

DOCTORAL THESIS

**Effects of future climate on carbon assimilation  
of boreal Norway spruce**

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*I am still confused,  
but at a higher level.*

*Enrico Fermi*



## Abstract

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In boreal forests, the main factors limiting biomass production are the harsh climate, which combines a short growing season and low annual levels of incoming solar energy, and the limited availability of nitrogen. These limitations will be directly affected by climate change, and may in turn substantially affect the carbon budget of the boreal forests, the production of wood and biofuel, biodiversity and other ecosystem services.

This thesis addresses the effects of climate change on the rate of carbon assimilation by boreal Norway spruce, *Picea abies* (L.) Karst. The study focussed on examining how the mechanisms regulating uptake of CO<sub>2</sub> in mature, field-grown trees are affected by exposure to elevated concentrations of atmospheric carbon dioxide [CO<sub>2</sub>] and air temperature. The experiment was conducted at the Flakaliden research site in northern Sweden. Twelve whole-tree chambers (WTCs) were used to impose combinations of [CO<sub>2</sub>] and temperature treatments as predicted for the region in the year 2100. Shoot CO<sub>2</sub> gas exchange was measured continuously within the chambers, using shoot cuvettes. The effect of the climate change treatments on developing shoots was studied during their first growing season; the effect of the treatments on spring recovery and annual photosynthetic performance in 1-year old shoots was also examined.

The elevated temperature induced an earlier start and completion of the structural development of the current year's shoots, as well as an earlier shift from negative to positive net carbon assimilation rate (NAR) by one to three weeks. The elevated CO<sub>2</sub> increased photosynthetic performance by 30% in high season. Consequently, the current year's shoots had assimilated their own mass in carbon 20-30 days earlier under the climate change conditions than under the current climatic conditions. For the 1-year old shoots, an increase in the maximum photosynthetic rate of ~50% was recorded, and the spring recovery of photosynthetic capacity was completed three to four weeks earlier than under the current climatic conditions.

Multiple environmental variables constantly affect the NAR. A model incorporating the most important variables – light, temperature and vapour pressure deficit – was fitted to the data from the 1-year old shoots. This linked changes in the carbon assimilation rate to each of the tested variables. An artificial neural network was used to reduce the noise present in the field data, and to benchmark the performance of the model. The climate change treatment increased the temperature optimum for gross carbon assimilation from 19.7 to 24.7 °C, and the model apparent quantum yield increased from 0.042 to 0.077 mol mol<sup>-1</sup>. In total, the annual gross carbon uptake increased by 84%, compared to that under current conditions. The lengthening of the growing season increased annual gross carbon uptake by 22%.

Finally, the influence of canopy processes on the rate of soil respiration and its carbon isotope signal ( $\delta^{13}\text{C}$ ) were investigated. The results indicated that canopy processes are likely to have a considerable influence on soil respiration rates, and it is suggested that ecosystem carbon balance models should include plant root allocation and aboveground productivity as driving variables with respect to soil respiration and carbon sequestration.

**Keywords:** *bud development, climate change, empirical models, gas exchange, photosynthesis, Picea abies, seasonality, whole-tree chambers*



## Sammanfattning

Det norra barrskogsbältet, även kallat de boreala skogarna, sträcker sig runt hela norra halvklotet. Det utgör en tredjedel av den globala skogsytan, och innehåller hälften av den totala mängden kol finns lagrat i samtliga skogsekosystem. Trots de låga temperaturerna, den korta vegetationssäsongen och en liten mängd inkommande solenergi under året, är dessa ekosystem viktiga för det globala klimatet. De boreala skogarna är ett av få landekosystem som anses kunna lagra in en större mängd kol från atmosfären under den närmsta hundraårsperioden, och därmed, åtminstone kortsiktigt, bidra till en inbromsning av den ökande växthuseffekten.

Projektets syfte var att fastställa hur de klimatförändringar som följer med den ökande halten växthusgaser i atmosfären, däribland koldioxid (CO<sub>2</sub>), kommer att påverka tillväxten hos skogsekosystem, speciellt fokuserat på granar, *Picea abies*, i norra Sverige. Scenariot för klimatförändringar som har använts är SWECLIMs klimatmodell, där en fördubbling av koldioxidhalten på hundra år, dvs. en ökning till 700 ppm år 2100, skulle medföra en temperaturökning på i genomsnitt 4 grader över året.

Fältförsök utfördes på Flakalidens försöksområde utanför Umeå. 12 vuxna granar inneslöts i helträdskammare, där temperatur och koldioxidhalt höjdes för att simulera det förväntade klimatet för år 2100. Uptaget och avgivningen av CO<sub>2</sub> hos träden följdes under tre år med hjälp av kuvetter som monterades på skott i övre delen av kronan. Det mätta utbytet av CO<sub>2</sub> användes för att beräkna fotosynteshastigheten. Hypotesen var, att den ökade koldioxidhalten och temperaturen, var för sig och tillsammans, skulle öka granarnas fotosynteshastighet, och därmed upptaget av kol vilket styr tillväxthastigheten. Liknande studier har gjorts av ett flertal forskargrupper både inom och utanför Sverige. Därför studien är speciell eftersom vuxna friväxande träd har studerats, för att ett extremt stort antal mätningar av gasutbytet har gjorts (~0.5 milj. per år), och för att försöket varat förhållandevis länge, från hösten 2001 till hösten 2004. Därmed har fotosyntesens utveckling under året kunnat studeras med hög tidsupplösning och parallellt inom olika behandlingar. Detta är nödvändigt för att kunna konstruera och utvärdera tillförlitliga simuleringsmodeller för att förutsäga effekterna av framtida klimat på den boreala skogen.

Fotosynteshastigheten hos granar i området runt Flakaliden är framförallt styrd av mängden inkommande ljus, lufttemperaturen, luftfuktigheten och näringsstatusen i barren. För att möjliggöra en djupare analys av hur ökningen av CO<sub>2</sub> och årsmedeltemperatur påverkade fotosyntesens respons mot dessa variabler, har en modell passats till mätdata. Modellen, ShootModel, består av ett antal ekvationer som beskriver hur fotosynteshastigheten drivs och begränsas av ovanstående variabler.

De viktigaste resultaten från studien var att kolupptaget ökade kraftigt när koldioxidhalten höjdes. Den maximala hastigheten för kolupptaget ökade med ungefär 50 %. Dessutom gjorde temperaturökningen att vegetationssäsongen startade cirka tre veckor tidigare på våren, vilket i sig ökade kolupptaget över året med 22 %. En förlängning av vegetationssäsongen är speciellt viktig på höga breddgrader, där mängden inkommande solenergi är en begränsande faktor för tillväxten under året. Även skottskjutningen påverkades av en förlängd vegetationssäsong, vilket gjorde att även årsskotten ökade sitt kolupptag under sitt första levnadsår. Kombinationen av ökad maxhastighet för kolupptag och längre vegetationssäsong medförde att granarna i förhöjd koldioxidhalt och ökad temperatur ökade sitt årliga kolupptag med 84 %, jämfört med granar i kammare som inte hade någon behandling utan följde dagens klimat.

Försöket visade alltså att vi kan förvänta oss en ökad hastighet på kolupptaget hos granar i norra Sverige. Däremot kan man inte direkt översätta ökningen i fotosynteshastighet till ökad virkesproduktion, eftersom många olika faktorer spelar in, däribland tillgången på näring. I ett framtida projekt ska därför kolupptagshastigheten, som i detta projekt mättes på skottnivå, skalas upp och användas för att beräkna kolupptag och kolavgång för hela träd och skogsbestånd.

## List of papers

The thesis is based on the following papers, referred to in the text by their Roman numerals.

- I. Hall M., Röntfors M., Slaney M., Linder S., Wallin G. CO<sub>2</sub> exchange of buds and developing shoots of boreal Norway spruce exposed to elevated and ambient [CO<sub>2</sub>] and temperature in whole tree chambers. *Submitted to Tree Physiology*.
- II. Wallin G., Slaney M., Hall M., Röntfors M., Medhurst J. Impacts of elevated [CO<sub>2</sub>] and temperature on photosynthetic capacity and chlorophyll fluorescence in boreal Norway spruce during spring. *Manuscript*.
- III. Hall M., Medlyn B., Röntfors M., Linder S., Wallin G. Impacts of CO<sub>2</sub> and temperature elevation on net shoot carbon assimilation rates in Norway spruce. *Manuscript*.
- IV. Betson, N. R., Göttlicher, S. G., Hall, M., Wallin, G., Richter, A., Högberg, P. (2007). No diurnal variation in rate or carbon isotope composition of soil respiration in a boreal forest. *Tree Physiology* 27, 749–756.



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## On the significance of boreal forests for the global climate

### The boreal forests – location, climate and growth conditions

Forest ecosystems are important as sources and sinks of atmospheric CO<sub>2</sub>, as well as for storing carbon within the standing crop, litter and soil. The boreal forest constitutes close to one third of the total global forest inventory (Bonan et al. 2008), covers 13.7 million square kilometres, and stores 559 Gt of carbon (C), which is almost 50% of the total C storage in forested areas, globally (Watson et al. 2000). Extending over a large proportion of the northern hemisphere, it stretches from Scandinavia across Siberia to the Pacific Ocean, and then across North America from Alaska to New Foundland. The climate is cold with a pronounced seasonality in temperature, below 6°C for 6-9 months, followed by short summers with mean temperatures exceeding 10°C; there is no dry season. Lakes, bogs and marshes are common. In three quarters of the area the permafrost starts less than a meter below the surface. In general, the soils of the boreal forests are podzolic, acidic, low in nutrients and poorly suited to agriculture (Raven et al. 1999).

In large areas of the boreal forests, the cold climate and short growing season, together with the limited availability of soil nitrogen, are the main factors limiting biomass production and forest-atmosphere carbon fluxes (Tamm 1991, Linder 1995). These limitations are directly and indirectly influenced by two major human-induced perturbations: rising atmospheric CO<sub>2</sub> concentration [CO<sub>2</sub>], causing an elevated global mean temperature, and atmospheric nitrogen (N) deposition. The deposition of N (wet and dry, oxidized and reduced) within the temperate and boreal forests amounts to between 1 and 100 kg ha<sup>-1</sup>yr<sup>-1</sup>. Deposition in the more remote forests, particularly in rural areas at high latitudes, is at the lower end of this range, while industrialized central Europe receives the higher levels (Jarvis and Fowler 2001).

Mean global [CO<sub>2</sub>] increased during the period 1995-2005 by 1.9 ppm yr<sup>-1</sup> (Forster et al. 2007). The increasing concentration of greenhouse gases in the atmosphere, including CO<sub>2</sub>, causes an increase in temperature at the earth's surface (e.g. Harvey 2000). Eleven years out of the twelve year period 1995-2006 rank amongst the twelve warmest years with respect to global surface temperature since 1850. The 100-year linear trend (1906-2005) for mean atmospheric temperature showed an increase of 0.74 °C (Forster et al. 2007). The increasing amounts of available soil N, the elevated levels of [CO<sub>2</sub>], and increasing temperatures can all be expected to have positive effects on annual production by the boreal forests (Watson et al. 2000).

Increasing temperature may be of particular importance for the annual carbon budgets in boreal forests, as a result of its impact on the length of the vegetation period. In the boreal regions, woody plants adapt to the freezing temperatures and low soil water availability during winter by changes in the state of their protoplasm, their metabolic activity, developmental processes and low-temperature resistance

(frost hardening), a state referred to as winter dormancy (Larcher 1995). The decreasing photoperiod and low temperatures in the autumn induce this state, which is maintained until dormancy is broken in early spring by increasing day length, air temperature and soil thawing. Spring and early summer are characterized by the growth and development of buds, restoration of the photosynthetic apparatus, and repairing any damage caused by freezing. All of these processes have been shown to be highly dependent on temperature (Linder and Lohammar 1981, Troeng and Linder 1982, Havranek and Tranquillini 1995, Bergh and Linder 1999, Leinonen and Kramer 2002, Slaney et al. 2007). An increase in mean seasonal temperatures during winter, spring and early summer may, therefore, have an impact on the length of the dormancy period, and on the rate of spring recovery and bud development. This may, in turn, affect the annual carbon budget of boreal forests, and the amount of carbon being sequestered in these northern regions.

### **Boreal forests for carbon storage**

Whilst increases in atmospheric CO<sub>2</sub>, with the associated effects on climate, have an impact on carbon sequestration by the boreal forests, the net uptake and release of carbon dioxide from the boreal forests have an effect on the atmospheric partial pressure of CO<sub>2</sub> (Urban 2003). The deep mineral soil of the boreal forests has been identified as one of the few possible terrestrial long-term carbon storage pools, capable of accumulating carbon throughout the next century (Steffen et al. 1998). There will, therefore, be significant environmental, political, and economic advantages resulting from a wise management strategy for the boreal forests. For example, one feature of the boreal forest identified within the 1997 Kyoto Protocol to the United Nations Framework Convention on Climate Change (UNFCCC), is the possibility that forests could act as carbon sinks, sequestering carbon from the atmosphere. It has been suggested that an increase in the total forested area as a result of afforestation or reforestation, especially in the higher latitudes of the globe, would help to mitigate climatic change as a result of carbon sequestration by trees and carbon storage in both aboveground biomass and the soil (Bala et al. 2007). Deforestation, on the other hand, is expected to exert a warming by CO<sub>2</sub> to the atmosphere, eliminating the possible increased storage of carbon in plants and soils (Bala et al. 2007).

The amount of carbon stored in the soil, and soil respiration rates (although strongly coupled to temperature) are ultimately dependent on the amount of incoming carbon sequestered from the atmosphere via autotrophic carbon assimilation (Janssens et al. 2001). The combination of cold temperatures, water logging and permafrost, together with the slow decomposition rates of plant litter, results in the soil organic matter in the soils of the boreal forests being quite stable (Hobbie et al. 2000). Over a longer time scale, disturbances and processes such as fires, permafrost dynamics and drainage need to be included in the carbon budget, and the net result at the landscape scale remains poorly understood (Hobbie et al.

2000). It has been predicted that acute events, such as extreme summer temperatures and rainfall deficits, will increase in frequency and severity as the climate changes (Meehl and Tebaldi 2004). Such events may cause a reduction in ecosystem productivity and large carbon releases from temperate and boreal ecosystems, as was reported after the 2003 heat wave in Europe (Ciais et al. 2005). Further research into both long term and short term effects on the carbon storage capacity of boreal forests is thus needed. This is particularly important in order to provide information to be used in support of international climate agreements.

### **Boreal forests and land surface albedo**

To estimate the net result of large scale afforestation and reforestation, changes in the physical properties of the earth's surface must also be taken into account. An increase in the forested area at the expense of non-forested areas would decrease the surface albedo (~ reflection of incoming light), the effect of which would be most pronounced in the boreal forest during the snow season. A decrease in albedo may lead to a greater increase in temperature than the predicted decrease resulting from the decreased levels of atmospheric CO<sub>2</sub> (Bonan 2008). Furthermore, the positive effects of afforestation and reforestation on the climate resulting from increased rates of carbon sequestration will only occur for up to a century, until the new forest reaches its carbon balance equilibrium (Steffen et al. 1998). The effect of the albedo decrease would not be time-limited, and may be further enhanced by a positive feed-back reducing glaciation (Snyder et al. 2004, Bonan 2008). Because of the strong albedo effect, the boreal forests may have the most important biogeophysical effect of all biomes on annual mean global temperature (Bonan 2008).

### **Climate change and carbon assimilation**

Increasing atmospheric [CO<sub>2</sub>] and a concomitant rise in temperatures are likely to, at least initially, result in a higher rate of CO<sub>2</sub> assimilation in boreal forest species (*cf.* Saxe et al. 1998, Luo et al. 1999, Saxe et al. 2001, Hyvönen et al. 2007). The main factors behind the increase in CO<sub>2</sub> assimilation include a temperature-induced lengthening of the growing season, increased photosynthetic capacity resulting from the elevated [CO<sub>2</sub>], and increased mineralisation of nitrogen and other nutrients in the soils due to a temperature-induced increase in the activity of soil organisms (Rustad et al. 2001, Melillo et al. 2002). Several ecosystem processes are involved, and their influence on the net CO<sub>2</sub> assimilation rate (NAR) of boreal forest trees means that all of these factors may prove to be of fundamental importance in controlling productivity. A direct relationship between stimulation of photosynthetic rate, and yield and biomass responses cannot, however, be assumed, as several feedback mechanisms are involved (*cf.* Morison and Lawlor 1999).

In many cases, models are used to transform measured responses established for one spatial scale to another, or from one timescale to another (Farquhar and von Caemmerer 1982, McMurtrie et al. 1990, Wang and Jarvis 1990, Sands 1995ab, 1996, Medlyn et al. 2003, Wang 2003, Lindroth et al. 2008). Many factors need then to be taken into account, including the sink capacity of non-photosynthetic tissue and structures, i.e. stems, branches, roots, fine roots and reproductive structures, as well as soil processes and nutrient and water relations (Stitt 1991, Kruijt et al. 1999, Morison and Lawlor 1999, Hobbie et al. 2000, Medlyn et al. 2000, Medlyn et al. 2001, Luo et al. 2004, Luo et al. 2008).

A key determinant of biomass production is the rate of carbon uptake as a result of shoot photosynthesis. Shoot photosynthesis is responsive to several environmental variables, particularly atmospheric  $[CO_2]$  (Saxe et al. 1998, Lloyd 1999, Ainsworth and Long 2005), incoming photosynthetic photon flux density PPF (e.g. Thornley 1990), air temperature  $T$  (cf. Farquhar et al. 1980, McMurtrie et al. 1990, Long 1991, McMurtrie and Wang 1993, Sands 1995b, Bernacchi et al. 2001, 2003) and atmospheric water vapour pressure deficit, VPD (Jarvis 1976, Wong et al. 1978, Morén 1999, Uddling et al. 2005). Of special importance for the annual carbon budgets of boreal forests are the length of the growing season, the reduction in photosynthetic capacity during the winter as a result of photosynthetic inhibition caused by the combination of low temperatures and high irradiance, and the rate and timing of the photosynthetic recovery in spring and early summer (Pelkonen and Hari 1980, Linder and Lohammar 1981, Troeng and Linder 1982, Repo et al. 1990, Havranek and Tranquillini 1995, Bergh and Linder 1999).

### **Spring events**

During spring and early summer, great changes occur in the carbon allocation pattern within the canopy of boreal evergreen conifers. The changes are initiated by phenological events driven mainly by temperature (Kramer et al. 2000). Such changes are characterised by the spring recovery of the photosynthetic apparatus, followed by an accumulation of starch in the needles and shoot axes from previous years (Ericsson 1978, Flower-Ellis 1993, Linder 1995). The next step in the phenological cycle is bud burst, followed by the elongation and growth of the current year's shoots. For various *Pinus* species, the accumulated starch has been shown to be the main support for the early growth of the current year's shoots (Kozlowski and Winget 1964, Gordon and Larson 1968, Ericsson 1978). To the best of my knowledge, there are no corresponding studies of Norway spruce. It has, however, been shown that the phase during which there is the most rapid elongation of shoots in Norway spruce coincides with a decline in the starch pool in needles on shoots from previous years (Flower-Ellis 1993, Linder 1995). A number of studies have shown that temperature sum ( $T_{sum}$ ) is the main factor controlling bud burst and the rate of shoot development (Hänninen 1995, Leinonen and Kramer 2002, Slaney et al. 2007), but day length (Heide 1993, Hänninen et al. 2007) and the accumulated duration of the light period (Partanen et al. 1998,

Partanen et al. 2001) have also been suggested as factors that contribute to the control of these processes.

Photosynthetic capacity refers to the status of the photosynthetic apparatus which, together with the prevailing environmental factors, determines the rate of photosynthesis at any given moment (Repo et al. 2006). During winter, the maximum photosynthetic capacity is reduced to 5-10 % of its late summer maximum, a reduction which starts with the first severe autumn frost (Troeng and Linder 1982, Bergh et al. 1998, Mäkelä et al. 2004). The reduction in capacity is the result of winter dormancy of the trees and damage to the photosynthetic apparatus caused by low temperatures and high photon flux densities while the needles are still frozen (Bergh 1997 and references therein). Recovery from winter damage in the spring is mainly temperature driven (Linder and Lohammar 1981, Tanja et al. 2003), but is also strongly coupled to soil thawing and water availability (e.g. Sevanto et al. 2006). Because of the strong link between temperature (air and soil) and the onset and rate of spring events, both bud burst and spring recovery of photosynthesis are likely to occur earlier in the future if climate change results in elevated temperatures.

### **The effect of CO<sub>2</sub> elevation on the carbon assimilation rate**

It has been suggested that any elevation in [CO<sub>2</sub>] will influence the productivity of forest trees as a result of CO<sub>2</sub> fertilization affecting the assimilation process, and because of changes in the nutrient and water responses (Saxe et al. 1998). Long-term (> 1 yr) field studies have shown a 21 % decrease in stomatal conductance in forest trees grown under a [CO<sub>2</sub>] of 700 μmol mol<sup>-1</sup>, a figure which was statistically significant. (Medlyn et al. 2001). The response was stronger in young trees compared to old, and in deciduous trees compared to coniferous. However, stomatal conductance at the stand-level is less investigated (Karnosky 2003).

On a molecular level, the maximum carbon assimilation rate under light saturation conditions is ultimately dependent on CO<sub>2</sub> availability, and the amount of Rubisco (Farquhar et al. 1980, Bernacchi et al. 2003) which is, in turn, dependent on nitrogen availability. An increase in [CO<sub>2</sub>], therefore, has a direct, positive impact on the maximum photosynthetic rate,  $A_{MAX}$ . At the shoot and canopy level, the maximum rate of light saturated photosynthesis also depends on the amount of chlorophyll, which in the boreal forests usually is limited by nitrogen availability (Tamm 1991, Linder 1995). In expanding canopies, an increase in [CO<sub>2</sub>] has been shown to result in an increase in LAI by as much as 22 %, however over a longer time period the increase in growth is likely to result in a dilution of foliage N content, leading to a down regulation of growth rate (Hyvönen et al. 2007).

### **The effect of temperature elevation on the carbon assimilation rate**

At boreal and temperate latitudes a temperature increase may enhance the NAR (Saxe et al. 2001). A temperature increase changes the temperature optimum for photosynthesis, and also influences the apparent quantum yield of photosynthesis (AQY, mol CO<sub>2</sub> mol<sup>-1</sup> photons), which can be estimated from the initial slope of a plot of photosynthesis *versus* intercepted light (Farquhar et al. 1980, Long 1991, McMurtrie and Wang 1993, Bernacchi et al. 2001, 2003). The apparent quantum yield is dependent on the regeneration of RuBP which, in turn, depends on the maximum rate of electron transport in the thylakoids and on the partitioning between carbon assimilation and photorespiration (Farquhar et al. 1980, Bernacchi et al. 2001). All of these processes are directly dependent on temperature. Partitioning between carboxylation and oxygenation is also dependent on the ratio of atmospheric O<sub>2</sub> to CO<sub>2</sub>. Furthermore, the separation of net photosynthetic rate into respiration (growth + maintenance) and biomass production is likely to be influenced by the availability of carbohydrates relative to other resources (Pleijel et al. 1999, Roberntz and Linder 1999, Tjoelker et al. 1999).

### **Effects of the changing climate on respiration**

The rate of maintenance respiration, which is the largest respiratory cost for aboveground tree components (Bergh 1997) increases exponentially with temperature. The relationship between temperature and maintenance respiration is described by the Q<sub>10</sub> value – the increase in respiration rate associated with an increase in temperature of 10 °C. The Q<sub>10</sub> value fluctuates seasonally, a range from 2.0 in July to 2.7 in February as been shown for boreal Norway spruce (Roberntz and Stockfors 1998). The response of respiration rate to temperature is likely to be down regulated as plants acclimatise to a future climate with a higher mean temperature (Saxe et al. 2001). Furthermore, the maintenance respiration rate at a constant temperature is proportional to the N content of the substrate (Stockfors and Linder 1998b, Ryan 1991), so a higher respiration proportion of the net carbon assimilation may be set of in case of production of biomass with lower nitrogen concentration.

### **On the importance of experimental design for the measured results**

Using a wide range of methods, including branch-bags (Barton et al. 1993, Kellomäki and Wang 1997, Saugier et al. 1997, Roberntz 1999), open top chambers (Whitehead et al. 1995, Jach and Ceulemans 1999, Murray et al. 2000), closed top chambers (Kellomäki et al. 2000, Medhurst et al. 2006), and the FACE-technique (Hendrey et al. 1999, Hamilton et al. 2001, Herrick and Thomas 2001, Körner et al. 2005), the impacts of temperature and [CO<sub>2</sub>] elevation have been investigated on seedlings, saplings, mature trees and ecosystems (see reviews by Saxe et al. 1998, Körner 2000, Medlyn et al. 2001, Saxe et al. 2001, Urban 2003, Hyvönen et al. 2007). Results from these experiments span over large intervals, with reported increases in NAR ranging from 12% to 98% in studies of coniferous

species in the genera *Picea* and *Pinus* (Dixon et al. 1995, Saxe et al. 1998, Tjoelker et al. 1998, Tissue et al. 2001, Sigurdsson et al. 2002, Bigras and Bertrand 2006, Hyvönen et al. 2007). The wide variation in results is a symptom of the multiple constraints affecting the growth rate at each instant, these include chamber effects and effects imposed by the experimental design. For example, in the experiments mentioned above, studies on seedlings or young trees in pots all produced results at the lower end of the range: a 12-50 % increase reported by Bigras and Bertrand (2006), 25 % reported by Tjoelker et al (1998) and 43% reported by Dixon et al (1995). No experiments that did not use plants in pots were found at this level of NAR responses. The highest response of 98% (Tissue et al. 2001), was reported for current-year needles on seedlings growing under well watered conditions in open-top chambers, i.e. in a phase of growth characterised by rapid expansion.

Some results indicate that it is the strength of the photosynthate sinks that regulate the responses of the trees to elevated [CO<sub>2</sub>] (Tissue et al 2001). This implies that experimental designs where only a part of the tree is exposed to elevated [CO<sub>2</sub>], for example branch bags, are not easily compared with experiments where the whole plant is being exposed; it also further separates results of experiments conducted on plants at different ages and growth conditions. Apart from this, the response to CO<sub>2</sub> is highly dependent on nutrient availability. In Free-Air CO<sub>2</sub> Enrichment (FACE) and open-top chamber experiments, N limitation has been shown to reduce the stimulation of biomass growth by CO<sub>2</sub> (Curtis and Wang 1998, Novak et al. 2004, de Graaf et al. 2006) Conversely, N addition has been shown to increase plant CO<sub>2</sub> responses (Oren et al. 2001, Schneider et al. 2004, Reich et al. 2006). Interpreting experimental results in the light of resource supply (Körner 2006) and experimental design is, therefore, extremely important.

## Scope

This thesis addresses the impact of climate change on the atmosphere–biosphere continuum, and focuses on carbon assimilation by boreal Norway spruce, *Picea abies* (L.) Karst. The main question that was addressed was how the mechanisms regulating uptake of carbon in mature field-grown Norway spruce trees are being affected by elevated atmospheric [CO<sub>2</sub>] and air temperature. A predicted climate scenario for the site, in year 2100, were used (atmospheric CO<sub>2</sub> concentration of ~ 700 μmol mol<sup>-1</sup> and a temperature increase of 2.8 and 5.6 °C in summer and winter, respectively).

The thesis project includes field studies of photosynthesis and soil respiration and a modelling study. The field studies was performed at the Flakaliden research site in northern Sweden. In the photosynthesis study, twelve whole-tree chambers (WTCs) were used to impose the temperature and CO<sub>2</sub> treatments on mature, field-grown Norway spruce trees (Figure 1). Shoot cuvettes (SCs) were used to take continuous measurements of the uptake and release of CO<sub>2</sub> by current-year shoots



(C-shoots) and one-year-old shoots (C+1-shoots), see Figure 2. In Papers *I* and *II* results from the field measurements were presented in the form of a descriptive data analysis. In Paper *I* the emphasis was on the development of current-year buds and shoots during their first spring and summer. Both the structural development and the gas exchange rates were examined. Paper *II* describes the treatment impacts on the photosynthetic capacity of one-year-old shoots during the spring.

The modelling study aimed to investigate how the treatments affected the photosynthetic response to the most important variables in the boreal forest, namely incoming photosynthetic photon flux density (PPFD), air temperature ( $T$ ), vapour pressure deficit (VPD), and foliage nitrogen content ( $N_F$ ). A semi-mechanistic model, the ShootModel, was fitted to the available field data (Paper *III*).

In the soil respiration study the influence of canopy processes on soil respiration rates was examined (Paper *IV*). Measurements of the diurnal variation in soil respiration rate and carbon isotope composition ( $\delta^{13}\text{C}$ ) of the respired  $\text{CO}_2$  were performed in one girdled and one non-girdled Norway spruce stand close to the chambers. The respiration rates were then compared with concurrent measurements of shoot carbon assimilation rate in the reference trees, and the carbon isotope composition of the respired  $\text{CO}_2$  was compared to the carbon isotope composition in the phloem sap of trees in the girdled plot.

## **The Flakaliden climate change experiment**

To investigate the impact of  $\text{CO}_2$  and temperature on mature Norway spruce under field conditions, a large scale experiment with whole tree chambers (WTCs) was conducted between 2001 and 2004 at the Flakaliden experimental site in northern Sweden (Medhurst et al. 2006, Slaney 2006).

### **Experimental site**

The Flakaliden forest experimental site is situated in northern Sweden (64°07' N, 19°27' E, 310 m a.s.l.). The site was planted in 1963 with four-year-old seedlings of a local provenance of boreal Norway spruce, the initial stand density was approximately 2500 trees  $\text{ha}^{-1}$ . The soil is a thin, podzolic, sandy, post-glacial till with a mean depth of about 120 cm. The thickness of the humus layer varies between 2 and 6 cm. Mean monthly air temperature for the period 1990–2004 varied from -7.3 °C in January to 14.6 °C in July (Slaney et al. 2007), the ground is usually frozen and covered by snow from mid-October to mid-May. Mean annual precipitation is approximately 600 mm, and soil water content does not usually limit biomass production. It has been proposed that the main growth limiting factor at this site is nitrogen availability (Linder 1995, Tamm 1991). For further details about the Flakaliden site, see Linder and Flower-Ellis (1992), Linder (1995) and Bergh and Linder (1999).

### The chamber treatments

From August 2001 to September 2004, twelve trees were enclosed in individual WTCs (Figure 1). The temperature and carbon dioxide treatment was designed to reflect the predicted conditions for the region in the year 2100, derived from the Swedish Regional Climate Modelling Programme, SWECLIM (Christensen et al. 2001, Räisänen and Joelsson 2001, Räisänen et al. 2001). The scenario used was a doubling of the atmospheric partial pressure of CO<sub>2</sub> to 700  $\mu\text{mol mol}^{-1}$ , with a concomitant temperature elevation by 2.8 °C (August) to 5.6 °C (December). The trees were exposed to a combination of two temperature treatments ( $T_A$ , ambient and  $T_E$ , elevated) and two [CO<sub>2</sub>] treatments ( $C_A$ , ambient:  $\sim 365 \mu\text{mol mol}^{-1}$ , and  $C_E$ , elevated:  $\sim 700 \mu\text{mol mol}^{-1}$ ) using a  $2 \times 2$  factorial design. To evaluate the chamber effect, three non-chambered reference trees ( $R$ ) were included in the experiment. The 15 selected trees were each randomly assigned to one of the five treatments ( $T_A C_A$ ,  $T_E C_A$ ,  $T_A C_E$ ,  $T_E C_E$ ,  $R$ ) with three replicates of each. The temperature in the  $T_A$ -WTCs continuously tracked the outdoor ambient air temperature, while in the  $T_E$ -WTCs the temperature increase was altered on a monthly basis, following the SWECLIM predictions (see Medhurst et al. 2006, Slaney et al. 2007).



a. Whole-tree chamber.



b. Reference tree.

**Figure 1.** At the Flakaliden research site, twelve whole-tree chambers (**a**) were used to impose combinations of elevated temperature and elevated [CO<sub>2</sub>] as predicted for the region in year 2100. Measurements of gas exchange were performed on two shoots from each tree. Three reference trees (**b**) were also selected, for quantification of chamber effects.

The WTCs comprised a circular frame ( $\varnothing$  3.25 m) approximately 8.5 m tall; the top 3.0 m was conical, and the lower 0.4 m constituted the soil compartment. An extra section of 2.5 m could be added for trees that outgrew the chamber. The walls consisted of 0.4 mm transparent PVC film, with 88 % transmittance of visible light (400-800 nm) for new material, decreasing by merely 4% during a 5 year period. For lower wavelengths the transmittance decreased sharply – at 350 nm only 4% and 1% transmittance was recorded for new and old material, respectively. A high transmittance (88% and 89% for new and old material, respectively) was measured for wavelengths of 800 to 1100 nm. The daily mean PPFD inside the chamber was 79% of the outside PPFD (recorded over a six-month period from 1 January to 30 June 2002 (Medhurst et al. 2006)).

Fresh air was continuously added to the WTC at a rate of approximately  $54 \text{ m}^3 \text{ h}^{-1}$ , and since the internal chamber volume was  $56.3 \text{ m}^3$  (including air pipes and cooling system), the chamber air was replaced approximately once an hour. During the dormant period the flow rate was reduced to  $42 \text{ m}^3 \text{ h}^{-1}$  to reduce costs.

The soil compartment was sealed off by a PVC film, allowing a separation between the above-ground and the soil compartment. The exhaust air from the above-ground compartment was ventilated through the soil compartment allowing similar treatments in both compartments. During the winter, external insulation was placed around the base of the chambers and thick polystyrene sections were placed over the floor inside the chambers, to simulate snow cover and to prevent deep frost forming in the soil. The precipitation was measured using rain gauges outside the chambers, and the trees were irrigated with the same amount of water by means of two micro-sprinklers installed in the soil compartment of the WTCs. The WTC system has been described in detail by Medhurst et al. (2006) and the treatment performance during the experimental period of the present study by Slaney et al. (2007).

The WTC system has been used in two other experiments. In the first one, at Flakaliden between 1997 and 2000, it was used to study the effect on Norway spruce of elevated  $[\text{CO}_2]$  in combination with irrigation and fertilization treatments (Fransson et al. 2001, Wallin et al. 2001, Kostianen et al. 2004). To the best of my knowledge, only two other experiments with mature field grown conifers subjected to both elevated  $[\text{CO}_2]$  and elevated temperature have been performed, both on Scots pine. In Finland, WTCs over individual trees were used (Kellomäki et al. 2000), and in Norway a large-scale enclosure was constructed in a small catchment enveloping a whole stand (Wright 1998, Rasmussen et al. 2002).

### **The gas exchange measurements**

Measurements of shoot gas exchange were performed from 2002 to 2004 on one-year old shoots (C+1-shoots), and from 2003 to 2004 on current-year shoots (C-shoots), using temperature controlled 0.15-l shoot cuvettes (SCs) fitted with a

transparent Perspex (Plexiglas) top (Figure 2). The base of the SC was coated with dark Teflon to avoid reflection of light. A total of 30 cuvettes were run simultaneously to measure shoot gas exchange, and an additional six air flow channels were run to measure reference gas flows. The gas exchange of each shoot sampled was measured for 30 seconds, every 30 minutes, amounting to a total of >15000 measurements per cuvette per year (including short stops for maintenance of the system). To minimise between-shoot variation, shoots on branches from the fourth to sixth whorl from the top were sampled on the south-facing side of the trees ( $\pm 90^\circ$ ). The  $\text{CO}_2$  exchange was expressed in relation to projected needle area measured after harvest, where the projected needle area was calculated from scanned images of the needles, using the WinSEEDLE software (WinSEEDLE Pro 5.1a, Regent Instruments Inc., Canada).



a) Current year shoot.

b) One-year old shoot.

**Figure 2.** Shoot cuvettes, for measurement of net  $\text{CO}_2$  exchange ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), incoming radiation ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), temperature ( $^\circ\text{C}$ ) and relative humidity in the air (%). Measurements were performed for 30 seconds, every 30 minutes throughout **a**) the first growing season (current year shoots) and **b**) throughout the year (one-year old shoots).

For the C-shoots, the measurements were performed by enclosing a bud in the SC (Figure 2a) from at least two weeks before bud burst and continuing until the maximum photosynthetic capacity had stabilised in mid- to late August, when the fully developed shoots were harvested (Paper I). To minimise the risk of C-shoots out-growing the SCs, apical buds of second or third order shoots were chosen. In order to seal the SC around the shoot axis next to the bud, the needles 1 cm from the bud were removed before the SC was installed. Measurements of C-shoots were performed with one SC per WTC during 2003. In 2004 measurements were also performed on the reference trees.

The measurements of the C+1 needles were performed continuously throughout the experimental period by enclosing a 55-mm portion of the shoot in the SC (Figure

2b). To ensure consistency in the measurements, and at the same time minimise potential chamber effects, the measured shoots were changed, on average, twice a year (Paper *II*). The shoots were trimmed to remove needles at the points where the shoot passed through the SC wall to allow the joint to be sealed with silicon rubber. Measurements of the C+1 shoots were performed using one SC per tree during the years 2003 and 2004, and two SCs per tree during 2002.

The SCs were connected by an insulated and heated tubing system to an open gas exchange system running in open mode. The meteorological measurements were analogous, and converted from analogue to digital form using A/D converters. The gas tubing and the digital data were conveyed to a hut close to the WTCs, and the SC system (gas tubing + digital data) was split into three parallel sub-systems operated by separate computers, allowing for continuous recording by the remaining two sub-systems in case of failure or maintenance of one sub-system. The CO<sub>2</sub> and H<sub>2</sub>O concentrations of the sampled air were measured using infrared gas analysers (CIRAS-1, PP Systems, Hitchin Herts, U.K.) which were calibrated monthly using an air source with a known CO<sub>2</sub> concentration and vapour pressure. The air-flow rates of the sample and reference air were set to 0.5 or 0.75 l min<sup>-1</sup>, depending on season and expected CO<sub>2</sub> exchange rates, using mass-flow controllers (F-201C, Bronkhorst Hightech, Ruurlo, The Netherlands). These were calibrated every second month using a piston-driven flow calibrator (DryCal DC-1, Bios International, Butler, NJ, U.S.A.). The temperature in the SC tracked the ambient temperature inside or outside the WTCs ( $T_A$ ,  $T_E$  and R treatments, respectively) by means of a Peltier heat exchanger. Condensation in the SC was prevented by setting the SC temperature +0.2 °C higher than the chamber air temperature and by drawing the incoming air through a condenser, maintained at 3 °C below the ambient air temperature by means of a second Peltier heat exchanger (Papers *I* and *II*). The transmittance of the Perspex lid was 85-90 % for wavelengths between 400 and 1100 nm. For wavelengths between 350 and 400 nm the transmittance decreased to 80 %. The cuvette system has previously been used in the Flakaliden [CO<sub>2</sub>]-fertilization experiment, 1997–2000 (Wallin et al. 2001).

### **Meteorological conditions and treatment performance**

Measurements of the meteorological conditions above the canopy – Air temperature ( $T$ , °C), total and diffuse photosynthetic photon flux density above the canopy (PPFD,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and relative humidity (RH, %) – were collected from a 15 m high mast close to the WTCs. PPFD was measured using a sunshine sensor (BF-2, Delta-T Devices Ltd, Cambridge, U.K.).

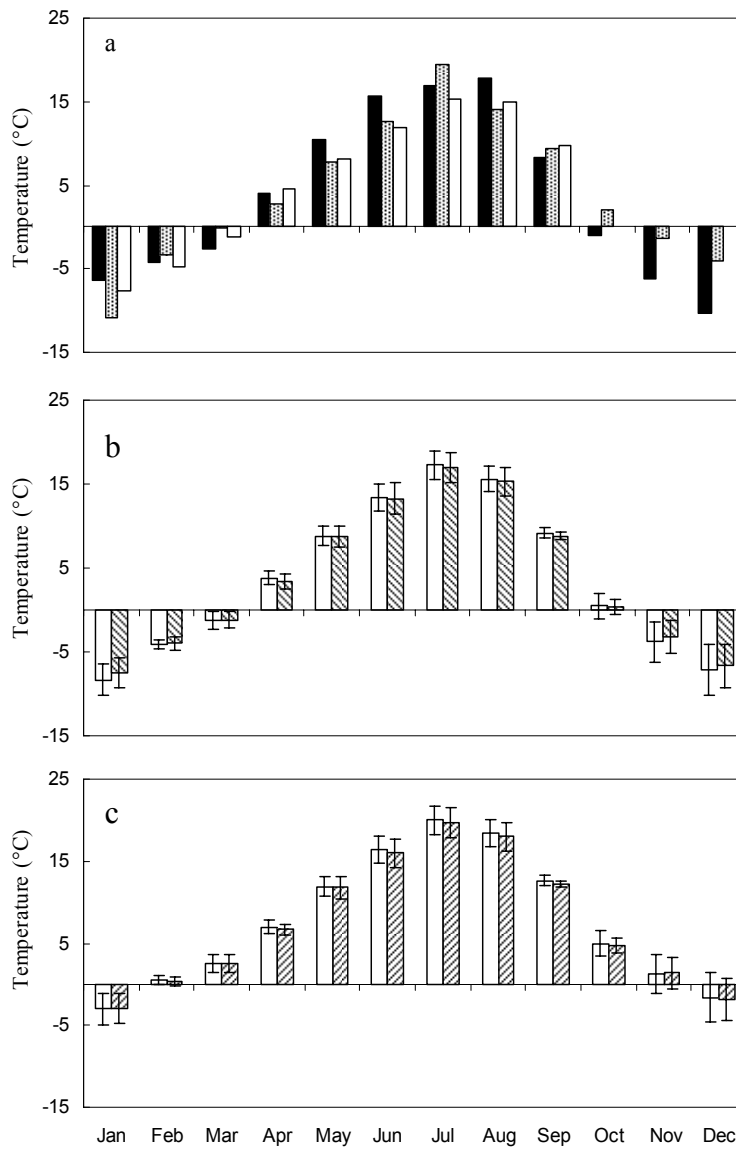
The annual mean temperature for the 15 year period 1990-2004 was 2.3 °C (Slaney 2006); this was exceeded in the warmest year of the experiment (2002) by 1.1 °C. The year 2002 had by far the warmest winter, spring and early summer of the three years, with a mean temperature for January–June of 2.9 °C, compared with 1.1 °C in 2003 and 0.9 °C in 2004 (Figure 3a). March differed from the pattern, with mean

temperatures of  $-2.7\text{ }^{\circ}\text{C}$ ,  $-0.2\text{ }^{\circ}\text{C}$  and  $-2.4\text{ }^{\circ}\text{C}$  in 2002, 2003 and 2004, respectively. When comparing the temperatures during the early growing season (April–June), 2003 and 2004 were close to the temperature mean for 1990–2004 ( $6.4\text{ }^{\circ}\text{C}$ ), but 2002 stands out as an extremely warm year ( $9.7^{\circ}\text{C}$ ). The difference of  $3.3\text{ }^{\circ}\text{C}$  is in the magnitude of the temperature elevation treatment, implying that during 2002 the  $T_E$  trees were exposed to almost a doubling of the intended temperature treatment, compared to the 15 year mean.

The temperature control in the chambers was effective over the experimental period (Figure 3b, c). During November–January, a reduction in cooling capacity resulted in an overheating by  $\sim 0.5\text{ }^{\circ}\text{C}$  in the  $T_A$ . The greatest overheating occurred in January 2003, when there was an increase in mean monthly temperature of  $1.44\text{ }^{\circ}\text{C}$  (data not shown). The temperature control of the  $T_E$  treatments performed better than the  $T_A$  control, with a slight overheating of the chambers in January–April and October–December ( $\ll 1\text{ }^{\circ}\text{C}$ ), but the target temperatures achieved in May–September.

The relative humidity of the air inside the WTCs was not regulated, leading to a higher VPD in the high temperature chambers compared to the outside air and the low temperature chambers (Medhurst et al. 2006). Medhurst et al. (2006) reported an increase in VPD of 0.19 and 0.30 kPa (SD = 0.06 and 0.08) for two 14 day measurement periods in February and May 2002, respectively. The maximum VPD of the outside air for these periods was 0.44 and 2.28 kPa, respectively. It is acknowledged that the greater VPD in the elevated temperature WTCs may have influenced the interactions between  $[\text{CO}_2]$  and temperature with respect to some physiological processes. However, Medhurst et al. (2006) point out that a study of the stable  $\delta^{13}\text{C}$  in the WTC trees at Flakaliden found no differences between  $T_A C_A$  and  $T_E C_A$  trees with respect to the  $\delta^{13}\text{C}$  of needle soluble sugars, starch and bulk material (Comstedt et al. 2006). This result suggests that the VPD disparity between  $T_A$  and  $T_E$  treatments had no major effect on stomatal behaviour. This is supported by the similar levels of  $\delta^{13}\text{C}$  in the  $T_A C_A$  and  $T_E C_A$  wood rings laid down during the course of the experiment (Medhurst et al. 2006 and references therein).

The temperature control of the shoot cuvettes preformed well under normal conditions (Wallin et al. 2001), however, individual cuvettes were occasionally subjected to overheating. When this occurred the measurements were terminated, the shoot was harvested and measurements restarted on a new shoot.



**Figure 3.** a) Monthly mean air temperature (°C) as measured in a climate mast nearby the chamber for 2002-2004. Black bars = 2002, grey bars = 2003, white bars = 2004. The performance of the chamber temperature treatments for b) ambient temperature and c) elevated temperature as predicted for the region, in the year 2100, by SWECLIM. The values are means for three years and six chambers in each temperature treatment. White bars = target temperature, hatched bars = chamber temperature. Error bars indicate standard deviation for the years ( $n = 3$ ).

## Modelling shoot level photosynthesis

Multiple environmental variables affect the rate of carbon assimilation at any given time. The most important variables in the boreal forest are the incoming photosynthetic photon flux density (PPFD), the air temperature ( $T$ ) and the vapour pressure deficit (VPD), together with the foliage nitrogen content. To understand how increasing  $[\text{CO}_2]$  and temperature will influence the flow of carbon into the plant–soil system, each of these variables needs to be examined alone and in combination with the others. This can be achieved by modelling, and a number of different shoot/leaf level photosynthesis models are available (Farquhar and von Caemmerer 1982, McMurtrie et al. 1990, Sands 1995b, Hari and Mäkelä 2003, Mäkelä et al. 2004, Mäkelä et al. 2006, Repo et al. 2006). However, most of these models rely on a large number of input parameters. To facilitate the estimation of carbon fluxes directly from readily available meteorological data, and to evaluate the photosynthetic response to these variables, the large available dataset collected during the experiment was used to fit response curves to the variables, generating a semi-mechanistic model. An Artificial Neural Network (ANN) was used to examine the relationship between gross photosynthesis and these variables and to determine the functional forms of the response curves (Paper III).

The semi-mechanistic model (ShootModel) comprises a set of equations that simulate shoot level net photosynthesis ( $A_{\text{NET}}$   $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) in boreal, evergreen coniferous forest species. The starting point for the development of the ShootModel was a simple model of PAR and  $T$  effects on foliage photosynthesis presented by Sands (1995b), combined with the springtime recovery model described by Pelkonen and Hari (1980) and Repo et al. (1990). Detecting model structural error is not straightforward (*cf.* Medlyn et al. 2005b), and therefore an Artificial Neural Network (ANN) model was used to identify where the simple model did not adequately capture the information content of the data and to correct the model structure. The data used to develop the model were measurements of the NAR of the C+1 shoots collected in 2002 from day 1 to day 151, to assess the spring recovery function, and for the whole of 2003 for the remaining variables, and to evaluate the model's performance. The development of the model is outlined in Paper III including: (i) a description of the ANN output; (ii) an explanation of the manner in which this was used to establish the model structure; (iii) a description of the resultant model, and (iv) an evaluation of the model performance. In this section, steps (i-iv) are described, along with a discussion of how well the chosen equations fitted the measured data and the ANN outputs.

In the ShootModel,  $A_{\text{NET}}$  is modelled as a function of the key variables identified above, i.e. foliage nitrogen content  $N_{\text{F}}$ , seasonality  $A(t)$ , photosynthetic photon flux density (PPFD), air temperature ( $T$ ), atmospheric vapour pressure deficit (VPD), and dark respiration ( $R_{\text{D}}$ ). Each of the equations used was parameterised using the gas exchange field measurements.



The functional forms of the PPFD, VPD and  $T$  responses were established directly from the field measurements of gas exchange obtained on days 152-275 in 2003; and an ANN was used to minimise noise in the data. The forms of the response curves obtained from the ANN simulations were then compared to response curves available in the literature. The literature response curves that corresponded to the results obtained from the ANN simulation were chosen for use in the ShootModel.

The maximum capacity for gross photosynthesis ( $A_{MAX}$ ) under non-limiting light and VPD conditions and optimal temperatures was calculated on the basis of a linear correlation with foliage N content (Reich et al. 1995, Roberntz and Stockfors 1998, Thornley 2002, Ellsworth et al. 2004).

The equations for the calculation of  $A(t)$  and  $R_D$  were derived from the literature. The seasonality function  $A(t)$  was driven by temperature in the form of an advanced temperature sum, and was multiplied (0-1, where 0 was full dormancy and 1 was complete recovery) to the gross photosynthetic rate ( $A_{GROSS} = A_{NET} + R_D$ ) as simulated from the functions above. The use of the  $A(t)$  function was as described for Scots pine, first by Pelkonen and Hari (1980) and Repo et al. (1990), and subsequently modified by Hänninen and Hari (2002).  $R_D$  was calculated on a mass basis from the  $Q_{10}$  values reported by Stockfors and Linder (1998ab), which were based on measurements made at Flakaliden 10 years before the present study. The values were multiplied by 0.6 to approximate the reduction of respiration rate in sunlight (PPFD >1  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) (Kirschbaum and Farquhar 1984).

### **Establishing the ShootModel response curves**

The ANN is an entirely statistical model; it determines a statistical relationship between the driving, independent variables and the dependent process under examination (i.e. VPD, air temperature and incoming radiation as driving input data and measured shoot level carbon fluxes as the dependent process that are of interest). The ANN in this project used only the systematic part of the training data with which it is provided to produce a simulation, so if only noise is fed into it, a zero simulation is produced (Abramowitz 2005). Therefore, the risk of finding a correlation “by chance”, which may be a problem in other statistical approaches to parameterization, is reduced. The ANN used was in the form of a self organizing feature map (SOFM; Kohonen 1989), which was run together with a self organizing map with linear output (SOLO; Hsu et al. 2002). The SOFM classifies the input data into nodes (groups), where each node represents a distinct region of the input space. The SOLO performs a linear regression between the grouped input variables and the corresponding target data at each node, resulting in a piecewise linear approximation of the training data (Abramowitz 2005). The SOFM-SOLO package (from here on referred to as simply SOLO) has been used previously for simulating of photosynthesis from meteorological data, as a tool for benchmarking the performance of mechanistic models, and for assessing model errors and uncertainties (Abramowitz 2005, Abramowitz et al. 2006).

As a first step towards establishing the functional forms of the ShootModel response curves, the relevance of the chosen variables was evaluated. The evaluation was based on the  $T_A C_A$  data, for which the individual measurements of the meteorological variables and the shoot gas exchange had been averaged over each day, to give more stability to the evaluation (Figure 4, Table 1). This was made both for the main growing season, DoY 152 – 273, and for the full year of 2003. First, the correlation between NAR and PPFD was established using SOLO. Then new SOLO simulations were run, with  $T$  and VPD added as driving variables, both separately and in combination (it makes no difference to the simulation the order in which the driving variables are added, each new SOLO run is independent of the previous one). The performance of each SOLO simulation was evaluated using three different measurements, namely the  $R^2$ , the root mean square error (RMSE, a measure of the mean deviation of the model predictions from the data; Medlyn et al. 2005b), and the model efficiency (ME). The ME estimates the proportion of variance of the data explained by the 1:1 relationship (Janssen and Heuberger 1995, Medlyn et al. 2005b) and was calculated as follows:

$$ME = 1 - \frac{\sum (y_i - \hat{y}_i)^2}{\sum (y_i - \bar{y})^2} \quad (1)$$

where  $y_i$  is the measured NAR,  $\hat{y}_i$  is the modelled  $A_{NET}$ , and  $\bar{y}$  is the mean measured NAR.

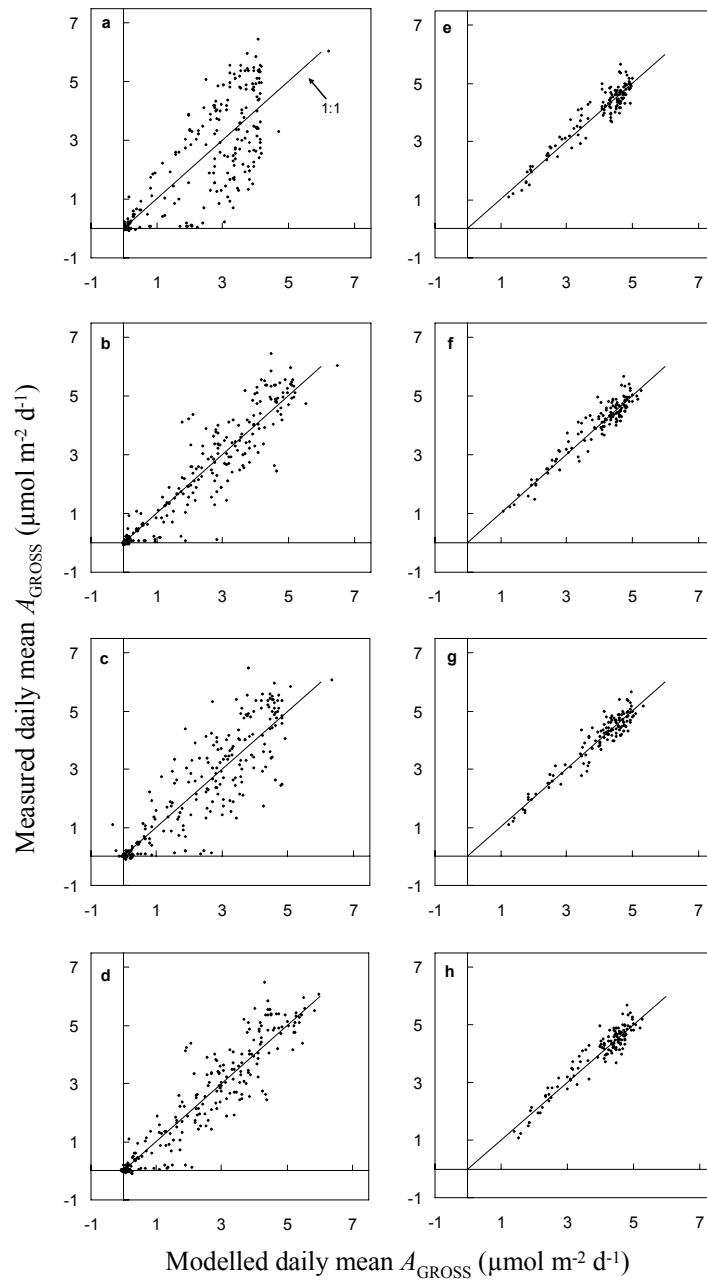
When the NAR was correlated to light alone for the full year of 2003, there was an underestimation of  $A_{NET}$  in the SOLO runs at high light intensities (Table 1, Figure 4). This can be explained by the lack of information in the data set describing the differences between high light intensities during winter, at low  $T$ s, and high light intensities during summer, resulting in a high rate of carbon uptake. When  $T$  was added as a driving variable, the SOLO performance improved (ME increased from 0.69 to 0.89, and the RMSE decreased from 1.08 to 0.63). Adding VPD alone to PPFD as a driving variable also improved the performance, but to a lesser extent (ME = 0.82 and RMSE = 0.83). No difference in the performance of the SOLO could be established between correlating NAR to the combination PPFD and  $T$  as input variables, or correlating NAR to the combination PPFD,  $T$  and VPD, when SOLO was run for the full year. This can be explained by the high correlation between VPD and  $T$ , and the lack of high VPDs during winter. For the summer period however, the ME was higher for the full combination of input variables (ME = 0.91, RMSE = 0.31), than when SOLO was run with only PPFD and  $T$  as input variables (ME = 0.90, RMSE = 0.33). Therefore, the full set of input variables were included in the next step of the parameterisation of the ShootModel.

As a second step, the functional forms of the meteorological variables were determined using separate SOLO runs for each variable. This was achieved using instantaneous measurements of VPD,  $T$ , PPFD and shoot gas exchange, instead of

daily means; in addition, the NAR was converted to  $A_{\text{GROSS}}$  by adding  $R_{\text{D}}$  to the measured value. To minimise the co-variance between the meteorological variables, SOLO was run for each variable separately using subsets of data in which only the relevant variable had an affect on  $A_{\text{GROSS}}$ . The steps to establish the correct interval for the optima and limitation to photosynthesis by the variables had to be repeated several times. First, preliminary intervals were determined by plotting the  $A_{\text{GROSS}}$  against the corresponding measurements of PPFD, VPD and  $T$ , then preliminary response curves were produced for each variable. These preliminary response curves were then used to determine new, more precise, intervals for the variables. The final filters for extracting data in which only one variable limited the  $A_{\text{GROSS}}$  were:  $\text{PPFD} > 500 \mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $T > 20 \text{ }^\circ\text{C}$  (for  $T_{\text{A}}C_{\text{A}}$   $T > 15 \text{ }^\circ\text{C}$ ) and  $\text{VPD} < 2000 \text{ Pa}$ .

**Table 1.** The relevance of the input variables PPFD,  $T$  and VPD for modelling gross photosynthetic rate,  $A_{\text{GROSS}}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). The artificial neural network (ANN) was trained on measured meteorological data and calculated  $A_{\text{GROSS}}$  data (daily means) obtained in the  $T_{\text{A}}C_{\text{A}}$  chambers during the main growing period day of year (DoY) 152-273, and for the full year of 2003. The ANN was run with combination of input variables as shown below. The model performance was evaluated using  $R^2$ , root mean square error (RMSE), and model efficiency (ME, estimates the proportion of data described by a 1:1 line in Figure 4). PPFD = photosynthetic photon flux density ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $T$  = air temperature ( $^\circ\text{C}$ ), VPD = vapour pressure deficit (Pa).

DoY	Input variables	$R^2$	RMSE	ME
1-365	PPFD	0.69	1.08	0.69
	PPFD, $T$	0.89	0.63	0.89
	PPFD, VPD	0.82	0.83	0.82
	PPFD, $T$ , VPD	0.89	0.63	0.89
152-273	PPFD	0.89	0.34	0.89
	PPFD, $T$	0.89	0.33	0.90
	PPFD, VPD	0.91	0.31	0.90
	PPFD, $T$ , VPD	0.90	0.31	0.91

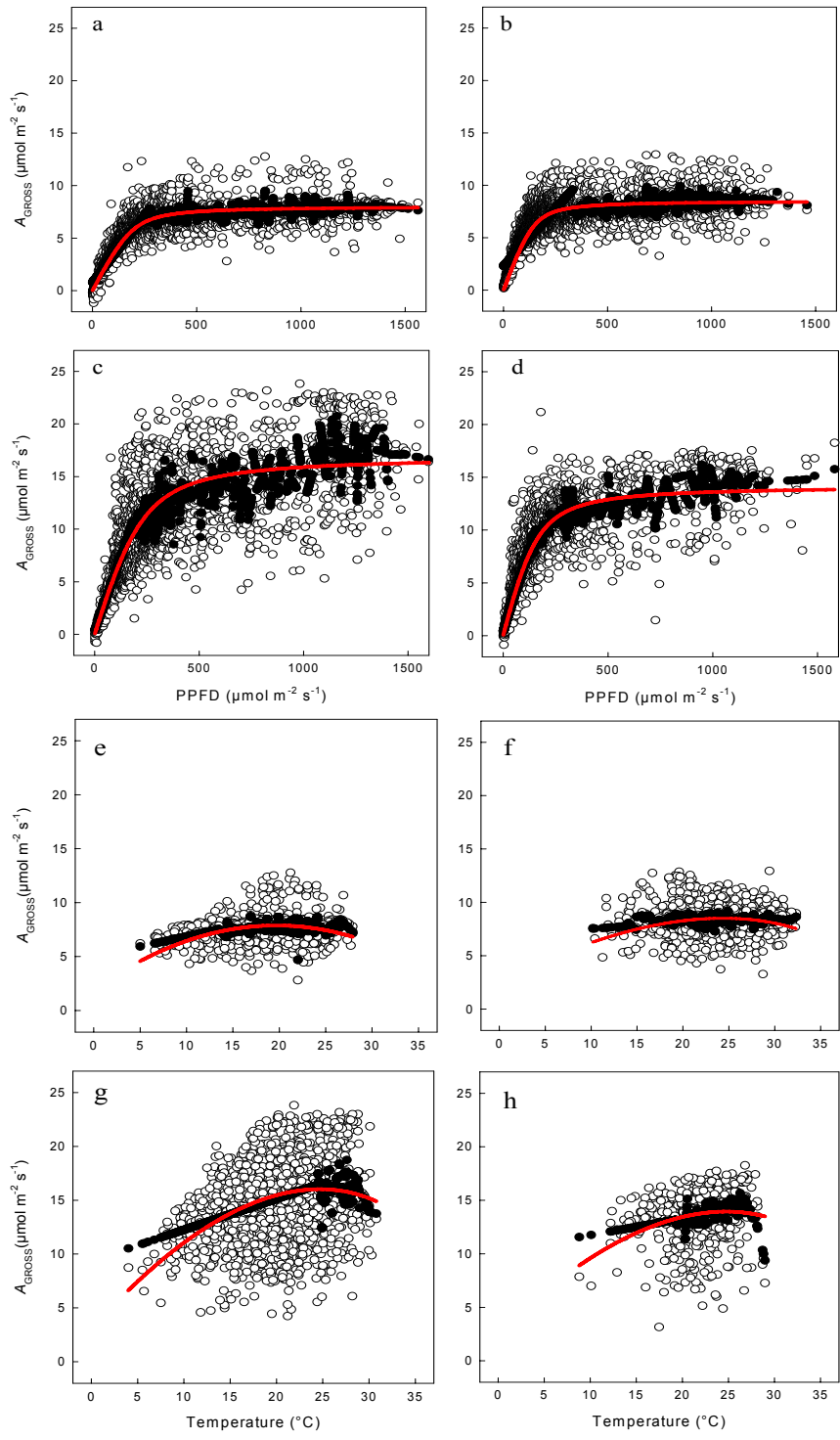


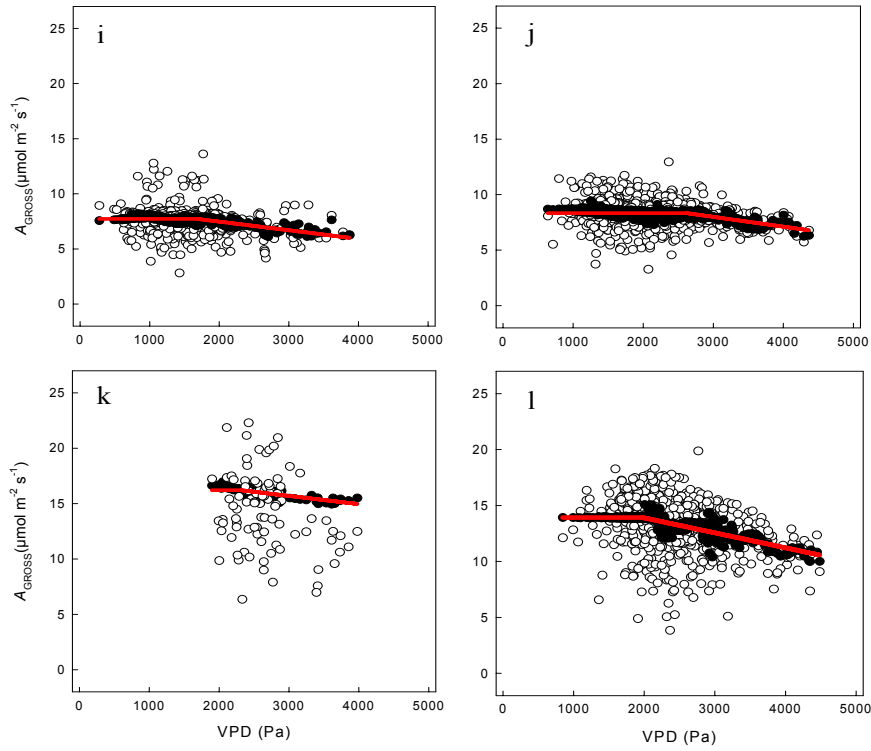
**Figure 4.** The relation between measured and modelled daily mean  $A_{\text{GROSS}}$  from simulations made by the ANN. **a-d)** daily means from the full year of 2003, **e-h)** daily mean from measurements performed day of year 152-273. Input variables used for simulation of  $A_{\text{GROSS}}$ : **a, e)** PPF; **b, f)** PPF,  $T$ ; **c, g)** PPF, VPD; **d, h)** PPF,  $T$ , VPD. For details of the data, and  $R^2$ , model efficiency and root mean square error, see Table 1

Because of the high correlation between VPD and  $T$ , distinguishing between these two parameters required several steps, as follows. A subset of data with PPFD >  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$  was extracted, and SOLO was run with both  $T$  and VPD as input variables. The SOLO  $A_{\text{GROSS}}$  output was plotted against  $T$ , a parabola was fitted to the data, and the optimum temperature point ( $T_{\text{VPD}}$ ) was determined for each treatment individually. Based on the findings of Fredeen and Sage (1999), it was assumed that in the temperature range 10–30 °C, temperature limited  $A_{\text{GROSS}}$  when  $T < T_{\text{VPD}}$ , while VPD limited  $A_{\text{GROSS}}$  when  $T > T_{\text{VPD}}$  via its effect on stomatal conductance.

In the final step, equations from the literature were parameterised against the SOLO output (Figure 5 a-l). The equations chosen were as follows. The light response function used was the common light response curve (*e.g.* Thornley 1990), i.e. a non-rectangular hyperbola similar to the one used by Sands (1995b). The temperature response curve used was an asymmetrical optimum curve, described in McMurtrie et al. (1990), instead of the symmetrical one as used by Sands (1995b). The VPD response applied was the regression established by SOLO: a linear decrease above a threshold value. The shape of the latter was similar to the VPD response reported by Fredeen and Sage (1999). Since VPD limitation mainly operates by reducing stomatal conductance, and not directly on the photosynthesis, it was included in the model as a multiplier (0-1).

The fitting of the VPD and the PPFD responses worked well, with the exception of the VPD response for the  $T_{\text{A}}C_{\text{E}}$  treatment. The  $T$ -response was, however, less clear-cut (Figure 5e-h). The VPD response in the  $T_{\text{A}}C_{\text{E}}$  treatment was weak (Figure 5k), and the amount of field data available for parameterisation was restricted, since the temperature optimum was unusually high for a tree exposed to the ambient temperature, 24.7 °C compared to 19.7 °C for the  $T_{\text{A}}C_{\text{A}}$  treatment. The chosen  $A_{\text{T}}$  parameter simulated the flat part of the temperature response well, but overestimated the decrease in photosynthetic activity at temperatures around 10 °C in the  $T_{\text{A}}$  treatments and 14 °C in the  $T_{\text{E}}$  treatments. Therefore, the bias introduced by the functional form of the  $A_{\text{T}}$  parameter underestimated  $A_{\text{GROSS}}$  at these temperatures by 3% and 8% in the  $T_{\text{A}}C_{\text{A}}$  and  $T_{\text{A}}C_{\text{E}}$  treatments, and 8% and 6% in the  $T_{\text{E}}C_{\text{A}}$  and  $T_{\text{E}}C_{\text{E}}$  treatments, respectively (Figure 5e-h).





**Figure 5.** The functional forms for the light (a-d), temperature (e-h) and VPD (i-l) response curves for  $A_{\text{GROSS}}$ . ( $\circ$ ) = measured data, ( $\bullet$ ) = simulation of  $A_{\text{GROSS}}$  by use of the artificial neural network (ANN) with light, temperature or VPD as driving variables, for a-d, e-h and i-l, respectively. (—) = the equation for each variable fitted to the ANN simulations. The temperature response curve overestimated the decrease of photosynthetic activity at temperatures around 10 °C in the  $T_A$  and 14 °C in the  $T_E$  treatments. This resulted in an underestimation of  $A_{\text{GROSS}}$  at these temperatures by 3% and 8% in  $T_A C_A$  and  $T_A C_E$ , and 8% and 6% in the  $T_E C_A$  and  $T_E C_E$  treatments, respectively, because of the bias introduced by the functional form of the temperature dependence. No seasonal adjustment of temperature optimum has been made, a simplification that may have introduced a minor error.

### The ShootModel

The final product of the process described above was the ShootModel, in which the net carbon assimilation rate  $A_{\text{NET}}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) is given by:

$$A_{\text{NET}} = \frac{(\alpha I + A_T) - \sqrt{(\alpha I + A_T)^2 - 4\theta\alpha I A_T}}{2\theta} * A_{\text{VPD}} * A(t) - R_D \quad (2)$$

where  $\alpha$  is the apparent quantum yield ( $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ photons}$ ),  $I$  is the irradiance (PPFD,  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ), and  $\theta$  is the curvature of the light response curve,  $A_T$ ,  $A_{\text{VPD}}$ ,  $A(t)$  and  $R_D$  are derived from the equations below.

( $A_T$ ) was taken from McMurtrie et al. (1990) (corrected for a misprint):

$$A_T = A_{\text{MAX}} * \chi * \frac{(T - T_L)(T_U - T)^{\chi}}{(T_U - T_O)^{1+\chi}} \quad (3)$$

$$\chi = \frac{T_U - T_O}{T_O - T_L} \quad (4)$$

where  $T$  is the air temperature ( $^{\circ}\text{C}$ ),  $T_L$  and  $T_U$  are, respectively, the minimum (Lower) and maximum (Upper) values of  $T$  for positive  $A_{\text{GROSS}}$  and  $T_O$  is the optimum air temperature for photosynthesis.  $A_{\text{MAX}}$  was calculated from the foliage nitrogen concentration:

$$A_{\text{MAX}} = N_S * N_F + N_I \quad (5)$$

where  $N_S$  is the slope of the linear relationship (determined by linear regression),  $N_F$  is the foliage nitrogen concentration ( $\text{g m}^{-2}$ ), and  $N_I$  is the intercept.

$A_{\text{VPD}}$  is the effect of VPD on  $A_{\text{GROSS}}$  applied as a multiplier (0-1):

$$A_{\text{VPD}} = \begin{cases} 1 & \text{for } \text{VPD} \leq \text{VPD}_T \\ \text{VPD}_S * \text{VPD} - \text{VPD}_I & \text{for } \text{VPD} > \text{VPD}_T \end{cases} \quad (6)$$

where  $\text{VPD}_T$  is the threshold value,  $\text{VPD}_S$  is the slope,  $\text{VPD}$  is the vapour pressure deficit in the air (Pa), and  $\text{VPD}_I$  is the intercept of the line describing the relationship between  $\text{VPD}$  and  $A_{\text{GROSS}}$ .



The seasonality function  $A(t)$  was driven by temperature in the form of an advanced temperature sum, and was multiplied (0-1, where 0 was full dormancy and 1 was complete recovery) to  $A_{\text{GROSS}}$  as simulated from the functions above. Thus,

$$A(t) = \min \left[ 1, \left( \frac{S(t)}{S_{\text{CRIT}}} \right) \right] \quad (7)$$

where  $S_{\text{CRIT}}$  is the critical state of development, indicating attainment of maximum photosynthetic capacity and  $S(t)$  is the state of recovery at time  $t$ .  $S(t)$  is calculated as the time integral of its time derivative,  $R(t)$ :

$$S(t) = \int_{t_0}^t R(t) dt \quad (8)$$

where  $R(t)$  is the rate of development calculated as a function of temperature:

$$R(t) = \left[ \frac{100}{1 + 100a^{-(T(t)-(S(t)/c)}} \right] - \left[ \frac{100}{1 + 100a^{(T(t)-(S(t)/c)}} \right] \quad (9)$$

where  $T(t)$  is the prevailing temperature and  $a$  and  $c$  are parameters determined statistically.

The dark respiration was calculated by:

$$R_D = R_0 * e^{kT} \quad (10)$$

where  $R_D$  is dark respiration (growth + maintenance,  $\mu\text{mol C m}^{-2} \text{ s}^{-1}$ ),  $k = (\ln Q_{10})/10$ ,  $T$  is the actual temperature and  $R_0$  is the respiration at 0 °C (Stockfors 1997).

The parameter values produced as a result of parameterisation against the gas exchange measurements are presented in Table 1 in Paper III; and the functional forms of the response curves are illustrated in Figure 1 in Paper III.

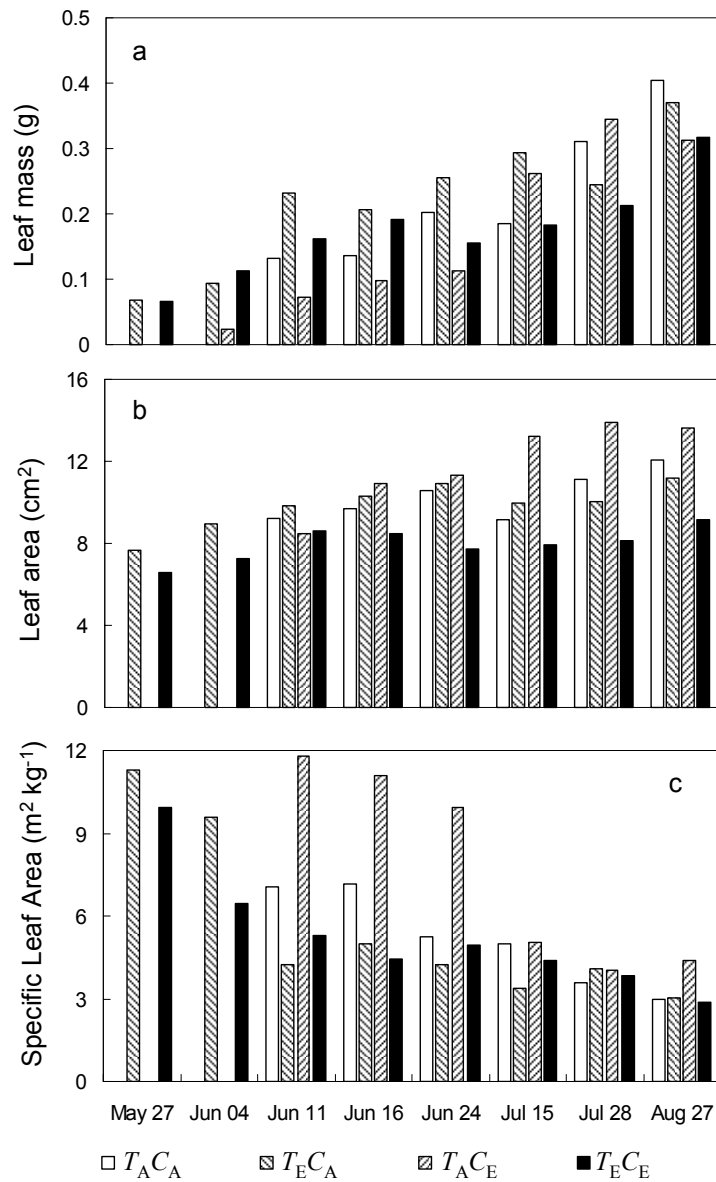
The evaluation of the performance of the ShootModel is described in detail in Paper III. The statistics  $R^2$ , RMSE, and ME were used to quantify the errors in the estimates produced using ShootModel and to make comparisons with the measured values used for parameterisation (Figures 3-4 and Table 4 in Paper III). For the 2003 data, the ShootModel explained 94% ( $T_A C_A$ ), 91% ( $T_E C_A$ ), 95% ( $T_A C_E$ ), and

87% ( $T_E C_E$ ) of the variation in the measured NAR. The modelled output was close to the 1:1 relationship for all treatments (Figure 3i-1 in Paper *III*). The performance of the ShootModel was also compared to the performance of SOLO runs using the entire dataset, and it was found that the ShootModel performed equally well or better than SOLO for all treatments for the 2003 data (Figure 3 and Table 4, in Paper *III*).

## Outcomes from the experiment

First, two methodological differences between the papers (*I-III*) need to be addressed. The photosynthetic rates and performances reported for the C-shoots must be considered in a slightly different way from the photosynthetic rates and performances for the C+1 shoots. For all shoots, photosynthesis was expressed in relation to projected needle area measured after harvest. The C-shoots were harvested in late August, while the C+1 shoots subjected to the gas exchange measurements were changed (followed by an immediate harvest), on average, twice a year on each tree – once in spring and once in autumn. While the changes in the needle area of the C+1 shoots are minor over the year, significant structural changes occur in the C-shoots throughout the growing season (Figure 6). The greatest changes occurred during spring and early summer, in the form of shoot elongation and an increase in the shoot area, which is completed in mid-July (Figure 6). The accumulation of mass, with a thereto connected growth respiration, was completed in late August (Figure 6; and Paper *I*). This means that it is impossible to determine whether the increase in NAR over the season in the C-shoots was an effect of increased photosynthetic capacity, reduced respiration, or increases in projected needle area. Therefore, the absolute rates of photosynthesis measured for the C-shoots cannot be compared directly with the absolute rates of photosynthesis in the C+1 shoots. The relative differences between the treatments for the C-shoots can, however, be compared with the relative differences between the treatments in the C+1 shoots.

The methods used to calculate the maximum rates of photosynthesis differed between the descriptive papers (*I* and *II*) and the modelling paper (*III*). In Papers *I* and *II*, the maximum photosynthetic rates were presented in the form of  $A_{SAT}$ .  $A_{SAT}$  was calculated as the net carbon assimilation rates under growth conditions when light was not limiting photosynthesis ( $PPFD > 400 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). The  $A_{SAT}$  should be regarded as apparent as the PPFD threshold is based on the light intensities at the light sensor and not at the shoot. In the modelling paper (Paper *III*), the impacts of environmental variables and nitrogen on gross photosynthesis were addressed specifically. Therefore, the maximum photosynthetic rate during high season was presented in the form  $A_{MAX}$ ; the maximum gross photosynthetic rate at the optimum temperature, with light and VPD not limiting, and related to the foliage N content  $N_F$ .



**Figure 6.** Shoot properties of developing shoots sampled at eight occasions during the summer 2004. **a)** Leaf mass (g), **b)** Leaf area (cm<sup>2</sup>), **c)** specific leaf area, SLA (m<sup>2</sup> kg<sup>-1</sup>). Statistical analysis was performed for June 16 and onwards by use of repeated measures ANOVA. No statistically significant interaction with time was found for leaf mass or leaf area. A significant CO<sub>2</sub> effect ( $p = 0.040$ ) for the period was obtained for the leaf area. A significant interaction between the CO<sub>2</sub> treatment and time was found for SLA ( $p=0.048$ ). A one-way ANOVA was thus performed, which gave a significant result for June 16 ( $p = 0.034$ ) and June 24 (0.039).

Statistical tests of the treatment effects were conducted using a two-way analysis of variance (ANOVA), and the changes in performance and shoot structure over time (Papers *I-III*) were tested using repeated measures ANOVA. In Papers *I* and *II*, all results from 2002-2004 (Paper *II*) and 2004 (Paper *I*) were statistically tested for chamber effects by comparing results from the  $T_A C_A$  chambers with the *R*-trees, using a one-way ANOVA. All statistical tests were performed using the SPSS software, version 14.0 (SPSS Inc, Chicago, IL, U.S.A.). No significant chamber effects were found with respect to either the net carbon assimilation rates or the bud development and shoot properties measured after harvest (Table 2; Tables 1-3 and 5 in Paper *I*; Table 2 in Paper *II*).

### **Effects of the temperature treatment**

The main effect of the elevated temperature treatment was a lengthening of the growing season and subsequently of the period with photosynthetic activity in both C and C+1 shoots (Paper *I-III*). The largest effect was due to earlier initiation of C shoot development and earlier photosynthetic spring recovery in C+1 shoots.

For the C-shoots in the elevated  $T_E$  chambers, budburst commenced two to three weeks earlier (Slaney et al. 2007) and these shoots reached 90% of the final shoot length two weeks earlier than in the  $T_A$  chambers, both in 2003 and 2004 (Table 2 in Paper *I*). The net carbon compensation point (NACP), i.e. the day when the NAR shifted from being negative to being positive (Figure 2 in Paper *I*), occurred 5–20 days earlier for the C-shoots in the  $T_E$  compared to  $T_A$  treatments (Figures 3, 5a,c and Table 2 in Paper *I*). No significant effect of temperature on the NAR during summer was found for the C shoots. Furthermore, no temperature effect was found with respect to the shoot properties measured after harvest in August (needle area, needle dry mass, axis dry mass, axis length, needle C content and specific needle area), except for needle N content on an area basis in 2004, which was reduced by 18% in the  $T_E$  treatment ( $p = 0.015$ ) (Table 1 in Paper *I*).

With respect to the C+1 shoots, elevated temperatures had a positive effect on spring recovery (Papers *II, III*) and altered the photosynthetic parameters in the summer (Paper *III*). The spring recovery of photosynthesis commenced ~ 10 days earlier in the  $T_E$  treatments than the  $T_A$  treatments (Figure 3 in Paper *II* and Table 1 and Figure 1e in Paper *III*), due to the higher air temperature. This was expressed in the form of a significantly higher photosynthetic capacity (AQY and  $A_{SAT}$ ) in  $T_E$  treatments compared to the  $T_A$  treatments during early spring (March to April) in all three years, except for  $A_{SAT}$  in April and AQY in March 2003 (Figure 4 and Table 3 in Paper *II*). Full recovery of photosynthetic capacity was achieved three to four weeks earlier in the  $T_E$  treatments than in the  $T_A$  treatments in 2002 to 2004 (Figure 3 in Paper *II* and Figure 1 and Table 2 in Paper *III*). Although, the average air temperature seems to be important for the recovery rate, the number and duration of severe frost events seems to have a larger influence on the date when

full and sustainable recovery was achieved (Paper II). Soil thawing may also be important, since a full and sustainable recovery did not occur until the soil temperature exceeded 0°C (Paper II-III). Thus, a warmer climate and an earlier and enhanced rate of photosynthetic efficiency can extend the period during which CO<sub>2</sub> uptake can take place.

Between June to August, elevated temperatures had no effect on the  $A_{MAX}$  (Figure 1a and Table 1 in Paper III), and no effect on the measured maximum rates of net carbon assimilation ( $NAR_{MAX}$ ) by the C-shoots (Table 2 in Paper I). The temperature optimum ( $T_O$ ) for photosynthesis in the C+1 shoots during high season increased from 19.7 in the  $T_A C_A$  treatment to 24.7 in the  $T_E C_A$  treatment (Figure 1 and Table 1 in Paper III). The flat nature of the temperature response curve for  $C_A$  (established by SOLO) suggests that the simulated  $T_O$  value in the present study should be considered the centre point of a temperature plateau rather than a real extreme. The low  $R^2$  values for fitting  $A_T$  in the  $T_A$  treatments (Table 1 in Paper III) are also explained by the flat response curve. A small response to temperature by gross photosynthesis has previously been reported for Norway spruce (*cf.* Bergh, 1997). This result contrasts with reports of  $A_{NET}$  responses to temperature, which have suggested that increased foliage respiration caused by higher temperatures causes a pronounced peak in the temperature response curve (*e.g.* Larcher 1995).

In Paper II, no significant temperature effect was recorded for AQY for June 2002 and 2003, but an average increase of 13 % in  $T_E$  compared to  $T_A$  was recorded in June 2004 ( $p = 0.034$ ). For the period June-August, the modelling results gave higher parameter values for AQY in the  $T_E$  treatments than the  $T_A$  treatments,  $\alpha = 0.042 \text{ mol mol}^{-1}$  in  $T_A C_A$  and  $0.061 \text{ mol mol}^{-1}$  in  $T_E C_A$  (Table 1 in Paper III). The response of AQY to both temperature and CO<sub>2</sub> is discussed in a separate section below.

The reduction in photosynthesis caused by both winter dormancy and frost damages to the photosynthetic apparatus during spring was much smaller in the present study (9-12 % for the ambient temperature and 4% for the elevated temperature, Table 3 in Paper III), than what has previously been reported for Norway spruce at the Flakaliden site (Bergh 1997, Bergh et al. 1998, Bergh et al. 2003). Using the boreal version of the BIOMASS model (Bergh, 1997, Bergh et al., 1998) a reduction of 21-28% of yearly GPP was estimated for ambient conditions as a result of the reduction in spring photosynthesis alone, and a reduction of 35-44% was predicted when frost damage to the photosynthetic apparatus in the autumn was included.

The differences were suggested to mainly be caused by meteorological differences between the years of the studies (Paper III). Especially air temperature, but also soil temperature has a large impact on the rate of recovery, leading to large differences between years in the timing of the completion of recovery (Linder and Flower-Ellis 1992). However, the intensity of incident light should also be

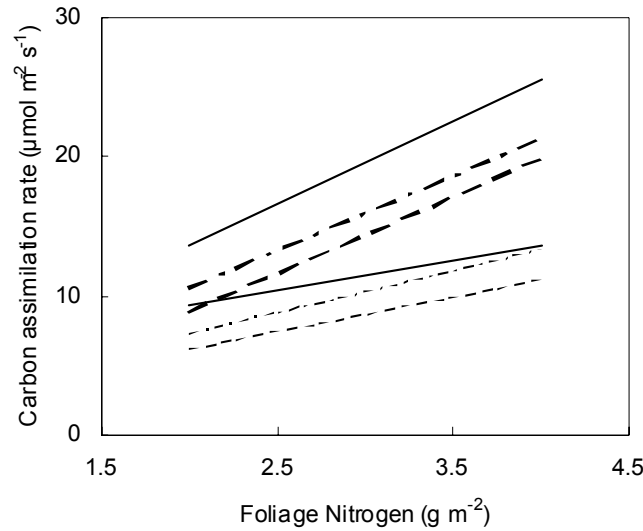
considered as low light intensities during periods with reduced photosynthesis will reduce the difference between actual and potential photosynthesis. Furthermore, it has been shown previously that the rate of photosynthetic recovery simulated by the equations used in the ShootModel is faster than the rate simulated by the seasonality parameter used in the boreal BIOMASS model, when the same conditions are used in both (Hänninen and Hari, 2002).

### Effects of the CO<sub>2</sub> treatment

The main effects of the elevated CO<sub>2</sub> treatment were an increase in the maximum rate of photosynthesis, seen in both the C and C+1 shoots (Papers *I- III*). The C<sub>E</sub> treatment resulted in a 51% rise in  $A_{SAT}$  in the C shoots in both years (Paper *I*), this increase was of the same magnitude as found for C+1 shoots described in Paper *II*, where the elevated CO<sub>2</sub> enhanced the light saturated CO<sub>2</sub> assimilation by 49% on average, a level that was sustained throughout the recovery period. This is consistent with the findings of Roberntz and Stockfors (1998) and two studies involving meta-analyses of experiments involving the effect of elevated [CO<sub>2</sub>] on European forest trees (Curtis and Wang 1998, Medlyn et al. 1999). The increase in the simulated maximum gross photosynthesis,  $A_{MAX}$ , was larger. For  $N_F = 3.0 \text{ g m}^{-2}$  the increase was 64% (Paper *III*), but this was still of the same magnitude as has been recorded previously for maximum net photosynthesis (Curtis and Wang 1998, Medlyn et al. 1999).

In both Papers *I* and *III* a greater response to CO<sub>2</sub> was recorded when there was higher foliage N content (Figure 7; Figure 7 in Paper *I*; Figure 1 in Paper *III*). This is consistent with previous findings for the site (Roberntz and Stockfors 1998), and findings from other sites, indicating that the photosynthetic response of Norway spruces exposed to elevated [CO<sub>2</sub>] depends to a large extent on the mineral nutrition status and duration of the CO<sub>2</sub> enrichment (Urban and Marek 1999, Urban 2003, Urban et al. 2003). In 2003, the mean  $N_F$  in the C<sub>E</sub> treatment was 10% lower than the mean  $N_F$  in the C<sub>A</sub> treatment ( $p < 0.001$ ) (Paper *III*). Similar differences were noted in Paper *II*, where the CO<sub>2</sub> stimulation in the treatment with a combination of elevated temperature and CO<sub>2</sub> was decreased 2004 compared to the previous years, which was also connected to a decrease in nitrogen content. The reason that the effect was observed in the combined treatment but not in the other treatments (Paper *II*) might be that both a longer growing season and an enhanced photosynthetic rate due to CO<sub>2</sub> stimulation may have resulted in higher growth, resulting in a dilution of nitrogen in the needles. A reduction in leaf nitrogen concentration of about 10% is regularly observed at elevated [CO<sub>2</sub>], even in short-term experiments (*cf.* Medlyn et al. 1999, meta-analysis by Ainsworth and Long 2005, Ainsworth and Rogers 2007). This feedback between increasing photosynthesis and nitrogen content has been found on a time-scale of months to years. The feedback results in a slight down-regulation of photosynthetic rate (10-20%), however elevated [CO<sub>2</sub>] still commonly results in photosynthesis being stimulated by approximately 50% (Medlyn et al. 1999, Ainsworth and Long 2005,

Medlyn et al. 2005a, Ainsworth and Rogers 2007). The limited biomass sampling that was performed during this project did not demonstrate any significant increase in biomass at the shoot level.



**Figure 7.** Illustration of the relationships between foliage nitrogen content ( $N_F$ ,  $\text{g m}^{-2}$ ) and  $A_{\text{SAT}}$  for the C-shoots (—);  $A_{\text{MAX}}$  for C+1 shoots (---); and  $A_{\text{SAT}}$  measured at Flakaliden by Roberntz and Stockfors (1998) (-.-). Thick lines are for elevated  $[\text{CO}_2]$ , and the thin lines are for ambient  $[\text{CO}_2]$ . *N.b.*, the slopes of the relationship between  $N_F$  and maximum photosynthetic rate can be compared between the C-shoots and the C+1 shoots, but the absolute numbers of maximum photosynthetic rate between the C-shoots and the C+1 shoots should not be compared, as the C-shoots are in a state of structural development, *cf.* Figure 6.

As has been observed previously, elevated  $[\text{CO}_2]$  affected neither the timing of bud burst nor the rate of shoot development in Norway spruce (Roberntz 1999, Slaney et al. 2007, Paper I). At the end of the season, the specific needle area ( $\text{SNA m}^{-2} \text{kg}^{-1}$ ) of the C-shoots was significantly lower ( $\sim 15\%$ ) in the  $C_E$  treatments than in the  $C_A$  treatments, both in 2003 and 2004 (Table 1 in Paper I). The N concentration in the needles ( $\text{mg g}^{-1}$  D.M.) was lower, although not significantly so, in the  $C_E$  compared to the  $C_A$  treatments (15% in 2003 and 10% in 2004). The result was that the N concentration on the basis of projected needle area was independent of the  $[\text{CO}_2]$  treatments. The  $T_E$  compared to the  $T_A$  treatments, however, produced a significantly lower N content per needle area (18%) during 2004, but not 2003.

Elevated CO<sub>2</sub> had no significant effect on the apparent quantum yield during spring (Figure 3, Table 2 in Paper II). During high season the AQY was higher in the C<sub>E</sub> treatment than in the C<sub>A</sub> treatment: the value of  $\alpha$  increased from 0.042 mol mol<sup>-1</sup> (T<sub>A</sub>C<sub>A</sub>) to 0.064 mol mol<sup>-1</sup> (T<sub>A</sub>C<sub>E</sub>) (Table 1 in Paper III), as will be discussed in the next section.

The optimum temperature for A<sub>GROSS</sub> during high season was influenced by the C<sub>E</sub> treatment; it increased by 5 °C in both T<sub>A</sub>C<sub>E</sub> and T<sub>E</sub>C<sub>E</sub>, compared to the T<sub>A</sub>C<sub>A</sub> treatment (Table 1 in Paper III). This is consistent with theoretical predictions, which suggest that the light saturated rate of gross photosynthesis has a more pronounced peak in the temperature response curve, and a higher optimum temperature in C<sub>E</sub> treatments than in ambient [CO<sub>2</sub>] (Farquhar et al. 1980, Farquhar and von Caemmerer 1982, McMurtrie and Wang 1993). At low temperatures the capacity for RuBP regeneration determines the A<sub>SAT</sub>. The transition to limitation caused by Rubisco-activity occurs at higher temperatures in higher [CO<sub>2</sub>], and therefore RuBP-limitation of gross photosynthesis is more important in high than in low [CO<sub>2</sub>] (McMurtrie and Wang 1993). However, the shift from a temperature optimum at 19.7 °C to 24.7 °C is lower than the 10 °C increase associated with doubling the amount of CO<sub>2</sub> that was suggested by McMurtrie and Wang (1993).

### **Treatment effects on Apparent Quantum Yield**

For the period June-August 2003, the model produced an AQY response where  $\alpha$  was lower in T<sub>A</sub>C<sub>A</sub> than in all the other treatments (Figure 1 and Table 1 in Paper III). The modelled values of  $\alpha$  for each treatment were: 0.042 mol mol<sup>-1</sup> (T<sub>A</sub>C<sub>A</sub>), 0.061 mol mol<sup>-1</sup> (T<sub>E</sub>C<sub>A</sub>), 0.064 mol mol<sup>-1</sup> (T<sub>A</sub>C<sub>E</sub>) and 0.072 mol mol<sup>-1</sup> (T<sub>E</sub>C<sub>E</sub>). There is little information available in the literature pertaining to field measurements of the impacts of CO<sub>2</sub> enrichment on the quantum yield of the light response curve. In theory, the foliage of C3 plants responds to elevated CO<sub>2</sub> because CO<sub>2</sub> and O<sub>2</sub> compete for ribulose biphosphate (RuBP), the primary acceptor molecule of C3 photosynthesis. It is the balance between the intercellular concentration of CO<sub>2</sub> and O<sub>2</sub> that determines the relative rates of carboxylation, which leads to photosynthesis and oxygenation followed by photorespiration (Farquhar et al. 1980, Farquhar and von Caemmerer 1982, McMurtrie and Wang 1993). Since oxygenation is favoured over carboxylation at high temperatures, the CO<sub>2</sub> response is, in turn, temperature-dependent, and the apparent quantum yield is expected to decrease linearly with increased temperature (Farquhar et al. 1980, McMurtrie and Wang 1993). This is the opposite response to that derived from the model described in Paper III and the measured results for June described in Paper II.

The electron transport chain responds to temperature: a temperature optimum for the quantum yield ranging between 25 and 40 °C has been reported in a study of tobacco (Bernacchi et al. 2003). This is similar to the behaviour of the modelled light response curve in the present study, and the findings for AQY in June



reported in Paper *II*. However, since the relationship between the quantum yield of electron transport and the quantum yield of photosynthesis is non-linear and highly temperature-dependent (McMurtrie and Wang 1993), the temperature response reported by Bernacchi et al. (2003) cannot directly explain the findings of the present study.

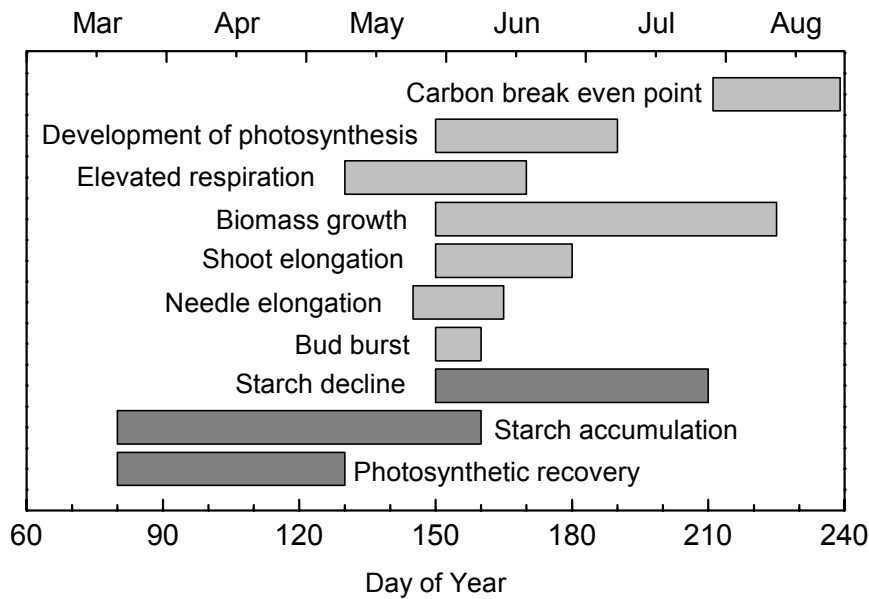
### **Combined effects of the treatments on carbon uptake**

The combined effect of the treatments was examined by measuring the accumulated assimilated C at the end of the experimental period (Paper *I, III*). For the C-shoots, the combined effects of the treatments were assessed on the basis of the carbon break even point (CBEP), i.e. the day the developing shoots had assimilated their own mass in carbon, and thus became net producers of carbohydrates instead of net consumers (Table 4 in Paper *I*). The CBEP was reached 20 and 32 days earlier in the  $T_E C_E$  treatment than in the  $T_A C_A$  treatment in 2003 and 2004 respectively. The  $T_A C_E$  and  $T_E C_A$  treatments both displayed intermediate results.

The main reasons for the treatment differences, which may independently contribute to the advancement of the CBEP, are earlier shoot development with elevated temperatures and higher NAR in the developed current-year shoots with elevated CO<sub>2</sub>. There was a great difference (28 days) in the timing of the CBEP in 2003 and 2004 in the  $T_A C_A$  treatment. This difference could have been caused by a difference in NAR, structural development, or a combination of the two. The structural development in terms of shoot elongation, however, was only four to five days later in 2004 compared to 2003 if expressed as the dates that the shoots reached 50% and 90% of their final length, indicating that only a small portion of the difference in the date of CBEP could be caused by differences in shoot development. Instead, it was suggested that difference between years partly was caused by differences in the growth development in terms of needle mass per area or volume at harvest (Paper *I*). Taking the change in dry mass into account, the CBEP of the 2003 needles would, on average, have been reached one week later. The remaining between-year differences in dates of the CBEP (once the later shoot development and SNA differences had been taken into account) were more than two weeks. It is proposed, therefore, that the large between-year variation in CBEP timing was caused by a combination of the slightly later shoot development in 2004, an underestimate of the final shoot biomass because shoots were harvested too early in 2003, and weather-induced differences in NAR.

The spring events for the current year and C+1 shoots under ambient conditions are summarised in Figure 8. The spring recovery of photosynthesis, and the starch accumulation in needles and shoot axis in one-year old and older shoots started approximately one month before bud burst. However, large variations between years can be expected, as these processes are so dependent on temperature. The shoot elongation of C-shoots was completed before the accumulation of biomass

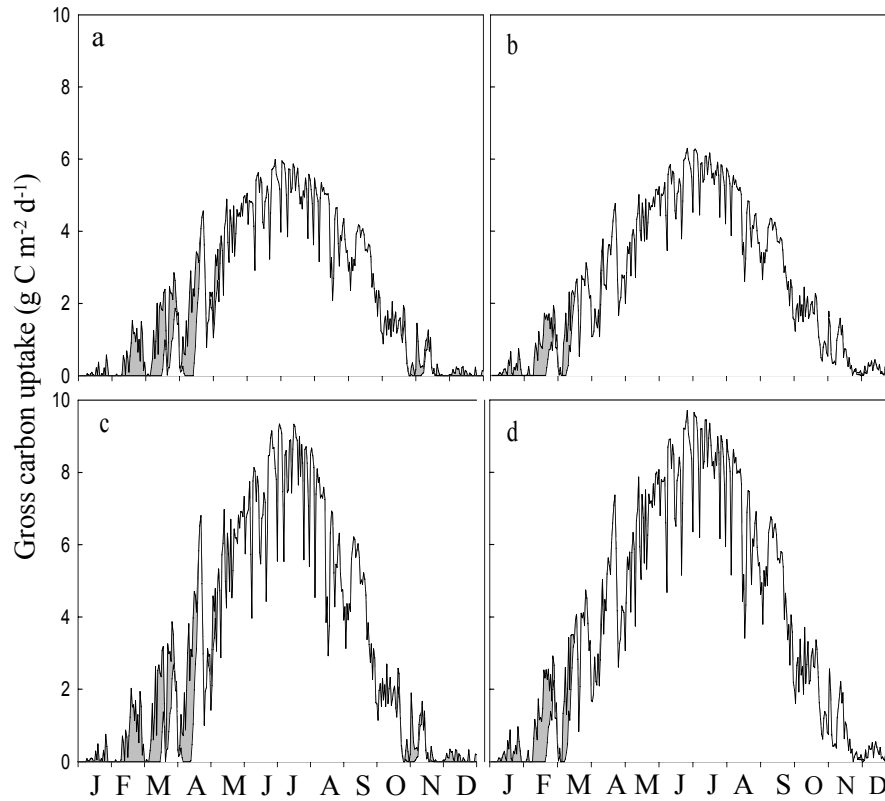
was completed. In early August, the current year shoots had reached CBEP, and the timing of this coincided with reported ending of starch decline in the older shoots (Linder 1995).



**Figure 8.** The phenological events taking place during spring and early summer are mainly driven by temperature. Therefore there are large differences in timing and rate of development between different years. In the one-year old and older shoots (dark grey) the recovery of photosynthetic capacity (Paper II) starts simultaneously with a starch accumulation in needles and shoot axis (Linder 1995). The starch content then declines (Linder 1995), while the development of current-year shoots (light grey) starts with increased respiration rates (Paper I), followed by bud burst and structural development (Slaney et al. 2007; Flower-Ellis 1993; Paper I). Carbon break even point, that is when the new shoot have assimilated its own mass in carbon and shifts from being a net consumer to a net provider of carbon, takes place in early August (Paper I).

There was a large combined effect of the WTC treatments and the  $A(t)$  parameter on the gross carbon assimilation in the C+1 shoots accumulated over the full year. The modelled annual gross C uptake at a constant N concentration ( $N_F = 3.0 \text{ g m}^{-2}$ ) was 723 ( $T_A C_A$ ), 882 ( $T_E C_A$ ), 1055 ( $T_A C_E$ ) and 1329 ( $T_E C_E$ )  $\text{g C m}^{-2}$  (Figure 9; Table 3 in Paper III). Thus, the combined effect of the  $T_E$  and  $C_E$  treatments increased the annual C uptake by 84%. The increase of 22% in the  $T_E C_A$  treatment compared to the  $T_A C_A$  treatment was mainly a result of the extended growing season.

The nitrogen status of the foliage was important for annual uptake, and a reduction in  $N_F$  from 3.0 to 2.5 g m<sup>-2</sup> in the ShootModel resulted in a reduced annual uptake of 12% in the  $C_A$  treatments and 16% in the  $C_E$  treatments. There was no difference in reduction between the temperature treatments.



**Figure 9.** The mean daily gross carbon uptake as simulated with the ShootModel at constant N concentration ( $N_F = 3.0 \text{ g m}^{-2}$ ) with (lower line) and without (upper line) the seasonality factor  $A(t)$  in the **a**)  $T_A C_A$ , **b**)  $T_E C_A$ , **c**)  $T_A C_E$  and **d**)  $T_E C_E$  treatments. The grey area is where photosynthesis is reduced due to winter dormancy of the trees and freezing damage to the photosynthetic apparatus. In the  $T_E$  treatments (**b**, **d**),  $A_{GROSS}$  is likely to be overestimated in late fall, when winter dormancy has begun, and frost events have damaged the photosynthetic apparatus.  $T_A$  = ambient temperature,  $T_E$  = elevated temperature  $C_A$  = ambient [CO<sub>2</sub>],  $C_E$  = elevated [CO<sub>2</sub>].

### Links between the canopy and the soil

As previously discussed in this thesis, it has been proposed that autotrophic carbon assimilation, i.e. the tree canopy and understory processes, ultimately control the rate of carbon sequestration by forest ecosystems (Cannell and Thornley 2000, Janssens et al. 2001, Ciais et al. 2005). Testing the performance of an ecosystem model for determining carbon budgets at the landscape level should, ideally, make use of field measurements of eddy covariance carbon flux data. It is necessary to partition the carbon fluxes into photosynthetic uptake and respiratory release, plant photosynthetic carbon isotope discrimination ( $\Delta^{13}\text{C}$ ) and the carbon isotope composition of ecosystem respiration ( $\delta^{13}\text{C}_{\text{R-E}}$ ), as well as the gross fluxes of  $\text{CO}_2$  into and out of the system (Paper IV). Much previous work on partitioning respiration and photosynthetic fluxes at the seasonal scale has relied on limited sampling, with instantaneous measurements collected throughout the growing season. Recent work has shown that there can be temporal variation in respiration rate (Knohl et al. 2005, Tang and Baldocchi 2005), and the associated stable carbon isotope ratio ( $\delta^{13}\text{C}$ ) (Bowling et al. 2002, McDowell et al. 2004, Scartazza et al. 2004, Bowling et al. 2005, Hemming et al. 2005, Hymus et al. 2005), including that associated with soil respiration ( $\delta^{13}\text{C}_\text{S}$ ) (Ekblad et al. 2005, Ekblad and Högberg 2001). To shed some light on this issue, and to investigate the impact of canopy processes on the soil carbon pool, the diurnal variation in the rate and carbon isotope composition of soil respiration in two stands close to the WTCs were investigated (Paper IV). The sampling was performed once every four hours during two 48h sampling periods, June 27-29 and August 5-7, 2004. The results were evaluated in relation to the meteorological conditions and compared with the shoot photosynthetic rate of two reference trees in the WTC experiment. To distinguish between autotrophic and heterotrophic soil respiration, the sampling was performed in one plot where the trees had been girdled two years earlier (Olsson et al. 2005), and in one control plot, both close to the WTCs. There were three replicates per plot.

Tree girdling had a large impact in both June (non-girdled mean =  $149 \text{ mg C m}^{-2} \text{ h}^{-1}$ ; girdled mean =  $69 \text{ mg C m}^{-2} \text{ h}^{-1}$ ;  $p = 0.005$ ) and August ( $215$  versus  $78 \text{ mg C m}^{-2} \text{ h}^{-1}$ ;  $p = 0.012$ ), and there was a close correlation between the  $\delta^{13}\text{C}$  of the phloem sap sugars and the soil-respired carbon. The respiration rates in the non-girdled plot measured in June were similar to measurements taken within the soil compartment in the WTCs during August 2002 (Comstedt et al. 2006). For the  $T_{\text{A}}C_{\text{A}}$  chambers, soil respiration of  $152 \text{ mg C m}^{-2} \text{ h}^{-1}$  was reported. However, Comstedt et al. (2006) also reported soil respiration for the same period in 2003 of merely  $90 \text{ mg C m}^{-2} \text{ h}^{-1}$ , and the differences between the years were not explained.

No systematic diurnal variation was found for either isotope composition or respiration rate, despite substantial variations in meteorological conditions and shoot photosynthetic rates (Figures 1 and 2 in Paper IV). The short nights (2 h in June and 4 h in August without direct light) may explain the lack of diurnal

variation. It is suggested that in the northern boreal forests during the summer period, validation of soil respiration based on single measurements is unlikely to be confounded by large errors induced by diurnal variations. However, large standard errors within the plots indicate that spatial variability, probably caused by heterogeneous microbial, tree and understory root activity, may be a problem and should be taken into account in any modelling project.

Based on the differences in respiration rates between the girdled and non-girdled plots, it can be concluded that, despite the lack of diurnal variation indicated by isotope composition or soil respiration rates, canopy processes do have a considerable influence on soil respiration (rate and carbon isotope signal), as previously demonstrated in an oak-grass savannah ecosystem (Tang et al. 2005). Ecosystem carbon balance models should, therefore, include plant root allocation and aboveground productivity as driving variables of soil respiration and carbon sequestration.

### **Concluding remarks**

The features of climate change – increases in temperature and atmospheric carbon dioxide concentration, and the secondary, reversed, effect of down regulation of foliage N content – had a large influence on the annual C uptake of Norway spruce shoots.

The main effect of the temperature treatment was a lengthening of the growing season, which affected the onset and rate of the development of the current year shoots, and the onset and rate of spring recovery of photosynthesis in the one-year old shoots. The elevated carbon dioxide concentration increased the maximum net carbon assimilation rate by ~50 % in both current year and one-year old shoots.

The combined effect of the climate change treatment was an increase of the annual gross carbon uptake by 84 %. This increase was partly attributed to the lengthening of the growing period (22 %) and partly to the increase in the maximum photosynthetic capacity. The gross C uptake response to elevated CO<sub>2</sub> concentrations was sensitive to the foliage Nitrogen status, and a reduction in  $N_F$  from 3.0 to 2.5 g m<sup>-2</sup> resulted in a reduction of 16% in the modelled gross C uptake in the climate change treatment and 12 % under ambient conditions.

Ultimately, the amount of carbon sequestered by the boreal forests is dependent on the amount of carbon assimilated by the vegetation and, therefore, ecosystem carbon balance models should include plant root allocation and aboveground productivity amongst the driving variables for soil respiration and carbon sequestration. The model presented in this thesis was intended to be used as a tool to determine shoot level carbon budgets from easily available meteorological data. A future project aims to scale the responses from shoot to stand level.

## References

- Abramowitz, G. 2005. Towards a benchmark for land surface models. *Geophysical Research Letters* 32, L22702, doi:10.1029/2005GL024419
- Abramowitz, G., H. Gupta, A. Pitman, Y.P. Wang, R. Leuning, H. Cleugh and K.L. Hsu 2006. Neural error regression diagnosis (NERD): A tool for model bias identification and prognostic data assimilation. *Journal of Hydrometeorology* 7:160-177.
- Ainsworth, E.A. and S.P. Long 2005. What have we learned from 15 years of free-air CO<sub>2</sub> enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO<sub>2</sub>. *New Phytologist* 165:351-371.
- Ainsworth, E.A. and A. Rogers 2007. The response of photosynthesis and stomatal conductance to rising [CO<sub>2</sub>]: mechanisms and environmental interactions. *Plant Cell and Environment* 30:258-270.
- Bala, G., K. Caldeira, M. Wickett, T.J. Phillips, D.B. Lobell, C. Delire and A. Mirin 2007. Combined climate and carbon-cycle effects of large-scale deforestation. *Proceedings of the National Academy of Sciences of the United States of America* 104:6550-6555.
- Barton, C.V.M., H.S.J. Lee and P.G. Jarvis 1993. A branch-bag and CO<sub>2</sub> control system for long-term CO<sub>2</sub> enrichment of mature Sitka spruce (*Picea sitchensis* (Bong.) Carr.). *Plant, Cell and Environment* 16:1139-1148.
- Bergh, J. 1997. Climatic and nutritional constraints to productivity in Norway Spruce. *Acta Universitatis Agriculturae Sueciae, Silvestria* 37, 34 pp. Doctoral thesis. ISBN 91-576-5321-6
- Bergh, J. and S. Linder 1999. Effects of soil warming during spring on photosynthetic recovery in boreal Norway spruce stands. *Global Change Biology*. 5:245-253.
- Bergh, J., R.E. McMurtrie and S. Linder 1998. Climatic factors controlling the productivity of Norway spruce: A model-based analysis. *Forest Ecology and Management* 110:127-139.
- Bergh, J., M. Freeman, B. Sigurdsson, S. Kellomäki, K. Laitinen, S. Niinisto, H. Peltola and S. Linder 2003. Modelling the short-term effects of climate change on the productivity of selected tree species in Nordic countries. *Forest Ecology and Management* 183:327-340.
- Bernacchi, C.J., E.L. Singaas, C. Pimentel, A.R. Portis and S.P. Long 2001. Improved temperature response functions for models of Rubisco-limited photosynthesis. *Plant Cell and Environment* 24:253-259.
- Bernacchi, C.J., C. Pimentel and S.P. Long 2003. In vivo temperature response functions of parameters required to model RuBP-limited photosynthesis. *Plant Cell and Environment* 26:1419-1430.
- Bigras, F.J. and A. Bertrand 2006. Responses of *Picea mariana* to elevated CO<sub>2</sub> concentration during growth, cold hardening and dehardening: phenology, cold tolerance, photosynthesis and growth. *Tree Physiology* 26:875-888.
- Bonan, G.B. 2008. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science* 320:1444-1449.

- Bowling, D.R., N.G. McDowell, B.J. Bond, B.E. Law and J.R. Ehleringer 2002. C-13 content of ecosystem respiration is linked to precipitation and vapor pressure deficit. *Oecologia* 131:113-124.
- Bowling, D.R., S.P. Burns, T.J. Conway, R.K. Monson and J.W.C. White 2005. Extensive observations of CO<sub>2</sub> carbon isotope content in and above a high-elevation subalpine forest. *Global Biogeochemical Cycles* 19:GB3023.
- Cannell, M.G.R. and J.H.M. Thornley 2000. Modelling the components of plant respiration: Some guiding principles. *Annals of Botany* 85:45-54.
- Christensen, J.H., J. Räisänen, T. Iversen, D. Bjorge, O.B. Christensen and M. Rummukainen 2001. A synthesis of regional climate change simulations - A Scandinavian perspective. *Geophysical Research Letters* 28:1003-1006.
- Ciais, P., M. Reichstein, N. Viovy, A. Granier, J. Ogee, V. Allard, M. Aubinet, N. Buchmann, C. Bernhofer, A. Carrara, F. Chevallier, N. De Noblet, A.D. Friend, P. Friedlingstein, T. Grünwald, B. Heinesch, P. Keronen, A. Knohl, G. Krinner, D. Loustau, G. Manca, G. Matteucci, F. Miglietta, J.M. Ourcival, D. Papale, K. Pilegaard, S. Rambal, G. Seufert, J.F. Soussana, M.J. Sanz, E.D. Schulze, T. Vesala and R. Valentini 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437:529-533.
- Comstedt, D., B. Boström, J.D. Marshall, A. Holm, M. Slaney, S. Linder and A. Ekblad 2006. Effects of elevated atmospheric carbon dioxide and temperature on soil respiration in a boreal forest using delta C-13 as a labeling tool. *Ecosystems* 9:1266-1277.
- Curtis, P.S. and X.Z. Wang 1998. A meta-analysis of elevated CO<sub>2</sub> effects on woody plant mass, form, and physiology. *Oecologia* 113:299-313.
- de Graaf, M.-A., K.-J.v. Groenigen, J. Six, B. Hungate and C.v. Kessel 2006. Interactions between plant growth and soil nutrient cycling under elevated CO<sub>2</sub>: a meta-analysis. *Global Change Biology* 12:2077-2091.
- Dixon, M., D. Le Thiec and J.P. Garrec 1995. The growth and gas exchange response of soil-planted Norway spruce [*Picea abies* (L.) Karst.] and red oak (*Quercus rubra* L.) exposed to elevated CO<sub>2</sub> and to naturally occurring drought. *New Phytologist* 129:265-273.
- Ekblad, A., B. Boström, A. Holm and D. Comstedt 2005. Forest soil respiration rate and delta C-13 is regulated by recent above ground weather conditions. *Oecologia* 143:136-142.
- Ekblad, A. and P. Högberg 2001. Natural abundance of C-13 in CO<sub>2</sub> respired from forest soils reveals speed of link between tree photosynthesis and root respiration. *Oecologia* 127:305-308.
- Ellsworth, D.S., P.B. Reich, E.S. Naumburg, G.W. Koch, M.E. Kubiske and S.D. Smith 2004. Photosynthesis, carboxylation and leaf nitrogen responses of 16 species to elevated pCO<sub>2</sub> across four free-air CO<sub>2</sub> enrichment experiments in forest, grassland and desert. *Global Change Biology* 10:2121-2138.
- Ericsson, A. 1978. Seasonal changes in translocation of <sup>14</sup>C from different age-classes of needles on 20-year-old Scots pine trees (*Pinus silvestris*). *Physiologia Plantarum* 43:351-358.
- Farquhar, G.D. and S. von Caemmerer 1982. Modelling of photosynthetic response to environmental conditions. In *Physiological plant ecology II: Water relations and carbon assimilation*. Eds. O.L. Lange, C.B. Nobel, B. Osmond and H. Ziegler. Springer-Verlag, Berlin, pp. 549-587.

- Farquhar, G.D., S. Von Caemmerer and J.A. Berry 1980. A biochemical model of photosynthetic carbon oxide assimilation in leaves of 3-carbon pathway species. *Planta* 149:78-90.
- Flower-Ellis, J.G.K. 1993. Dry-matter allocation in Norway spruce branches: a demographic approach. *Studia Forestalia Suecica* 191:51-73.
- Forster, P., V. Ramaswamy, P. Artaxo, T. Berntsen, R. Betts, D.W. Fahey, J. Haywood, J. Lean, D.C. Lowe, G. Myhre, J. Nganga, R. Prinn, G. Raga, M. Schulz and R.v. Dorland 2007. Changes in atmospheric constituents and in radiative forcing. *In* Climate Change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Ed. S. Solomon. Cambridge University Press, Cambridge.
- Fransson, P.M.A., A.F.S. Taylor and R.D. Finlay 2001. Elevated atmospheric CO<sub>2</sub> alters root symbiont community structure in forest trees. *New Phytologist* 152:431-442.
- Fredeen, A.L. and R.F. Sage 1999. Temperature and humidity effects on branchlet gas-exchange in white spruce: an explanation for the increase in transpiration with branchlet temperature. *Trees* 14:161-168.
- Gordon, J.C. and P.R. Larson 1968. Seasonal course of photosynthesis, respiration, and distribution of <sup>14</sup>C in young *Pinus resinosa* trees as related to wood formation. *Plant Physiology* 43:1617-1624.
- Hamilton, J.G., R.B. Thomas and E.H. Delucia 2001. Direct and indirect effects of elevated CO<sub>2</sub> on leaf respiration in a forest ecosystem. *Plant Cell and Environment* 24:975-982.
- Hänninen, H. 1995. Effects of climatic-change on trees from cool and temperate regions - an ecophysiological approach to modeling of bud burst phenology. *Canadian Journal of Botany* 73:183-199.
- Hänninen, H. and P. Hari 2002. Recovery of photosynthesis of boreal conifers during spring: a comparison of two models. *Forest Ecology and Management* 169:53-64.
- Hänninen, H., M. Slaney and S. Linder 2007. Dormancy release of Norway spruce under climatic warming: testing ecophysiological models of bud burst with a whole-tree chamber experiment *Tree Physiology* 27:291-300.
- Hari, P. and A. Mäkelä 2003. Annual pattern of photosynthesis in Scots pine in the boreal zone. *Tree Physiology* 23:145-155.
- Harvey, L.D.D. 2000. *Global Warming - The Hard Science*. Prentice Hall, Singapore. 336 p.
- Havranek, W.H. and W. Tranquillini 1995. Physiological processes during winter dormancy and their ecological significance. *In* *Ecophysiology of coniferous forests*. Eds. W.K. Smith and T.M. Hinckley. Academic Press, London, pp. 95-124.
- Heide, O.M. 1993. Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. *Physiologia Plantarum* 88:531-540.
- Hemming, D., D. Yakir, P. Ambus, M. Aurela, C. Besson, K. Black, N. Buchmann, R. Burllett, A. Cescatti, R. Clement, P. Gross, A. Granier, T. Grunwald, K. Havrankova, D. Janous, I.A. Janssens, A. Knohl, B.K. Ostner, A. Kowalski, T. Laurila, C. Mata, B. Marcolla, G. Matteucci, J. Moncrieff, E.J. Moors, B. Osborne, J.S. Pereira, M. Pihlatie, K. Pilegaard, F. Ponti, Z. Rosova, F. Rossi, A. Scartazza and T. Vesala 2005. Pan-European delta C-13 values of air and organic matter from forest ecosystems. *Global Change Biology* 11:1065-1093.
- Hendrey, G.R., D.S. Ellsworth, K.F. Lewin and J. Nagy 1999. A free-air enrichment system for exposing tall forest vegetation to elevated atmospheric CO<sub>2</sub>. *Global Change Biology* 5:293-309.



- Herrick, J.D. and R.B. Thomas 2001. No photosynthetic down-regulation in sweetgum trees (*Liquidambar styraciflua* L.) after three years of CO<sub>2</sub> enrichment at the Duke Forest FACE experiment. *Plant Cell and Environment* 24:53-64.
- Hobbie, S.E., J.P. Schimel, S.E. Trumbore and J.R. Randerson 2000. Controls over carbon storage and turnover in high-latitude soils. *Global Change Biology* 6:196-210.
- Hsu, K.-l., H.V. Gupta, X. Gao, S. Sorooshian and B. Imam 2002. Self-Organizing Linear Output map (SOLO): An artificial neural network suitable for hydrologic modeling and analysis. *Water Resources Research* 38:1302, doi:10.1029/2001WR000795.
- Hymus, G.J., K. Maseyk, R. Valentini and D. Yakir 2005. Large daily variation in C-13-enrichment of leaf-respired CO<sub>2</sub> in two *Quercus* forest canopies. *New Phytologist* 167:377-384.
- Hyvönen, R., G.I. Ågren, S. Linder, T. Persson, M.F. Cotrufo, A. Ekblad, M. Freeman, A. Grelle, I.A. Janssens, P.G. Jarvis, S. Kellomäki, A. Lindroth, D. Loustau, T. Lundmark, R.J. Norby, R. Oren, K. Pilegaard, M.G. Ryan, B.D. Sigurdsson, M. Strömberg, M. van Oijen and G. Wallin 2007. The likely impact of elevated [CO<sub>2</sub>], nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review. *New Phytologist* 173:463-480.
- Jach, M.E. and R. Ceulemans 1999. Effects of elevated atmospheric CO<sub>2</sub> on phenology, growth and crown structure of Scots pine (*Pinus sylvestris*) seedlings after two years of exposure in field. *Tree Physiology* 19:289-300.
- Janssen, P.H.M. and P.S.C. Heuberger 1995. Calibration of process-oriented models. *Ecological Modelling* 83:55-66.
- Janssens, I.A., H. Lankreijer, G. Matteucci, A.S. Kowalski, N. Buchmann, D. Epron, K. Pilegaard, W. Kutsch, B. Longdoz, T. Grünwald, L. Montagnani, S. Dore, C. Rebmann, E.J. Moors, A. Grelle, Ü. Rannik, K. Morgenstern, S. Oltehev, R. Clement, J. Gudmundsson, S. Minerbi, P. Berbigier, A. Ibrom, J. Moncrieff, M. Aubinet, C. Bernhofer, N.O. Jensen, T. Vesala, A. Granier, E.D. Schulze, A. Lindroth, A.J. Dolman, P.G. Jarvis, R. Ceulemans and R. Valentini 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology* 7:269-278.
- Jarvis, P.G. 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 273:593-610.
- Jarvis, P.G. and D.G. Fowler 2001. Forests and the atmosphere. *In* The forests handbook Ed. J. Evans. Blackwell Science, Oxford, U.K. 229–281 pp.
- Karnosky, D.F. 2003. Impacts of elevated atmospheric CO<sub>2</sub> on forest trees and forest ecosystems: knowledge gaps. *Environment International* 29:161-169.
- Kellomäki, S. and J.-P. Wang 1997. Effects of elevated O<sub>3</sub> and CO<sub>2</sub> on chlorophyll fluorescence and gas exchange in Scots pine during the third growing seasons. *Environmental Pollution* 97:17-27.
- Kellomäki, S., K. Wang and M. Lemettinen 2000. Controlled environmental chambers for investigating tree response to elevated CO<sub>2</sub> and temperature under boreal conditions. *Photosynthetica* 38:69-81.
- Kirschbaum, M.U.F. and G.D. Farquhar. 1984 Temperature dependence of whole-leaf photosynthesis in *Eucalyptus pauciflora* Sieb. ex Spreng. *Australian Journal of Plant Physiology* 11:519–538

- Knohl, A., R.A. Werner, W.A. Brand and N. Buchmann 2005. Short-term variations in delta C-13 of ecosystem respiration reveals link between assimilation and respiration in a deciduous forest. *Oecologia* 142:70-82.
- Kohonen, T. 1989. *Self-organization and associative memory*. Springer, New York.
- Körner, C. 2000. Biosphere responses to CO<sub>2</sub> enrichment. *Ecological Applications* 10:1590-1619.
- Körner, C. 2006. Plant CO<sub>2</sub> responses: an issue of definition, time and resource supply. *New Phytologist* 172:393-411.
- Körner, C., R. Asshoff, O. Bignucolo, S. Hattenschwiler, S.G. Keel, S. Pelaez-Riedl, S. Pepin, R.T.W. Siegwolf and G. Zotz 2005. Carbon flux and growth in mature deciduous forest trees exposed to elevated CO<sub>2</sub>. *Science* 309:1360-1362.
- Kostiainen, K., S. Kaakinen, P. Saranpää, B.D. Sigurdsson, S. Linder and E. Vapaavuori 2004. Effect of elevated [CO<sub>2</sub>] on stem wood properties of mature Norway spruce grown at different soil nutrient availability. *Global Change Biology* 10:1526-1538.
- Kozlowski, T.T. and C.H. Winget 1964. The role of reserves in leaves, branches, stems, and roots on shoot growth of red pine. *American Journal of Botany* 51:522-529.
- Kramer, K., I. Leinonen and D. Loustau 2000. The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forests ecosystems: an overview. *International Journal of Biometeorology* 44:67-75.
- Kruijt, B., C. Barton, A. Rey and P.G. Jarvis 1999. The sensitivity of stand-scale photosynthesis and transpiration to changes in atmospheric CO<sub>2</sub> concentration and climate. *Hydrology and Earth System Sciences* 3:55-69.
- Larcher, W. 1995. *Physiological plant ecology*. Springer Verlag, Berlin Heidelberg.
- Leinonen, I. and K. Kramer 2002. Applications of phenological models to predict the future carbon sequestration potential of boreal forests. *Climatic Change* 55:99-113.
- Linder, S. 1995. Foliar analysis for detecting and correcting nutrient imbalances in Norway spruce. *Ecological Bulletins (Copenhagen)* 44:178-190.
- Linder, S. and J.G.K. Flower-Ellis 1992. Environmental and physiological constraints to forest yield. *In Responses of Forest Ecosystems to environmental changes*. Eds. A. Teller, P. Mathy and J.N.R. Jeffers. Elsevier Applied Science, London, pp. 149-164.
- Linder, S. and T. Lohammar 1981. Amount and quality of information on CO<sub>2</sub> gas exchange required for estimating annual carbon balance of coniferous trees. *Studia Forestalia Suecica* 160:73-87.
- Lindroth, A., F. Lagergren, M. Aurela, B. Bjarnadottir, T. Christensen, E. Dellwik, A. Grelle, A. Ibrom, T. Johansson, H. Lankreijer, S. Launiainen, T. Laurila, M. Molder, E. Nikinmaa, K. Pilegaard, B.D. Sigurdsson and T. Vesala 2008. Leaf area index is the principal scaling parameter for both gross photosynthesis and ecosystem respiration of Northern deciduous and coniferous forests. *Tellus Series B* 60:129-142.
- Lloyd, J. 1999. The CO<sub>2</sub> dependence of photosynthesis, plant growth responses to elevated CO<sub>2</sub> concentrations and their interaction with soil nutrient status, II. Temperate and boreal forest productivity and the combined effects of increasing CO<sub>2</sub> concentrations and increased nitrogen deposition at a global scale. *Functional Ecology* 13:439-459.
- Long, S.P. 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO<sub>2</sub> concentrations - Has its importance been underestimated? *Plant Cell and Environment* 14:729-739.

- Luo, Y.Q., J. Reynolds, Y.P. Wang and D. Wolfe 1999. A search for predictive understanding of plant responses to elevated [CO<sub>2</sub>]. *Global Change Biology* 5:143-156.
- Luo, Y., B. Su, W.S. Currie, J.S. Dukes, A. Finzi, U. Hartwig, B. Hungate, R.E. McMurtrie, R. Oren, W.J. Parton, D.E. Pataki, M.R. Shaw, D.R. Zak and C.B. Field 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *Bioscience* 54:731-739.
- Luo, Y.Q., D. Gerten, G. Le Maire, W.J. Parton, E.S. Weng, X.H. Zhou, C. Keough, C. Beier, P. Ciais, W. Cramer, J.S. Dukes, B. Emmett, P.J. Hanson, A. Knapp, S. Linder, D. Nepstad and L. Rustad 2008. Modeled interactive effects of precipitation, temperature, and [CO<sub>2</sub>] on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology* 14:1986-1999.
- Mäkelä, A., P. Hari, F. Berninger, H. Hänninen and E. Nikinmaa 2004. Acclimation of photosynthetic capacity in Scots pine to the annual cycle of temperature. *Tree Physiology* 24:369-376.
- Mäkelä, A., P. Kolari, J. Karimäki, E. Nikinmaa, M. Perämäki and P. Hari 2006. Modelling five years of weather-driven variation of GPP in a boreal forest. *Agricultural and Forest Meteorology* 139:382-398.
- McDowell, N.G., D.R. Bowling, A. Schauer, J. Irvine, B.J. Bond, B.E. Law and J.R. Ehleringer 2004. Associations between carbon isotope ratios of ecosystem respiration, water availability and canopy conductance. *Global Change Biology* 10:1767-1784.
- McMurtrie, R.E. and J.-P. Wang 1993. Mathematical models of the photosynthetic response of tree stands to rising CO<sub>2</sub> concentrations and temperatures. *Plant, Cell and Environment* 16:1-13.
- McMurtrie, R.E., D.A. Rook and F.M. Kelliher 1990. Modelling the yield of *Pinus-radiata* on a site limited by water and nitrogen. *Forest Ecology and Management* 30:381-413.
- Medhurst, J., J. Parsby, S. Linder, G. Wallin, E. Ceschia and M. Slaney 2006. A whole-tree chamber system for examining tree-level physiological responses of field-grown trees to environmental variation and climate change. *Plant Cell and Environment* 29:1853-1869.
- Medlyn, B.E., F.W. Badeck, D.G.G. De Pury, C.V.M. Barton, M. Broadmeadow, R. Ceulemans, P. De Angelis, M. Forstreuter, M.E. Jach, S. Kellomäki, E. Laitat, M. Marek, S. Philippot, A. Rey, J. Strassemer, K. Laitinen, R. Liozon, B. Portier, P. Roberntz, K. Wang and P.G. Jarvis 1999. Effects of elevated [CO<sub>2</sub>] on photosynthesis in European forest species: a meta-analysis of model parameters. *Plant Cell and Environment* 22:1475-1495.
- Medlyn, B.E., R.E. McMurtrie, R.C. Dewar and M.P. Jeffreys 2000. Soil processes dominate the long-term response of forest net primary productivity to increased temperature and atmospheric CO<sub>2</sub> concentration. *Canadian Journal of Forest Research* 30:873-888.
- Medlyn, B.E., C.V.M. Barton, M.S.J. Broadmeadow, R. Ceulemans, P. De Angelis, M. Forstreuter, M. Freeman, S.B. Jackson, S. Kellomäki, E. Laitat, A. Rey, P. Roberntz, B.D. Sigurdsson, J. Strassemer, K. Wang, P.S. Curtis and P.G. Jarvis 2001. Stomatal conductance of forest species after long-term exposure to elevated CO<sub>2</sub> concentration: a synthesis. *New Phytologist* 149:247-264.
- Medlyn, B.E., D. Barrett, J. Landsberg, P. Sands and R. Clement 2003. Conversion of canopy intercepted radiation to photosynthate: review of modelling approaches for regional scales. *Functional Plant Biology* 30:153-169.

- Medlyn, B.E., P. Berbigier, R. Clement, A. Grelle, D. Loustau, S. Linder, L. Wingate, P.G. Jarvis, B.D. Sigurdsson and R.E. McMurtrie 2005a. Carbon balance of coniferous forests growing in contrasting climates: Model-based analysis. *Agricultural and Forest Meteorology* 131:97-124.
- Medlyn, B.E., A.P. Robinson, R. Clement and R.E. McMurtrie 2005b. On the validation of models of forest CO<sub>2</sub> exchange using eddy covariance data: some perils and pitfalls. *Tree Physiology* 25:839-857.
- Meehl, G.A. and C. Tebaldi 2004. More intense, more frequent, and longer lasting heat waves in the 21st century. *Science* 305:994-997.
- Melillo, J.M., P.A. Steudler, J.D. Aber, K. Newkirk, H. Lux, F.P. Bowles, C. Catricala, A. Magill, T. Ahrens and S. Morrisseau 2002. Soil warming and carbon-cycle feedbacks to the climate system. *Science* 298:2173-2176.
- Morén, A.S. 1999. Modelling branch conductance of Norway spruce and Scots pine in relation to climate. *Agricultural and Forest Meteorology* 98-9:579-593.
- Morison, J.I.L. and D.W. Lawlor 1999. Interactions between increasing CO<sub>2</sub> concentration and temperature on plant growth. *Plant Cell and Environment* 22:659-682.
- Murray, M.B., R.I. Smith, A.D. Friend and P.G. Jarvis 2000. Effect of elevated [CO<sub>2</sub>] and varying nutrient application rates on physiology and biomass accumulation of Sitka spruce (*Picea sitchensis*). *Tree Physiology* 20:421-434.
- Novak, R.S., D.S. Ellsworth and S.D. Smith 2004. Functional responses of plants to elevated atmospheric CO<sub>2</sub> - do photosynthetic and productivity data from FACE experiments support early predictions? *New Phytologist* 162:253-280.
- Olsson, P., S. Linder, R. Giesler and P. Högberg 2005. Fertilization of boreal forest reduces both autotrophic and heterotrophic soil respiration. *Global Change Biology* 11:1745-1753.
- Oren, R., D.S. Ellsworth, K.H. Johnson, N. Phillips, B.E. Ewers, C. Maier, K.V.R. Schäfer, H. McCarthy, G.R. Hendrey, S.G. McNulty and G.G. Katul 2001. Soil fertility limits carbon sequestration by a forest ecosystem in a CO<sub>2</sub>-enriched atmosphere. *Nature* 411:469-472.
- Partanen, J., V. Koski and H. Hänninen 1998. Effects of photoperiod and temperature on the timing of bud burst in Norway spruce (*Picea abies*). *Tree Physiology* 18:811-816.
- Partanen, J., I. Leinonen and T. Repo 2001. Effect of accumulated duration of the light period on bud burst in Norway spruce (*Picea abies*) of varying ages. *Silva Fennica* 35:111-117.
- Pelkonen, P. and P. Hari 1980. The dependence of the springtime recovery of CO<sub>2</sub> uptake in Scots pine on temperature and internal factors. *Flora* 169:398-404.
- Pleijel, H., L. Mortensen, J. Fuhrer, K. Ojanperä and H. Danielsson 1999. Grain protein accumulation in relation to grain yield of spring wheat (*Triticum aestivum* L.) grown in open-top chambers with different concentrations of ozone, carbon dioxide and water availability. *Agriculture, Ecosystems & Environment* 72:265-270.
- Räisänen, J. and R. Joëlsson 2001. Changes in average and extreme precipitation in two regional climate model experiments. *Tellus Series A* 53:547-566.
- Räisänen, J., M. Rummukainen and A. Ullerstig 2001. Downscaling of greenhouse gas induced climate change in two GCMs with the Rossby Centre regional climate model for northern Europe. *Tellus Series A* 53:168-191.
- Rasmussen, L., C. Beier and A. Bergstedt 2002. Experimental manipulations of old pine ecosystems to predict the potential tree growth effects of increased CO<sub>2</sub> and temperature in a future climate. *Forest Ecology and Management* 158:179-188.

- Raven, P.H., R.F. Evert and S.E. Eichhorn 1999. Biology of plants. W. H. Freeman and Company, Worth Publishers, New York.
- Reich, P.B., B.D. Kloeppel, D.S. Ellsworth and M.B. Walters 1995. Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. *Oecologia* 104:24-30.
- Reich, P.B., S.E. Hobbie, T. Lee, D.S. Ellsworth, J.B. West, D. Tilman, J.M.H. Knops, S. Naeem and J. Trost 2006. Nitrogen limitation constrains sustainability of ecosystem response to CO<sub>2</sub>. *Nature* 440:922-925.
- Repo, T., A. Mäkelä and H. Hänninen 1990. Modelling frost resistance of trees. *In* Modelling to understand forest functions Ed. H. Jozefek. *Silva Carelica*, pp. 61-74.
- Repo, T., I. Leinonen, K.Y. Wang and H. Hanninen 2006. Relation between photosynthetic capacity and cold hardiness in Scots pine. *Physiologia Plantarum* 126:224-231.
- Roberntz, P. 1999. Effects of long-term CO<sub>2</sub> enrichment and nutrient availability in Norway spruce. I. Phenology and morphology of branches. *Trees* 13:188-198.
- Roberntz, P. and S. Linder 1999. Effects of long-term CO<sub>2</sub> enrichment and nutrient availability in Norway spruce. II. Foliar chemistry. *Trees* 14:17-27.
- Roberntz, P. and J. Stockfors 1998. Effects of elevated CO<sub>2</sub> concentration and nutrition on net photosynthesis, stomatal conductance and needle respiration of field-grown Norway spruce trees. *Tree Physiology* 18:233-241.
- Rustad, L.E., J.L. Campbell, G.M. Marion, R.J. Norby, M.J. Mitchell, A.E. Hartley, J.H.C. Cornelissen and J. Gurevitch 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126:543-562.
- Ryan, M.G. 1991. Effects of climate change on plant respiration. *Ecological Applications* 1:157-167.
- Sands, P.J. 1995a. Modelling Canopy Production. I. Optimal distribution of photosynthetic resources. *Australian Journal of Plant Physiology* 22:593-601.
- Sands, P.J. 1995b. Modelling canopy production. II. From single-leaf photosynthetic parameters to daily canopy photosynthesis. *Australian Journal of Plant Physiology* 22:603-614.
- Sands, P.J. 1996. Modelling canopy production. III. CanopyLight-utilisation efficiency and its sensitivity to physiological and environmental variables. *Australian Journal of Plant Physiology* 23:103-114.
- Saugier, B., A. Granier, J.Y. Pontallier, E. Dufrêne and D.D. Baldocchi 1997. Transpiration of a boreal pine forest measured by branch-bag, sap-flow and micrometeorological methods. *Tree Physiology* 17:511-519.
- Saxe, H., D.S. Ellsworth and J. Heath 1998. Tree and forest functioning in an enriched CO<sub>2</sub> atmosphere. *New Phytologist* 139:395-436.
- Saxe, H., M.G.R. Cannell, B. Johnsen, M.G. Ryan and G. Vourlitis 2001. Tree and forest functioning in response to global warming. *New Phytologist* 149:369-399.
- Scartazza, A., C. Mata, G. Matteucci, D. Yakir, S. Moscatello and E. Brugnoli 2004. Comparisons of delta C-13 of photosynthetic products and ecosystem respiratory CO<sub>2</sub> and their response to seasonal climate variability. *Oecologia* 140:340-351.
- Schneider, M.K., A. Lüscher, M. Richter, U. Aeschlimann, U.A. Hartwig, H. Blum, E. Frossard and J. Nösberger 2004. Ten years of free-air CO<sub>2</sub> enrichment altered the mobilization of N from soil in *Lolium perenne* L. swards. *Global Change Biology* 10:1377-1388.
- Sevanto, S., T. Suni, J. Pumpanen, T. Grönholm, P. Kolari, E. Nikinmaa, P. Hari and T. Vesala 2006. Wintertime photosynthesis and water uptake in a boreal forest. *Tree Physiology* 26:749-757.

- Sigurdsson, B.D., P. Roberntz, M. Freeman, M. Naess, H. Saxe, H. Thorgeirsson and S. Linder 2002. Impact studies on Nordic forests: effects of elevated CO<sub>2</sub> and fertilization on gas exchange. *Canadian Journal of Forest Research* 32:779-788.
- Slaney, M. 2006. Impact of elevated temperature and [CO<sub>2</sub>] on spring phenology and photosynthetic recovery of boreal Norway spruce. *Acta Universitatis Agriculturae Sueciae*. Doctoral Thesis 2006:3, 47 pp. ISSN 1652-6880, ISBN 91-576-7052-8
- Slaney, M., G. Wallin, J. Medhurst and S. Linder 2007. Impact of elevated carbon dioxide concentration and temperature on bud burst and shoot growth of boreal Norway spruce. *Tree Physiology* 27:301-312.
- Snyder, P.K., C. Delire and J.A. Foley 2004. Evaluating the influence of different vegetation biomes on the global climate. *Climate Dynamics* 23:279-302.
- Steffen, W., I.N.J. Canadell, M. Apps, E.-D. Schulze, P.G. Jarvis, D. Baldocchi, P. Ciais, W. Cramer, J. Ehleringer, G. Farquhar, C.B. Field, A. Ghazi, R. Gifford, M. Heimann, R. Houghton, P. Kabat, C. Körner, E. Lambin, S. Linder, H.A. Mooney, D. Murdiyarsa, W.M. Post, I.C. Prentice, M.R. Raupach, D.S. Schimel, A. Shvidenko and R. Valentini 1998. The terrestrial carbon cycle: Implications for the Kyoto Protocol. *Science* 280:1393-1394.
- Stitt, M. 1991. Rising CO<sub>2</sub> Levels and Their Potential Significance for Carbon Flow in Photosynthetic Cells. *Plant Cell and Environment* 14:741-762.
- Stockfors, J. 1997. Respiratory losses in Norway spruce: the effect of growth and nutrition. *Acta Universitatis Agriculturae Sueciae, Silvestria* 20, 41 pp. Doctoral thesis. ISBN 91-576-5304-6
- Stockfors, J. and S. Linder 1998a. Effect of nitrogen on the seasonal course of growth and maintenance respiration in stems of Norway spruce trees. *Tree Physiology* 18:155-166.
- Stockfors, J. and S. Linder 1998b. The effect of nutrition on the seasonal course of needle respiration in Norway spruce stands. *Trees* 12:130-138.
- Tamm, C.O. 1991. Nitrogen in terrestrial ecosystems - Questions of productivity, vegetational changes, and ecosystem stability. *Ecological Studies* 81. Springer-Verlag, 115 p.
- Tang, J.W. and D.D. Baldocchi 2005a. Spatial-temporal variation in soil respiration in an oak-grass savanna ecosystem in California and its partitioning into autotrophic and heterotrophic components. *Biogeochemistry* 73:183-207.
- Tang, J.W., D.D. Baldocchi and L. Xu 2005b. Tree photosynthesis modulates soil respiration on a diurnal time scale. *Global Change Biology* 11:1298-1304.
- Tanja, S., F. Berninger, T. Vesala, T. Markkanen, P. Hari, A. Mäkelä, H. Ilvesniemi, H. Hänninen, E. Nikinmaa, T. Huttula, T. Laurila, M. Aurela, A. Grelle, A. Lindroth, A. Arneth, O. Shibistova and J. Lloyd 2003. Air temperature triggers the recovery of evergreen boreal forest photosynthesis in spring. *Global Change Biology* 9:1410-1426.
- Thornley, J.H.M. 1990. *Plant and crop modelling: a mathematical approach to plant and crop physiology*. Clarendon Press, Oxford [England], New York.
- Thornley, J.H.M. 2002. Instantaneous canopy photosynthesis: Analytical expressions for sun and shade leaves based on exponential light decay down the canopy and an acclimated non-rectangular hyperbola for leaf photosynthesis. *Annals of Botany* 89:451-458.
- Tissue, D.T., K.L. Griffin, M.H. Turnbull and D. Whitehead 2001. Canopy position and needle age affect photosynthetic response in field-grown *Pinus radiata* after five years of exposure to elevated carbon dioxide partial pressure. *Tree Physiology* 21:915-923.

- Tjoelker, M.G., J. Oleksyn and P.B. Reich 1998. Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO<sub>2</sub> and temperature. *Tree Physiology* 18:715-726.
- Tjoelker, M.G., P.B. Reich and J. Oleksyn 1999. Changes in leaf nitrogen and carbohydrates underlie temperature and CO<sub>2</sub> acclimation of dark respiration in five boreal tree species. *Plant Cell and Environment* 22:767-778.
- Troeng, E. and S. Linder 1982. Gas exchange in a 20-year-old stand of Scots pine. I. Net photosynthesis of current and one-year-old shoots within and between seasons. *Physiologia Plantarum* 54:7-14.
- Uddling, J., M. Hall, G. Wallin and P.E. Karlsson 2005. Measuring and modelling stomatal conductance and photosynthesis in mature birch in Sweden. *Agricultural and Forest Meteorology* 132:115-131.
- Urban, O. 2003. Physiological impacts of elevated CO<sub>2</sub> concentration ranging from molecular to whole plant responses. *Photosynthetica* 41:9-20.
- Urban, O. and M.V. Marek 1999. Seasonal changes of selected parameters of CO<sub>2</sub> fixation biochemistry of Norway spruce under the long-term impact of elevated CO<sub>2</sub>. *Photosynthetica* 36:533-545.
- Urban, O., R. Pokorny, J. Kalina and M.V. Marek 2003. Control mechanisms of photosynthetic capacity under elevated CO<sub>2</sub> concentration: evidence from three experiments with Norway spruce trees. *Photosynthetica* 41:69-75.
- Wallin, G., S. Linder, A. Lindroth, M. Rantfors, S. Flemberg and A. Grelle 2001. Carbon dioxide exchange in Norway spruce at the shoot, tree and ecosystem scale. *Tree Physiology* 21:969-976.
- Wang, Y.P. 2003. A comparison of three different canopy radiation models commonly used in plant modelling. *Functional Plant Biology* 30:143-152.
- Wang, Y.P. and P.G. Jarvis 1990. Description and validation of an array model - Maestro. *Agricultural and Forest Meteorology* 51:257-280.
- Watson, R.T., I.R. Noble, B. Bolin, N.H. Ravindranath, D.J. Verardo and D.J. Dokken 2000. Land use, land-use change, and forestry. A special report of the IPCC. Cambridge University Press, Cambridge. 377 p.
- Whitehead, D., K.P. Hogan, G.N.D. Rogers, J.N. Byers, J.E. Hunt, T.M. McSeveny, D.Y. Hollinger, R.J. Dungan, W.B. Earl and M.P. Bourke 1995. Performance of large open-top chambers for long-term field investigations of tree-response to elevated carbon dioxide concentration. *Journal of Biogeography* 22:307-313.
- Wong, S.C., I.R. Cowan and G.D. Farquhar 1978. Stomatal conductance correlates with photosynthetic capacity. *Nature* 282:424-426.
- Wright, R.F. 1998. Effects of increased CO<sub>2</sub> and temperature on runoff chemistry at a forested catchment in southern Norway (CLIMEX project). *Ecosystems* 1:216-225.

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