dieback (Körner, 2003). The evergreen and the wintergreen heath types had a more stable pattern as they start the growing season with a significant amount of over-wintering leaves (Shaver and Kummerow, 1992), and they shed their leaves more gradually (Chapin, 1980). However, both the *Cassiope* and the *Dryas* heaths showed unexpectedly sudden drops in leaf mass by mid August, which may be due to leaf shedding by subdominant deciduous plants. Leaf shedding in the evergreen *C. tetragona* elsewhere takes place during the first half of the growing season (Shaver and Chapin, 1991), and the *Dryas* sp. is often described as a wintergreen plant, with a leaf longevity of about one year (Karlsson, 1992). It is possible, though, that *Dryas* sp. in high arctic areas sheds a relatively large proportion of the leaves at the end of the growing season, as found for *Dryas octopetala* in high alpine settings in Japan (Wada, 2003).

Leaf biomass of *Salix* heath peaked in mid July, one week earlier than the other vegetation types, which was unexpected as the late snowmelt in this heath type is expected to delay growth. High soil temperatures have been shown to cause higher stomatal conductance in *Salix arctica* at Devon Island in high arctic Canada, causing a potential higher photosynthetic gain (Dawson and Bliss, 1989). Also, Moore et al. (2006) suggested that cold temperatures in the vascular rooting zone were a primary limitation on the development of shrub photosynthesis in a cool temperate bog. The early peak leaf biomass could therefore be due to the early snowmelt in the year of sampling due to limited snow cover and unusually warm temperatures. The summer of 2004 was among the warmest on record since 1996 and snowmelt was early (Sigsgaard et al., 2005), leading to a longer growing season. This may be one of the reasons for the high biomass estimates in our study compared to earlier estimates as that of Christensen et al. (2000), also from Zackenberg.

In general, the plant biomasses and C pools in the Zackenberg valley are high compared to that of other, less productive high arctic sites, e.g. those studied by Welker et al. (2004) and Sjögersten et al. (2006). The aboveground biomass in the *Cassiope* and *Dryas* heath even exceeded that of some similar heath tundra types near Toolik Lake in low arctic Alaska (Shaver and Chapin, 1991; Hobbie and Chapin, 1998) and Abisko in subarctic N Sweden (Sorensen et al., 2006).

The increase in leaf biomass in the fen was larger than in any other vegetation type, and the high leaf biomass (Fig. 3) and photosynthesis (Fig. 8) by mid August indicates that the growing season had not ceased completely in this vegetation type when we ended harvesting. By this time the high moss cover and soil water content may improve growth conditions for the dominant graminoids due to the stabilizing effect on soil temperature at the end of the growing season. The late senescence in the fen ecosystems will enhance plant production more in this than other ecosystem types if the growing season expands due to warming. The significant difference in leaf biomass between the fen, and the *Salix* heath and the grassland clearly shows the great production and growth potential in the fen.

MOSS BIOMASS

The moss biomass varied sixfold among the vegetation types and dominated the total biomass in the grassland, the fen, and the *Salix* heath (Fig. 5), in agreement with the few other comparable studies from the Arctic (Chapin, 1995; Hobbie and Chapin, 1998; Rastorfer, 1978).

The increasing moss biomass in the fen throughout the growing season (Fig. 4) suggests that moss growth was not limited by the lower temperature or decreasing solar radiation at the end of the growing season, unlike leaf growth in the same vegetation type. Mosses have no roots and their photosynthesis is independent of peat temperatures (Moore et al., 2006). Earlier moss studies have also found lack of senescence of the photosynthetic tissue in late summer (Longton, 1988; Oechel and Sveinbjörnsson, 1978). This indicates that mosses are capable of utilizing the lower solar irradiance towards the last weeks of the arctic summer, while some vascular plants senescence. In general, bryophytes are adapted to low light, relative to other land plants, and most taxa have a low light compensation point and a low light saturation point (Glime, 2007) and are important contributors to plant production also in spring when the vascular plant canopy is not fully developed (Douma et al., 2007). Hence, the mosses and not the graminoids may be the main cause of enhanced C sink in the currently moss-dominated high arctic ecosystems as fen and grassland, if the potential growing season is extended due to warming.

Soil water content is presently not a limiting factor for mosses in most ecosystems, as the grassland, the fen, and the *Cassiope* heath all had high moss biomass despite differences in soil water content. Many mosses tolerate periods of desiccation (Longton, 1988), which might explain the lack of significant differences in moss biomass. The reason for the significantly lower moss biomass in the *Dryas* heath was probably the almost complete cover of *Dryas* sp., which forms cushions under which moss growth is difficult, unlike under for instance *C. tetragona*.

The leaf and moss cover data essentially showed the same seasonal pattern as the biomass (carbon) data, although with higher variance. This provides additional support for the differences in GEP and biomass among vegetation types. However, due to high variance the quick method of visual estimation of plant cover is not recommendable if a fine-grained analysis of changes in plant biomass is required.

CARBON AND NITROGEN POOLS

The significantly higher total C pool in the evergreen vegetation types (Fig. 5) was due to the high mass of woody tissue in the evergreen species which are slow growing and invest in C-rich compounds as lignin and cellulose, which increase with stem age (Chapin et al., 1986).

The mosses contributed proportionally less to the total C content than to the total biomass in comparison with the vascular plants, due to lack of structural tissue in mosses and consequently lower tissue C concentration. However, mosses still made up the major part of the plant C pool in all vegetation types except the *Dryas* and the *Cassiope* heaths.

The higher total aboveground N pool size in the *Cassiope* and the *Dryas* heaths (Fig. 6) was caused by the high stem fraction in these vegetation types, while the major part of the N pool in the fen, the grassland, and the *Salix* heath was due to mosses. N_2-fixing cyanobacteria are often closely associated with mosses and benefit from the moist conditions in their environment (Alexander et al., 1978). High rates of N_2 fixation in wet, moss covered areas (Sorensen et al., 2006) are probably a major reason for the high productivity in the fen and the grassland, where all aboveground plant N is found in non-woody, photosynthetically active tissue types.

Leaf N showed a pronounced seasonal pattern in the deciduous vegetation types while the two evergreen vegetation types had similar leaf N content without significant seasonal variation (Fig. 7). The stable N content suggests that there is a steady loss and uptake of N in the *Cassiope* and the *Dryas* heaths. Evergreens are less dependent on new N uptake from soil because leaves persist and they use stored N, while the deciduous types are more likely to become nutrient limited during leaf expansion and the period of formation of new leaves in the middle of the growing season. This is consistent with the lower soil ammonium concentrations in July in the rooting zone in these deciduous vegetation types (Elberling et al., 2008).

In general, the leaf biomass and C pool peaked in mid to late July, while the total aboveground plant C pool peaked in early August. This is because the mosses and woody stems continued to gain C in August while plant leaf mass was constant or even reduced. Hence, the timing of sampling of "peak biomass" in high arctic settings such as Zackenberg must depend upon whether the focus is on vascular plant leaves, stems, or mosses. If the aim is to estimate peak leaf biomass or leaf N pool size across vegetation types, sampling should generally not be done before early August in vegetation types dominated by deciduous shrubs or graminoids, while sampling in evergreen or deciduous types could start earlier. However, maximal biomass, C and N pools for woody stems and mosses are found in mid to late August, when leaf biomasses have started to decline. Also, vegetation types differed in the timing of total plant peak C and N pool as the *Dryas* heath and the *Salix* heath had clearly started to decline by mid August while the other types had not. This complicates comparisons of C pools among different vegetation types based on single harvests alone. Furthermore, the high seasonal variation in some vegetation types complicates comparison of carbon pool sizes among different studies. For instance, the biomasses of some of the same vegetation types in Zackenberg reported earlier in Christensen et al (2000) are far lower than our peak estimates, partly because the single sampling by Christensen et al (2000) was done in late August, when biomasses had started to decline. Consequently, biomass estimates with high time resolution are required for evaluation and comparisons of C and N pools in arctic ecosystems.

GROSS ECOSYSTEM PRODUCTION

Gross ecosystem production varied by more than fourfold in week 7, from the lowest values in the *Cassiope* heath to the highest in the fen (Fig. 8) and with intermediate values in the grassland and the *Salix* heath, which is comparable to data from peak season at Zackenberg (Christensen et al., 2000) and elsewhere (Johnson and Tieszen, 1976; Semikhatova et al., 1992), but higher than GEP in the more sparsely vegetated high arctic sites studied by Welker et al. (2004). Increased leaf longevity in plants implies that the photosynthetic rate declines with leaf age and becomes lower in evergreen plants (Chapin, 1980; Johnson and Tieszen, 1976). This might explain the non-significantly higher GEP in the *Dryas* than in the *Cassiope* heath, as *Dryas* sp. is wintergreen with a shorter leaf life span than the "real" evergreen *C. tetragona*. Long leaf life span increases the need for investment in chemical defenses as a means of protection against herbivores, and decreases investment in the photosynthetic apparatus (Johnson and Tieszen, 1976; Chapin et al., 2002).

Across vegetation types there was high correlation between GEP and leaf N, moss N, and leaf chlorophyll. This suggests that N may be limiting plant production in these vegetation types.

The difference in GEP among vegetation types is most likely due to differences in N content in photosynthesizing tissues. Plants with high leaf N have higher potential rates of photosynthesis, unlike slow growing wintergreens and evergreens such as *Dryas* sp. and *C. tetragona*, which often have a higher nutrient use efficiency (NUE), but lower photosynthetic efficiency than faster growing species (Chapin, 1980; Aerts and Chapin, 2000), explaining the lower GEP in these vegetation types.

GEP WITHIN VEGETATION TYPES

In the evergreen *Cassiope* vegetation the GEP correlated positively with leaf biomass and the leaf N pool, as leaf area and the length of time the leaf area is photosynthetically active are determinant factors of GEP. In the grassland the total chlorophyll *a* content in vascular plants had the lowest total mean compared to the other vegetation types and low chlorophyll may therefore limit GEP, explaining the positive correlation between chlorophyll *a* and GEP, which is similar to other results from the Arctic (Gerasimenko et al., 1993). In the fen, by mid August the GEP was still more than four times higher than in mid June, which suggests that the fen retains high photosynthesis longer than the other vegetation types, as was also indicated in the high leaf and moss biomass in mid August. By this time the graminoids in the fen were senescing, as indicated by the declining leaf N, but the moss biomass contributed considerably to the late season production, in agreement with the high correlation between GEP and moss N. In a similar study GEP at snowmelt was associated with the mosses, which have no roots and can photosynthesize as soon as they thaw and receive light (Moore et al., 2006). Moss growth has also no strict period of senescence (O'Neill, 2000) and is thereby able to take greater advantage of the late summer. The mosses have a lower light compensation point and light saturation intensity than the vascular plants and can maintain a positive net assimilation under cold and low light conditions (Longton, 1997; Tenhunen et al., 1992; Mogensen, 2001). The aboveground productivity of the mosses is generally considered lower than that of the vascular plants in the Arctic (Oechel and Sveinbjörnsson, 1978). However, the low specific productivity is compensated by a greater biomass of photosynthetically active tissue. This was found in three of the five major vegetation types in the Zackenberg Valley. The large moss biomass probably contributed indirectly to the GEP, as the moss mats enable the cyanobacteria to reach a larger biomass than on bare soil, thus enhancing N fixation and N availability (Billings, 1992; Zielke et al., 2005). This may enable the high chlorophyll and N leaf pool size, which also contributed to the high GEP in the fen.

The *Salix* heath showed high positive correlation between GEP and both leaf biomass and N pool, and GEP peaked in mid July, coinciding with the peak in leaf N. As the seasonal progression of maximum photosynthetic rates is mainly determined by the activity of ribulose-1,5-diphosphate carboxylase activity (Tieszen and Johnson, 1975), and this and other photosynthetic enzymes account for c. 50% of leaf N (Field and Mooney, 1983), this explains the influence of leaf N on GEP.

Conclusions

This study has demonstrated clear differences among five major high arctic vegetation types. The fen, which had the highest leaf N, leaf chlorophyll, and moss N content per unit ground area, was also the most productive vegetation type in terms of GEP. The other four vegetation types were not significantly different in their seasonal GEP mean, which indicates that different species and growth forms may have relatively similar mean daily rates of net photosynthesis throughout the growing season. However, the vegetation types differed in the variables that influence the seasonal plant production. In the *Cassiope* heath, production relied on the evergreen leaf biomass and N pool, leading to relatively stable biomass production throughout the growing season. Despite physiognomical differences the grassland and the *Salix* heath shared the same variables that were correlated with GEP, namely leaf biomass, leaf chlorophyll, and leaf N pool. The GEP of the fen was, in addition, positively influenced by the moss N content, indicating the great role of the mosses in this ecosystem.

The mosses dominated both biomass C and N pools in the grassland, the fen, and the *Salix* heath, and contributed importantly to the ecosystem production, as suggested by the positive correlation between the moss N and GEP across vegetation types. Although the relative contribution of the mosses and the vascular plants to C uptake cannot be evaluated from this study, it is evident that the role of the mosses should be examined in more detail, especially in the light of possible future climatic changes in the High Arctic.

The results furthermore demonstrated a significant seasonal variation, most pronounced in the deciduous vegetation. The peak of GEP, biomass, chlorophyll, and N content in the vascular plant and the moss biomass did not coincide. This is important, as other studies often upscale a single measurement estimate at an expected time of "peak growing season." This emphasizes the importance of sampling throughout the growing season when using field data from the Arctic to estimate plant biomasses and modeling carbon fluxes and pool sizes.

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