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Discussions

Effects of nitrogen fertilization on the understorey carbon balance over the growing season in a boreal Pine forest

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Abstract

Boreal forests play a key role in the global carbon cycle and are facing rapid shifts in nitrogen availability with poorly understood consequences for ecosystem function and global climate. We quantified the effects of nitrogen availability on carbon fluxes
5 from a relatively understudied component of these forests – understorey vegetation – at three intervals over the summer growing period in a northern Swedish Scots Pine stand. Nitrogen addition altered both photosynthetic carbon uptake and respiratory release, but the magnitude and direction of this effect depended on the time during the growing season and the amount of nitrogen added. Specifically, nitrogen addition stim-
10 ulated net ecosystem carbon uptake only in the late growing season. We find evidence for species-specific control of understorey carbon sink strength, as photosynthesis per unit ground area was positively correlated only with the abundance of the vascular plant *Vaccinium myrtillus* and no others. Comparison of photosynthetic carbon uptake with data on plant carbon dioxide release from the study site, indicate that understorey
15 vegetation photosynthate was mainly supplying respiratory demands for much of the year. Only in the late season with nitrogen addition did understorey vegetation appear to experience a large surplus of carbon in excess of respiratory requirements. Further work, simultaneously comparing all major biomass and respiratory carbon fluxes in understorey and tree vegetation, is required to resolve the likely impacts of environmental
20 changes on whole-ecosystem carbon sequestration in boreal forests.

1 Introduction

Boreal forests store around 25 % of global terrestrial carbon (C) (Gower et al., 2001) and are currently estimated to be a net C sink (Myneni et al., 2001; Pan et al., 2011). These ecosystems are critically constrained across large areas by the availability of N
25 (Tamm, 1991; Vitousek and Howarth, 1997) which is greatly increased across managed forests due to intensive fertilization and, across all systems, via elevated N inputs from

atmospheric deposition (Galloway et al., 2008; Reay et al., 2008). Therefore, increasing N availability in boreal forests could have major implications for future climate change, both directly by affecting the net flux of carbon dioxide (CO_2) to the atmosphere, and indirectly by mediating the relative impacts of other climate change agents on boreal vegetation and soils.

Most research to date about the effects of N on boreal forest C cycling has focused on trees. By comparison relatively little is known about the effects of fertilization on understorey vegetation CO_2 fluxes despite evidence that understorey vegetation accounts for a large proportion of whole ecosystem photosynthesis and respiration (Goulden and Crill, 1997; Heijmans et al., 2004; Kolari et al., 2006), and exerts a powerful influence over soil nutrient and C cycling (Wardle et al., 1998; Nilsson and Wardle, 2005). The few available studies within boreal forest N manipulation experiments all suggest that N addition causes either no change or a slight decline in ground CO_2 efflux (Gärdenäs, 2000; Olsson et al., 2005; Allison et al., 2008 but see Hasselquist et al., 2012), but a number of major questions remain. For example, none of these studies partitioned net CO_2 efflux from the ground into uptake from photosynthesis and release via soil and plant respiration, so it remains unclear to what extent any N-induced shifts in respiration could be offset by concurrent changes in photosynthetic uptake.

A wide range of studies showing inhibited decomposition and soil CO_2 efflux following N addition have formed the empirical foundation for model predictions that global rises in N deposition will reduce soil C loss, and hence promote ecosystem C storage (Berg and Matzner, 1997; Ågren et al. 2001; Janssens et al., 2010 and references therein). However, the majority of N addition experiments (Bond-Lamberty and Thomson, 2010) have fertilized at rates which are several times greater than even the most severe N deposition scenarios (Lamarque et al., 2005; Galloway et al., 2008; Reay et al. 2008). Yet, several studies have highlighted the potential for non-linear soil C responses to N addition rates, (Knorr et al., 2005; Hasselquist et al., 2012). For example, in a boreal *Pinus sylvestris* L. forest, Hasselquist et al. (2012) found that soil CO_2 efflux was stimulated by low soil doses of N but suppressed at higher N addition

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rates. The underlying mechanism for this pattern appears to be an increase in the abundance and/or activity of mycorrhizae, with an associated rise in autotrophic respiration (R_a), under low N addition but a strong decrease in the plant-mycorrhizal symbiosis under higher N loads (Hasselquist et al., 2012) which is consistent with the findings of other studies in the same ecosystem type (Nilsson and Wallander, 2003; Högberg et al., 2010; Vallack et al., 2011). If such non-linear responses are widespread, projections of ecosystem C sequestration under future N deposition scenarios may need to be revised.

We measured understorey vegetation Net Ecosystem Exchange of CO_2 (NEE), and its components – uptake via photosynthesis (Gross Primary Productivity, GPP) and release through respiration (R) – over a full growing season in the same N addition experiment described in Hasselquist et al. (2012). For the experiment, N has been added to the soil since 2006 at two distinct rates in adjacent *P. sylvestris* forest plots, to distinguish between the likely impacts of future atmospheric N deposition vs. intensive N fertilization similar to the rate applied by many scientific studies. Specifically, we asked the following questions:

1. Is understorey NEE, and its component fluxes, affected in the same way by different N addition rates?

2. How does N addition affect the seasonality of NEE, and its components?

3. Which abiotic (temperature, soil moisture) and biotic (vegetation density, tree proximity) factors explain observed differences in NEE, and its components?

Finally, as an index of the C status of the understorey plants measured, and how this changes over the growing season and amongst plots, we compare GPP measured in this study with data on R_a of understorey vegetation from nearby locations on all plots and measurement periods (Hasselquist et al., 2012).

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2 Methods

2.1 Study site and experimental design

The study was located within a homogenous 70 yr old *Pinus sylvestris* stand at the Rosinedal experimental forest in northern Sweden (64°10′ N, 19°45′ E). The site is ~ 145 m a.s.l., on fine podzolized sand with a thin surface organic mor-layer. Mean annual temperature is ~1 °C, annual rainfall is 520 mm and the snow-free growing season extends for approximately 6 months from May to October. A continuous ground-layer of vegetation exists, composed of shrubs (*Vaccinium myrtillus* L., *Vaccinium vitis-idaea* L.), mosses (*Pleurozium schreberi* (Bird.) Mitt., *Hylocomium splendens* (Hedw.) Schimp), and lichens (*Cladonia spp.*). A detailed site summary is presented in Table 1.

At the site, two 15 ha plots have each been subjected to a different fertilization treatments since 2006: addition of 20 kg N ha^{-1} yr^{-1} as NH_4NO_3 to replicate a typical rate of atmospheric N deposition in southern Sweden (low N plot) (Lamarque et al., 2005), and addition of 100 kg N ha^{-1} yr^{-1} to represent a fertilization intensity typical of many scientific fertilization experiments (high N plot) (Bond-Lamberty and Thomson, 2010; Hasselquist et al., 2012). Adjacent to these plots is a matching 15 ha area of unfertilized forest which acts as an experimental control.

2.2 Sampling and data analyses

Understorey CO_2 exchange was surveyed on all three plots over a two week time-window in June, July and August of 2011 to capture variation over the active growing period for understorey vegetation in boreal forests. In each plot, 17 locations were selected for understorey vegetation CO_2 flux measurements. Prior to measurements, 40 cm × 40 cm metal bases were inserted ~ 2 cm into the soil surface, taking care to minimize disturbance to surrounding vegetation and roots. After allowing a minimum of two days for equilibration, understorey vegetation CO_2 fluxes were recorded by sealing a 40 cm high transparent plastic chamber to the chamber base, and recording the

linear accumulation of CO_2 within the chamber over two minutes using an infra-red gas analyzer or IRGA (EGM-4, PP Systems, PP Systems, Hitchin, UK). A light sensor was placed inside the chamber to continuously record the amount of photosynthetically active radiation (PAR, $\mu mol\,m^{-2}\,s^{-1}$) received by the vegetation within the chamber

5 during CO_2 measurements. The air inside the chamber was thoroughly mixed during measurements with a fan. The measurement duration was sufficiently short to minimize changes in air temperature and humidity within the chamber. At each location, CO_2 fluxes were recorded eight times, five records under different PAR levels and three replicate measurements in complete darkness. Mesh covers were used to reduce PAR

10 within the chamber, while a completely opaque cover was used to reduce PAR to zero. The flux measured represents net ecosystem exchange of CO_2 from the understorey vegetation, soil and tree roots (NEE, $g\,CO_2\,m^{-2}\,h^{-1}$):

$$NEE = R - GPP \qquad (1)$$

where GPP is gross primary productivity ($g\,CO_2\,m^{-2}\,h^{-1}$), and R is ecosystem respira-

15 tion of CO_2 ($g\,CO_2\,m^{-2}\,h^{-1}$). A negative value of NEE indicates that GPP is greater than R and therefore that the location at that time is sequestering CO_2, whereas a positive value of NEE indicates that R is dominating and so the location is a net source of CO_2 to the atmosphere. Under complete darkness, photosynthesis does not occur so the CO_2 flux represents R. GPP may then be estimated for each location by adding mean

20 R_{eco} to NEE at a particular level of PAR. For each location, we fit a three-parameter decay model to the relationship between PAR and measured NEE:

$$y = a + b \cdot \exp^{-c \cdot p} \qquad (2)$$

where y represents modelled NEE, a, b and c represent the three fitted curve parameters and p refers to PAR. Across all plots and time periods of measurements, there was

25 a close agreement between measured and modelled NEE (Fig. 1). Fitted curve parameters for each location were then used to predict NEE and GPP for a standardized PAR value of $600\,\mu mol\,m^{-2}\,s^{-1}$.

After CO_2 flux measurement, a range of abiotic and biotic plot variables were measured at each location. Surface (0–10 cm soil depth) soil moisture and temperature was recorded with probes at four replicate points within the metal base at each location. The depth of the organic layer was visually estimated, and the number of *V. myrtillus* and *V. vitis-idaea* stems was counted as a estimate of vegetative density. Finally, to investigate and, if necessary, control for the effects of tree proximity on root biomass and respiration, and hence ground CO_2 efflux, we measured the diameter of all trees within 3.5 m radius of each location and computed a tree proximity index (T).

$$T = \sum s \times (1/d) \tag{3}$$

where s represents tree size as diameter at 1.3 m (cm) and d represents tree distance from the CO_2 flux measurement location (cm). Seasonal shifts in CO_2 fluxes were assessed with a parametric repeated-measures analysis of variance (ANOVA). Where the condition of sphericity was violated, we applied a lower-bound adjustment to the degrees of freedom to provide a conservative test for significance. Within each time period, we tested for plot differences with parametric univariate ANOVA followed by a Bonferroni post-hoc test. All measured locations within plots were spaced more than 20 m apart, so the degree of spatial autocorrelation in CO_2 fluxes among locations within each plot should be minimal (Stoyan et al., 2000, and references therein). Therefore, we treat the 17 locations measured within each plot as statistically independant replicates in our analysis. Finally, we conducted a non-parametric Spearman's rank test to assess correlations amongst the CO_2 fluxes measured and a range of abiotic and biotic variables recorded at each location. Where necessary, variables were transformed to conform to the assumptions of parametric analysis. All statistical analyses were conducted with IBM SPSS Statistics 19 software.

3 Results

N addition altered both R and GPP but the magnitude and direction of the effect depended strongly on timing during the season and, to a lesser extent, the amount of N added (Fig. 2). Across all measurements, R significantly increased over the growing season, but the pattern of this increase was significantly modified by N treatment (Fig. 2). In the early season, R was generally low across all plots, but was only stimulated on the low N treatment relative to the control. In contrast, from July onwards R was suppressed on the low N treatment, and to an even greater extent, on the high N treatment compared to the control. In comparison with R, the flux of CO_2 as GPP was generally lower in magnitude, more variable and showed no clear N treatment effect (Fig. 2). Hence, seasonal and treatment patterns of NEE were mainly driven by shifts in R. There was no overall N treatment effect on NEE across all measurement campaigns. However, considering each measurement period individually some significant plot differences were detected (Fig. 2). The high N treatment was a significantly smaller net C source than the control in July, mainly due to plot differences in R rather than GPP. In addition, both N treatments were substantially greater net C sinks than the control in the later part of the growing season in August, although these differences were marginally insignificant ($P = 0.054$–0.067).

R and GPP displayed distinct seasonal patterns which had an important impact on NEE (Fig. 2). Thus, R reached maximal levels from July onwards whereas GPP peaked only later in August. This lag between R and GPP meant that the understorey on all plots had a greater tendency towards being a large net C source in the middle of the growing season (Fig. 2). By contrast, in the early and late portions of the growing season, NEE was more neutral because R and GPP approximately offset each other (Fig. 2).

No significant correlation was found between tree proximity and any of the CO_2 fluxes measured (Table 2), so we conclude that it was not a major source of confounding variation in our analyses. Across all plots and measurement periods, R showed a sig-

nificant positive association with both soil surface moisture and temperature (Table 2). Surprisingly, no clear link was found between R and metrics of total vegetation density or organic layer depth (Table 2), both of which were elevated on the N addition plots relative to the control (Table 1). Like R, GPP was also significantly greater under conditions of higher soil moisture but, in addition, vegetation abundance was also linked to higher GPP (Table 2). We find evidence for species-specific effects on CO_2 uptake, since GPP was significantly positively correlated with the abundance of *V. myrtillus* but not *V. vitis-idaea* (Table 2). Vegetation density stimulated GPP but not R, with the result that NEE increased with metrics of vegetation density (Table 2). In contrast, soil temperature strongly affected R but not GPP, so that the understorey tended to be a greater net C source under warmer temperatures (Table 2). Soil moisture stimulated both CO_2 uptake via GPP and release as R, so there was no net effect of soil moisture on NEE (Table 2). With the exception of the relationship between R and soil temperature, none of these variables in isolation explained much variation in the measured fluxes (Table 2), despite the significance of some correlations.

As a rough indicator of the internal C balance of understorey plants, we compared measured GPP in each plot and time period during the growing season with understorey R_a (Fig. 3). At a light intensity of $600\,\mu mol\,m^2\,s^{-1}$, which is generally higher than that predominating at the ground level at the study site, uptake of CO_2 via GPP only just covered plant respiratory demand on all plots in the early and middle growing season (Fig. 3). By August, however, understorey vegetation in the N addition plots were operating a large C surplus at $600\,\mu mol\,m^2\,s^{-1}$, acquiring $515 \pm 128\,\%$ and $702 \pm 199\,\%$ more CO_2 than was required for plant respiration on the low and high N plots, respectively (Fig. 3). In contrast, at the same time in the late growing season, the C surplus at $600\,\mu mol\,m^2\,s^{-1}$ in control plot vegetation was much lower and largely unchanged from early growing season levels.

4   Discussion

Boreal forests are currently estimated to be a net C sink (Myneni et al., 2001; Pan et al., 2011), but the contribution of understorey vegetation to this sink is currently poorly understood. One striking pattern emerging from this study was that understorey vegetation was generally a very weak net sink for CO_2 (Fig. 2). Understorey vegetation CO_2 uptake at a light intensity of $600\,\mu mol\,m^{-2}\,s^{-1}$ (equivalent to full sun with a typical canopy light interception for this type of forest of $\sim 80\,\%$, Mencuccini and Grace, 1996) could barely cover respiratory demand for much of the year (Fig. 3). It is possible that these plants may derive a disproportionate amount of photosynthate from short-lived sunflecks (Lieff et al., 1999). Indeed, we found little sign of GPP saturating at high light levels, contrary to previous reports from similar systems (Kolari et al., 2006; Whitehead and Gower, 2001), indicating that understorey plants at the site may have high photosynthetic capacity to exploit ephemeral bright periods. Nevertheless, the fact that full sun conditions are rare, and that light intensity drops at night even at these high latitudes in summer, suggests that little assimilated C remains for other functions (growth, herbivore defense and reproduction) in understorey plant species at this site after basic metabolic demands have been satisfied. This appears incongruent with widely cited reports that understorey NPP is over half of above-ground tree NPP in a chronosequence of boreal forest (Wardle et al., 2003; Nilsson and Wardle, 2005) but total above-ground NPP in these systems is very low, at less than $150\,g\,C\,m^{-2}\,yr^{-1}$ compared to $232\,g\,C\,m^{-2}\,yr^{-1}$ from a pan-boreal synthesis (Gower et al., 2001). Thus, in absolute terms, understorey NPP along the chronosequence sites is still low ($< 45\,g\,C\,m^{-2}\,yr^{-1}$, Nilsson and Wardle, 2005), and likely to be lower still in more dense forests where carbon uptake in the understorey is more strongly light limited. A preliminary comparison of understorey C allocation in boreal forests supports this hypothesis: taking typical published values for understorey GPP and NPP of $131\,g\,C\,m^{-2}\,yr^{-1}$ and $22\,g\,C\,m^{-2}\,yr^{-1}$ respectively (Kolari et al., 2006; Gower et al., 2001), the portion of understorey photosynthate allocated to biomass growth is extremely low (17 %) compared to mean values

for boreal trees of 40–50 % (Vicca et al., 2012). Indeed, clonal plant growth and efficient nutrient resorption are relatively common strategies amongst boreal understorey plants, and are thought to be an adaptive trait to increase resource use efficiency (Eckstein et al., 1999; Svensson et al., 2009). This does not necessarily mean that the contribution of boreal understorey plants to ecosystem C storage is insignificant, since many such plants turnover biomass rapidly and produce recalcitrant organic litter that retards soil microbial activity thereby promoting soil C sequestration (Chapin, 1983; Wardle et al., 1998; Nilsson and Wardle, 1999; Wardle and Zackrisson, 2005).

This study shows that N fertilization effects on understorey CO_2 fluxes were strongly dependent firstly, on the time during the growing season and secondly, on the amount of N added (Fig. 2). In the early growing season, R responded in a similar way to N addition as that noted by Hasselquist et al. (2010) from the same study site: with greater levels of CO_2 released as R under low levels of N addition compared to both the control and high N plots. However, later in the season we recorded a different response, more in line with the consensus view (Janssens et al., 2010, and references therein) – showing successively lower R on the low and high plots relative to the control (Fig. 2). The reasons for the differences between the current study and Hasselquist et al. (2010) may be partly due to differences in the timing of measurements. The stimulation of R_a, and hence total R, on the low N treatment was maximal in late August and September, after the period of sampling in this study. However, we note that our results still highlight the risks of inferring likely effects of atmospheric N deposition from fertilization experiments which apply N at much higher rates, since we do not observe a monotonic linear response to the four-fold increase in N addition from the low to high plot. Instead, the effects of N on understorey CO_2 fluxes tended to saturate with increasing rates of N addition.

N availability will also have large impacts on the composition and diversity of understorey plant communities (Bobbink et al., 2010). In this study, we find evidence for species-specific effects on ecosystem-level CO_2 fluxes, since GPP was significantly positively correlated with the abundance of *V. myrtillus* but not related to the amount

of *V. vitis-idaea* (Table 2). Important impacts of fertilization on CO_2 fluxes, beyond the short-term increases in leaf N and soil microbial activity, could therefore operate over longer time-scales by shifting the relative abundance of species with different capacities to take up and store C in plant tissue and soil. Although we have not yet observed

5 a substantial shift in *V. myrtillus* abundance at the study site (Table 1), longer-term forest fertilization experiments have demonstrated substantial declines in *V. myrtillus* abundance, even up to nine years after nitrogen addition ceased (Strengbom et al., 2001; Nordin et al., 2005; Strengbom and Nordin, 2008). Our results suggest that such a plant community shift could reduce understorey GPP, and therefore partly offset the

10 beneficial effects of forest fertilization in terms of enhanced tree C uptake (De Vries et al., 2006). Integration of such longer-term, indirect effects of environmental changes on ecosystem C storage via shifts in plant community composition are poorly constrained in global models compared to the direct impacts of abiotic factors such as temperature and moisture (Ostle et al., 2009; Metcalfe et al., 2011). Therefore, further

15 work linking together community ecology and C cycling are required to improve model predictions of forest C sequestration in a changing world.

5 Conclusions

To improve understanding of C and N interactions in boreal forests, we studied seasonal C fluxes from an important but often overlooked component of forests – un-

20 derstorey vegetation – in a large-scale forest N manipulation experiment. Overall, we found that N addition to understorey vegetation tends to increase the likelihood that it will be a net C sink, but that this is strongly contingent upon the timing during the growing season and, to a lesser extent, the amount of N added. Whether this additional C taken up under fertilized conditions will contribute to long-term C sequestration

25 is, however, unclear because most assimilated C is apparently directly respired. This tentative conclusion would be reinforced by simultaneous measurements of biomass growth and respiratory C fluxes in understorey vegetation, but is consistent with avail-

able information about the carbon allocation and life history strategies of understorey plants.

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Interactive Discussion

Table 1. Summary of plot characteristics. Values represent mean ± SE ($n = 17$). Soil moisture and temperature means across the growing season (June–August).

	Control	Low	High
Tree stem growth ($g\,m^{-2}\,yr^{-1}$)[*]	280	340	500
V. myrtillus density (stems m^{-2})	76 ± 8	75 ± 12	79 ± 11
V. vitis-idaea density (stems m^{-2})	151 ± 12	205 ± 11	208 ± 14
Organic layer depth (cm)	10.0 ± 0.8	9.4 ± 0.6	9.3 ± 0.7
Organic layer C : N ratio[*]	39.2 ± 1.3	40.7 ± 1.3	40.2 ± 1.3
Soil moisture (%)	10.3 ± 0.4	10.5 ± 0.5	10.2 ± 0.4
Soil temperature (°C)	11.1 ± 0.4	11.7 ± 0.4	10.8 ± 0.4

[*] From Hasselquist et al. (2012).

Table 2. Results of a spearman's rank correlation between CO_2 fluxes and a range of abiotic and biotic variables. Significant correlations (≤ 0.05) are highlighted in bold. CC refers to the correlation coefficient, negative and positive CC values denote a negative and positive correlation respectively.

	R			GPP			NEE		
	R^2	CC	P	R^2	CC	P	R^2	CC	P
Tree proximity index	0.01	0.065	0.428	< 0.01	0.043	0.596	< 0.01	−0.026	0.746
Organic layer depth (cm)	< 0.01	0.066	0.415	0.01	0.052	0.522	< 0.01	−0.110	0.176
V. myrtillus density (stemsm^{-2})	< 0.01	0.085	0.295	**0.05**	**0.219**	**0.007**	0.01	−0.121	0.137
V. vitis-idaea density (stemsm^{-2})	0.01	−0.068	0.403	< 0.01	−0.007	0.935	0.05	−0.066	0.420
Vegetation density (stemsm^{-2})	< 0.01	−0.023	0.773	**0.03**	**0.199**	**0.014**	**0.02**	**−0.177**	**0.029**
Soil moisture (%)	**0.09**	**0.431**	**< 0.001**	**0.03**	**0.314**	**< 0.001**	< 0.01	0.016	0.849
Soil temperature (°C)	**0.41**	**0.777**	**< 0.001**	0.01	0.087	0.291	**0.03**	**0.480**	**< 0.001**

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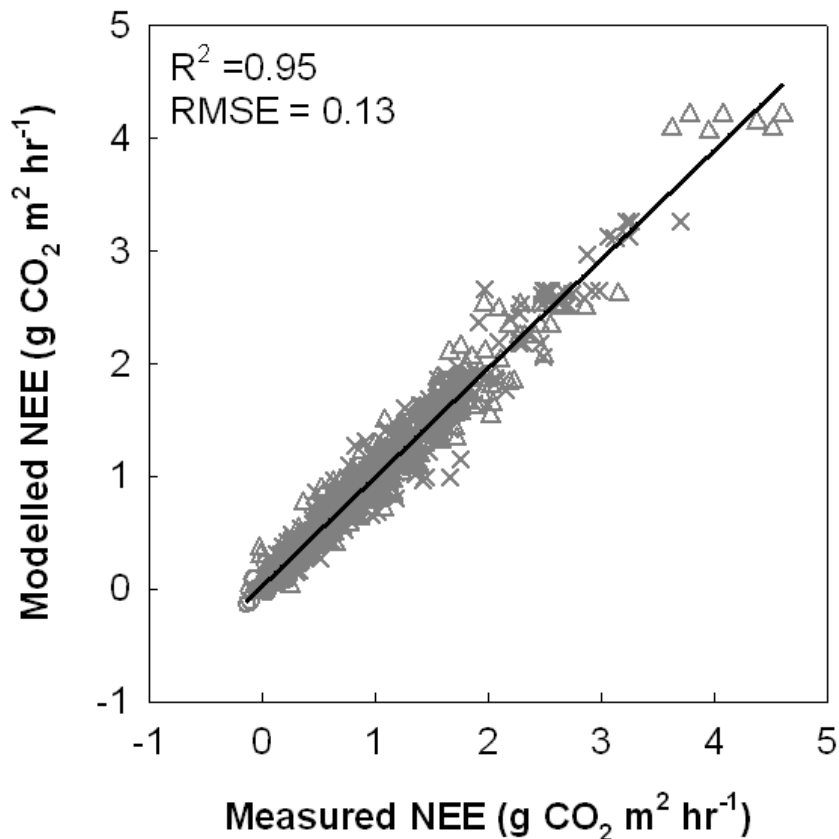Printer-friendly Version

Interactive Discussion

Fig. 1. Measured vs. modelled NEE. Modelled NEE was estimated from a three parameter decay model fit to measurements. Negative values denote net uptake of CO_2 into vegetation from the atmosphere. Circles, triangles and crosses represent measurements in the early, middle and late growing season respectively. The line is a linear regression fit through all the data (y = 0.9652x + 0.0268).

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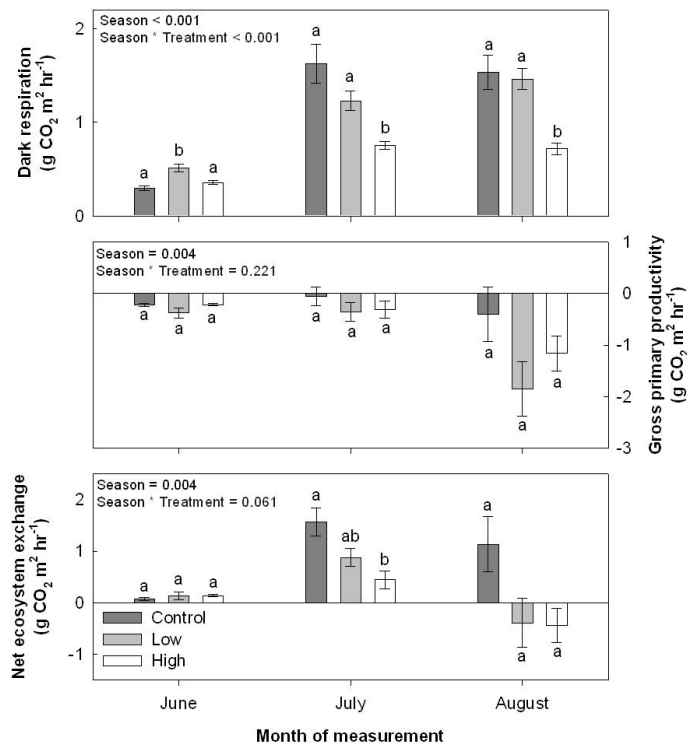Printer-friendly Version

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Fig. 2. Understorey fluxes of CO_2 from R (upper panel), GPP (middle panel) and NEE (lower panel) in plots with different N addition rates over the growing season. Values of GPP and NEE are standardized to a light intensity of $600 \, \mu mol \, m^{-2} \, s^{-1}$. Negative values denote uptake of CO_2 into the vegetation from the atmosphere, error bars represent SE ($n = 17$). Letters next to error bars denote significant differences amongst plots within each time period. The overall significance P values of season and its interaction with N treatment are noted in the upper left corner of each panel.

Fig. 3. Plant carbon surplus potential – calculated as GPP at light intensity of 600 µmol m^{-2} s^{-1} minus R_a – in plots with different N addition rates over the growing season. Error bars represent SE (n = 17 and 2 for GPP and R_a respectively). R_a values were derived from Hasselquist et al. (2010) from locations < 20 m from the points measured in this study in all plots and measurement periods.