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## Editorial: Part of a special section on the Flakaliden experiments

# Three decades of research at Flakaliden advancing whole-tree physiology, forest ecosystem and global change research

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Nutrient supply often limits growth in forest ecosystems and may limit the response of growth to an increase in other resources, or to more favorable environmental factors such as temperature and soil water. To explore the consequences and mechanisms of optimum nutrient supply for forest growth, the Flakaliden research site was established in 1986 on a young Norway spruce site with nutrient-poor soil. This special section on research at Flakaliden presents five papers that explore different facets of nutrition, atmospheric CO<sub>2</sub> concentration, [CO<sub>2</sub>], and increased temperature treatments, using the original experiment as a base. Research at Flakaliden shows the dominant role of nutrition in controlling the response of growth to the increased photosynthesis promoted by elevated [CO<sub>2</sub>] and temperature. Experiments with whole-tree chambers showed that all treatments (air temperature warming, elevated [CO<sub>2</sub>] and optimum nutrition) increased shoot photosynthesis by 30–50%, but growth only increased with [CO<sub>2</sub>] when combined with the optimum nutrition treatment. Elevated [CO<sub>2</sub>] and temperature increased shoot photosynthesis by increasing the slope between light-saturated photosynthesis and foliar nitrogen by 122%, the initial slope of the light response curve by 52% and apparent quantum yield by 10%. Optimum nutrition also decreased photosynthetic capacity by 17%, but increased it by 62% in elevated [CO<sub>2</sub>], as estimated from wood δ<sup>13</sup>C. Elevated air temperature advanced spring recovery of photosynthesis by 37%, but spring frost events remained the controlling factor for photosynthetic recovery, and elevated [CO<sub>2</sub>] did not affect this. Increased nutrient availability increased wood growth primarily through a 50% increase in tracheid formation, mostly during the peak growth season. Other notable contributions of research at Flakaliden include exploring the role of optimal nutrition in large-scale field trials with foliar analysis, using an ecosystem approach for multifactor experiments, development of whole-tree chambers allowing inexpensive environmental manipulations, long-term deployment of shoot chambers for continuous measurements of gas exchange and exploring the ecosystem response to soil and aboveground tree warming. The enduring legacy of Flakaliden will be the rich data set of long-term, multifactor experiments that has been and will continue to be used in many modeling and cross-site comparison studies.

**Keywords:** autotrophic respiration, δ<sup>13</sup>C, elevated [CO<sub>2</sub>], long-term research, Norway spruce, photosynthetic recovery, *Picea abies*, soil respiration, soil warming, temperature, tree nutrition, whole-tree chamber, wood formation.

## Introduction

Low nutrient availability (mainly nitrogen, N) has often been identified as an important factor limiting growth in boreal forests (Tamm 1991, Binkley and Högberg 1997, Bergh et al. 1999, 2005, Hyvönen et al. 2007, Lukac et al. 2010). The

Flakaliden research site was established in 1986 with the aim of assessing nutrient and water limitations, and determining the potential productivity under optimal nutrition and irrigation for young forests in northern Sweden (Linder 1995, Bergh et al. 1999). The study was designed to be a long-term exploration

of resource limitation using the then newly identified concepts of production efficiency (biomass production per unit of light absorbed (Linder 1985) or leaf area (Waring 1983)) and light-use efficiency (Monteith 1977, Jarvis and Leverenz 1983)—particularly how nutrition altered light absorption and use.

Flakaliden is located in northern Sweden ~15 km southwest of Vindeln (64.1134N, 19.4737E, 310 m elevation). The climate is mid-boreal (Sjörs 1999) with a mean annual temperature of 2.4 °C, and mean annual precipitation of ~600 mm, enough for soil water content to not normally limit tree growth (Bergh et al. 1999). One-third of the precipitation falls as snow, which usually covers the frozen ground from mid-October to early May. Flakaliden has long, cool days in the summer (14.6 °C mean temperature in July for 1990–2009), and cold, short days in winter (−7.5 °C mean temperature in February for 1990–2009). The length of the growth season, when daily mean air temperature is  $\geq 5$  °C, averages ~150 days, with large between-year variability. Soil at the site is a thin, very rocky, well-developed iron podzolic and sandy post-glacial till of gneissic origin with a mean depth of ~120 cm and a 2- to 6-cm-thick humus layer, with low nutrient availability (Bergh et al. 1999). Nitrogen deposition in the region averages 3 kg ha<sup>-1</sup> year<sup>-1</sup> (references cited in Sigurdsson et al. 2013), and the overstory is Norway spruce (*Picea abies* L. Karst.).

Flakaliden is particularly suited for understanding the role of nutrition and interactions with other resources and the environment, because nutrients are very limited, particularly N (Linder 1995, Bergh et al. 1999). As an example of nutrient limitations to tree growth at Flakaliden, 10 years of optimal nutrient application increased annual stem wood volume increment to 14 m<sup>3</sup> ha<sup>-1</sup> year<sup>-1</sup> compared with 3 m<sup>3</sup> ha<sup>-1</sup> year<sup>-1</sup> on control plots (Bergh et al. 1999). After 24 years of optimal nutrition, representative trees in the optimal nutrition treatment were 4 m taller than the control trees, and had ~4× the aboveground biomass (Sigurdsson et al. 2013).

The original nutrient optimization experiment was established in a Norway spruce forest that was planted in 1963 with local provenance 4-year-old seedlings after the site had been clear-felled, burned and scarified (Linder 1995, Bergh et al. 1999). This experiment had 32 large plots (50 × 50 m) for control, irrigation, optimum fertilization, irrigation plus optimum fertilization and other treatments replicated four times in a randomized block design. By 2004, the irrigated and optimally fertilized treatment had cumulatively received 1125 kg N ha<sup>-1</sup> and all other nutrients in optimum proportion to N (Sigurdsson et al. 2013). Photographs of a control and an irrigated plus optimum fertilization plot can be seen in Strengbom et al. (2011).

A key focus of the research over the second and third decades of the study has been the interactions among nutrition and atmospheric CO<sub>2</sub> concentration, [CO<sub>2</sub>], temperature and water at the whole tree and ecosystem scale, using the control and irrigation plus optimum fertilization treatments.

## Important contributions of research at Flakaliden

Research at Flakaliden has made enormous contributions to our understanding of the role of nutrient supply in boreal forest growth and ecosystem function, in addition to clearly identifying the critical importance of nutrient availability in the response of forest growth to increased air temperature and elevated [CO<sub>2</sub>] described below. These contributions include: (i) exploring the role of optimal nutrition in large-scale field trials using foliar nutrition analysis (Linder 1995, Bergh et al. 1999); (ii) exploring the consequences of optimal nutrient supply on tree growth (Bergh et al. 1999) and ecosystem function with many studies focused at the same site, including root growth (Majdi 2001, Majdi and Öhrvik 2004), mycorrhizal function (Fransson et al. 2000), water use (Phillips et al. 2001) and light interception (Stenberg et al. 1995, 1999, Palmroth et al. 2002), providing a very rich data set for model development and application (Bergh et al. 1998, Bergh and Linder 1999, McMurtrie et al. 2000, 2001, Medlyn et al. 2000, Eliasson et al. 2005, Pepper et al. 2005); (iii) pioneering the development and use of whole-tree chambers to independently manipulate [CO<sub>2</sub>], temperature, humidity, nutrient supply for the aboveground portion of a tree and eventually to enable the measurement of the aboveground tree carbon balance (Medhurst et al. 2006); (iv) application of shoot chambers (Wallin et al. 1990) to continually measure shoot gas exchange before, during and after the growth season to study environmental regulation and extrapolation (Hall et al. 2009, 2013, Uddling and Wallin 2012, Wallin et al. 2013); (v) exploring the mechanisms of an initial increase and ultimate homeostasis of soil respiration to soil warming (Strömgren 2001, Eliasson et al. 2005), and the effect of soil warming on nutrient availability and forest growth (Strömgren and Linder 2002); and finally (vi) maintenance of the original nutrient optimization and irrigation experiment that enabled many additional experiments, and allowed the long-term treatment response to be explored.

One keystone contribution was taking the discoveries about the role of balanced nutrient *supply* developed for seedling growth (for example, Ingestad 1979, and other papers listed in Linder 1995) and applying them to a developing forest (Linder 1995, Bergh et al. 1999). Using foliar analysis and targeting nutrient concentrations, sustained annual increases in wood production of ~400% were achieved at Flakaliden without leaching nutrients below the rooting zone into groundwater (Linder 1995, Bergh et al. 1999). A key finding of several years of foliar analysis on the suite of treatments throughout the growth season was that nutrient ratios relative to nitrogen in 1-year-old foliage were less sensitive to seasonal changes in carbohydrate concentrations. Using ratios of nutrients to nitrogen enables the optimum nutrition concept to be more easily applied on an operational basis.

The development of the whole-tree chambers at Flakaliden was a major technological advance for whole-tree physiology.

Controlling [CO<sub>2</sub>], temperature and humidity with a relatively low chamber net air exchange (Medhurst et al. 2006) enables lower cost experiments on the dominant tree in the ecosystem. In the studies described below, the whole-tree chambers helped promote our mechanistic understanding of interactions among elevated [CO<sub>2</sub>], temperature and nutrition. These chambers continue to be used for whole-tree experiments including soil water availability in Australia (Barton et al. 2010, 2012) as part of the Hawkesbury Forest Experiment at the Hawkesbury Institute for the Environment at the University of Western Sydney (Figure 1).

A notable contribution of research at Flakaliden was the early identification of a reduction of soil respiration to nearly that of the unheated treatment after an initial spike (Strömngren 2001, Eliasson et al. 2005). These results have also been seen in a temperate forest and a temperate grassland (Luo et al. 2001, Melillo et al. 2002). Analysis of the Flakaliden soil respiration data with a simulation model suggests that the faster decomposition of the most labile pools of soil carbon causes the initial spike but quickly depletes the labile pool (Eliasson et al. 2005). Warmer temperatures also maintain a higher decomposition rate of a smaller labile pool, resulting in about the same heterotrophic respiration after the initial spike (Eliasson et al. 2005). Higher nutrient availability and tree growth in the plots with soil heating (Strömngren and Linder 2002), coupled with similar soil respiration for the heated and unheated plots after the initial spike (Strömngren 2001, Eliasson et al. 2005), also suggest lower partitioning of photosynthesis belowground in the heated treatment (Giardina and Ryan 2002).

The original study and those that capitalized on the original design contributed enormously to knowledge on the consequences of nutrient availability on ecosystem and tree-level physiology, and on the interactions of nutrition and forest responses to elevated [CO<sub>2</sub>] and temperature. This research has

made Flakaliden a globally important site for research on the response of boreal forests to nutrition and global change. Data from Flakaliden have provided grist for many modeling studies and cross-site comparisons of ecosystem function and remote sensing (see Appendix S1 available as Supplementary Data at *Tree Physiology* Online). Studies at Flakaliden or data from Flakaliden have to date contributed to 245 publications in refereed journals, 65 book chapters, books and proceedings publications, as well as 59 dissertations and theses (see Appendix S1 available as Supplementary Data at *Tree Physiology* Online).

### Photosynthesis response to elevated [CO<sub>2</sub>] and temperature

Leaf-level photosynthesis consistently increases in experiments that elevate [CO<sub>2</sub>], and the elevated photosynthesis generally persists even though photosynthetic capacity and stomatal conductance can decrease over time (see reviews by Curtis 1996, Saxe et al. 1998, Medlyn et al. 1999, Ainsworth and Long 2005, Wang et al. 2012). In boreal forests and at Flakaliden, elevated [CO<sub>2</sub>] also consistently increased photosynthesis (Robertz and Stockfors 1998, Sigurdsson et al. 2002, Riikonen et al. 2008, Hall et al. 2009, Uddling and Wallin 2012, Marshall and Linder 2013, Wallin et al. 2013). Studies in two separate experiments with whole-tree chambers (Figure 2) have measured consistent increases in photosynthesis with elevated [CO<sub>2</sub>] under conditions of poor nutrient availability (control 33–67%, Table 1) and optimal nutrient supply (55–62%, Table 1), and by 50% in conditions of poor nutrient availability with air temperature increased 2.8 °C above the ambient during the growth season (Table 1, Hall et al. 2009, 2013, Uddling and Wallin 2012, Marshall and Linder 2013, Wallin et al. 2013). These increases in photosynthesis were sustained over the 3-year duration of each experiment.

For the Flakaliden experiments, an artificial neural network coupled with an empirical photosynthesis model and continuous measurements of shoot photosynthesis showed that the elevated [CO<sub>2</sub>] increased seasonal photosynthesis by 44% and the initial slope of the light response function by 52% in the nutrient-poor treatment (Hall et al. 2013). Maximum photosynthesis rates also increased 122% with increased foliar N based on the tree-to-tree variability in N among the trees in the nutrient-poor treatments (Table 1, Hall et al. 2013). Carbohydrates produced by photosynthesis, integrated over the growth season and incorporated into wood, indicated that photosynthesis increased 38% in elevated [CO<sub>2</sub>] (700 ppm) for nutrient-poor trees under ambient air temperature, but increased 60% in elevated [CO<sub>2</sub>] for optimally fertilized trees (Marshall and Linder 2013). In this study, wood growth only increased for the optimally fertilized trees (Sigurdsson et al. 2013). Interestingly, in the Marshall and Linder (2013) study, bulk foliage tissue δ<sup>13</sup>C showed contamination from years prior to the elevated [CO<sub>2</sub>] treatment, but δ<sup>13</sup>C



Figure 1. Infrared camera (FLIR) photograph showing control (orange) and elevated temperatures (yellow) in new experiments with the whole tree chambers at the Hawkesbury Institute for the Environment at the University of Western Sydney. (Photo J. Marshall.)





Figure 2. A whole-tree chamber enclosing a tree grown under ambient (poor) nutrient availability, ambient air temperature and ambient  $[\text{CO}_2]$ . (Photo S. Linder.)

from bulk wood tissue did not. Marshall and Linder (2013) conclude that  $\delta^{13}\text{C}$  for conifer leaves should not be used to infer integrated intercellular  $[\text{CO}_2]$  because of  $\delta^{13}\text{C}$  contamination by turnover of starch reserves and other metabolic pools.

Annual tree radial and volume growth in boreal forests is strongly correlated with growth season air temperature or temperature sums (Henttonen 1984, Briffa et al. 1990, Miina 2000, Seo et al. 2008, Lloyd et al. 2011). At Flakaliden, elevating temperatures around nutrient-poor trees increased annual leaf carbon uptake by 44% (Hall et al. 2013), primarily because of the increased length of time photosynthesis could operate through earlier budbreak (Slaney et al. 2007) and both earlier spring onset and later fall cessation of photosynthesis (Hall et al. 2013, Wallin et al. 2013). The combination of elevated temperature and elevated  $[\text{CO}_2]$  increased maximum rates of photosynthesis by 67% for nutrient-poor trees and increased annual leaf carbon uptake by 50% compared with ambient conditions; there were no clear interactive effects of temperature and  $[\text{CO}_2]$  on parameter values of the photosynthesis model (Hall et al. 2013).

Elevated air temperature in the whole-tree chambers increased early season (March–June) leaf photosynthesis by

increasing apparent quantum yield and light-saturated photosynthesis and by a 10-day acceleration of the recovery of these values in the spring (Table 1, Slaney et al. 2007, Wallin et al. 2013). Elevated  $[\text{CO}_2]$  also increased early season leaf photosynthesis by increasing the recovery of apparent quantum yield and light-saturated photosynthesis (Table 1, Wallin et al. 2013). However, frosts delayed the onset of complete photosynthetic recovery in all treatments, suggesting that climate change increases in air temperature will only aid photosynthetic recovery in the spring if frost events become rarer. The study also suggests that frost events, not accumulated temperature, are the key to understanding spring photosynthetic recovery (Wallin et al. 2013). Elevated  $[\text{CO}_2]$  had small or mixed effects on photosynthetic recovery in the spring under the current ambient air temperature (Wallin et al. 2013).

Results from Flakaliden and other studies with elevated  $[\text{CO}_2]$  suggest some important lessons for modeling photosynthesis to predict future ecosystem fluxes under global change. First, elevated  $[\text{CO}_2]$  can promote lower photosynthetic capacity (Robertz and Stockfors 1998, Smith and Dukes 2013), even if photosynthesis at the higher  $[\text{CO}_2]$  remains greater than that at current  $[\text{CO}_2]$ . Second, photosynthesis remains enhanced under elevated  $[\text{CO}_2]$ , even when other resources or environments limit aboveground growth sinks (Sigurdsson et al. 2013, and other studies described in the following section). This photosynthetic enhancement may occur to increase nutrient acquisition (Phillips et al. 2011), or because feedbacks to photosynthesis are poorly developed and increased carbohydrate can be lost through respiration (Robertz and Stockfors 1998, Ceschia 2001). Third, even though enhanced carbohydrate levels and warmer temperatures can speed spring recovery of photosynthesis for boreal conifers, it is frost occurrence, not recovery rate that ultimately determines seasonal integrated photosynthesis (Wallin et al. 2013). These insights suggest that models for global change predictions will need to incorporate additional factors to accurately estimate photosynthesis for boreal conifers: (i) feedbacks between nutrient availability and demand and carbon partitioning; (ii) feedbacks between carbon demand and photosynthesis and respiration; and (iii) frost occurrence and frequency.

### Nutrition regulates the response of growth to elevated $[\text{CO}_2]$ and temperature

Tree biomass growth does not always increase with elevated  $[\text{CO}_2]$  and temperature (Koch and Mooney 1996, Curtis and Wang 1998, Nowak et al. 2004, Körner 2006, Hyvönen et al. 2007, Way and Oren 2010, Wang et al. 2012). In boreal forests, the increased photosynthesis observed under elevated  $[\text{CO}_2]$  sometimes increased biomass growth (Peltola et al. 2002, Riikonen et al. 2008), and sometimes not (Kubiske et al. 1998, Sigurdsson et al. 2001, Pokorný et al. 2010, Norby and Zak

Table 1. The effect size of treatment responses for given variables for treatments in whole-tree chambers, in percentage, relative to a whole-tree chamber at ambient  $[\text{CO}_2]$  and temperature and low nutrient availability (the chamber control treatment). Note that elevated  $[\text{CO}_2]$  and temperature changed growth only with increased nutrient availability, even though leaf photosynthesis increased.

Treatment	$T_A C_A$ -IL <sup>1</sup>	$T_A C_E$ -C	$T_A C_E$ -IL	$T_E C_A$ -C	$T_A C_E$ -C	$T_E C_E$ -C	Reference
$[\text{CO}_2]$ $\mu\text{mol mol}^{-1}$	380	700	700	380	700	700	
Air temperature	Ambient	Ambient	Ambient	+2.8 °C	Ambient	+2.8 °C	
Nutrients (other nutrients in optimum ratio to N)	Optimum N	Low N	Optimum N	Low N	Low N	Low N	
Tree biomass at the end of the experiment	229%	0%	229%	0%	0%	0%	Sigurdsson et al. (2013)
Tree growth rate	100%	0%	150%	0%	0%	0%	Sigurdsson et al. (2013)
Annual shoot C uptake				20%	44%	50%	Hall et al. (2013)
Slope of $A_{\text{max}}^2$ with foliar N				0%	122%	122%	Hall et al. (2013)
Initial slope of the light response curve				45%	52%	52%	Hall et al. (2013)
$C_a$ - $C_i$ <sup>3</sup> ( $\mu\text{mol mol}^{-1}$ ) from wood $\delta^{13}\text{C}$ , year = 2000	-17%	38%	60%				Marshall and Linder (2013)
No. of tracheids	50%						Kalliokoski et al. (2013)
Days of tracheid formation	34%						Kalliokoski et al. (2013)
C uptake March 1 to June 30				44%	33%	61%	Wallin et al. (2013)
Date when apparent quantum yield reached 90% of the maximum value				-38%	-9%	-36%	Wallin et al. (2013)
Date when $A_{\text{sat}}^4$ reached 90% of the maximum value				-15%	-8%	-22%	Wallin et al. (2013)
Net photosynthesis		67%					Uddling and Wallin (2012)
$V_{\text{cmax}}^5$		-19%					Uddling and Wallin (2012)
Dark respiration		44%					Uddling and Wallin (2012)
Dark respiration: net photosynthesis		-14%					Uddling and Wallin (2012)
Mean photosynthesis of expanded shoots				0%	33%	30%	Hall et al. (2009)
Light-saturated photosynthesis <sup>6</sup>	14%	50%	55%				Robertz and Stockfors (1998)

$T$ , temperature;  $C$ ,  $[\text{CO}_2]$ ;  $A$ , ambient;  $E$ , elevated;  $-IL$ , irrigated with optimum nutrition;  $-C$ , rain-fed.

<sup>1</sup>Abbreviations for treatments used in references.

<sup>2</sup>Maximum photosynthesis.

<sup>3</sup>Difference between ambient and intercellular  $[\text{CO}_2]$ .

<sup>4</sup>Photosynthesis at saturating light.

<sup>5</sup>Maximum rate of carboxylation.

<sup>6</sup>Experiment done with branch bags, not in whole-tree chambers.

2011, Sigurdsson et al. 2013). As predicted by models that linked photosynthesis and soil nutrition to estimate biomass growth (Rastetter et al. 1991, 1992, McMurtrie et al. 1992, Comins and McMurtrie 1993, Kirschbaum et al. 1994, McMurtrie and Comins 1996, Rastetter et al. 2005), studies in both boreal and temperate forests have now clearly linked resource availability (primarily nutrients but also water) to the use of increased photosynthesis under elevated  $[\text{CO}_2]$  to increase biomass growth (Curtis and Wang 1998, Oren et al. 2001, Sigurdsson et al. 2002, Norby et al. 2010, Norby and Zak 2011).

The responses of photosynthesis and growth to nutrition, temperature and  $[\text{CO}_2]$  at Flakaliden are the strongest support yet that nutrient availability is a critical control of  $[\text{CO}_2]$  response. At Flakaliden, the increased photosynthesis in elevated  $[\text{CO}_2]$  or under higher air temperature only increased tree growth when nutrient supply was increased (Table 1, Sigurdsson et al. 2013). Optimally fertilized trees at an elevated  $[\text{CO}_2]$  of ~700 ppm annually grew ~25% more than the optimally fertilized trees at ambient  $[\text{CO}_2]$  (Sigurdsson et al. 2013)—the trees in the elevated  $[\text{CO}_2]$ , increased air tempera-

ture or increased air temperature plus elevated  $[\text{CO}_2]$  treatments (all in the control treatment with poor natural nutrient availability) did not show any increased biomass growth after 3 years of treatment (Sigurdsson et al. 2013).

What is the mechanism by which increased nutrient supply increases wood growth, and where elevated  $[\text{CO}_2]$  amplifies wood growth under optimal nutrient supply? At the level of tracheid formation, optimized nutrition resulted in the formation of more tracheids (~50%) and extended the duration of tracheid formation by 20–50%, compared with control trees (Kalliokoski et al. 2013). Much of the >4× wood production for the optimally fertilized trees (Bergh et al. 1999) was a result of an enhanced tracheid formation rate during the middle of the growth season (Kalliokoski et al. 2013). Temperature appears to drive the initiation and ending of tracheid formation, but the tracheid formation rate appears to respond largely to nutrition (Kalliokoski et al. 2013).

The exact mechanism by which trees sense increased nutrient availability and what triggers a higher rate of tracheid formation and growth in other tissues are unknown. Increased nutrient

supply increases internal N (Näsholm et al. 1994), foliar N (Linder 1995), maximum photosynthesis (Roberntz 2001), and tree and forest leaf area (Bergh et al. 1999, Sigurdsson et al. 2013). Increased nutrient and water availability can also decrease the absolute flux of photosynthetic sugars belowground and/or decrease the proportion of annual photosynthesis going belowground (Linder and Axelsson 1982, Ryan et al. 2004, 2010, Palmroth et al. 2006, Litton et al. 2007). At Flakaliden, optimum nutrition increased fine root production and turnover, compared with control plots (Majdi 2001, Majdi and Andersson 2005), and increased soil temperature amplified the effect (Majdi and Öhrvik 2004). On a forest basis at Flakaliden, however, increased nutrients decreased both autotrophic and heterotrophic respiration compared with that of controls (Olsson et al. 2005), which suggests that both the flux to belowground and the partitioning of photosynthesis to belowground decreased under increased nutrients (Giardina and Ryan 2002). An increase in growth efficiency for the optimally fertilized treatments compared with controls (Bergh et al. 2005, Sigurdsson et al. 2013) also suggests that either photosynthesis or partitioning to wood, or both, increased with greater nutrient availability.

Research at Flakaliden provides important insights into the mechanism behind the widely observed correlations of annual tree ring growth with temperature, because experimental increases in soil and aboveground air temperature were both done at the site. The response to elevated air temperature of photosynthesis and the lack of response of wood growth for the same trees described above suggest that carbon supply does not limit growth for the nutrient-poor treatment. A soil warming treatment at the same site, from spring to late autumn (5 °C, no aboveground warming), increased aboveground growth by 115% after 6 years, compared with the control stand in non-heated soil, because warming resulted in earlier and faster spring recovery of photosynthesis (Bergh and Linder 1999), and increased decomposition and nutrient supply (Strömgren and Linder 2002). Soil warming also increased wood growth in optimally fertilized and irrigated plots relative to the non-heated (but optimally fertilized and irrigated) controls (Strömgren and Linder 2002). The increased growth in the heated and optimally fertilized and irrigated plots suggests that soil warming either increased nutrient availability over that supplied in the experiment, or warmer soils enabled more nutrient uptake over a longer 'root activity' season.

What happens to the increased carbohydrate supply from increased photosynthesis under elevated [CO<sub>2</sub>] when nutrient supply is poor and biomass growth does not occur? Sigurdsson et al. (2013) present an excellent discussion of the possibilities, including increased foliar respiration (Roberntz and Stockfors 1998, Uddling and Wallin 2012), increased stem CO<sub>2</sub> efflux (Ceschia 2001), increased allocation to non-woody parts (Sigurdsson et al. 2013) and increased belowground flux to capture more nutrients (Comstedt et al. 2006). At the Duke

FACE experiment, elevated [CO<sub>2</sub>] increased carbon flux belowground (Palmroth et al. 2006, Drake et al. 2011), including exudates (Phillips et al. 2009) and stimulated nutrient acquisition (Phillips et al. 2011). Shifts in mycorrhizal composition under elevated [CO<sub>2</sub>] in the nutrient-poor treatment at Flakaliden suggested increased carbon allocation for nutrient uptake (Fransson et al. 2001).

Other factors besides nutrition may also limit the ability of trees to use the sugars produced by increased photosynthesis under elevated [CO<sub>2</sub>]. Forest-level [CO<sub>2</sub>] studies at the Duke FACE study demonstrated that soil water availability is also an important limiting control for the biomass growth response to elevated [CO<sub>2</sub>] (McCarthy et al. 2010). Mature trees may also not respond to elevated [CO<sub>2</sub>] by increasing growth (Körner et al. 2005) even with a sustained increase in photosynthesis (Bader et al. 2010), because of physiological limitations to growth (Woodruff et al. 2004, Ryan et al. 2006). The increased photosynthetic response of many trees and plants in cold temperatures and treelines to elevated [CO<sub>2</sub>] (Inauen et al. 2012, Dawes et al. 2013) may not translate to growth because of the effects of cold temperature on cell division (Körner 2003, Dawes et al. 2011). Elevated [CO<sub>2</sub>] may also increase susceptibility to frost damage (Martin et al. 2010).

The results from the [CO<sub>2</sub>] × nutrition and [CO<sub>2</sub>] × temperature experiments at Flakaliden and elsewhere and the results for mature trees, where low soil water availability and low temperature limit growth, suggest that we should explore a different approach than currently used for predicting future terrestrial ecosystem responses to global change. Current approaches used to model global change effects in a wide variety of models (Smith and Dukes 2013) suggest that growth can be estimated from an accumulation of leaf-level photosynthesis, and that leaf-level and canopy photosynthesis can be estimated from leaf-level responses to environment, nutrition and [CO<sub>2</sub>]. The Flakaliden results alone should thoroughly disabuse us of the notion that an understanding of leaf-level photosynthesis to elevated [CO<sub>2</sub>] and temperature will allow any prediction of the response of biomass growth or ecosystem carbon storage. Forests growing under nutrient limitations, low soil water and cold temperature are widespread, as are forests with mature trees. An understanding of how these other factors limit growth (Körner 2003) and how photosynthesis interacts with growth will be necessary to accurately model global change responses.

### The legacy of Flakaliden

Perhaps the greatest contribution of Flakaliden is the very rich data set that includes numerous measurements in response to a variety of experimental manipulations that were measured over long-term studies or that used the now 27-year nutrient optimization treatment to assess long-term responses. These data have provided a wealth of material for many modeling studies



and for many cross-site comparisons of ecosystem function and remote sensing (see Appendix S1 available as Supplementary Data at *Tree Physiology* Online). Maintenance of the original experiment has likely been challenging at times because of the short duration of most grants. That the site was established and the experiments maintained is a fitting legacy for Sune Linder, whose vision and persistence enabled this research.

## Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

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## Conflict of interest

None declared.

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