Increased photosynthesis compensates for shorter growing season in subarctic tundra—8 years of snow accumulation manipulations

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Abstract This study was initiated to analyze the effect of increased snow cover on plant photosynthesis in subarctic mires underlain by permafrost. Snow fences were used to increase the accumulation of snow on a subarctic permafrost mire in northern Sweden. By measuring reflected photosynthetic active radiation (PAR) the effect of snow thickness and associated delay of the start of the growing season was assessed in terms of absorbed PAR and estimated gross primary production (GPP). Six plots experienced increased snow accumulation and six plots were untreated. Incoming and reflected PAR was logged hourly from August 2010 to October 2013. In 2010 PAR measurements were coupled with flux chamber measurements to assess GPP and light use efficiency of the plots. The increased snow thickness prolonged the duration of the snow cover in spring. The delay of the growing season start in the treated plots was 18 days in 2011, 3 days in 2012 and 22 days in 2013. Results show higher PAR absorption, together with almost 35 % higher light use efficiency, in treated plots compared to untreated plots. Estimations of GPP suggest that the loss in early season photosynthesis, due to the shortening of the growing season in the treatment plots, is well compensated for by the increased absorption of PAR and higher light use efficiency throughout the whole growing seasons. This compensation is likely to be explained by increased soil moisture and nutrients together with a shift in vegetation composition associated with the accelerated permafrost thaw in the treatment plots.

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1 Introduction

Snow is one of the most important factors controlling vegetation and ecosystem functions in higher latitudes and alpine areas (Walker et al. 1993; Høye et al. 2007). The duration of snow cover and snow cover thickness directly govern fluxes of CO_2 in plant communities (Grøndahl et al. 2007; Larsen et al. 2007; Nobrega and Grogan 2007; Grogan 2012) and in the colder regions, where the growing season is short, a few weeks of change in season length may have significant impact on phenology and ecosystem functions (Walker et al. 1999; Høye et al. 2007; Post et al. 2009; Elmendorf et al. 2012). Snow also serves as an insulating and protecting cover for many plants, as well as storage of water being released when snow melts in spring (Olsen et al. 2011).

Observations show that, although changes in snow depth and snow cover duration is not uniform over the Arctic (Brown and Mote 2009), winter snow depth increased in Scandinavia and Eurasia during the 20th century (Callaghan et al. 2011). Projections made by General Circulation Models indicate that hydrological processes are expected to intensify with climate change (Christensen et al. 2007) and many regions in the Arctic and subarctic will experience an increase in snow water content (SWC) (Callaghan et al. 2011). Understanding of how temporal and spatial changes in snow patterns affect arctic and subarctic ecosystems is therefore crucial to better estimate the global carbon balance with a changing climate. In subarctic Fennoscandia, permafrost mires are currently subjected to climate related thawing (Åkerman and Johansson 2008; Callaghan et al. 2012) and shift in vegetational and hydrological patterns (Malmer et al. 2005; Bosiö et al. 2012). These changes exert a significant impact on atmospheric CO_2 sink function and CH_4 emissions (Christensen et al. 2004; Johansson et al. 2006) and on soil hydrologic dynamics (O'Donnell et al. 2012; Jorgenson et al. 2013).

Snow manipulation experiments have been carried out in various arctic, subarctic and alpine environments. Most common are snow fence manipulations where the snow is accumulated over the season, delaying the melt off, and snow removal and plot warming to simulate warmer climate and earlier snowmelt. A review over snow manipulation experiments in alpine and arctic environments show that the majority of the experiments run for 3 years or shorter, while some experiments (mainly focused on changes in species composition and phenology) run for longer time periods (4–32 years) (Wipf and Rixen 2010). Several studies have investigated productivity and plant growth (Walker et al. 1999; Welker et al. 2000; Chimner and Welker 2005; La Puma et al. 2007; Rixen et al. 2008). However, the results are not all conclusive: Plant biomass has shown to increase with increased snow cover (Walker et al. 1995, 1999; Wahren et al. 2005), but others report a decline in the overall ecosystem productivity due to delayed snowmelt and shortened growing season (Aurela et al. 2004; Grøndahl et al. 2007; Wipf and Rixen 2010). The effect of the snow manipulation experiments varied between a few decimeters to over two meters in increased snow depth. All the studies indicate no clear pattern with regard to the level of snow manipulation. Plant productivity and growth rates generally varied between species, showing negative response for grasses, positive response for forbs and no clear pattern for deciduous and evergreen dwarf shrubs (Wipf and Rixen 2010). Although changes in climate may have drastic effects upon the arctic tundra, the ecosystems response is slow in terms of equilibration and adaptation (Walker et al. 1999). It may take decades before the full impact of changes in the environmental conditions is visible. It is therefore essential to study the long term effects of increased winter snow cover on plant communities (Walker et al. 1999; Wipf and Rixen 2010).

A number of snow manipulation studies in the area surrounding Abisko have previously been reported (Grogan and Jonasson 2006; Larsen et al. 2007; Torp et al. 2010; Olofsson et al.

2011). Enhanced snow depth and prolonged snow cover duration resulted in increased ecosystem respiration during late winter but had no effects during spring snowmelt (Larsen et al. 2007). Prolonged snow cover delayed plant phenology but favored plant growth and nutrient availability. Plant biomass decreased over the observation periods due to higher herbivore leaf damage and plant diseases (Larsen et al. 2007; Torp et al. 2010). After 3 years of snow manipulation at a lowland permafrost site Johansson et al. (2013) could observe increased soil wetness on the manipulated plots, especially after snowmelt. However, no statistically significant difference in plant species composition could be observed although the vegetation on the manipulated plots showed an increased "greening" by the end of the growing season. Carbon fluxes, measured during parts of the growing season in 2009 at the experimental plots, using manual closed chamber systems (unpublished), showed only a weak or non-significant correlation between the "greening" and the snow manipulation experiment.

Quantifying carbon fluxes of terrestrial ecosystems to predict current and future carbon sink activity has been a major challenge (Kicklighter et al. 2014). One commonly used method to estimate GPP of terrestrial biomes is the canopy light-use efficiency (ε), defined as the ratio of GPP (or NPP) to absorbed light (Kergoat et al. 2008). Because of its theoretical basis and practicality, ε provides an accurate description of terrestrial ecosystem productivity and is used at various spatial and temporal scales (Turner et al. 2002; Xiao et al. 2004; Bradford et al. 2005; Schwalm et al. 2006; Yuan et al. 2007).

1.1 Aims and hypothesis

Our main objective was to investigate how increased snow cover and prolonged snow cover duration affect plant photosynthesis in two subarctic tundra vegetation types: dry heath and moist tussock tundra. More specifically our aims were 1) to estimate the effect of the delayed date of snowmelt (DOSM) on the accumulated gross primary production (GPP) over the growing season for the two vegetation types and 2) to estimate to what extent areas subjected to several years of increased snow cover and prolonged snow cover duration, can compensate for the shortened growing season by increased photosynthesis. Based on previous visual observations, such as increased soil moisture and a greening effect of the vegetation, we hypothesize that the photosynthesis rate is higher in plots subjected to increased snow cover than plots under ambient snow cover conditions, and that the higher photosynthesis rate to some extent compensates for a shorter snow free period.

2 Materials and methods

2.1 Study site

We measured reflected photosynthetic active radiation (PAR) and carbon dioxide flux on Storflaket, a subarctic ombrotrophic mire underlain by permafrost located 6 km east of Abisko in northern Sweden (68° 20.8′N, 18° 58.2′E, 383 m.a.s.l). The orographic effect of the surrounding Scandes mountains leaves the area in rain shadow, with as little as 362 mm precipitation per year, mean annual temperature is +0.49 °C for the period 2002–2011 (official data from Abisko Scientific Research Station) . The mire covers approximately 13 ha and is characterized by a 60–90 cm thick peat layer underlain by silty sediments (Klaminder et al. 2008; Åkerman and Johansson 2008). Because of underlying permafrost, the plant community is tundra-like, even if the surrounding is not strictly classified as tundra (Wielgolaski 1972). The dryer upraised palsa areas are characterized by dry heath vegetation with low growing

dwarf shrubs, short sedges, bryophytes, lichens and barren soil. In hollows (thermokarst) and depressions, dominant vegetation consists of tussock-forming sedges and sphagnum mosses. In some areas dwarf shrubs, such as *Betula nana,* grow higher. The surrounding area is vegetated by birch and willow forest, tall shrubs and heath vegetation.

2.2 Experimental setup

2.2.1 Snow manipulations

Since 2005 the snow cover thickness has been manipulated by using snow fences (10 m long, 1 m high) to accumulate snow over six randomly selected experimental plots (+Snow). Snow fences were installed every year in September–October, perpendicular to the prevailing east–west wind direction, and removed every year after snowmelt. Initially, snow accumulates on the west side and by the end of the snow season the effect of the snow manipulation covers approximately 20×10 m. Six control plots (Cont.) were selected randomly for comparison. For detailed description of the site and the experimental setup, see Johansson et al. (2013).

2.2.2 PAR measurements

Using the light use efficiency (ε) model, GPP can directly be related to the amount of photosynthetic active radiation (PAR) absorbed by plants (APAR) (Monteith 1972, 1977) with the following equation (Monteith 1977):

$$GPP = \varepsilon \cdot APAR \tag{1}$$

where GPP is given in μg CO_2-C m^{-2} s^{-1} and ε is the light use efficiency parameter (μg CO_2-C μmol^{-1}).

The amount of APAR can be derived from the incident light PAR (μmol m^{-2} s^{-1}) and the fraction of PAR absorbed by vegetation (fAPAR) (Gobron and Verstraete 2009):

$$APAR = fAPAR \cdot PAR \tag{2}$$

Photosynthetic photon flux density (PPFD) is a quantitative measure of PAR, i.e. the energy of the electromagnetic radiation in the interval 400–700 nm, and fAPAR was calculated with the following equation:

$$fAPAR = (PPFD_{in} - PPFD_{refl})/PPFD_{in} \tag{3}$$

where $PPFD_{in}$ is the incident light and $PPFD_{refl}$ is the reflected light, both in μmol m^{-2} s^{-1}.

Assessing the photosynthetic activity by using PAR sensors is a non-intrusive method that allows high temporal resolution and requires little maintenance. In July 2010 Minikin QT loggers from EMS Brno were installed at 50 cm height in the middle of each plot to measure $PPFD_{refl}$ by the vegetated surface. On the treatment plots, the loggers were installed within a 5 m radius on the western side of the snow fence and one upward facing logger was installed to measure incident PPFD ($PPFD_{in}$) for the site. Since all control (Cont.) and treatment (+Snow) plots are located within an area of less than 2 ha, one logger was considered enough to represent the incident light of all 12 plots. Measurements of incident PPFD from the nearby Abisko Scientific Research Station were used to validate the $PPFD_{in}$ logger at Storflaket. In

2010 and 2011 $PPFD_{refl}$ was recorded and stored once per hour; in 2012 and 2013 $PPFD_{refl}$ was recorded once per minute and an hourly average was derived.

2.2.3 Flux chamber measurements in 2010

CO_2 fluxes were measured manually using a PP Systems' gas analyzer (EGM-4) attached to a Plexiglas chamber. The chamber was equipped with a fan for air mixing during measurements. Net ecosystem exchange (NEE) was measured as the net exchange of CO_2 between the uptake (mainly due to plant CO_2 sequestration) and emissions (autotrophic and heterotrophic respiration). NEE was measured in a transparent chamber to quantify the effect of photosynthesis. Ecosystem dark respiration (R_{eco}) was measured by shading the transparent chamber with a dark cloth. GPP was calculated as the difference between NEE and R_{eco}. The measurements were carried out on 15 days without precipitation between July and September. On each plot the measurements of NEE and R_{eco} were conducted between 10 and 14 h (CET) three times per day, from which daily means of NEE, R_{eco} and GPP were computed. Together with the chamber measurements, soil water content (SWC) and soil temperature was measured manually at 5 cm depth on three points per plot using a Theta Probe kit. Air temperature was not measured plot-wise but for the whole site during the chamber measurements. Results of NEE, R_{eco}, soil moisture, and soil and air temperature are presented in the appendix (App. 1; App. 2; App. 3).

2.3 Data processing and statistical analysis

Since vegetation covers the surface completely in the studied plots, with a moss layer closest to the ground, we assumed that all of the $PPFD_{in}$ that was not reflected by the surface was absorbed by vegetation (Frolking et al. 1998; Huemmrich et al. 2010a). For each plot we calculated fAPAR separately in 1-h intervals throughout the whole growing season. In 2010, $PPFD_{in}$ was taken from the nearby logger at Abisko Scientific Research Station. We assumed the growing season is equivalent to the period starting by the DOSM in spring and ending by the first day of snowfall in autumn.

Since DOSM differed between the control (Cont.) and the treatment plots (+Snow), DOSM was computed individually for Cont. ($DOSM_C$) and + Snow ($DOSM_S$). DOSM was defined as the date when all control and treatment plots were snow free. The high albedo of snow gives a clear signal in $PPFD_{refl}$ when snow is present or not. Therefore, DOSM was determined by the day when the maximum PPFD equaled or showed higher values of PPFD than the highest value of PPFD between 1 June and 31 August.

Hourly fAPAR ($fAPAR_h$) was computed (Eq. 3) for each sensor separately, for three parts of the snow free season: Early season, peak season and late season. The early season was defined as the time period between DOSM until the daily average air temperature reached >10.0 °C within five consecutive days. The peak season was defined as the time period with daily average air temperatures >10.0 °C, and the late season was defined as the time period when daily average air temperatures dropped below 10.0 °C within five consecutive days until the first day of snowfall.

Since loggers were installed in the end of July 2010, $fAPAR_h$ could only be computed for the peak- and late season that year. Values of $PPFD_{in} < 1$ μmol m^{-2} s^{-1} were filtered out, as they were regarded as nighttime; $fAPAR_h < 0$ was also excluded from the analysis. From $fAPAR_h$ we computed (plot-wise) daily mean fAPAR ($fAPAR_d$). Due to sensor maintenance (15–17 June 2012) $fAPAR_d$ was gap-filled using linear interpolation. During 27 July 2011 and 16 June

2012 data of one sensor at Cont. was removed from the analysis because it had fallen down (the exact date could be detected from a sharp increase in the reflected PAR).

Both PPFD$_{refl}$ and fAPAR$_d$ of Cont. and + Snow were tested against normality. A non-parametric test (Mann–Whitney U-test) was performed to test the significance of the difference between control and treatment measurements.

2.3.1 Estimation of ε and GPP

Plot-specific ε values (ε$_{plot}$) were estimated using CO_2 flux measurements and APAR from the 15 days in 2010. ε$_{plot}$ was computed for each plot by fitting a linear curve to the measured daily GPP and APAR values of each plot, assuming a linear relationship between GPP and APAR (Eq. 1), and that GPP is zero at APAR=0. Since the chamber measurements were carried out between 10 and 14 h (CET), the daily APAR was computed as a mean of APAR-values during the same time period. ε$_{plot}$ was tested for correlation with day of year (DOY), soil water content (SWC) and soil temperature. Since only very weak and non-significant correlations were found (App. 1), we assumed ε$_{plot}$ to be relatively constant over the season. This assumption is supported by previous research, concluding that the light use efficiency differs among species and locations but is relatively fixed over the growing season, between years and even under manipulations of seasonal patterns in snow and temperature (Starr et al. 2008; Huemmrich et al. 2010a, b).

The photosynthetic capacity is assumed to quickly increases to its maximum to take advantage of the short growing season (Starr et al. 2008). We thus assumed ε$_{plot}$ to represent the specific vegetation, soil and water conditions of each plot, and used the ε$_{plot}$ to model hourly GPP (GPP$_h$) from the hourly PAR measurements between 2010 and 2013. GPP$_h$ was computed plot wise for all years, according to Eqs. 1 and 2, where ε equals ε$_{plot}$ for each plot, fAPAR equals the fAPAR$_h$ for each plot and PAR equals the hourly values of PPFD$_{in}$ for the site. Accumulated GPP (GPP$_{accum}$) was computed for each plot by summing all GPP$_h$ (24 values/day) for each part of the season. The plot where the sensor had fallen down in July 2011 was excluded from the GPP$_{accum}$ computations, since GPP$_h$ could not be computed for most of the growing season in 2011 and parts of the growing season in 2012. The GPP$_{accum}$ was computed from the date of snowmelt until the first day of snowfall.

3 Results

3.1 Snow and climate monitoring

Since the installation of snow fences in the winter season 2005/06, the snow depth at + Snow was twice the depth of Cont. (~20 cm and 10 cm respectively) (Johansson et al. 2013). Between 2011 and 2013 the thicker snow cover, caused by the snow fences hindering snow drift, prolonged the duration of snow cover in the treated plots. In 2011, DOSM was 10 May in + Snow compared to 22 April in Cont., i.e. a delay of 18 days. In 2012 the spring was late and snow melted rapidly in both Cont. and + Snow. DOSM was 18 May in + Snow compared to 15 May in Cont., hence a delay in DOSM in + Snow of only 3 days. In 2013, DOSM was 11 May in + Snow compared to 19 April in Cont., i.e. a delay of 22 days. Comparing the 3 years, the total length of the snow free season was 193 days for Cont. (175 days for + Snow) in 2011, 162 (159) days in 2012 and 178 (156) days in 2013.

The snow free season in 2013 was warmer than the two preceding years. From the early season until end of late season the daily mean temperature was 9.0 °C in 2013, 7.0 °C in 2012

and 8.8 °C in 2011. 2011 was drier than the following years with accumulated precipitation of 228.4 mm, compared to 262.4 mm in 2012 and 232.3 mm in 2013. The accumulated winter precipitation (precipitation from the day of first snow in the preceding year until $DOSM_C$) was higher in the winter season 2010/11 (140.8 mm) than in 2011/12 (116.2 mm) and in 2012/13 (81.9 mm). The maximum snow depth (precipitation and snow depth data from the Abisko Scientific Research Station, 6 km west of the site) in 2011 and 2012 was 66 and 54 cm respectively; In 2013 the maximum snow depth reached 55 cm. Due to wind drift, the ambient snow depth at the site (i.e. snow depth in control plots) is lower (~10 cm).

3.2 Carbon flux measurements in 2010

The chamber flux measurements showed a significant ($p < 0.001$) difference in GPP between Cont. and + Snow. GPP was on average 57 % higher (medians compared) in + Snow than in Cont., ranging between 0.04 and 0.28 g CO_2-C m^{-2} h^{-1} for + Snow and 0.02–0.20 g CO_2-C m^{-2} h^{-1} for Cont. from peak season (mid of July) to late season (end of September). The ε_d parameter computed from GPP_d and APAR measurements in 2010, showed a significant ($p < 0.001$) difference in ε_d between + Snow and Cont. (Fig. 1). ε_{plot} was on average 0.0486 μg CO_2-C μmol^{-1} in Cont. and 0.0692 μg CO_2-C μmol^{-1} in + Snow, i.e. 0.0206 μg CO_2-C μmol^{-1} higher in + Snow than in Cont. (App. 2). No significant trend could be seen in ε_{plot} with changing DOY over the snow free period (App. 1), thus we assumed ε_{plot} to be constant over the growing season.

3.3 fAPAR

Median + Snow $fAPAR_d$ in late season is strongly significantly ($p < 0.001$) lower in 2013 than in 2012 and 2011. +Snow $fAPAR_d$ during peak season is highest in 2011 whereas no clear difference between median $fAPAR_d$ was observed in the other years. In the early season, differences in median $fAPAR_d$ between years are small (Fig. 2).

Cont. shows a similar pattern for late season, with highest $fAPAR_d$ in 2011 and 2012. During peak season no pronounced difference in $fAPAR_d$ was observed in 2011 and 2013. In
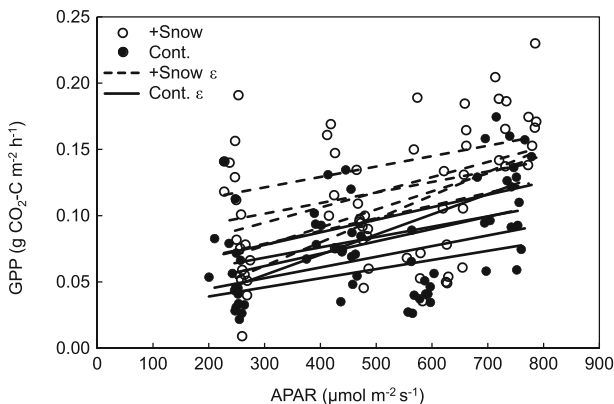

Fig. 1 Relationship between daytime GPP and APAR measured in 2010. The slope of the linear relationship between APAR and GPP represents ε_{plot} for control plots (*filled circles, solid lines*) and treatment plots (*empty circles, dashed lines*)
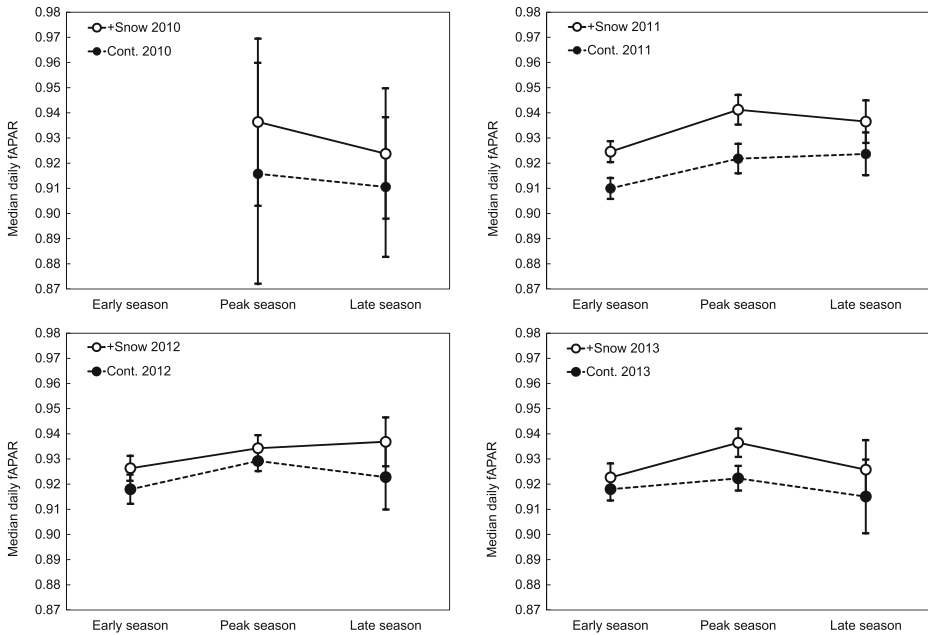
Fig. 2 Median daily fAPAR for early, peak and late season from 2010 to 2013. *Filled circles* indicate median values for control plots, *empty circles* indicate treatment plots. *Bars* show the median absolute deviation (MAD)

early season, $fAPAR_d$ is lowest in 2011, for 2013 and 2012 no clear difference was observed (Fig. 2).

For 2011–2013 the difference in $fAPAR_d$ between + Snow and Cont. ($\Delta fAPAR$ = median $fAPAR_{d,T}$ - median $fAPAR_{d,C}$) was strongly significant ($p < 0.001$), where median $fAPAR_d$ for + Snow is generally higher than for Cont. On average, $fAPAR_d$ is 1.3 % higher in + Snow than in Cont. with a strong significance through all parts of the seasons and years. The difference is most pronounced during peak season (1.6 %) and late season (1.4 %), whereas during early season the difference is 1.0 %.

Mid-day (10–14 h) fAPAR in 2010, to estimate the seasonal GPP, showed significant difference ($p < 0.001$) between + Snow and Cont., where mean fAPAR was 0.90 in Cont. and 0.93 in + Snow.

3.4 Estimated seasonal GPP

Figure 3 illustrates the accumulated GPP over the seasons for Cont. and + Snow during 2010–2013. The modeled GPP_{accum} showed that a delayed start of the growing season in + Snow, compared to Cont., results in a lower GPP_{accum} in + Snow (medians compared). The difference in GPP_{accum} is strongest in 2011 and 2013, when average delay of the growing season between + Snow and Cont. was 20 days. In 2012 the delay was 3 days, resulting in higher GPP_{accum} in + Snow.

For the peak season the modeled GPP_{accum} is, on average, 14.9 g C m^{-2} higher in + Snow than in Cont. (2011–2013). GPP_{accum} for the same years in the late season is, on average, 2.5 g C m^{-2} higher in + Snow than in Cont. Compared to 2011 and 2013, lower average air temperatures during the growing season in 2012 resulted in lower total GPP_{accum} for both +
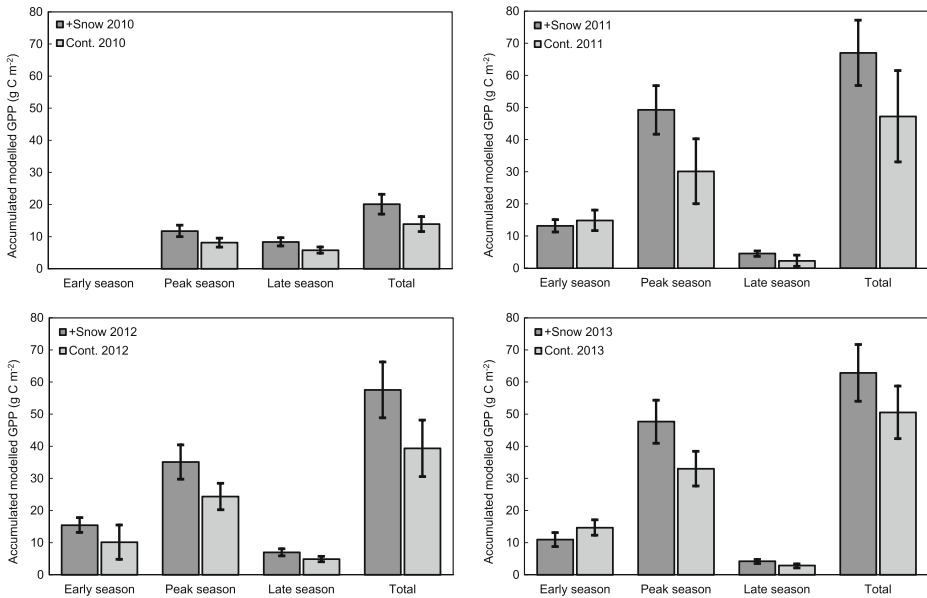
Fig. 3 Modeled GPP$_{accum}$ for control (Cont.) and treatment (+Snow) plots for early, peak and late season from 2010 to 2013. *Bars* show the standard deviation

Snow and Cont. Although the measurement period in 2010 is reduced due to the late start of our measurements, GPP$_{accum}$ in + Snow is higher than in Cont. for both peak and late season.

4 Discussion

4.1 Observed differences between control and treatment plots

Measured fAPAR and estimated GPP showed significant differences between + Snow and Cont., where both fAPAR and accumulated GPP over the growing season, was higher in + Snow than in Cont. Previous studies on snow-vegetation interaction have observed similar effects (Walker et al. 1995, 1999; Wahren et al. 2005), although increased plant growth may be a short-term response (Walker et al. 1995). Several studies report no (Starr et al. 2008) or even negative (Aurela et al. 2004; Larsen et al. 2007; Torp et al. 2010; Wipf and Rixen 2010) effect on plant growth or photosynthesis from increased snow cover or delayed snowmelt. We conclude that our plots with experimentally increased snow cover still benefit compared to plots under ambient snow conditions.

The accumulation of snow affects the abiotic conditions both directly and indirectly, e.g. it acts as insulating layer during winter, preventing soil temperatures to drop as low as under ambient conditions. Increased snow depth has induced permafrost thawing and associated ground subsidence in + Snow with water table closer to (and sometimes above) ground level and thicker active layer (Johansson et al. 2013). In tundra regions, where plants are adapted to short growing seasons but often are moisture limited (Keuper et al. 2012a), the timing of snowmelt and the availability of water during the peak growing season are important factors regulating plant growth and annual carbon balance (Aurela et al. 2004). In line with our observations from Storflaket, increased productivity due to permafrost thawing was reported

from Alaskan tundra sites (Trucco et al. 2012) and from five peatland sites in northern subarctic Sweden (Keuper et al 2012b).

The insulation effect of the snow and thicker active layer exposes larger volumes of unfrozen organic soil to microbial decomposition. The thicker active layer allows roots to penetrate deeper into the soil substrate and thus increases nutrient uptake (Schimel et al. 2004). According to Johansson et al. (2013) the treated plots at Storflaket have significantly higher soil temperatures than control plots at both 15 and 50 cm depth during winter (November–April). We hypothesize that the combined effects of increased moisture and temperature promotes nutrient availability and graminoid growth.

4.2 Interannual variability

When comparing our fAPAR and GPP measurements between the years 2011 and 2013 and vegetation analysis from Johansson et al. (2013) the picture becomes more complex. In + Snow they observed a dominance of *Eriophorum vaginatum*, with higher tillers compared to Cont., and a pronounced greening at the end of the summer but no statistically significant change in the abundance of plant functional types between Cont. and + Snow.

In 2012, snow melted almost a month later than in 2011 and 2013 (Cont. compared). The modeled accumulated GPP was lower for both Cont. and + Snow in 2012 than in 2011 and 2013, likely due to the overall shorter season. The lower cumulative GPP in + Snow in 2012 may also be an effect of climate conditions during that growing season. +Snow appears to overcompensate for the shorter growing season but the climate conditions were less favorable that year by showing lower peak season fAPAR in 2012 than in the other years. However, Cont. did not seem to be negatively affected by the colder and wetter weather in 2012 with significantly highest fAPAR in 2012 during early and peak season, i.e. the periods of most importance for production (when temperature and light availability is at its highest). This indicates that, in spite of a colder and wetter growing season, the delayed snowmelt promoted plant growth in Cont. but it was not enough to offset the delayed snowmelt and subsequent shortening of the growing season. This suggests that the overall species composition in Cont. is better adapted to colder growing season temperatures. Vegetation in Cont., where soil is drier than in + Snow (App. 3), benefits from more precipitation. On the other hand, vegetation in + Snow is not limited by moisture and is likely to be favored by higher growing season temperature (as in 2011 and 2013) rather than wet and cold growing season conditions as in 2012. Our results indicate that interannual variability, i.e. snow cover duration and length of the growing season, primarily affects the cumulative GPP. Photosynthetic capacity of the vegetation is mainly controlled by the indirect, long-term effects such as hydrological changes, nutrient availability, diseases, and shifts in species composition (Larsen et al. 2007; Torp et al. 2010). According to Walker et al. (1999) the long term effect of climatic changes depend greatly on the species adaptation ability. Therefore, increased snow cover and delayed snowmelt may favor species such as *Betula nana* and *Eriophorum vaginatum*, with high photosynthetic capacity in relation to evergreen shrubs (Bigger and Oechel 1982; Starr et al. 2008), and higher potential to take advantage of increased soil temperature, soil moisture and nutrient availability (Bigger and Oechel 1982; Shaver et al. 1986; Schimel et al. 2004; Wahren et al. 2005; Starr et al. 2008).

4.3 Potential feedback mechanisms

In spite of increased GPP, the observed changes in plant community structure towards a dominance of graminoids (Johansson et al. 2013) may have a large impact on the regions carbon balance and act as a positive feedback to climate. Existing lowland permafrost in

northern Fennoscandia is under severe threat of disappearance with projected climate change (Åkerman and Johansson 2008), and large areas of predominantly dry hummock vegetation is facing a shift towards wetter conditions and an increase in graminoid vegetation (Bosiö et al. 2012). If the thawed peatlands remains waterlogged for long periods of the year the increased carbon uptake through photosynthesis is offset by increased methane emissions, with much stronger global warming potential on a 100 year time frame (Bäckstrand et al. 2010; Jackowicz-Korczynski et al. 2010).

4.4 Uncertainties and future research

In previous studies, it has been shown that the light use efficiency is dependent on a number of variables such as temperature, soil type, soil moisture, nutrient availability, plant type, growth state, plant age, and plant health (Prince 1991; Potter et al. 1993; Ruimy et al. 1994; Brogaard et al. 2005; Alton et al. 2007). Further, the light use efficiency parameter varies with time of the year and location but shows little interannual variation (Turner et al. 2002; Schwalm et al. 2006; Connolly et al. 2009). Since the light use efficiency for our study was estimated from field measurements made during mid- and late part of the season, we have no indication of how ε varies in the very beginning of the season. Starr et al. (2008) argues that since interannual variations in photosynthetic capacity is small for most species, it is more important to focus on the species composition and total photosynthetic leaf area than variations within species-level when estimating the effects of climate change on carbon assimilation. Huemmrich et al. (2010a, b) also found that the light use efficiency parameter is constant throughout the growing season, but varies between species and that soil moisture was the key variable in regulating the carbon assimilation in tundra environment. We assumed that ε_{plot} was constant over the whole growing season and may thus have overestimated ε_{plot} during the early season. Since ε_{plot} shows only very weak correlation with DOY, soil moisture and soil temperature (App. 1), we assume this overestimation of ε_{plot} during the early season as negligible.

Previous studies have shown that date of snowmelt is a good predictor for determining growing season productivity (Aurela et al. 2004; Grøndahl et al. 2007; Wipf and Rixen 2010). Nevertheless, interactions between date of snowmelt and plant productivity are complex. Our measurements suggest that a thicker snow cover initiates potential feedback effects such as changes in soil hydrology. The increase in soil moisture alters plant growth and results in higher fAPAR and GPP. In contrast to theories suggesting that increased growth due to prolonged snow cover is a transitional short term effect (Walker et al. 1995), we hypothesize that this effect is due to shift in vegetation community as plants adapt to changed conditions, and hence an effect that will last for as long as the snow cover remains thicker than under ambient conditions.

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