APPENDIX A

Carbon in boreal forest ecosystems

- The influence of climate change, nitrogen fertilization, whole-tree harvest and stump harvest on the carbon cycle

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This report is an appendix to the report “Effects of climate change, nitrogen fertilization, whole-tree harvesting and stump harvesting on boreal forest ecosystems - A review of current knowledge and an evaluation of how these factors may influence the possibilities to reach the Swedish environmental objectives”. January 2013.

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Acknowledgements

This work was funded by the research program “Climate Change and Environmental Objectives” (CLEO) hosted by IVL Swedish Environmental Research Institute and the strategic research area “Biodiversity and Ecosystem Services in a Changing Climate” (BECC) hosted by Lund University. The photos in the report are from dreamstime.com, freedigitalphotos.net and shutterstock.com.

SUMMARY

This report consists of a literature review about the effects of climate change and forest management on carbon (C) cycling in boreal forest ecosystems, with specific emphasis on Swedish conditions and the terrestrial part of the C cycle. With regard to climate change, the influence of temperature, moisture and increased levels of carbon dioxide (CO_2) on C cycling have been evaluated. With regard to forest management practices, the effects of nitrogen (N) fertilization, whole-tree harvesting (WTH) and stump harvesting (SH) have been evaluated. Results from empirical as well as modelling studies are included in the review.

Background

The C concentration in the atmosphere has risen from close to 280 ppm before the industrial revolution to a value of 350 ppm in the late 1950s and 379 ppm in 2005. About three-quarters of this increase is due to emissions from fossil fuel burning, with emissions as a consequence of land-use changes (such as deforestation) being responsible for the rest of the increase. Terrestrial ecosystems are, together with oceans, the major regulators of atmospheric CO_2 levels. Calculations show that the terrestrial C sink has absorbed around 30% of anthropogenic emissions over the period 2000 to 2007, emphasizing C sequestration by land vegetation as a major ecosystem service. Forests store approximately 45% of the terrestrial C. In Europe, forest standing-stocks have nearly tripled during the past 50 years and forests currently constitute a significant C sink. Changes in the forested area, a juvenile age structure of the forests and an increasing NPP as a consequence of CO_2 fertilization, elevated N deposition and climate change are likely reasons behind the increase.

C in plants

Plants take in CO_2 from the atmosphere and convert it into organic compounds by the process of photosynthesis. Since boreal forests are temperature-limited ecosystems, it is reasonable to assume that an increase in temperature is followed by an increase in the rate of photosynthesis. However, the biggest impact of an increase in temperature may be through its influence on the recovery of photosynthesis in spring. The extremely low temperatures that occur in the boreal region in winter may inactivate, or even partly destroy, the photosynthetic apparatus. The rate of recovery is closely related to air temperature, making temperature conditions during spring and early summer of great importance for the total photosynthetic production during the season. If most of the temperature increase in a changing climate falls in winter and spring, with an earlier start of the growing season as a consequence, the net annual photosynthesis could increase, something that has been indicated in empirical as well as modelling studies. In coherence with these results are the increases in above-ground plant production and growing season length which have been demonstrated for several different forest ecosystems during recent decades. Water stress, on the other hand, usually results in a down-regulation of photosynthetic capacity. Several different modelling studies have indicated that drought stress episodes, in particular during summer, may become more frequent in Scandinavia in the future. Results from these modelling studies suggest that the southern parts of Sweden and Finland are most susceptible to water limitation.

Many studies, in particular those investigating trees, have shown that elevated CO_2 concentrations result in increased rates of photosynthesis. The stimulation seems to be greater at higher temperatures. However, a downward acclimation has also often been reported. The reason behind this acclimation is still debated, but it has been related to both growth forms and environmental conditions (i.e. nutrient limitation). Considering the latter, an increased N availability has often been suggested to have a positive effect on photosynthesis, and the photosynthetic capacity has been shown to increase linearly with leaf N concentration. In coherence with the results for photosynthesis, many studies (empirical and modelling) also show increased growth at elevated CO_2. However, a 1:1 translation of photosynthetic responses to growth responses cannot be assumed and responses vary from large increases in growth to no change. Some of the reasons why photosynthetic up-regulation does not translate into increased growth include increased exudation of non-structural carbohydrates from leaves and roots, increased C transfer to symbionts, changes in the C allocation patterns within the plant and nutrient and water limitation of growth.

Boreal and temperate forest ecosystems have generally been regarded as N limited, and many old fertilization experiments have indicated a positive response of tree growth to N. Recent investigations have shown more variable results, ranging from positive effects, to no effects or even negative effects on growth as a consequence of N addition. The observed reductions in growth have most often been attributed to the increased N concentrations in plant tissue, together with the acidifying effect of N, resulting in imbalanced nutrient to N proportions in plants. However, several other explanations have also been brought forward as likely mechanisms behind the decreased growth, for example changes in the allocation patterns of plants, reduced ectomycorrhizal colonization and growth, and more frequent and intensive pathogen attacks.

With regard to WTH and SH, we are not aware of any studies examining the impact of these management practices on the photosynthetic capacity of trees in the subsequent generation. However, the majority of studies (both Scandinavian ones and those from other countries) indicate a negative effect of WTH on the growth of trees in the subsequent generation as compared with conventional stem harvesting (CH). Several different explanations for the reduced growth have been put forward, the most convincing one being the reduction in nutrient availability as a consequence of the removal of logging residues. Whether the productivity remains lower after WTH as compared with CH during the whole rotation period or if it is a transient phenomenon is currently not clear. The effects of SH on tree productivity is also unclear, since most studies hitherto have been performed with the purpose of investigating the efficacy of SH as a sanitation measure on pathogen infested sites.

Root systems comprise up to half the total tree biomass and the flux of C below-ground in terrestrial ecosystems exceeds the C emitted to the atmosphere through combustion of fossil fuels by an order of magnitude. Yet, it remains one of the least understood C fluxes in the terrestrial C cycle. For boreal forests, the partitioning of GPP to total belowground C flux tends to decrease with increasing mean annual temperature, possibly as a consequence of the increased soil nutrient availability when temperature increases. Increased resource supply generally decreases the fraction of GPP partitioned to below-ground. Consequently, mild droughts and reduced nutrient availability often results in increased allocation to below-ground organs while plentiful of the two generally results in the opposite. With regard to the impact of N on growth and diversity of ectomycorrhiza (EM), results are inconclusive and the predictability for any given ecosystem is relatively low.

Elevated CO_2 generally results in an increase in the allocation of C below-ground. Furthermore, fine roots of trees exposed to elevated CO_2 are distributed more deeply in the soil profile relative to trees grown under ambient CO_2 (i.e. a larger proportion of root biomass at deeper soil depths). The causes and consequences of the increased root proliferation at depth are still poorly understood, but one likely cause is an increased resource demand as a consequence of increased forest production at elevated CO_2.

There are very few studies on the effects of WTH and SH on root growth and mycorrhiza, and it is thus not yet possible to draw any conclusions about their impact on below-ground growth of trees in the subsequent generation.

The quantity of C transferred from trees to soil by litterfall is primarily a function of tree biomass. Generally, increases in temperature, moisture, CO_2 and N are all regarded to result in increased production and thus litterfall. WTH and SH, on the other hand, implies a removal of potential litter, and thus C, from the ecosystems.

C in soils

Globally, soils contains more than three times as much C as either the atmosphere or the terrestrial vegetation. In boreal forests, C stocks in soil exceed those in vegetation by 5:1. With regard to forest C budgets, changes in soil C stocks can thus be significantly more important than changes in vegetation C stocks.

Climate is the most important factor determining decomposition of plant litter. The effects of temperature and moisture are generally both positive, at least within a certain range and for easily decomposable pools of soil organic matter (SOM). Whether the later stages of decomposition and SOM are sensitive to temperature is unclear, but several recent studies indicate that more recalcitrant material is at least as, or even more, sensitive to warming as easily soluble SOM. Also the impact of elevated CO_2 on the SOM pool is unclear, with studies showing increases, decreases and no change in SOM, as well as studies showing initial decreases followed by increases. The latter result is usually attributed to an initial priming effect of SOM as a consequence of new substrate fuelling larger decomposition fluxes.

N has been suggested to have a dual effect on decomposition, where initial litter decomposition rates usually respond positively to N while later stages do not. In fact, high N concentrations may even have a rate-retarding effect on degradation of litter in later stages. This retardation has been shown to be due to suppression of lignolytic enzymes but also to be a consequence of the formation of chemically stable recalcitrant compounds (that are formed when low-molecular N reacts with lignin). However, experimental evidence of the impact of N on SOC in non-agricultural soils are inconclusive with studies showing both positive and negative as well as negligible effects.

In general, management operations such as harvesting and thinning affect the litter input as well as the microclimate, and hence both decomposition rates and the soil C pool. However, most empirical Scandinavian studies have found no significant effects of WTH on soil C. The modelling studies, on the other hand, generally indicate a decrease in the soil C storage as a consequence of WTH. There is currently a lack of peer-reviewed literature on the effects of SH on soil C pools. The few studies that do exist indicate a decrease, something that is coherent with the view that intensive site preparation usually results in soil C losses.

C losses

C is lost from terrestrial ecosystems via several different pathways: autotrophic plant respiration, heterotrophic respiration, leaching of dissolved inorganic and organic C, and by disturbances, in which large amounts of organic matter are oxidized in short periods of time.

Plant respiration generally increases with increasing temperature and when plants are suddenly exposed to water stress. However, there are indications that the respiration rate acclimates when the exposure continues for long periods of time. With regard to elevated CO_2, leaf respiration is usually inhibited immediately upon exposure, but most longer-term studies seem to shown an opposite trend, i.e. an increase in respiration as a consequence of elevated CO_2. A positive correlation between respiration rate and N concentration has also been observed. However, it has been suggested that the long-term effects of CO_2 and N are indirect consequences of changes in for example allocation patterns and plant growth rate rather than accounted for by direct effects. We are not aware of any studies investigating the influence of WTH and SH on plant respiration rates of the subsequent forest stands.

Most studies indicate a strong positive link also between temperature and heterotrophic respiration and/or soil respiration (heterotrophic respiration together with autotrophic respiration from roots and mycorrhizal fungi). Drought, on the other hand, commonly leads to decreased respiration rates. Consequently, C loss through respiration may primarily be determined by soil

temperature in the dormant season. The results with regard to the effects of elevated CO_2 on heterotrophic respiration are unclear, with studies showing increases as well as no change in response to elevated CO_2. Some of the variation may possibly be explained by variable soil properties. Increased concentrations of ions, such as N, usually result in increases in root respiration. However, the rate of root respiration per ion absorbed or per unit root biomass produced at a low supply of for example nitrate may be high compared with those of plants that grow and take up ions at a much higher rate. A Swedish fertilization experiment showed that N fertilization of two pine forests resulted in significant decreases in respiration rates when expressed per gram of C. However, since the amount of C per m^2 was higher in fertilized plots there was no difference between fertilized and control treatments on an area basis.

The information available with regard to the influence of WTH and SH on soil respiration rates is very sparse. WTH was shown to result in decreased CO_2 efflux from soil as compared to where logging residues were left on site in one study - a logical consequence considering the rapid decomposition of fresh litter during the first years following harvest where residues are left on site. The only Swedish study that has been published with regard to SH shows an initial increase in respiration rate as a consequence of SH. However, the difference as compared with the control disappeared rather quickly.

With regard to leaching of organic and inorganic C, the information available is sparse and straggling. Some studies suggest that leaching losses from forest ecosystems are relatively small and hardly affect the net ecosystem C balance, while others suggest that ignoring it may lead to over-estimations of the C accumulation rates within terrestrial ecosystems. Considering the lack of coherent information, the summary of the state of knowledge presented by Fan *et al.* (2010) seems appropriate: "…the mechanisms that control DOC production and loss are complex, and future projections of climate impacts remain highly uncertain."

C accumulation in forests

In general, the amount of C stored in forests in many parts of the world, including Scandinavia, has increased during the last half-century. Most life-cycle assessment type studies currently available indicate that intensive forest management will result in reductions in net C emissions, emphasizing the role of forests as major C regulators also in the future. However, although interesting, a major draw-back of these life-cycle studies is their inadequate consideration of soil C. In boreal forests, only around 13% of the C is estimated to be in biomass. If boreal forest soils are loosing C, it thus seems unlikely that boreal forest biomass can sequester sufficient amounts to compensate for it. Several recent studies (empirical and modelling ones) also indicate that not all forest currently accumulate C. Instead, their average balance is near zero, or they may even be loosing C. Furthermore, the view of old-growth forests as C neutral or C sources has recently been challenged, emphasizing the need for more detailed and legitimate information before firm conclusions about the best practices with regard to the future C storage capacity of forests can be drawn.

Conclusions

Although recent advances have resulted in a more comprehensive understanding of how climate change and forest management practices affect the processes controlling the C dynamics of boreal forest ecosystems, much information is still lacking - in particular with regard to the impact on processes controlling soil C. The current knowledge about the effects of the microbial community structure on C storage and ecosystem C balances in forest ecosystems has been described as a black box, and long-term data on the effects of climate change and forest management practices on tree productivity and soil biogeochemistry is scarce. Improving our knowledge about soil C, endeavouring in obtaining long-term data sets and including realistic information on soil C pools in current modelling and life cycle assessment approaches are crucial if reliable predictions about future cycling of C in boreal forest ecosystems are to be made.

TABLE OF CONTENTS

1. BRIEF

This report consists of a literature review about the effects of climate change and forest management on carbon (C) cycling in boreal forest ecosystems, with specific emphasis on Swedish conditions. The literature review is an appendix to the report "Effects of climate change, nitrogen fertilization, whole-tree harvesting and stump harvesting on boreal forest ecosystems - A review of current knowledge and an evaluation of how these factors may influence the possibilities to reach the Swedish environmental objectives", published by Belyazid Consulting & Communication AB in January 2013.

The aims of this review are:

1) To identify what processes are controlling the C dynamics in boreal and temperate forest ecosystems.

2) To investigate how these processes are influenced by climate change and some forest management practices that are likely to become more common in Sweden in the future, namely nitrogen (N) fertilization, whole-tree harvesting (WTH) and stump harvesting (SH). With regard to climate change, the influence of temperature and moisture as well as increased levels of carbon dioxide (CO_2) on the various processes included in the C cycle are evaluated.

The focus of the literature review is on the terrestrial part of the C cycle. Atmospheric and ocean C is only briefly described. Methane production has not been included since it is mainly associated with wetlands (Mosier, 1998), an ecosystem that is not investigated in this review. Due to the lack of information on dissolved C (in particular dissolved inorganic C) and suspended C, the production and transport of these are not described in any detail in this review.

We are aware of the difficulty in drawing coherence from a large number of studies, which to varying degrees are site-, age- and species-specific. However, we have tried to include as much information as possible within the limited time available. Foremost, we have collected information from scientifically published articles concerning boreal forest ecosystems in Scandinavia. When the information available was scarce, we extended the literature search to other types of forest ecosystems and other regions of the world. Both empirical and modelled data have been included in the review.

2. CARBON CYCLING - AN OVERVIEW

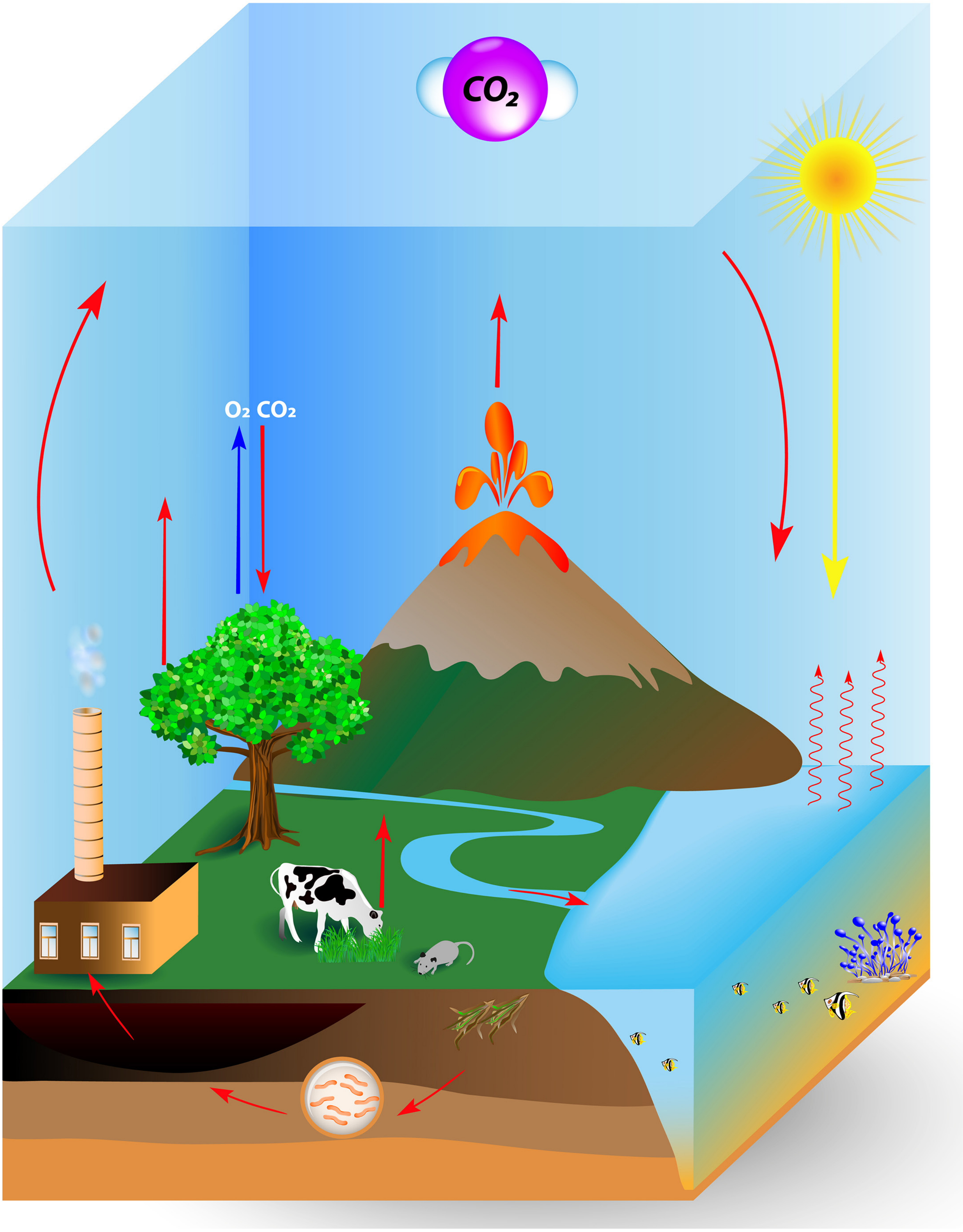
The overview is mainly based on the description provided by Brady & Weil (1999).

Plants take in CO_2 from the atmosphere and, through the process of photosynthesis, the energy of sunlight is trapped in the C to C bonds of organic molecules. Some of these organic compounds are used as a source of energy, via respiration, by the plants themselves, with the C being returned to the atmosphere as CO_2. The remaining are stored temporarily as constituents of the standing vegetation. Some of the plant material may be eaten by animals (including humans), in which case about half of the C is exhaled into the atmosphere as CO_2. The C not returned to the atmosphere is eventually returned to the soil as plant litter, bodily wastes or bodily tissues. Once deposited on or in the soil, the litter is metabolized by soil organisms by the process of decomposition. Decomposition gradually returns the C to the atmosphere as CO_2 (Brady & Weil, 1999). Forests contain large amounts of C in biomass, dead organic matter and soil, and thus contribute to significant annual C exchanges with the atmosphere (Denman *et al.*, 2007).

Carbohydrates (which range in complexity from simple sugars and starches to cellulose) are usually the most plentiful organic compounds in plant and animal tissues, and are relatively easily decomposable. In general, very little of the original residue material thus persist in soil. However, plants contain some more complex compounds, such as lignin and polyphenols, which are considerably more resistant to decomposition. Decades, or even centuries, may pass before the C in them is returned to the atmosphere as CO_2. In addition, small particles may become physically protected from decay by lodging inside soil pores too tight to allow access by most organisms. Some of the C may also become chemically protected by conversion into soil humus (modified lignin and newly synthesized organic compounds) that is highly resistant to decay. Some of the fine humus is further protected by binding strongly to clay particles. Thus, a small percentage of the C in the added residues is retained, continuously increasing the pool of stable organic matter in the soil (Brady & Weil, 1999). Some small amounts of CO_2 also react in the soil to produce carbonic acid (H_2CO_3) and the carbonates and bicarbonates of calcium (Ca), potassium (K), magnesium (Mg) and other base-forming cations. The bicarbonates are readily soluble and may be removed in drainage. However, eventually, much of the C in the carbonates and bicarbonates is also returned to the atmosphere as CO_2 (Brady & Weil, 1999).

Globally, approximately 2 400 Pg (10^{15}) of C is stored as soil organic matter (SOM; excluding surface litter). About one third of that is stored at depths below 1 meter. An additional 700 Pg of C is stored as soil carbonates, which can release CO_2 upon weathering. Altogether, about three times as much C is stored in the soil as in the world's vegetation and atmosphere combined (Schmidt *et al.*, 2011).

In a mature natural ecosystem, the release of C as CO_2 by oxidation of SOM is generally balanced by the input of C into the soil as plant residues (and to a far smaller degree, animal residues). However, certain perturbations of the system, such as deforestation, some types of fire, tillage and artificial drainage, may result in a net loss of C from the soil system (Brady & Weil, 1999). Globally, the release of C from soils into the atmosphere is about 62 Pg per year, while only about 60 Pg per year enter the soils from the atmosphere via plant residues (Brady & Weil, 1999). This imbalance of about 2 Pg per year, along with about 5 Pg per year of carbon released from burning of fossil fuels, is only partially offset by increased absorption of atmospheric CO_2 by the ocean. Fossil fuel burning and degrading land-use practices have thus increased the atmospheric concentration of CO_2 at accelerating rates, from 280 ppm to 379 ppm during the last century alone (IPCC, 2007).


CO_2
O_2 CO_2

3. THREE DIFFERENT CARBON COMPARTMENTS

3.1 C in the atmosphere

The concentration of CO_2 in the atmosphere has risen from close to 280 ppm before the industrial revolution, at first slowly and then progressively faster, to a value of 350 ppm in the late 1950s and 379 ppm in 2005 (IPCC, 2007). About three-quarters of this increase is due to emissions from fossil fuel burning (between 5.4 and 6.3 Pg C yr^{-1} from 1980 to 1999), with emissions as a consequence of land-use changes (deforestation, conversion of old-growth to second growth forest etcetera) being responsible for the rest of the increase (Prentice *et al.*, 2001).

However, the observed increase in atmospheric CO_2 cannot account for the estimated releases of CO_2 from fossil fuel burning and other sources. This is because some of the emitted CO_2 dissolves in the ocean, and some is taken up by terrestrial ecosystems. For 1980 to 1989, the ocean-atmosphere flux was estimated to be -1.9 ± 0.6 Pg C yr^{-1}, and the land-atmosphere flux was estimated to be -0.2 ± 0.7 Pg C yr^{-1} (negative signs denote net uptake). For 1990 to 1999, the corresponding values were -1.7 ± 0.5 Pg C yr^{-1} and -1.4 ± 0.7 Pg C yr^{-1}, respectively (Prentice *et al.*, 2001). The variability that is apparent between individual years is mainly caused by variations in land and ocean uptake. That terrestrial systems comprise a sink has several likely causes, including changes in land management practices and fertilisation effects of increased atmospheric CO_2 and N deposition, leading to increased vegetation and soil C (Prentice *et al.*, 2001). Modelling based on atmospheric observations imply substantial terrestrial sinks for anthropogenic CO_2 in northern and tropical forests. Terrestrial C inventory data are consistent with these results (Prentice *et al.*, 2001).

The present atmospheric CO_2 concentration has not been exceeded during the past 420 000 years, and likely not during the past million years, and the rate of increase over the past century is unprecedented, at least during the past 20 000 years (Prentice *et al.*, 2001). Since the uptake and release processes of CO_2 to the atmosphere are climate and temperature dependent (e.g. Friedlingstein *et al.*, 2006), climate change creates potential for feedbacks. Measurements have shown that the increase in atmospheric CO_2 has continued during recent years (Dolman *et al.*, 2010) and the first-generation coupled climate-C cycle models also indicate that global warming will increase the fraction of anthropogenic CO_2 that remains in the atmosphere. In models run under the IPCC (2000a) special report on emission scenarios (SRES) A2 emission scenario, this positive climate-C cycle feedback leads to an additional increase in atmospheric CO_2 concentration of 20 to 224 ppm by year 2100 (Denman *et al.*, 2007).

3.2 C dissolution in the oceans

Oceans are, together with terrestrial ecosystems, the major regulator of atmospheric CO_2 levels. According to Prentice *et al.* (2001), the total amount of C in the ocean is about 50 times greater than the amount in the atmosphere, and is exchanged with the atmosphere on a time-scale of several hundred years. The uptake of anthropogenic CO_2 by the ocean is primarily governed by ocean circulation and carbonate chemistry (Prentice *et al.*, 2001). As long as atmospheric CO_2 concentration is increasing, there is net uptake of C by the ocean, driven by atmosphere-ocean difference in partial pressure of CO_2. However, the fraction taken up by the ocean declines with increasing CO_2 concentration due to reduced buffer capacity of the carbonate system (Prentice *et al.*, 2001). Furthermore, the fraction taken up by the ocean also declines with the rate of increase in atmospheric CO_2, because the rate of mixing between deep water and surface water limits CO_2 uptake (Prentice *et al.*, 2001).

According to Denman *et al.* (2007), improved estimates of ocean uptake of CO_2 suggest little change in the ocean C sink of 2.2 ± 0.5 Gt C yr^{-1} between 1990s and the first five years of the 21st century. However, models indicate that the fraction of CO_2 taken up by the ocean will decline if atmospheric CO_2 continues to increase (Denman *et al.*, 2007). According to Dolman *et al.* (2010), the North Atlantic and Southern ocean now take up less CO_2, but is unclear whether this is part of the natural decadal scale variability.

Previously, it has been suggested that the increasing atmospheric concentrations of CO_2 has no significant fertilization effect on the marine biological productivity (Prentice *et al.*, 2001). However, recent studies have shown that ocean CO_2 uptake has lowered the average ocean pH (see for example Denman *et al.*, 2007). Consequences for marine ecosystems may include reduced calcification by shell-forming organisms, and in the longer term, the dissolution of carbonate sediments (Denman *et al.*, 2007).

3.3 Terrestrial C

In contrast with the ocean, most C cycling through land takes place locally within ecosystems. Each year, photosynthesizing land plants remove (fix) one in eight molecules of atmospheric CO_2, and respiring land plants and soil organisms return a similar number (Reich, 2010). The two processes remain surprisingly well-coupled across C cycling rates that vary by several orders of magnitude (Chapin *et al.*, 2009). According to Chapin *et al.* (2009), one possible explanation is that climate and soil resources exert primary controls over net primary production (NPP) and that decomposition is "donor-controlled" by the transfer of dead organic C to soils and the coupling of C and N cycles. Chapin *et al.* (2009) argue, however, that recent rapid changes in climate, atmospheric CO_2, land cover, species composition and element inputs and losses have fundamentally altered the relationship between the climate drivers and the ecosystem C dynamics. NPP and decomposition are thus likely to differ in their rate and/or pattern of response to these changes. According to Chapin *et al.* (2009), these biogeochemical complexities warrant inclusion in global-scale climate-C cycle models, since the exchange determines whether terrestrial ecosystems are net C sinks or sources.

Calculations by Canadell *et al.* (2007) have shown that globally, the terrestrial C sink has absorbed about 30% of anthropogenic emissions over the period 2000 to 2007. C sequestration by land vegetation thus constitutes a major ecosystem service (Schulze *et al.*, 2010). More recently, Beer *et al.* (2010) estimated the total annual terrestrial gross primary production (GPP). They produced estimates of global GPP that varied from approximately 105 to 130 Pg C yr^{-1}, with a 95% probability that the value lies between 102 and 135 Pg C yr^{-1}. According to Reich (2010), this estimate is more solidly based on data than previous simple approximations and is thus the best and most broad-based estimate we have. He emphasized, however, that although an advance, this estimate shows how far we still are from an accurate estimate of global GPP – the 33 Pg C yr^{-1} difference between low and high values is roughly four times the annual CO_2 emission from fossil-fuel burning.

Schulze *et al.* (2009), exploiting the full benefits of both a top down estimate from inverse models and bottom up estimates from models and observations, provided the C balance and the first complete greenhouse gas (GHG) balance of Europe. They concluded that the overall GHG balance of Europe is nearly neutral, with emissions of N_2O and CH_4 caused largely by agriculture in the west, and balanced by uptake of CO_2 by forest and grassland in the east.

3.3.1 C in forest ecosystems

According to Bonan (2008), forests store approximately 45% of terrestrial C and can sequester large amounts of C annually. In Europe, forest standing-stocks have nearly tripled during the past 50 years (Schulze *et al.*, 2010). Luyssaert *et al.* (2010) found, using three independent approaches (ecosystem modelling, forest inventories and up-scaling of ecological data), that the overall mean NPP in forests of 25 member states of the European Union (EU-25) was 520 ± 75 g C m^{-2} yr^{-1}. In the EU-25, forests are thus a C sink, according to the authors as a result of changes in forested area (i.e. 5-10%), a juvenile age structure of the forests and an increasing NPP because of CO_2 fertilization, elevated N deposition and climate change (i.e. 20-50%). The relatively large forest net biome production (NBP) is thought to be the result of a sustained difference between NPP and C losses primarily by harvest and heterotrophic respiration, which increased less over the same period (Ciais *et al.*, 2008a,b; Luyssaert *et al.*, 2010).

According to Schulze *et al.* (2010), the current accumulation of C in forests should not hide the fact that C incorporated into forest biomass is vulnerable to natural disturbances such as fire or pests and that the magnitude of the forest sink depends on stand age (Luyssaert *et al.*, 2008), atmospheric N deposition (Magnani *et al.*, 2007; Reay *et al.*, 2008; de Vries *et al.*, 2009) and forest management (de Vries *et al.*, 2006; Ciais *et al.*, 2008a,b). Consequently, it should not be regarded as permanent or secure (Schulze *et al.*, 2010).

4. CARBON IN PLANTS

4.1 Photosynthesis

Higher plants acquire CO_2 by diffusion through tiny pores (stomata) into leaves and thus to the sites of photosynthesis. The total amount of CO_2 that dissolves in leaf water is around 270 Pg C yr^{-1}, i.e. more than one-third of all the CO_2 in the atmosphere. Most of this CO_2 diffuses out again without participating in the photosynthesis. Terrestrial GPP has been estimated to be around 120 Pg yr^{-1}. Autotrophic respiration (respiration by plants) returns approximately half of this C to the atmosphere and global NPP has been estimated to be around 60 Pg C yr^{-1} (Prentice *et al.*, 2001).

4.1.1 Effects of temperature

Many plants show an optimum temperature for photosynthesis close to their normal growth temperature (Lambers *et al.*, 1998). Since the boreal forest is a temperature-limited ecosystem, it is reasonable to assume that an increase in temperature is followed by an increase in photosynthesis. Optimum values for photosynthesis for Norway spruce (Bergh, 1997) and Scots pine (Troeng & Linder, 1982) has been reported to be 14-15°C. For most conifers, however, the response curve is relatively flat (Teskey *et al.*, 1995) and an increase of 10°C above optimum typically reduces the photosynthesis by 10-20%, indicating that respiration generally responds more rapidly to temperature changes than does photosynthesis (see for example Lindroth *et al.,* 1998).

Temperature may influence photosynthesis in several different ways. Through the growing season, leaf temperature has an effect on the maximum rate of photosynthesis by affecting Rubisco specificity for CO_2 and O_2, and in particular by enhancing photorespiration at high temperatures (Long, 1991). The latter is because

the solubility of CO_2 decreases with increasing temperature more strongly than does that of O_2 (Lambers *et al.*, 1998). Another effect of temperature, evident only in cold climates, is that at the extremely low temperatures that occur in the boreal region in winter, the photosynthetic apparatus may become inactivated, or even partly destroyed (Strand & Öquist, 1985; Öquist & Strand, 1986). It may take eight or more weeks during the spring to fully recover (Troeng & Linder, 1982; Strand & Lundmark, 1995; Bergh & Linder, 1999), resulting in a loss of potential photosynthetic production equal to 30% of the total annual C gain in Scots pine growing in central Sweden (in Bergh & Linder, 1999 and based on Linder & Lohammar, 1981). The rate of recovery is closely related to the air temperature (Lundmark *et al.*, 1988; 1998; Strand & Lundmark, 1995; Bergh & Linder, 1999; Strand *et al.*, 2002), making temperature conditions during spring and early summer of great importance for the total photosynthetic production during the season. If most of the temperature increase in a changing climate falls in winter and spring, with an earlier start of the growing season as a consequence, the net annual photosynthesis could thus increase.

Bergh *et al.* (1998) simulated "potential" (not including an effect of the soil being frozen during winter or effects of low air temperatures on post-winter recovery and autumn decline of photosynthesis) and "actual" photosynthesis (photosynthesis could not occur prior to soil thawing and temperature effects on the recovery of photosynthesis in spring as well as the decline in autumn were incorporated) in a Norway spruce stand in northern Sweden during three years using the model BIOMASS. The restrictions induced in the "actual" photosynthesis scenario reduced the period of positive C gain to six months per year, a result that is consistent with earlier findings regarding the annual C balance of Scots pine in central Sweden where 95% of annual C gain occurred from May to October (Troeng & Linder, 1982). The total effect of introducing the boreal modifications was a reduction of potential annual GPP by 34-44%, depending on the year. The loss of photosynthetic capacity in winter and the time taken in spring and early summer to repair the damage resulted in the largest difference between "potential" and "actual" photosynthesis, reducing annual GPP with approximately 20% (one year 27%). This is, according to the authors, in coherence with results by Linder & Lohammar (1981) and Linder & Flower-Ellis (1992), who found a 30% loss of potential annual photosynthetic production as a consequence of damage of the photosynthetic apparatus and early decline of photosynthesis in autumn in a Scots pine stand in southern Sweden. The estimated time for photosynthetic capacity to recover fully varied between the three years (62-85 days), with faster recovery during warm springs without severe frost nights. A similar inter-year variation was reported from field-measurements of gas-exchange in Scots pine (Bergh *et al.*, 1997; based on Linder & Lohammar, 1981 and Linder & Flower-Ellis, 1992). The restrictions on C gain caused by frozen soils in spring had a moderate effect, reducing annual GPP with around 12%, while the frost-induced decline of photosynthetic capacity in late autumn had a minor effect (2.5-4.5%) on estimated annual GPP. The latter is in agreement with earlier reports (Linder & Lohammar, 1981; Troeng & Linder, 1982). That low day-time air temperature and freezing nights can adversely affect the recovery process have also been shown by Lundmark *et al.* (1988; 1998), Bergh & Linder (1999) and Strand *et al.* (2002). After regaining full photosynthetic capacity, the rate of photosynthesis is mainly controlled by irradiance, air temperature and access to water (Troeng & Linder, 1982) and even if severe summer frosts can reduce light saturated photosynthesis (Amax) substantially (Lundmark *et al.*, 1988), full recovery from such low-temperature stress is normally attained within a few days of the frost event (Berg & Linder, 1999).

4.1.2 Effects of moisture

The inevitable loss of water when the stomata open to allow photosynthesis may lead to a decrease in leaf relative water content (RWC), if the water supply from the roots does not match the loss from the leaves (Lambers *et al.*, 2008). A decline in RWC may directly or indirectly affect photosynthesis. When a plant is subjected to water stress, stomata tend to close, turgor potential in the leaves decrease and stomatal conductance decrease. The result of these regulatory mechanisms is that, in many cases, transpiration is kept constant over a range of vapour pressure differences (between leaf and the air) and leaf water potential is kept constant over a range of soil water potentials. Water loss is therefore restricted when dry air is likely to impose water stress or when the plant experiences incipient water stress (Lambers *et al.*, 1998). Since water stress affect both the supply (stomatal conductance) and demand (A_{max}) functions of photosynthesis, there is a down-regulation of photosynthethic capacity in response to water stress (Lambers *et al.*, 1998). The mechanism behind this down-regulation is not fully understood. Because high irradiance and high temperature often coincides with drought, however, photoinhibition may be involved. Similarly, because growth is inhibited more strongly than photosynthesis by drought, feedback inhibition may play an additional role (Lambers *et al.*, 1998).

According to Mahli *et al.* (1999), soil moisture reserves in high and mid-latitudes are largely replenished by autumn and winter precipitation, so lack of soil moisture is likely to have little impact on spring growth, but may restrict photosynthesis and growth in the late summer, primarily by reducing C uptake by inducing stomatal closure upon drought. However, the sensitivity to water may vary substantially between species.

At high latitudes, the availability of soil water may have an effect on the recovery of the photosynthetic capacity in spring and early summer (Jarvis & Linder, 2000). Frozen soil prevents water uptake by roots so that leaf turgor and stomatal opening are dependent on the limited supply of stored water within the trees (Waring *et al.*, 1979; Troeng & Linder, 1982), sometimes resulting in a temporary decrease in net photosynthesis after the initial start (Troeng & Linder, 1982). As air temperature rises and the snow cover begins to thaw, melt water close to 0°C percolates down through the soil, replacing the ice and enabling water uptake. The freezing of the ground, with consequent restriction of the water supply, sets an ultimate stop to net photosynthesis in autumn (Troeng & Linder, 1982).

4.1.3 Effects of CO_2

Photosynthesis is generally limited by the availability of CO_2, and elevated CO_2 concentrations generally increase photosynthesis by 1) increasing the carboxylation rate of Rubisco and 2) competitively inhibiting the oxygenation of Ribulose-1,5-biphosphate (RubP) (Lambers *et al.*, 1998). The world's vegetation, and especially the world's forests, thus acts as a negative feedback regulator that helps to moderate changes in atmospheric CO_2 concentrations (Kimmins, 1997).

Because of technical and economic considerations, many CO_2 enrichment studies of woody plants have been restricted to seedlings and young trees grown under laboratory conditions. Seedling responses may be quite different from mature trees and responses under laboratory conditions may differ from responses under field conditions. Free-air CO_2 enrichment (FACE) experiments allow the study of effects of elevated CO_2 on plants and ecosystems grown under natural open-air conditions. In a review of FACE experiments by Ainsworth & Long (2005), the effects of elevated CO_2 on forests, grasslands, deserts and agricultural lands were examined. The levels of CO_2 ranged from 475 to 600 ppm CO_2. Exposure to elevated concentrations of CO_2 resulted in a 31% increase in the light-saturated leaf photosynthetic rate (A_{sat}) and a 28% increase in the diurnal photosynthetic C assimilation when averaged across all FACE experiments and species. Trees were generally more responsive than grass, forbs, legumes and crops, showing an average 47% stimulation in A_{sat}. The strong response of trees compared with herbaceous species is according to Ainsworth & Long (2005) somewhat surprising, but is probably due to the fact that most of the trees grown under FACE conditions are young and rapidly growing. Nevertheless, in contrast to chamber studies, trees have been grown to canopy closure and 6 to 20 m in height (Ainsworth & Long, 2005).

Stomatal conductance (g_s), on the other hand, was reduced by 20% as a consequence of elevated CO_2 (when averaged for 40 species grown at all 12 FACE experiments), resulting in a large increase in intrinsic water-use efficiency. Growth under stressful condition (low N, drought) exacerbated the decrease in g_s (Ainsworth & Long, 2005). Similar results were found by Medlyn *et al.* (2001) when performing a meta-analysis on the response stomatal conductance of trees grown at elevated CO_2 across a set of 13 long-term studies on European forest tree species. The response tended to be stronger in young trees than old trees, in deciduous trees as compared with coniferous trees and in water-stressed trees as compared with nutrient-stressed trees. No evidence of acclimation of stomatal conductance to elevated CO_2 was found.

In Scandinavia, Roberntz & Stockfors (1998) investigated the effects of elevated CO_2 on gas exchange in a 30-year old Norway spruce stand in northern Sweden using the branch bag technique. They found that the elevated CO_2 enhanced A_{max} by 50 to 55% compared with rates under ambient conditions. A continuation of the study in the years that followed (Roberntz, 2001) resulted in a relative increase in A_{max} of 15 to 90% at elevated CO_2 compared with ambient. In coherence with the studies by Roberntz & Stockfors (1998) and Roberntz (2001), Sigurdsson *et al.* (2002), investigating four field-grown tree species (*Picea abies* L. Karst, *Pinus sylvestris* L., *Fagus sylvatica* L. and *Populus trichocarpa*) in Scandinavia (including the site investigated in Roberntz & Stockfors, 1998) found that long-term CO_2 enrichment increased A_{sat} significantly for all tree species (49-114%; *P. trichocarpa* showed the lowest response and *P. sylvestris* the highest).

However, trees grown at elevated CO_2 eventually and frequently exhibit a downward acclimation of light-saturated photosynthesis and carboxylation efficiency (Sage, 1994; Pettersson & McDonald, 1994; Curtis, 1996; Drake *et al.*, 1997; Ainsworth & Long, 2005). The photosynthetic acclimation is often reported along with an accumulation of leaf non-structural carbohydrates (sugars and starch) and a decrease in N concentration in the leaf and plant, in FACE experiments (not trees) as well as in other experiments (Ainsworth & Long, 2005 and references therein). A downward acclimation, which was greater at low N, was also reported by Roberntz & Stockfors (1998) and Roberntz (2001) for the Norway spruce site in northern Sweden. Furthermore, the needles exposed to elevated CO_2 had significantly higher starch, glucose and fructose concentrations than needles exposed to ambient CO_2 (Roberntz & Stockfors, 1998). In contrast to the studies mentioned above, the degree of photosynthetic acclimation and the increase in leaf carbohydrates in trees in the FACE experiments were low (Nowak *et al.*, 2004; Ainsworth & Long, 2005). Sigurdsson *et al.* (2002) also reported a lack of photosynthetic acclimation (A_{sat}) for the trees investigated in their Scandinavian study.

The reason behind the down-regulation found in many studies is still debated. Stitt & Krapp (1999) and Isopp *et al.* (2000) reported acclimation to be more pronounced when plants were N limited, and to be absent when N supply was adequate. In the majority of the FACE experiments where down-regulations were reported, the down-regulation was observed under particular conditions such as low nutrient conditions or in older but not younger leaves of evergreen species (Nowak *et al.*, 2004). Nowak *et al.* (2004) thus concluded that the photosynthetic down-regulation response seems to be both growth-form and environment specific.

Stimulation of photosynthesis at elevated concentration of CO_2 is theoretically predicted to be greater at higher temperatures (Drake *et al.*, 1997). When FACE data were divided between experiments conducted below 25°C and those conducted above 25°C, this prediction was supported. At lower temperatures (<25°C), A_{sat} was increased by 19%. At temperatures above 25°C, A_{sat} was increased by 30%. In coherence with the FACE-results, Sigurdsson *et al.* (2002) found that the effect of CO_2 was greater at temperatures around 20°C than at 10°C.

4.1.4 Effects of N

The photosynthetic machinery accounts for more than half of the N in a leaf, and photosynthesis is thus strongly affected by N availability (Lambers *et al.*, 1998). A_{max} increases linearly with leaf N concentration, regardless of whether the variation in leaf N is caused by differences in soil N availability, leaf age or species composition. However, the slope of this relationship is much steeper for C_4 plants than it is for C_3 plants (i.e. forest trees; Lambers *et al.*, 1998). According to Lambers *et al.* (1998), the strong A_{max} versus N relationship cannot be due to any simple direct N limitation on photosynthesis. Instead, the entire photosynthetic process is down-regulated under conditions of N limitation, with declines in Rubisco, chlorophyll and g_s. Over longer periods, plants acclimate and adapt to low soil N (and soil moisture) by producing long-lived leaves that are thicker, have a high leaf-mass density (low specific leaf area, SLA) and low leaf N concentrations.

Several studies on forest tree species have shown that high needle N concentrations have a positive effect on photosynthesis. Strand & Lundmark (1995) found that liquid fertilization with a complete nutrient solution reduced winter damage and improved recovery of photosynthesis during spring in Norway spruce stands in northern Sweden. That needle N status strongly affected A_{max} was found by Roberntz & Stockfors (1998), investigating the effects of elevated CO_2 and N on a Norway spruce stand in northern Sweden using the branch bag technique (Figure 1). The latter result was supported by Sigurdsson *et al.* (2002), who found a linear relation between foliage N content and A_{sat} in four field-grown tree species (*P. abies* (L.) Karst, *P. sylvestris* L., *F. sylvatica* L. and *P. trichocarpa*) in a Scandinavian investigation. Furthermore, Roberntz (2001) found that the response of A_{max} to N increased with temperature and that the photosynthetic temperature optimum increased with N status.

Reich *et al.* (1995), investigating the relationship between photosynthetic capacity (A_{max}) and leaf N concentration for trees in the US, also found that mass-based A_{max} was highly correlated with leaf N, in particular for broad-leaved deciduous trees. For evergreen conifers, mass-based A_{max} was also correlated with leaf N. However, the slope of regression was much lower than in broad-leaved species (i.e. a “flatter” relation between A_{max} and N), leading the authors to conclude that “A_{max} -N relationships are fundamentally different for ecologically distinct species groups with differing suites of foliage characteristics: species with long leaf life-spans and low SLA, whether broad-leaved or needle-leaved, tend to have lower A_{max} per unit leaf N and a lower slope and higher intercept of the A_{max} -N relation than do species with shorter leaf life-span and higher SLA”. Reich *et al.* (1995) suggested that there may be indirect advantages of a low poten-

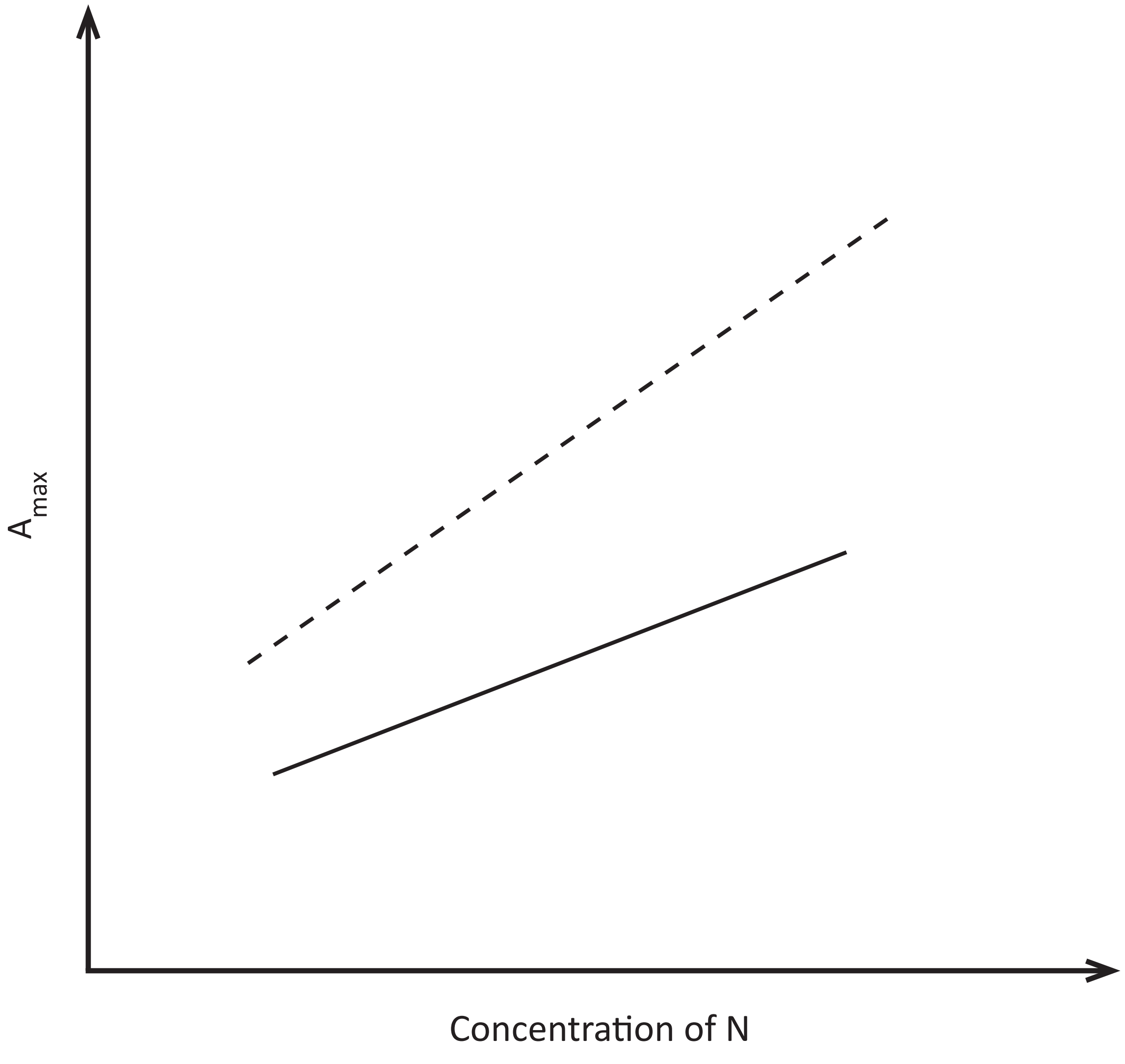


Figure 1. A schematic picture of the relationship between light-saturated photosynthesis (A_{max}) and N concentration in shoots of Picea abies grown at ambient (solid line) and elevated CO_2 (dashed line) using the branch bag technique. Based on graph presented in Roberntz & Stockfors (1998).

tial photosynthetic N-use efficiency, such as lower respiratory costs, extended leaf durability, carbohydrate and N storage functions – characteristics that may enhance competitiveness on nutrient-poor and/or shaded microsites. There may also be other potential N-based functions for evergreen needles outside the context of C gain. Reich *et al.* (1995) suggested that leaf N and SLA together may be more useful in predicting A_{max} among disparate species groups, than either variable alone.

Recently, Ollinger *et al.* (2008) reported that ecosystem CO_2 uptake capacity in temperate and boreal forests scales directly with whole-canopy N concentrations, mirroring the leaf-level trend between photosynthesis and N concentrations that has been observed worldwide.

4.1.5 Effects of WTH

We are not aware of any studies examining the impact of WTH on the photosynthetic capacity of trees in the subsequent generation.

4.1.6 Effects of SH

We are not aware of any studies examining the impact of SH on the photosynthetic capacity of trees in the subsequent generation.

4.2 Plant growth and above-ground production

4.2.1 Effects of temperature

There are many studies that have investigated the impact of an increasing temperature on plant growth. Using a diverse set of forest ecosystem data from across the globe, Litton & Giardina (2008) found that GPP increased linearly with mean annual temperature. Rustad *et al.* (2001), investigating the influence of warming at some grassland, forest and tundra sites, found that above-ground plant productivity increased by on average 19% across the 20 sites for which data was available. In general, the response was greatest in colder ecosystems characterized by lower mean annual precipitation. Suggested reasons for the productivity increase was increased rates of photosynthesis, longer growing season and increased nutrient availability as a consequence of increased rates of litter decomposition and N mineralization. Similar results were found by Beier *et al.* (2008), performing a soil warming experiment along a north-south temperature gradient in European shrubland ecosystems. While warming had significant effects on growth at the northern sites, it had no effect on plant productivity at the warm Mediterranean site. There were no differences in productivity between control plots along the European temperature gradient.

With regard to Sweden, Strömgren & Linder (2002) investigated the impact of soil warming on stem volume growth in a Norway spruce stand in the north of the country. After six seasons of warming, stem volume production (m^3 ha^{-1} yr^{-1}) was 115% higher on heated than on non-heated plots. Heated and irrigated-fertilized plots also tended to have a higher production than unheated and irrigated-fertilized plots. However, this difference was not significant. According to the authors, the increase in growth may be explained by a longer growing season and/or an increased availability of soil nutrients as a consequence of increased mineralization in the heated plots.

Remotely sensed data (Myneni *et al.*, 1997; Lucht *et al.*, 2002) and phenological observations (Menzel & Fabian, 1999; Ahas *et al.*, 2002) do indicate that there has been an increase in the length of the growing season in boreal and northern temperate regions during recent decades. The phenology of boreal forests is mainly driven by temperature, which affects the beginning of the growing season and thereby its duration (Kramer *et al.*, 2000). The main factor determining the timing of budburst (apart from a chilling requirement which is a prerequisite for bud development in the boreal region and which occurs every winter) is the occurrence of mild temperatures in spring (Leinonen & Kramer, 2002). Both Slaney *et al.* (2007) and Hall *et al.* (2009) found that elevated air temperature (trees were grown in whole-tree chambers at temperatures projected to occur at year 2100) hastened both bud development and the initiation and termination of shoot growth in Norway spruce growing in northern Sweden by 2-3 weeks and there was a 1-3 week earlier shift from negative to positive net CO_2 assimilation rate (NAR) compared with the ambient temperature treatment. Once the net C assimilation compensation point (NACP) had been reached, elevated temperature had little or no effect on the development of NAR performance. Similar results were found in experiments with elevated temperature in whole-tree chambers with Scots pine in Finland, where an increase in temperature of 4-5°C resulted in 4-8 weeks earlier budburst (Hänninen, 1995). Earlier budburst could increase the risk of frost injury (Hänninen, 1991; Jönsson & Bärring, 2011). The magnitude of this risk can be debated, however, because climatic warming may also reduce the risk of late frosts (se discussion in Jönsson & Bärring, 2011).

A simulation study using a coupled model describing abiotic and biotic processes in the soil-plant-atmosphere system (the COUP model) at four sites situated in different regions of Sweden showed that an increase in temperature of 2 or 3°C would increase GPP by 24 to 32% in northern Sweden and by 32 to 43% in the southern part of the country (Jansson *et al.*, 2008). The net ecosystem exchange (NEE) increased between 20 and 25% at all sites, according to the authors more or less solely due to increased accumulation of C in tree biomass (changes in soil C were small compared with the current climate). In the north, the increase was related to the combined effect of air and soil temperature extending the growing season. In the south, it was mainly governed by increased N availability due to increased soil temperature and thus mineralization. In coherence with the results of Jansson *et al.* (2008), Finnish model simulations have also indicated an increased yield of boreal Scots pine in response to increasing temperatures (Kellomäki & Kolström, 1993). However, in Finland the enhanced production was more pronounced in the northern part of the country than in the southern part (Kellomäki & Kolström, 1993). An increase in NPP (5-27% for coniferous stands) as a consequence of elevated temperature was also found by Bergh *et al.* (2003), using the process-based simulation model BIOMASS to quantify the effects of increased temperature and CO_2 on NPP of both coniferous and deciduous broad-leaved stands in the Nordic countries. The response was smaller in the milder maritime climate where the current mean temperature rises above 0°C in February and March (5-14%), compared with the colder continental climate (13-27%). The increase in NPP could largely be ascribed to the earlier start of the growing season and more rapid recovery of the winter-damaged photosynthetic apparatus. However, temperature-driven increases in respiration reduced the C gain for all species and sites.

4.2.2 Effects of moisture

In a recent study, Ge *et al.* (2011) investigated the impacts of climate change on the productivity of Norway spruce dominated mixed stands in relation to water availability in southern and northern Finland using the process-based ecosystem model FinnFor. They found that both annual net canopy photosynthesis and total stem wood growth were lower on the southern site under the changing climate compared with current climate, while the opposite was the case for the northern site. In northern Finland, the elevation of temperature lengthened the growing season and increased total photosynthesis over the years. Furthermore, photosynthetic production was increased by the higher atmospheric CO_2 in this part of the country where soil moisture seldom limits forest growth. In southern Finland, on the other hand, less summer precipitation as a consequence of climate change led to water deficit in the rooting zone. Together with enhanced evapotranspiration, this resulted in a decline in stomatal conductance and C uptake. The elevation of CO_2 increased the water use efficiency, but not enough to fully compensate for the effects of the reduced soil moisture in the south. When comparing the results from pure stands of spruce, pine and birch with those from mixed stands, Ge *et al.* (2011) found that the growth of pure Norway spruce stands in southern Finland could be even lower than the growth of Norway spruce in mixed stands under changing climate. The opposite was found for pure Scots pine and birch stands. According to the authors the difference was due to the lower water depletion in the Scots pine and birch stands compared with the Norway spruce stands, since the former have smaller total leaf area than the latter. In coherence with the results of Ge *et al.* (2011), Ge *et al.* (2010) and Kellomäki *et al.* (2008) also found that drought stress episodes may become more frequent in Finland in the future and that they may influence the productivity of Norway spruce stands. While the needle-canopy area expanded under a changing climate, the increasing soil water deficit reduced the canopy stomatal conductance, the transpiration, the humus yield and the nitrogen uptake of the trees (Ge *et al.*, 2010).

Jansson *et al.* (2008), simulating the effects of climate change on four sites across Sweden using the COUP model, also found water stress to be an important limiting factor in the future, especially in southern forests during summer. Water limitation counteracted the improved availability of N, and July GPP in the future climate was thus only slightly higher than July GPP under current climate. According to Jansson *et al.* (2008), summer water stress is not only a consequence of lower summertime precipitation rates, but also of longer growing seasons, increased leaf area index (LAI) values and, consequently, evaporative demand from the atmosphere.

That water deficit can override the positive growth effect of increasing concentrations of CO_2 in the future was also found by Loustau *et al.* (2005) when evaluating the impact of climate change on French forests using the process-based models Castanea, Graeco and Orchidee.

4.2.3 Effects of CO_2

In the short term, rising concentrations of CO_2 increases photosynthesis in many of the woody species that have been studied, which has the potential to yield significant increases in rates of biomass accumulation (Ainsworth & Long, 2005; Körner, 2006; Hyvönen *et al.*, 2007). This is evident in short-term experiments with seedlings grown under controlled conditions as well as in longer-term, whole-stand manipulations. In the FACE experiments, growth and above-ground biomass production generally increased with exposure to elevated concentrations of CO_2 (see reviews by Nowak *et al.*, 2004 and Ainsworth & Long, 2005). However, the magnitude of the response varied between species, growing seasons and experimental conditions. For woody plants and trees grown under non-nutrient limiting conditions, elevated concentrations of CO_2 resulted in greater allocation to wood and woody structures (stem diameter increased on average 9%) and a 28% increase in above-ground dry matter production (Ainsworth & Long, 2005). Trees grown under nutrient limitation, on the other hand, had a non-significant 14% stimulation in above-ground biomass (Ainsworth & Long, 2005). According to Ainsworth & Long (2005), stimulation of growth was generally greater in the third growing season than in the first and second growing season, something that contrasts with the expectation that initial stimulation of growth in response to elevated CO_2 will diminish over time. Persistent growth responses of trees were also reported by Saxe *et al.* (1998). In general, larger responses in growth, biomass and LAI have been observed in trees than other functional types of plants (Saxe *et al.*, 1998; Ainsworth & Long, 2005).

Most studies using various kinds of modelling approaches have also projected increases in boreal forest production as a consequence of climate change. The increases have been suggested to range from 10 to 50% (Briceño-Elizondo *et al.*, 2006; Kirilenko & Sedjo, 2007; Eggers *et al.*, 2008). Pussinen *et al.* (2002) suggested that in the future, the length of the rotation period for Scots pine in southern Finland may decrease by 5-10 years. With regard to Swedish forests, the Swedish Forest Agency (2008) projected a 25% increase in annual stem wood production due to the direct effects of climate change over the next 100 years. Poudel *et al.* (2011), performing the most recent estimate using the process-based model BIOMASS and the empirical forecast model HUGIN, predicted annual forest production in Sweden to increase by 33% and potential annual harvest by 32% over the next hundred years as compared to a reference case without climate change.

Although many studies show increased growth at elevated CO_2, there is often a poor correlation between photosynthetic capacity measured as A_{max} and total biomass production (Lambers *et al.*, 1998). Pinkard *et al.* (2010) concluded that while increases in both NPP and total biomass have been reported at elevated CO_2 concentrations (Saxe *et al.*, 1998; Nowak *et al.*, 2004; Ainsworth & Long, 2005; Hyvönen *et al.*, 2007), a 1:1 translation of photosynthetic responses to growth responses cannot be assumed, and responses can vary from large increases in growth to no change (Körner, 2006). Schleppi *et al.* (2012), for example, found that elevated CO_2 had no overall or sustained effect on growth of trees in a temperate deciduous forest stand in Switzerland over eight years of measurements, despite an enhanced N availability. Tognetti *et al.* (2000) found no radial growth enhancement in their long-term study of five Mediterranean tree species growing near CO_2 vents. Peñuelas *et al.* (2010), investigating the intrinsic water-use efficiency and tree growth at 47 study sites including boreal, wet temperate, Mediterranean, semi-arid and tropical biomes over the past decades using $\Delta^{13}C$ changes and tree ring growth, found that although water use efficiency had increased by 20.5% over the last 40 years, there was no significant overall increase in tree growth and there were no significant trends within biomes or among biomes. Peñuelas *et al.* (2010) thus concluded that the changing climate is already influencing the gas exchange of forests and may be decreasing plant water-use, but that other factors have overridden the potential growth benefits of increased CO_2 levels at many sites, and that the rate of biomass sequestration may not increase with increasing CO_2 concentrations to the same extent as is often implied by biospheric models and short-term elevated CO_2 experiments. In one of the longest studies of continuous exposure of forest trees to elevated CO_2 that exist, holm oak (*Quercus ilex* L.) were grown for 30 years in the vicinity of two natural CO_2 springs in Italy (Hättenschwiler *et al.*, 1997). From this study, early growth enhancements included a near doubling of the annual growth ring size under elevated CO_2. However, a diminishing trend was noted throughout the duration of the study, and at years 25 to 30 there was no additional stimulation of annual growth rings and the CO_2 exposed trees were only marginally larger than the control trees.

According to Pinkard *et al.* (2010), some of the reasons why photosynthetic up-regulation may not translate into increased growth include:

1) Increased exudation of non-structural carbohydrates (NSC) from leaves and roots and increased C transfer to symbionts. Studies of ectomycorrhozal associations with conifers have demonstrated that up to 30% of the assimilated C can be transferred to symbiotic fungi (Söderström, 2002). These sorts of emissions have been found to increase under elevated concentrations of CO_2 in some species (Millard *et al.*, 2007).

2) Increased allocation of NSC to organs with high turnover rates, such as fine roots and leaves. Under elevated concentrations of CO_2, patterns of biomass allocation may change to promote leaf and fine root development (Hyvönen *et al.*, 2007; Lukac *et al.*, 2009 and references therein), both of which constitute temporary stores of biomass.

3) Age-related decline in responses to elevated concentrations of CO_2. Trees can capitalise most rapidly on elevated concentrations of CO_2 when they are in the exponential growth phase prior to canopy closure (Körner, 2006). Hence, an initial large increase in biomass is commonly reported, followed by a decline once canopy closure has occurred (Idso, 1999). This response pattern is supported by long-term dendrochronological studies of trees growing near natural CO_2 vents compared to those growing under ambient CO_2 concentrations, where increased stem diameter growth associated with elevated concentrations of CO_2 was largest when trees were young (Hättenschwiler *et al.*, 1997).

4) Competition for resources. Whether post-canopy closure forests exhibit an increase in biomass at elevated concentrations of CO_2 depend at least partly on whether resources other than C are limiting growth. Oren *et al.* (2001) found that potential increases in biomass of maturing pine were related to N availability, with little or no increase in biomass when N was limiting and large increases when nutrients were added. Also Ise & Moorcroft (2010) emphasized the importance of soil fertility for the effect of CO_2 fertilization on boreal forest dynamics in Canada. Nutrient-limited trees grown at elevated CO_2 generally increased their allocation to below-ground sinks (Linder & Murray, 1998; Oren *et al.*, 2001; Palmroth *et al.*, 2006). King *et al.* (2001), for example, observed a 96% increase in fine-root biomass in a mixed stand of trembling aspen and paper birch, and fine-root production more than doubled under elevated CO_2 in a N-limited *L. styraciflua* forest, the increased presence of fine roots being related to increased N uptake (Norby *et al.*, 2004). However, the increased production does not always result in larger standing root biomass, as root turnover may also increase (Phillips *et al.*, 2006). Elevated concentrations of CO_2 may also accelerate the development of nutrient limitations because of more rapid initial growth rates (Saxe *et al.*, 1998). In a similar fashion, a faster depletion of available water as a consequence of more rapid growth may reduce C assimilation and offset the benefits of elevated CO_2, despite the improvements in leaf-level water-use efficiency (Hyvönen *et al.*, 2007) and whole-tree water use (Cech *et al.*, 2003) that have been observed.

Since tree species differ in their inherent rates of growth and the times during their life cycle when their highest growth rates occur, Pinkard *et al.* (2010) suggested that elevated concentrations of CO_2 is likely to favour more responsive taxa in mixed forest ecosystems, but that other factors such as soil type (as suggested by Körner, 2006), may ultimately determine which species become dominant. In an analysis of C limitation of trees at several different scales, Millard *et al.* (2007) came to a similar conclusion and stated that "the growth of trees is not carbon-limited, with the key to understanding future responses to climate change being turnover of soil organic matter and nutrient cycling".

Although elevated CO_2 is generally assumed to not have any significant effects on spring phenology of trees, such as timing of budburst or rate of shoot development (Jarvis, 1998; Roberntz, 1999, Slaney *et al.*, 2007; Hall *et al.*, 2009), Hall *et al.* (2009) found that later in the season, after the net assimilation compensation point (NACP) had been reached, trees growing at elevated CO_2 had a 30% increase in net assimilation rate (NAR) compared with trees in the ambient CO_2 treatment. Consequently, shoots grown at elevated CO_2 assimilated their own mass in terms of C earlier than shoots growing at ambient CO_2. Hall *et al.* (2009) thus concluded that under the climate regime predicted for Sweden in 2100 (Swedish Regional Climate Modelling Programme, SWECLIM; Christensen *et al.*, 2001), current-year shoots of Norway spruce will assimilate their own mass in terms of C 20 to 30 days earlier compared with current climate, and thereby significantly contribute to canopy assimilation during their first year.

4.2.4 Effects of N

The well-known growth-nutrient response curve (Figure 2) has three clearly defined regions: 1) the deficient range, where growth rate increases with increasing nutrient supply, 2) the adequate range, where growth rate reaches a maximum and remains unaffected by nutrient supply and 3) the toxic range, where growth rate falls with increasing nutrient supply (Kimmins, 1997; Marschner, 2003). Boreal and temperate forests have generally been regarded as N limited ecosystems and many old fertilization experiments in Sweden have indicated a positive response of N on tree growth (reviewed in Nohrstedt, 2001). N addition has thus most often been regarded as a positive measure from a forest production perspective. However, recent investigations have demonstrated rather variable reactions of forests to an increased input of N. In these studies, no significant effects on tree growth (Christ *et al.*, 1995; Persson *et al.*, 1995; Magill *et al.*, 1997; Sikström 1997; 2002; Emmett *et al.*, 1998; Pettersson & Högbom, 2004) are as common as positive ones (Mälkönen, 1990; Andersson *et al.*, 1998; Tamm *et al.*, 1999; Jacobson & Pettersson, 2001). In some areas, particularly those with acid soils and high N deposition, N fertilization may even result in a decrease in tree growth. Nilsson *et al.* (2001), for example, reported a decline in tree growth rate in the Skogaby experiment in southern Sweden. Initial increases in tree growth in

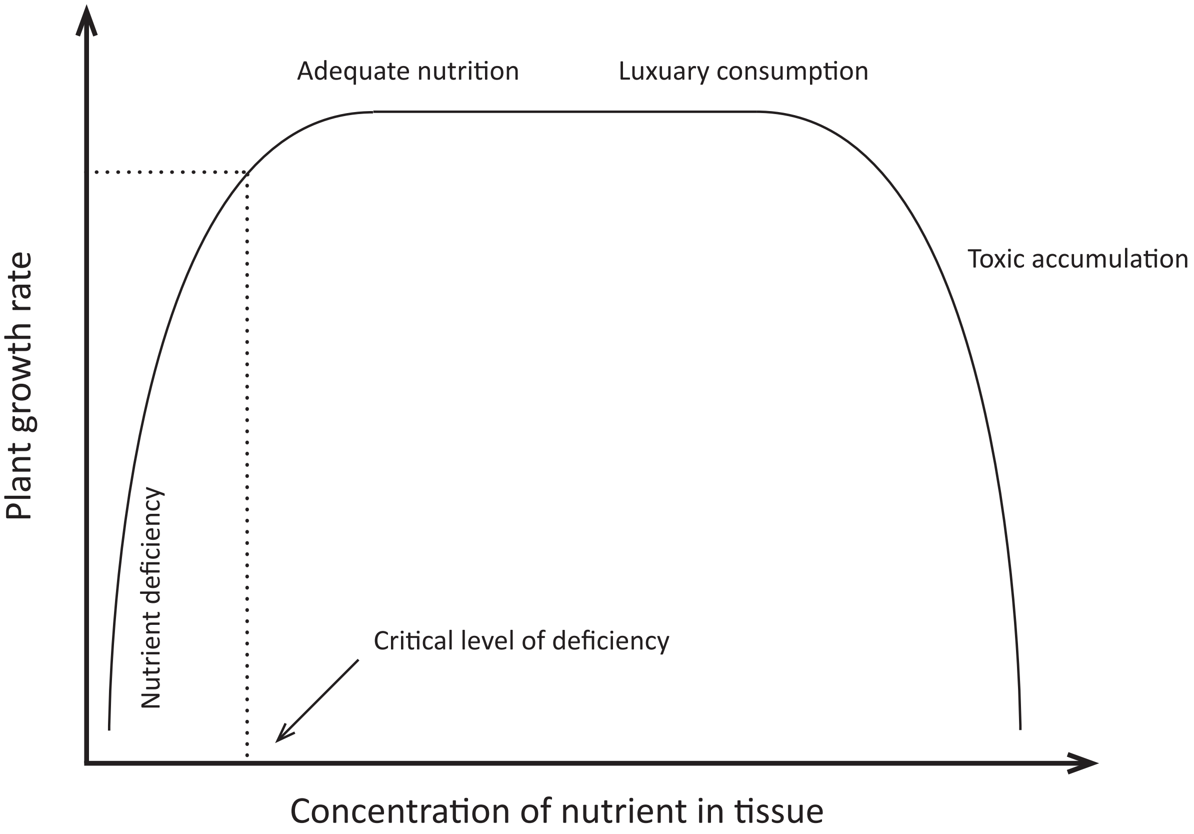


Figure 2. Relationship between the growth of a plant and the concentration of nutrient in its tissue. If an addition of a nutrient increases plant growth but has little effect on the concentration of the nutrient in the plant, the plant is nutrient deficient. If such an addition results in little change in growth but an increase in the concentration of the nutrient in the plant tissue, the plant is adequately nourished. If the addition results in high concentrations of the nutrient in plant tissue but a decrease in growth, the nutrient has reached toxic levels. Modified from Kimmins (1997).

response to inputs of 100 kg N ha^{-1} yr^{-1} as $(NH_4)_2SO_4$ were replaced by decreased production rates after the first six years of N additions. After an additional four years, production values of fertilized trees were 15% below production values of the control. Similar results have been found in forest stands in Switzerland (Braun *et al.*, 2010) and in spruce-fir stands in New England (McNulty *et al.*, 1996; 2005). Consistent declines in wood accumulation rates from the very start of the fertilizer application have been demonstrated for a heavily polluted spruce forest in the French Ardennes, following an addition of 100 kg N ha^{-1} yr^{-1} as NH_4NO_3 in 1981 and 1983 (Bonneau *et al.*, 1990), and in a pine stand in the United States after application of 150 kg N ha^{-1} yr^{-1} as NH_4NO_3 (Magill *et al.*, 1997; 2004). Another example of a negative growth response to N is provided by Boxman *et al.* (1998), showing a 50 percent increase in tree growth at a Scots pine stand in the Netherlands, following a reduction of N and S inputs using an exclusion roof.

Another approach was taken by Nelleman & Thomsen (2001). They analysed radial increment data from increment cores of more than 31 000 spruce forest plots in southern Norway from 1954 to 1996. Using a combination of a biostratification model and a catchment model for acidification, they demonstrated a spatial and temporal co-variation between forest growth and N deposition and acidification. The initial increase in growth as a consequence of long-term atmospheric input of acidifying and fertilising compounds was turned into a decrease in growth when the critical loads for acidification were exceeded.

The observed reductions in growth reported in the studies referred to above have most often been attributed to the acidifying effect of N, a result of NH_4^+ uptake and/or nitrification of the applied NH_4^+. The subsequent increase in solubility and consequently uptake and leaching of base cations (Binkley & Högberg, 1997) may result in imbalanced nutrient to N proportions in the photosynthetic tissue (Mohren *et al.*, 1986; Flückiger & Braun, 1998; Flückiger & Braun, 1999). The presence of NO_3^- ions have commonly been reported to enhance the leaching of base cations, and the increased concentrations of N in foliage tissue commonly observed at elevated N input (Hüttl 1990; Sikström, 1997; 2002; Jacobson & Pettersson, 2001) to accelerate the nutrient imbalances.

However, several other explanations have also been brought forward as likely mechanisms behind the decreased growth rates. It is well-known that an increased availability of N increases the allocation of C to growth, particularly shoot growth, resulting in changes in the root: shoot ratios of plants (Ericsson *et al.*, 1996; Marschner, 2003). For forest trees, this change has been demonstrated to be apparent already at 25 kg N ha^{-1} yr^{-1} (Flückiger & Braun, 1999), an addition rate that is rather modest even for practical forestry. Another consequence of an elevated N input into forest ecosystems is a reduction in the EM colonization and growth of external mycelia (Brunner, 2001; Nilsson & Wallander, 2003; Nilsson, 2004). Both of these changes are likely to influence tree uptake of nutrients. In a modelling study by Eliasson & Ågren (2011), investigating the feedback from slowly increasing soil inorganic N levels (comparable to deposition) on N mineralisation and tree growth in six boreal Scots pine stands in Sweden using the Q-model, the reduced growth response of trees to N was found to be a function of N immobilisation increasing with increasing soil N availability. The interaction between N and secondary stress factors is another mechanism that may be of importance for tree growth responses to N. A decrease in the protein precipitating capacity of trees and in the foliar concentrations of phenolics and tannins in response to increased N has commonly been observed in both gymnosperms and deciduous trees (Balsberg-Påhlsson, 1992; Muzika & Pregitzer, 1992; Joseph *et al.*, 1993; Schafellner *et al.*, 1994; Hättenschwiler & Schafellner, 1999), but only a few studies have demonstrated increased pathogen attacks with increasing fertilization levels (Flückiger & Braun, 1998; Flückiger & Braun, 1999).

4.2.5 Effects of WTH

Most Scandinavian studies to date show no effect (Egnell & Leijon, 1999; Egnell & Valinger, 2003; Saarsalmi *et al.*, 2010) or a positive effect (Egnell & Leijon, 1999) of WTH as compared with conventional stem harvesting (CH) on seedling survival of coniferous trees, although there are exceptions (Wall & Hytönen, 2011).

Growth, on the other hand, seems to be more negatively affected. The total basal area over bark at breast height, wood biomass and height growth in a Scots pine stand in southern Sweden were all reduced 24 years after WTH (Egnell & Valinger, 2003). The trees that were grown on CH plots produced 20% more wood and bark biomass above stump than trees on WTH plots. Negative effects of WTH on growth was also found by Egnell & Leijon (1999), investigating the effects of WTH on growth in four coniferous stands (including the one referred to in Egnell & Valinger, 2003), two of them situated in the southern part of the country and two of them in the northern part. Furthermore, Helmisaari *et al.* (2011) presented results from comparisons of 22 field experiments in Finland, Norway and Sweden (representing a range of site types and climatic conditions) where volume increments of pine stands were 4 and 8% lower, and those of spruce stands 5 and 13% lower, on WTH plots as compared with CH plots during the first and second decades after clear-cut (Jacobson *et al.*, 2000; Helmisaari *et al.*, 2011). In a Norway spruce stand in central Finland, Wall & Hytönen (2011) found that WTH with needles left on site reduced the total stem volume of the stand, and, consequently, site productivity, 30 years after planting because of lower density of naturally regenerated seedlings. Jacobson (2000), investigating the effects of slash removal in four whole-tree thinned stands distributed across Sweden (one fertile Norway spruce stand in the south-west and three Scots pine stands in south, south-central and central Sweden), also found significant negative effects on growth of trees (7-17%) during the first ten years after the first thinning.

Results similar to those of the Nordic studies have also been found for other tree species and in other countries – for Sitka spruce in the UK (Proe & Dutch, 1994; Proe *et al.*, 1996; Walmsley *et al.*, 2009; Vanguelova *et al.*, 2010; Mason *et al.*, 2012), for Douglas fir in coastal Washington (Ares *et al.*, 2007) and for loblolly pine (*Pinus taeda* L.) in south-eastern US (Scott & Dean, 2006). In Mason *et al.* (2012), the benefits of leaving brash on site was not clearly evident until the last stages of the establishment period for Sitka spruce (which is after around ten years), highlighting the need for long-term studies if valid conclusion about the effects of WTH on growth are to be drawn. Today, longer-term scientifically published experiments (>30 years) on the effects of WTH on growth of trees are basically missing.

Although many studies show decreased growth as a consequence of WTH, there are exceptions. In the North American long-term soil productivity (LTSP) program, no significant effects of WTH on tree growth was found (Fleming *et al.*, 2006). Similar results were presented by Saarsalmi *et al.* (2010) for two Scots pine stands in eastern Finland 22 years after clearcut and in one of the pine stands investigated in Egnell & Leijon (1999). A modelling study by Belyazid *et al.* (2008), using the dynamic models ForSAFE-VEG to investigate the effects of WTH compared with CH on several different parameters in spruce-dominated forest stands in Sweden, also showed no effect of WTH on growth in any part of the country. De Jong & Lönnberg (2010) refer to several studies where there are no significant negative effects, or even positive ones, on growth as a consequence of WTH. However, none of these studies are peer-reviewed and published in international scientific journals.

Several different explanations for the reduced growth of trees after WTH have been put forward, for example changes in the microclimatic conditions and less competition from weeds where logging residues were retained (Proe & Dutch, 1994; Devine & Harrington, 2007). Egnell & Leijon (1999), however, found that mean height and basal area were almost the same on plots where needles had been left (while removing branches and stems) as on plots exposed to CH. They thus suggested that the reduced growth after WTH was a consequence of reduced nutrient availability after WTH. Their finding was supported by Helmisaari *et al.* (2011), who showed that compensatory fertilization with NPK increased the volume increment in WTH plots, so that it equalled that of CH plots. Similar conclusions were drawn by Mason *et al.* (2012), investigating the influence of WTH on growth of three Sitka spruce stands in upland Britain. They found that the growth reduction as a consequence of WTH was largest at the site classified as a high-risk site (i.e. a nutrient poor site). At all three sites, the reductions in growth as a consequence of WTH could be avoided if fertilizer was applied. The effect of the fertilizer was much reduced where brash had been retained on site. Also Scott & Dean (2006) found that the magnitude of the growth response in a loblolly pine stand subjected to WTH was related to the inherent productivity of the site and to the soil P availability. Tan *et al.* (2009) reported that

the effects of WTH on lodgepole pine (*Pinus contorta* Dougl. Ex. Loud.) and Douglas fir (*Pseudotsuga menziesii* var. menziesii) in Canada was site and soil specific. In non-compacted soil, there was a positive growth effect on seedlings three years after WTH. In moderately compacted soil, on the other hand, WTH reduced growth of both tree species.

An important question is whether the reduced productivity as a consequence of WTH remains during the whole rotation period, or if it is a transient phenomenon. A calculation by Egnell & Valinger (2003), based on the 20% decrease in wood and bark biomass in trees grown on WTH plots, showed that for one rotation this reduction corresponded to a production loss of 0,8 m^3 ha^{-1} yr^{-1}, resulting in a total loss of 68 m^3 for the entire rotation period (if final stand age is 85 years). In other words, trees on sites where WTH has been applied must grow approximately 13 years longer before the same total production is achieved as for trees on sites with CH (Egnell & Valinger, 2003). Egnell & Valinger (2003) suggested, however, that at a stand age of 24 years (i.e. at the age of their measurements), all negative effects on growth have been reached. No more loss of volume growth can be expected and an increase in the rotation period of only three years will thus be the result, the argument being that the initial growth reduction is a consequence of N deficiency at seedling establishment. Egnell & Leijon (1999) also suggest that a short-term decrease in growth rate will to some extent be offset by a more successful regeneration, resulting in a denser stocking if logging residues are utilized. However, looking at the data on basal area, height and volume presented in Egnell & Leijon (1999) and Egnell & Valinger (2003), there is no convincing trend of the negative growth effects diminishing over time. In contrast to Egnell & Valinger (2003), several other authors have suggested that logging residues are a slow-release fertilizer (Smolander *et al.*, 2008; Hyvönen *et al.*, 2000). Hyvönen *et al.* (2000), for example, reported that Scots pine and Norway spruce needles loose only 30-50% of their initial amount of N within the first six to eight years after harvest, and that no net release of N from branches occurs during the first eight years. Modelling approaches have shown that at some sites, it takes more than 20 years for half of the initial N to be released from the logging residues, indicating that nutritional constraints may be rather long-lived.

Several studies investigating the effects of WTH have emphasized the differences between the controlled conditions in experimental manipulations and the current conditions during forest harvest operations. Under experimental conditions, logging residues are generally evenly distributed and there are no strip roads on the plots. At forest harvest operations, logging residues are usually left on the strip roads and in small heaps, possibly leading to more small-scale variation (see for example Helmisaari *et al.*, 2011).

4.2.6 Effects of SH

With regard to disturbance level, SH is sometimes compared with mechanical site preparation. Such preparation generally promotes rapid establishment of seedlings by improving seedling nutrient supply, raising soil temperatures during the growing period, improving the soil structure in the seedling rooting zone and reducing competition (both above- and below-ground; Örlander *et al.*, 1996; Hope, 2007). Egnell *et al.* (2007) concluded, mainly based on a number of reports by Kardell (not published in peer-reviewed scientific journals), that SH is unlikely to reduce stand productivity in the short term. However, there is still not sufficient information available to conclude about the long-term impact.

Furthermore, the majority of studies on SH effects have been performed on pathogen-infested sites. Root rot is a wide-spread problem in Sweden and other European countries as well as in North-America, and SH has been regarded as one of the most efficient ways to reduce disease levels of root rot fungi such as *Heterobasidion*, *Armillaria* and *Phellinus*. A recent review by Vasaitis *et al.* (2008) showed that when SH is undertaken to remove root-rot infested stumps, root rot in the next generation of trees is generally reduced. This is not surprising considering that tree stumps play a major role in the life cycles of pathogens, promoting disease development in several different ways. The compilation of data by Vasaitis *et al.* (2008) showed that of 29 trials, a growth increase was reported in 13 cases (45%; six different tree species from western North America and Europe), low or no impact was reported in 10 cases (34%; six different tree species from western North America and Europe), and a growth decrease was reported in 6 cases (21%; three tree species from North America). A review by Walmsley & Godbold (2010), also compiling a number of studies investigating the effect of SH and site preparation treatments (that may be comparable in terms of disturbance) on various tree species from Europe and North America gives a somewhat more pessimistic view. In their review, five studies reported an increase or no change in productivity (i.e. increased productivity at some sites included in the study while no change at others), five reported a decrease, and two reported no change. Looking only at studies where actual SH took place, two showed increased productivity, two showed decreased productivity, one showed no change and two showed increased productivity or no change. Based on their findings, Walmsley & Godbold (2010) concluded that productivity on sandy loams and podzols tended to benefit from SH, whereas productivity was generally more negatively affected on organic and ash-cap soils.

The effects of SH on growth also seem to depend on the tree species. Hope (2007) found that SH in combination with soil scarification in a lodgepole pine (*P. contorta*) and hybrid spruce (*Picea glauca* (Moench) Voss x *Picea engelmanii* Parry) stand in Canada had differing effects depending on the species and the age of trees. Height and diameter growth of pine was positively affected by SH and scarification under the whole ten-year period when the study took place. SH alone had a somewhat smaller effect on pine growth. Spruce, on the other hand, only showed a positive effect as compared to the control at year three. Page-Dumroese *et al.* (1998) found that both Douglas fir (*Pseudotzuga menziesii* var. glauca [Beissn.] Franco) and western white pine (*Pinus monticola* Dougl. ex D. Don) were negatively affected by stump removal, but that the Douglas fir was considerably more so than the white pine.

Vasaitis *et al.* (2008) also emphasized that it is unclear if, and to what extent, SH for biofuel on clear-felled sites could reduce the occurrence of *Heterobasidion* and *Armillaria* in the next forest generation, and thus improve seedling survival and growth, since harvest for sanitation purposes usually require a rather thorough removal. Furthermore, the efficacy of SH in reducing the incidence of damage from other pests and pathogens, such as the large pine weevil (*Hylobius abietis*) and the European spruce bark beetle (*Ips typographus*), remains unclear (Vasaitis *et al.*, 2008).

4.3 Root growth and mycorrhiza production

Root systems comprise up to half the total tree biomass (Karnosky, 2003) and Giardina *et al.* (2005) estimated that globally, the flux of C to below-ground in terrestrial ecosystems exceeds the C emitted to the atmosphere through combustion of fossil fuels by an order of magnitude (approximately 6 versus 60 Gt C yr^{-1}). Despite the magnitude of the flux, it remains one of the least understood C fluxes in the terrestrial C cycle. It has been estimated that between 33 and 67% of forest NPP may be allocated to fine roots (Matamala *et al.*, 2003) and Chapin *et al.* (2009) recently emphasized plant C allocation to below-ground as a critical determinant of soil C sequestration.

4.3.1 Effects of temperature

With respect to the effects of temperature on C allocation within trees and root production, the relationships are complicated. For non-arid temperate and tropical forests, partitioning to total below-ground C flux (TBCF) increases with increasing mean annual temperature (MAT; Giardina *et al.*, 2005; Litton & Giardina, 2008). However, for boreal forests, the partitioning of GPP to TBCF tends to decrease with MAT (although not significantly; Litton & Giardina, 2008). Similar results were found by Vogel *et al.* (2008), investigating a North American gradient of boreal black spruce (*Picea mariana*) forests. The decrease in partitioning of GPP to TBCF with increasing MAT at boreal sites might be related to increases in soil nutrient availability as a consequence of increased annual average soil temperatures (Vogel *et al.*, 2008), as seen in some soil warming experiments (Rustad *et al.*, 2001; Melillo *et al.*, 2002). Increased resource supply has previously been found to decrease the fraction of GPP partitioned to below-ground (Litton *et al.*, 2007). Litton & Giardina (2008) also found that the fraction of TBCF that is used for below-ground net primary production (BNPP; that what is not used for autotrophic respiration, i.e. coarse and fine root production, root mortality, losses to herbivory, root exudation, mycorrhizal growth and turnover) varied between 0.26 and 0.53 across the entire MAT gradient (-5 to +30°C), with a much narrower range for temperate and tropical systems (0.42 to 0.53). Both TBCF and BNPP were positively and linearly related to MAT, with the fraction of TBCF that is BNPP appearing to increase with both temperature and below-ground resource supply (water and nutrients; Litton & Giardina, 2008).

The review by Pendall *et al.* (2004) showed that higher root temperatures are generally associated with increased fine root production, but also mortality and thus turnover rates. Lambers (1998), on the other hand, suggested that the investment of biomass in roots is lowest at a certain optimum temperature and that it increases at both higher and lower temperatures.

4.3.2 Effects of moisture

In a meta-analysis on EM roots by Cudlin *et al.* (2007), the most evident effect found was the decrease in fine-root biomass during drought. A relative increase in the allocation of C to below-ground organs at the expense of above-ground ones during a mild drought has often been found, and even absolute root growth may increase during a mild drought (Becker *et al.*, 1987), as can bee seen in for example *Quercus* species which have a proportionally large investment in roots under moderately dry conditions (Osonubi & Davies, 1981; van Hees, 1997; Vivin & Guehl, 1997). However, when the water stress becomes more severe, reductions in root growth are common (Joslin *et al.*, 2000). Reduced input of labile C to the soil under drought conditions were also observed by Ruehr *et al.* (2009).

By contrast, the fractional colonization of EM in the meta-analysis by Cudlin *et al.* (2007) did not show a reduction as a consequence of water stress. This may, according to the authors, be due to a negative effect of drought on the total number of root tips. The rates of recovery of roots from drought have been very little studied. However, there are studies indicating that fine-root growth and root tip formation can respond very quickly to resumed soil moisture (Joslin *et al.*, 2000).

4.3.3. Effects of CO_2

According to the review by Lukac *et al.* (2009), a common response to elevated CO_2 is an increase in the allocation of C below-ground. This increase might be the result of a shift in C allocation between foliage and roots, increased production and turnover of fine roots, greater proliferation of mycorrhizal symbionts or increased root exudation, all but the exudation having been observed in FACE experiments (Lukac *et al.*, 2009). The largest increase in C allocation below-ground was found in forest ecosystems still in their initial expanding state (Lukac *et al.*, 2009). In coherence with the FACE results, Treseder (2004) reported a near 50% increase in mycorrhizal abundance as a consequence of elevated CO_2, and a meta-analysis by Cudlin *et al.* (2007) also demonstrated a positive response of EM roots to elevated CO_2. Furthermore, Hu *et al.* (2006) reported that about two-thirds of 135 experiments on trees and herbaceous plants observed an increase in the infection and external fungal hyphae of both arbuscular mycorrhizae (AM) and EM under elevated CO_2. No studies reported negative effects on mycorrhizal colonization or extraradical biomass. An increase in root tip abundance under elevated CO_2 is consistent with reported changes in root:shoot ratio under elevated CO_2, especially under conditions of nutrient limitation (see review by Cudlin *et al.*, 2007). According to Iversen (2010), increased fine-root allocation could drive changes in soil C storage and N cycling because fine roots turn over quickly in forests and contribute large amounts of C and N to the soil system. At the FACE sites, the increase in fine root biomass as a consequence of elevated CO_2 was in most cases accompanied by a higher fine root turnover (27-55%), which resulted in higher C input into soil via root necromass (Lukac *et al.*, 2009). King *et al.* (2001) reported a 140% increase of fine root necromass, alongside an increase of live fine-root biomass in one of the FACE forest experiments (Aspen). In addition to C input from necromass, Lukac *et al.* (2009) emphasized the C inputs thought to occur from exudation of low molecular weight organic acids or root mucilage. There are very few field studies of root exudation. Of the few studies that do exist, some have reported an increase in exudation as a consequence of elevated CO_2, while others have reported no effect (see Lukac *et al.*, 2009 and references therein). A significant increase of water soluble C and extractable C, representing the most labile C fraction in the soil and thus thought to at least partly originate from root exudates, have been reported in the EuroFACE experiment and in the Duke forest experiment (Lukac *et al.*, 2009 and references therein).

Experimental evidence from a diverse set of forested ecosystems (ranging from FACE experiments in mature forest plantations to tree seedlings and saplings planted in open-top chambers) have also indicated that fine roots of trees exposed to elevated CO_2 are distributed more deeply in the soil profile relative to trees grown under ambient CO_2 (see review by Iversen, 2010). According to Iversen (2010), 73% of the studies examining rooting depth responses to elevated CO_2 found deeper rooting distributions under elevated CO_2. This does not mean that fine roots developed under elevated CO_2 are generally found deeper in the soil than fine roots developed under ambient CO_2. Rather, the relative increase in root production under elevated CO_2 is often greatest below 15 centimeters depth, resulting in a larger proportion of root biomass at deeper soil depths under elevated CO_2 (Iversen, 2010). Deeper rooting distributions have also been observed under elevated CO_2 without an overall increase in root production (i.e. a redistribution of roots below-ground). According to Iversen (2010), the increased proliferation at depth is not limited to fine roots, but evidence exists also for coarse roots and mycorrhizas (see references in Iversen, 2010). While mycorrhizal infection rates tend to decline with soil depth in natural ecosystems, there is evidence that both EM and AM has higher root infection rates deeper in the soil profile when CO_2 is elevated (Iversen, 2010 and references therein).

While much work has been done to examine root proliferation in the soil in response to resource patches, the causes of increased root proliferation throughout the soil under elevated CO_2 remain relatively unexplored. Iversen (2010) stated three factors to which the deeper rooting distributions are likely to be related: 1) increased resource demand as forest production increases in response to CO_2 enrichment, 2) increased C available for allocation to root growth, 3) limited resource availability in shallower soil as a result of increased microbial or plant competition. These three factors will according to Iversen (2010) probably interact to determine root distribution throughout the soil profile, but mining for nutrients is likely to be one of the main factors responsible for greater root proliferation at depth under elevated CO_2. This reasoning is supported by the review of Stitt & Krapp (1999), giving examples showing that increases of the R:S ratio generally occurs only when plants are N limited, while it is absent when plants are well fertilized. However, roots also proliferate in water zones (Hodge, 2004) and greater root production at depth may thus also occur in response to increased tree water-use under elevated CO_2 (Uddling *et al.*, 2008). In fact, some studies have indicated that drought stress might be, or may become, one of the major limiting factors for growth, at least in certain parts of the boreal and temperate regions (see section 4.2.2).

The consequences of increased fine-root proliferation and turnover at depth are still poorly understood, but are expected to affect important ecosystem processes. In general, as soil depth increases, microbial activity, nutrient availability and root decomposition rates often decline, changes that according to Iversen (2010) might result in altered nutrient uptake rates, slower turnover and changes in the rate at which root detritus is incorporated into SOM. In addition, the increased proliferation of roots at relatively unexplored depths under elevated CO_2 may affect previously stable organic matter pools deeper in the soil. According to Iversen (2010), the energy gained in deeper soils from fresh inputs of labile C and N compounds from root exudates or of detritus from root turnover may be more important than temperature and moisture in stimulating the decomposition of ancient C situated deeper in the soil profile. Rhizosphere priming through exudation by living roots has been shown to stimulate decomposition of organic matter and also stimulate N mineralization (see Iversen, 2010 and references therein). As up to 50% of soil C is stored below 20 cm in forests, even small changes in C inputs at depth in soil can, according to Iversen (2010), have drastic consequences for long-term C storage. In contrast to the stimulatory effect of fine-root inputs on the decomposition of organic matter at depth in soil, root-derived inputs have been shown to be disproportionally important for the formation of stable microaggregates in the soil system (Iversen, 2010).

4.3.4 Effects of N

Nutrient availability plays a major role in determining the allocation of C between above- and below-ground growth of forest trees, but there exists an important interaction with moisture (Kimmins, 1997). Lack of soil moisture reduces soil animal abundance and activity, reducing litter communition and soil mixing, promoting slowly the decomposing, acidic, fungal-dominated forest floors with lower rates of nutrient mineralization, and leading to poor nutrition. Poor tree nutrition will reduce the quality and quantity of litterfall, reducing nutrient availability even further, ultimately resulting in greater allocation to fine roots (Kimmins, 1997).

In contrast, increasing N supply usually enhances both shoot and root growth. Generally, shoot growth is more stimulated than the root growth, leading to a fall in root-shoot dry weight ratio (Marschner, 2003), with subsequent implications for nutrient uptake in the long term. However, there are exceptions. Some N deposition studies have suggested that root turnover and production instead increases with increasing N (Gundersen *et al.*, 1998).

With regard to mycorrhiza, there are many studies indicating no effect at all on EM fungi as a consequence of N fertilization (Cudlin *et al.*, 2007 and references therein), including some from Scandinavian coniferous stands. Arnebrant & Söderström (1989) noted little change with regard to mycorrhizal infection frequency when investigating a *P. sylvestris* stand that had received N fertilization 13 years prior to sampling. Exposure of *P. sylvestris* seedlings to NO_X for short periods of time (<39 days) had no significant effect on EM colonization levels (Näsholm *et al.*, 1991). Furthermore, Kårén & Nylund (1997) observed no decline in fractional EM colonization of *P. abies* following continued fertilization (around 5 years), although the number of short lateral roots, and hence the total EM number, decreased. Similar results were reported by Nilsén *et al.* (1998), who found no significant effects on mycorrhizal colonization or mycorrhizal types when investigating a Norway spruce stand in southern Norway.

However, there are also studies reporting the opposite result. Brunner (2001) and Nilsson (2004), for example, found that a high N input influenced the EM colonization of roots and mycelial growth negatively. Treseder (2004), performing a meta-analysis on only field-based manipulations of N, found that the fractional colonization decreased significantly (15%) across studies. In the review by Cudlin *et al.* (2007), several of the studies included also reported a decrease in the fractional colonization by EM fungi or in the total number of EM roots as a consequence of N fertilization. However, the decrease in the EM colonization was sometimes rather short-lived and disappeared after only a few years of treatment (Cudlin *et al.*, 2007).

With regard to the diversity of EM fungi, the response to fertilization seems to vary among species with certain taxa declining in abundance and diversity, while others continue to flourish at higher deposition levels (Lilleskov, 2005; Cudlin *et al.*, 2007). Considering the large variation in N responses among studies, Cudlin *et al.* (2007) suggested that the predictability of N effects on fine roots and mycorrhizas for any given ecosystem is relatively low, and that it may be influenced by factors such as the amount and form of fertilizer added, site conditions, tree species and stand age.

4.3.5 Effects of WTH

There are very few studies investigating the impact of WTH on root growth and mycorrhiza. With regard to root growth, we are not aware of any. With regard to EM, repeated removal of harvesting residues (after clear-cut and in subsequent thinnings) was found to have no effect on the production of external mycelium in a Norway spruce stand in south-western Sweden slightly less than 40 years after clear-cut (Hagerberg & Wallander, 2002). Furthermore, no effect on the species composition of EM was detected (Mahmood *et al.*, 1999). However, Mahmood *et al.* (1999) found a decrease in the number of EM root tips, both per metre root length and per unit humus volume, something that could result in a lower capacity to access nutrients.

4.3.6 Effects of SH

Menkis *et al.* (2010) reported a negative effect on mycorrhization of Norway spruce seedlings grown in plots that had stumps removed as compared with other treatments (mounding, mounding and removal of slash and removal of slash and stumps). Since SH had a positive effect on growth of the seedlings, Menkis *et al.* (2010) suggested that the altered soil conditions due to the site disturbance by stump and slash removal might be more favourable for tree growth than more abundant mycorrhization of their root systems in less disturbed soils. However, the treatments were not replicated and Menkis *et al.* (2010) emphasized that results should be interpreted with caution.

4.4 Litterfall

The quantity of C transferred from trees to soil by above- and below-ground litterfall is primarily a function of the tree biomass. Within Sweden, tree litter production has been shown to be related to the above-ground tree biomass (see for example Berggren Kleja *et al.*, 2008) and, accordingly, shows a clear south-north gradient. However, a growing number of studies have indicated that also forest floor vegetation contribute significantly (10-30%) to NPP in boreal forests (O'Connell *et al.*, 2003). The longevity of above- and below-ground components of major forest floor species is poorly known, making estimates of their contribution to litter production uncertain. In the study by Berggren Kleja *et al.* (2008), no clear north-south gradient in total litterflux at three Swedish Norway spruce stands (situated in the north, middle and south of the country) were found. The tree litter input was highest at the southernmost site, but at the two northern sites the lower tree litter input was largely balanced by a considerable input of litter (27%) from the field layer (shrubs, herbs and grasses) and bottom layer (mosses, lichens) vegetation, indicating that field and bottom layer vegetation contribute significantly to litter production. The importance of the field-layer vegetation for the C and nutrient cycling of northern boreal forests have also been emphasized in the studies by Kolari *et al.* (2006) and Helmisaari *et al.* (2007).

In many types of forest, shrub and herbaceous communities, there is a greater annual turnover of organic matter below-ground than above-ground. Although very little studied, recent investigations have shown that below-ground litterfall is a major pathway of nutrient loss from plants (Kimmins, 1997), and it does seem like fine-root litterfall varies according to both stand age and site productivity (Vogt *et al.*, 1996; Attiwill & Adams, 1993).

4.4.1 Effects of temperature

Higher temperatures are generally associated with higher NPP (see section 4.2.1). Provided no other resources are limiting, increased temperature thus has the potential to provide more substrate to the soil (Pendall *et al.*, 2004).

4.4.2 Effects of moisture

In general, both total above-ground litterfall and leaf litterfall of forests increase from polar regions towards the equator, paralleling an increase in biomass and NPP (Kimmins, 1997). Since factors affecting production positively also affect litterfall positively, litterfall losses are generally greatest on moist, warm, fertile and other high-productivity sites and least on dry, cold, infertile and other low-productivity sites (Kimmins, 1997).

4.4.3 Effects of CO_2

The higher production under elevated CO_2 (see section 4.2.3) will most likely result in production of additional litter. According to the review by Hyvönen *et al.* (2007), this litter is expected to be energy-rich but nutrient poor with high C/N ratios. Norby *et al.* (2001) found that N was reduced by on average 7.1% and lignin by 6.5% in leaves of plants grown at elevated CO_2 compared with those grown at ambient levels. Other studies have also showed effects of elevated CO_2 on leaf chemistry, for example decreased N concentrations (Norby *et al.*, 1999) and changes in foliar concentrations of starch (Kainulainen *et al.*, 1998). In contrast to Norby *et al.* (2001), Verburg *et al.* (1999) found decreased lignin concentrations in leaves of *Betula pubescens* as a consequence of elevated CO_2. Chapin *et al.* (2009), linking plant-soil C dynamics to global consequences, emphasized that elevated CO_2 can give rise to litter that is more resistant to microbial breakdown. Growth at elevated CO_2 may also affect decomposition by changing the amount of and the dynamics of litterfall (Schlesinger & Lichter, 2001) or by modifying litter quality through changes in plant community composition.

4.4.4 Effects of N

An increase in the amount of available N has in many studies been associated withincreased growth (section 4.2.4) and, consequently, increased litter production.

A decrease in the rate of root turnover with increasing litterfall and return of N from plant to soil in litterfall for broad-leaved forests across the world was reported by Attiwill & Adams (1993), based on results by Vogt *et al.* (1986) as well as on their own data. The authors suggested the decrease to be a function of the decrease in root:shoot ratio with increasing productivity.

4.4.5 Effects of WTH

In a forest subjected to WTH, slash is removed from the forest with the result that litter is lost from the ecosystem. According to Palviainen *et al.* (2010), the amount of C contained in above-ground logging residues amounts to 10 000 kg C ha^{-1} for pine stands and 17 000-20 000 kg C ha^{-1} for spruce stands.

4.4.6 Effects of SH

In a forest subjected to SH, the stumps and the roots that are attached to the stumps are removed from the system and, subsequently, the C in them is lost from the ecosystem. Of the total below-ground biomass, coarse and structural roots make up by far the greatest portion and for Fennoscandian mature forest stands, Palviainen *et al.* (2010) reported that stumps account for 15-20% of the C found in tree biomass. Pine stumps contain 8 200-10 900 kg C ha^{-1} and spruce stumps 3 900-5 100 kg C ha^{-1} (Palviainen *et al.*, 2010). According to the literature reviewed in Palviainen *et al.* (2010), C pools in stumps are thus relatively large compared to the pools in the tree seedlings and ground vegetation on recently clear-cut areas (2 000-3 000 kg C ha^{-1}), but small compared to the pools in the soil (60 000-70 000 kg C ha^{-1}). Since stumps are the largest coarse woody debris (CWD) component of the litterfall and have high C/N ratios, they often decompose substantially slower than roots, branches and needles. They have thus been suggested to be important long-term C pools (Palviainen *et al.*, 2010 and references therein).

5. CARBON IN SOILS

Globally, soil organic matter (SOM) contains more than three times as much C as either the atmosphere or the terrestrial vegetation (Schmidt *et al.*, 2011). In total, around 70% of the forest C pool is in soils (IPCC, 2000b). The main source of SOM is plant tissue and SOM may reside in the soil for hundreds to thousands of years. In temperate forests, C stocks in soil exceed those in vegetation by a little bit less than 2:1, while in boreal forests, C stocks in soil exceed those in vegetation by 5:1 (IPCC, 2000b). Changes in soil C stocks can thus be significantly more important than changes in vegetation C stocks for forest C budgets (Medlyn *et al.*, 2001) and below-ground processes currently regulate fluxes to the atmosphere that are approximately ten times the current anthropogenic CO_2 loading rate (Pendall *et al.*, 2008).

5.1 Decomposition

5.1.1 Effects of temperature and moisture

Climate is the most important factor determining decomposition of plant litter (Swift *et al.*, 1979; Aerts, 1997; Berg & McClaugherty, 2003), and variation in decomposition rates between climatic regions have been shown to reflect the variations in macroclimate, primarily soil moisture and temperature (Meentemeyer, 1978). The effects of soil temperature and soil moisture are generally both positive, at least within a certain range (Donnelly *et al.*, 1990) and for easily decomposable pools of SOM (Melillo *et al.*, 2002; Pendall *et al.*, 2004 and references therein). Labile substrates are generally regarded as making up approximately 10% of the total SOM pool. Whether the later stages of decomposition and SOM are sensitive to temperature has hitherto been unclear, with some studies suggesting increasing sensitivity with decreasing quality (Ågren & Bosatta, 2002; Fierer *et al.*, 2005; Knorr *et al.*, 2005) while others have suggested no effect (Giardina & Ryan, 2000; Fang *et al.*, 2005).

Recently, however, Craine *et al.* (2010) presented convincing evidence, using results from a large-scale soil incubation experiment, that the more recalcitrant the organic matter, the more sensitive it is to warming. When compiling their own findings with those from other studies, they found that the temperature sensitivity was highly variable. Yet, there was a positive correlation between the temperature sensitivity of decay and the biogeochemical recalcitrance of the organic matter across all of these studies, showing that the relationship holds across multiple scales and soil types. Biogeochemical recalcitrance captured over 40% of the variability in the temperature response of decomposition (Craine *et al.*, 2010). Karhu *et al.* (2010), investigating the temperature sensitivity of decomposition by incubating two upland boreal forest soils, found similar results. In their study, the temperature sensitivity of decomposition increased substantially from the youngest annually cycling fraction (Q_{10}<2) to a decadally cycling fraction (Q_{10}=4.2-6.9) and then decreased again for a centennially cycled fraction (Q_{10}=2.4-2.8). Applying the same temperature sensitivity of decomposition for all soil organic C (SOC) fractions may thus, according to Karhu *et al.* (2010), give a biased picture of future SOC cycling. Janssens & Vicca (2010) emphasizes, however, that it remains to be seen whether the rates of organic matter decay observed in laboratory incubations are representative of, or scalable to, rates in the field since the microbial assemblages are highly diverse and adaptable. Furthermore, a multitude of stabilization and activation mechanisms exist in the field, either protecting the organic matter from microbial decay, or rendering it more prone to decay (Janssens & Vicca, 2010).

Davidson & Janssens (2006) raised the issue of intrinsic and apparent temperature sensitivity. It is well known that SOM consists of more or less of a soup of thousands of different organic C compounds, each with its own inherent kinetic properties. The inherent kinetic properties based on molecular structure and ambient temperature is called intrinsic temperature sensitivity of decomposition (Davidson & Janssens, 2006). In addition to the complex structures of the organic matter, the enzymes for decomposition may be physically or chemically excluded from many of the organic C substrates within the heterogenous soil environment, causing substrate limitation at the reaction microsite. The observed response to temperature under these environmental constraints is called apparent temperature sensitivity (Davidson & Janssens, 2006). The apparent temperature sensitivity may thus be much lower than the intrinsic temperature sensitivity of the substrate. On the other hand, it may also be higher since if a temperature sensitive process alleviates an environmental constraint to decomposition, the subsequent increase in substrate availability could result in the apparent temperature sensitivity temporarily exceeding the intrinsic temperature sensitivity of the substrate. Davidson & Janssens (2006) lists a number of factors that can temporarily or indefinitely affect the apparent temperature sensitivity of decomposition:

- Physical properties: Organic matter may become physically protected in the interior of soil aggregates. They can also be physically protected from degradation by water-soluble enzymes if they have low water solubility, or if they occur in hydrophobic domains of humified organic matter.
- Chemical protection: Organic matter may become adsorbed onto mineral surfaces, through covalent or electrostatical bonds, thus chemically protecting it from decomposition.
- Drought: Drought reduces the thickness of soil water films, thus inhibiting diffusion of extracellular enzymes and soluble organic C substrates.
- Flooding: Flooding slows oxygen diffusion to decomposition reaction sites.
- Freezing: The diffusion of substrates and extracellular enzymes within the soil is extremely slow when soil water is frozen.

Each of these environmental constraints affects decomposition reaction rates directly or indirectly, by decreasing substrate concentrations at enzymatic reaction sites.

5.1.2 Effects of CO_2

Elevated concentrations of CO_2 have often been found to result in increased allocation of C below-ground, including increased root exudation (see section 4.3.3). Although root exudation has rarely been measured in the field and is believed to represent only 1 to 10% of annual NPP, it may be of uttermost importance to the C cycling in soil by providing substrates that fuel larger decomposition fluxes, mediate nutrient cycling and stimulate microbial activity (Pendall *et al.*, 2008).

Despite the increased allocation below-ground, studies have rarely found measurable changes in SOM pools as a consequence of elevated CO_2 using conventional C analyses (Pendall *et al.*, 2004). According to Pendall *et al.* (2004) this may be due to the difficulties of measuring small changes in SOC in soils where C have been accumulating for thousands of years. However, studies exist where changes have been reported. Leavitt *et al.* (2001) detected a 5 to 6% increase in SOC over two years, when using stable C isotope labelling in a FACE experiment on wheat. Pendall *et al.* (2004) found that the new C inputs to soil in a semi-arid grassland roughly doubled at CO_2 concentrations twice the ambient over four years. However, the increased turnover of old SOM negated the gain of new C, resulting in no difference in net ecosystem production (NEP, i.e. the balance between net primary production and heterotrophic respiration) between elevated and ambient CO_2. In the FACE experiment on poplar in Italy, Hoosbeek *et al.* (2004) initially found a decrease in the total soil C content in the upper mineral soil under elevated CO_2 as compared with ambient CO_2. However, this pattern was later reversed and at then end of the first two years of the second rotation, an increase in total soil C content was observed under elevated CO_2 (Hoosbeek *et al.*, 2006). The authors suggested the initial decrease to be a result of the priming effect, with decomposition initially being stimulated as a consequence of the addition of labile substrates under elevated CO_2, but where the extra C input eventually started to accumulate due to a limitation by N. Consistent with their theory, an increase in the labile fractions of C was observed in the upper mineral soil in the latter study, while N-mineralization rates remained at levels similar to those observed at ambient CO_2.

Bradford *et al.* (2008) emphasized the importance of the C input rate for the magnitude of the priming effect. In their laboratory study without plants, they found that decomposition of SOC was attenuated at high C amendment rates, i.e. SOC formation was higher at higher C amendment rates. However, when adding low rates of C, SOC decomposition was stimulated. According to the authors, the higher SOC formation at higher C amendment rates is to be expected if much of the new SOC is in the form of microbially derived products, something that seems to have been the case since microbial biomass and activity were both greatest at the highest C amendment rate. Bradford *et al.* (2008) thus concluded that to accurately predict how changes in below-ground C supply to soils will impact stocks of SOC, quantification of the C input rates are necessary.

However, the responses of soil microbes to increased levels of CO_2 are not unambiguous. In their reviews, Zak *et al.* (2000) and Pendall *et al.* (2004) reported increases, decreases and neutral responses in microbial biomass as a consequence of increased inputs of labile C at elevated CO_2. More recent studies have continued to report variable responses. Gielen *et al.* (2005) showed a significant increase of the microbial C in FACE soils (i.e. the fraction of microbial biomass in relation to total soil C) compared with control soils, while Carney *et al.* (2007) demonstrated an alteration of the microbial community as a result of elevated concentrations of CO_2. In the latter study, soils exposed to elevated CO_2 had higher relative abundance of fungi and higher activities of a C-degrading enzyme than soils exposed to ambient CO_2, which led to more rapid rates of SOM degradation and loss of soil C at elevated CO_2. This contrasts with the hypothesis of Bradford *et al.* (2008), suggesting that the attenuation of SOC decomposition at higher C amendment rates is a consequence of certain soil microbes outcompeting the SOC decomposing microbes, thereby slowing decomposition at high C input rates.

Van Groeningen *et al.* (2006), performing a meta-analysis on 80 observations from 41 published and unpublished studies of the effects of CO_2 enrichment on soil C, found that elevated CO_2 only causes an accumulation of soil C when N is added at rates well above the typical atmospheric N inputs. Elevated CO_2 was also found to enhance N_2 fixation only when other major nutrients (P, Mo, K) were added. Hence, according to van Groeningen *et al.* (2006), soil sequestration of C under elevated CO_2 is constrained both by N availability and by nutrients needed to support N fixation. Similar conclusions were drawn by Johnson (2006).

Temperature-CO_2 experiments focusing on changes in belowground C pools are rare. However, Loiseau & Soussana (1999), investigating the effects of elevated temperature, CO_2 and N on ryegrass swards, found that decomposition was more strongly stimulated by elevated CO_2 and warming together than by elevated CO_2 alone. Elevated CO_2 alone resulted in increases in particulate organic matter, warming increased turnover rates and the interaction of CO_2 and warming strongly enhanced old pool C decomposition. However, this interaction was dependent on an adequate supply of N. In a study of a shortgrass steppe, Q_{10} for decomposition was found to be lower under elevated than ambient CO_2 (Pendall *et al.*, 2003). Pendall *et al.* (2004) suggested that the reduction in temperature sensitivity may be a result of a diminished substrate quality or an altered composition of the microbial community (fungal dominance instead of bacterial, since fungi generally have lower temperature response than bacteria).

5.1.3 Effects of N

Apart from climate, the quality of litter in terms of its susceptibility to attack by decomposers seems to be the most important factor affecting the rate of decomposition (Attiwill & Adams, 1993). Traditionally, the C/N ratio has been regarded as a good indicator of decomposability. However, nowadays, the initial concentration of N and the lignin/N ratio are often considered as the best predictors of litter decomposition rates (Kimmins, 1997; Berg, 2000). It has been suggested that decomposition can be divided into two phases; an early stage in which climate as well as concentrations of the major nutrients and water soluble substances has a

clear influence on decomposition rate, and a later phase where the decomposition of lignin dominate over the influence of nutrients and thus rule the decomposition (Berg & Staaf, 1980; Taylor *et al.*, 1989; 1991). The mechanism was further explained in Berg (2000): In fresh litter, the degradation process is dominated by easily soluble C compounds. Consequently, the amount of C is high in relation to macronutrients such as N. Net N immobilization may thus occur, resulting in a deficit of N in relation to C. Consequently, initial litter decomposition rates respond positively to increased N availability. With the disappearance of celluloses, the concentration of the more recalcitrant compound lignin increases and in partly decomposed litter the degradation rate of lignin thus determines the decomposition rate. The suppressing effect of lignin on litter mass-loss rates can be described as a linear relationship (Berg & Lundmark, 1987), which for pine litter may start already at approximately 20 to 30% mass loss. In contrast to the early phase, high N concentrations will now have a rate-retarding effect on degradation and thus on the litter decomposition. This retardation has been shown to be due to suppression of lignolytic enzymes in white rot fungi, but can also be a result of the formation of chemically stable recalcitrant compounds, which are formed when low-molecular N reacts with lignin (Berg, 2000).

Another explanation was suggested by Chapin *et al.* (2009). In the presence of adequate N, the priming effect is diminished as microorganisms preferentially utilize C-rich substrate additions. Accordingly, the end result is that increases in soil N may promote SOM conservation. When N availability is low, on the other hand, microorganisms mine SOM for N, increasing the SOM-C respired. Chapin *et al.* (2009) also suggested that the differences in C sequestration in response to N addition might depend on whether the largest effect of N in soils is to increase the non-biological formation of recalcitrant SOM (reduces decomposability) or to increase growth and metabolism of soil decomposers (N stimulation of decomposition).

The geographical pattern of SOC found in many Swedish studies (Akselsson *et al.*, 2005; 2007; Berggren Kleja *et al.*, 2008; Svensson *et al.*, 2008; Ågren *et al.*, 2008) has been suggested to be caused by differences in litter input together with differences in N deposition and N availability (and partly also historical land-use) resulting in a slower turnover of SOM in the northern part of the country (Olsson, 2008; Berggren Kleja *et al.*, 2008; Ågren *et al.*, 2008). However, experimental evidence with regard to the impact of N on SOC stocks in non-agricultural soils is inconclusive. Positive (Waldrop *et al.*, 2004; Bradford *et al.*, 2009), negative (Mack *et al.*, 2004; Waldrop *et al.*, 2004) and negligible (Neff *et al.*, 2002) effects have all been documented, with the study by Waldrop *et al.* (2004) emphasizing the importance of ecosystem-specific responses of soil C to elevated N and the one by Neff *et al.* (2002) highlighting the need to take different C fractions into consideration when looking at the impact of N on soil C pools.

5.1.4 Effects of WTH

WTH may influence decomposition not only by reducing the substrate availability but also by changing the abiotic environment. Soil moisture levels are generally lower where logging residues have been removed (Pérez-Batallón *et al.*, 2001), although this effect may eventually disappear as a consequence of canopy factors (Vanguelova *et al.*, 2010).

In general, unmanaged stands typically show higher C stocks than managed forest stands (Lindner *et al.*, 2008). Management operations, like thinning and harvesting, affect the litter input as well as the microclimate, and hence the decomposition and the soil C pool (Jandl *et al.*, 2007). Nave *et al.* (2010), synthesizing data (432 soil C response ratios) for temperate forests all over the world, found that harvesting reduced soil C by an average of 8±3% (95% CI). C stored in the forest floor was more vulnerable to harvest-induced loss (-30% on average) than C stored in the mineral soil (no significant change). Species composition had a significant effect on the forest floor C response to harvest, with hardwoods (-36%) generally loosing more C than coniferous/mixed stands (-20%). Variation among mineral soils was best explained by soil taxonomy, with Spodosols and Alfisols showing no significant changes while Inceptisols and Ultisols lost mineral soil C at harvest. According to Nave *et al.* (2010), reductions in forest floor C probably have a greater impact on the soil C budgets of Spodosols than on other soil orders, since Spodosols store large amounts of C in forest floors relative to mineral soils and require 50 to 70 years to recover lost forest floor C.

Despite the effects of forest management reported above, most Scandinavian studies have found no effect of WTH on soil C. Wall (2008) and Wall & Hytönen (2011) reported no significant short-term (four years) or long-term (30 years) effects on SOM pools of Norway spruce stands in central Finland. However, in the latter long-term study, needles were left on site. In coherence with these studies, Rosenberg & Jacobson (2004) found no effects on soil content of C when investigating the effects of slash removal after the second removal of logging residues in four whole-tree thinned stands distributed across Sweden (one fertile Norway spruce stand in the south-west and three Scots pine stands in south, south-central and central Sweden). Also Olsson *et al.* (1996) found no general effect of removing logging residues on soil C pools 15 to 16 years after the harvest, when investigating four coniferous forest sites situated in southern as well as northern Sweden. However, there was a tendency for lower concentrations of C both in the humus layer and the mineral soil, and at a later sampling occasion (approximately 25 years after harvest), the concentration of C at 5-10 cm depth in the mineral soil was significantly lower after WTH as compared with CH. At the other soil depths, the differences were not significant, rendering conclusions about the general effect difficult. Saarsalmi *et al.* (2010) also found significant effects of WTH on total amount of C in the organic layer of Scots pine in eastern Finland 22 years after harvest. However, the effect was only apparent for the more fertile Scots pine stand investigated. In the less fertile stand investigated, there was no difference between WTH and CH.

Smolander *et al.* (2008), investigating a Norway spruce stand in central Finland ten years after harvesting, found that although the mass loss of litter and the C/N ratio was not significantly affected by WTH, the rate of C mineralisation and the amount of C in the microbial biomass tended to be lower (not statistically significant) in WTH plots compared with CH plots. Furthermore, the concentrations of total water-soluble phenols and an important group of phenols, condensed tannins, were both lower in the humus layer of WTH plots than in plots subjected to CH. The decay rates of

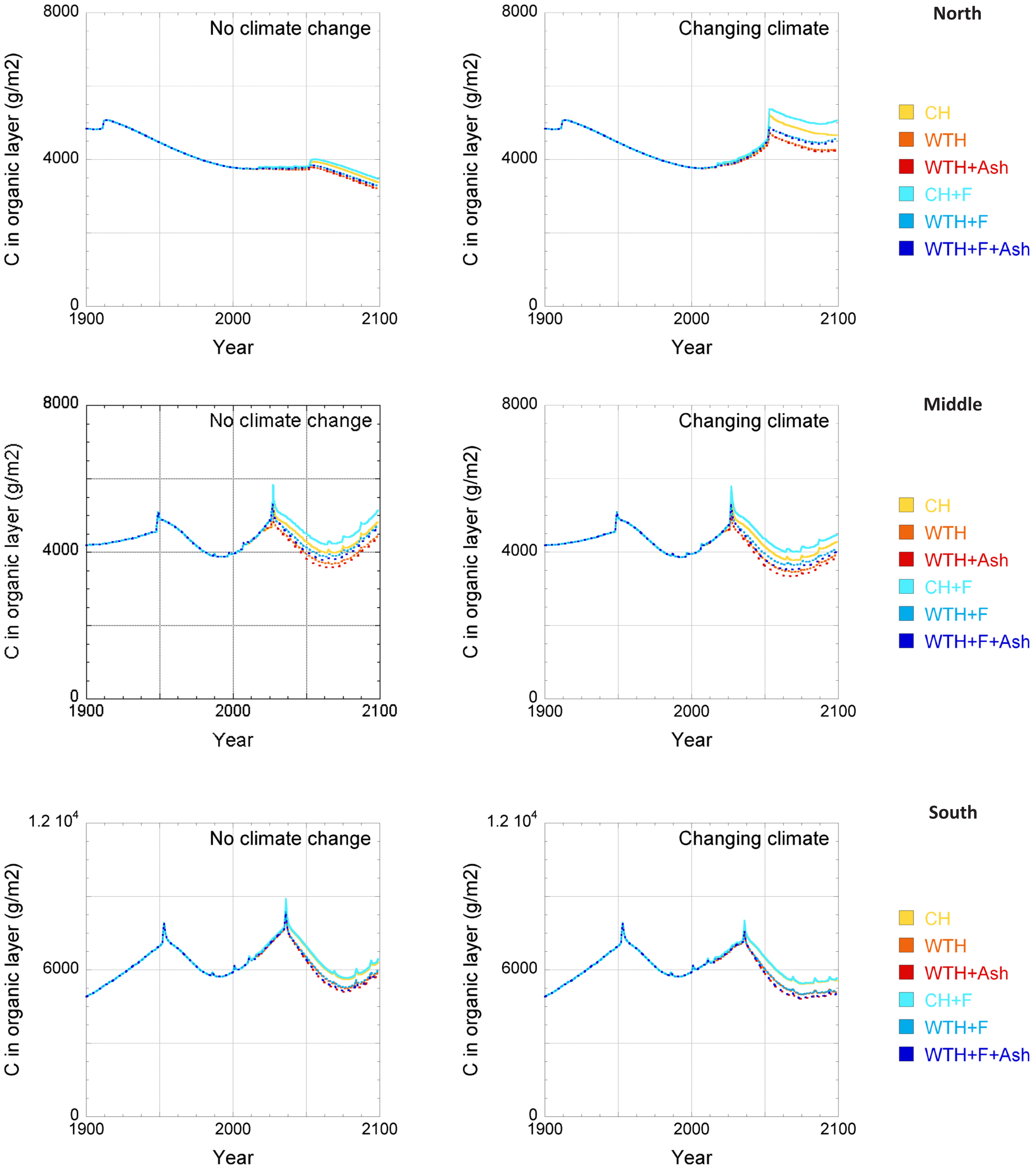


Figure 3. Concentration of C in the organic layer of three different forest soils (situated in the north, middle and south of Sweden) as modelled with the forest ecosystem model ForSAFE. The graphs to the left represent a situation without climate change whereas the graphs on the right-hand side represent a situation where the climate is changing (scenario A2; Houghton et al., 2001). Each site experiences two harvests during the simulation period. CH=conventional stem harvest, WTH=whole-tree harvest, WTH+Ash=whole-tree harvest followed by ash recycling (2 ton ha^{-1}), CH+F=conventional stem harvest and fertilization with N according to Swedish recommendations (Swedish Forest Agency, 2007), WTH+F=whole-tree harvest and fertilization with N according to Swedish recommendations (Swedish Forest Agency, 2007), WTH+F+Ash= whole-tree harvest and fertilization with N according to Swedish recommendations (Swedish Forest Agency, 2007) and ash recycling (2 ton ha^{-1}). For more information, see Belyazid et al. (2008).

litters from various plant species and the mineralization of C and N in the litter and humus layers have, according to Smolander *et al.* (2008), all been observed to correlate with the concentration of total soluble phenols. However, considering the limited information available, the authors emphasized that it cannot be concluded whether the decrease in soluble phenolic compounds due to WTH has any ecological consequences. That repeated removal of logging residues tended (not significant) to decrease rates of net C and N mineralisation was also found by Smolander *et al.* (2010), when investigating the effects of thinning on four Norway spruce stands in southern and central Finland. The changes were greatest where site index, i.e. site fertility, was lowest. In the more fertile site, no effect of removal of logging residue was seen.

In coherence with the latter studies, modelling exercises have generally showed significant effects of WTH on soil C. Ågren & Hyvönen (2003) found that WTH reduced the soil C store by 59 Tg over 150 years, equivalent to 0.4 Tg yr^{-1} (which according to the authors should be compared to the annual C harvest of 11 Tg and the total soil C store of 1 700 Tg). Belyazid *et al.* (2008), using the dynamic model ForSAFE-VEG to model the potential effects of various forestry practices, found that WTH decreased the amount of C incorporated into the humus layer as a consequence of reduced litter input (Figure 3). Results were similar for southern, central and northern Sweden. However, while the effect was permanent in the northern part of the country (the C store in the humus layer did not recover before the end of the rotation period), soil C storage in the central and southern parts of the country were restored before the end of the rotation period. The differences between WTH and CH persisted for all three regions when including climate change, although the total amount of C in the humus layer in the northern part increased as a consequence of increased growth and thus litter input. In the southern and central parts, on the other hand, increases in decomposition rates as a consequence of climate change resulted in decreases in humus layer C.

Results from other countries are as inconclusive as the Scandinavian ones. Johnson & Curtis (2001) reviewed and summarized results from 73 observations (from 26 publications) of temperate forest sites around the world. Their meta-analysis showed that harvesting had small, or no, effect on soil C and N across the entire data set. However, residue removal caused a 6% reduction in A-horizon C and N, whereas leaving residues on site caused an 18% increase compared to not harvested control plots. According to Johnson & Curtis (2001), the positive effects on soil C and N of leaving residues on site seem to be restricted to coniferous species, since several studies showed that residues had little or no effect on soil C and N in hardwood or mixed forests (Johnson & Curtis, 2001 and references therein). For some boreal forests in Canada, Thiffault *et al.* (2006) reported that WTH had a negative effect on CEC compared with CH 15 to 20 years after harvest. This effect was apparent in both forest floor and mineral soil and was linked to decreased levels of organic C (not statistically significant). Similar effects were found by Bélanger *et al.* (2003), also studying boreal forests in Canada. Walmsley *et al.* (2009), on the other hand, found no evidence that WTH led to decreased SOM in a Sitka spruce stand in Northern Wales 23 years after harvest. Instead, SOM tended to be higher after WTH as compared with CH. A significantly increased content of SOC as a consequence of WTH was found by Vanguelova *et al.* (2010) for a second rotation Sitka spruce stand growing on a peaty gley soil in the UK. In CH plots, the residues left on site increased the mineralisation rates and resulted in increased tree growth as compared with WTH plots, subsequently reducing the water content of the soil. Where residues were removed, on the other hand, both mineralisation and tree growth was significantly lower, resulting in increased C and N stocks in soil at WTH plots compared with CH plots. Vanguelova *et al.* (2010) suggested the response of soil C to brash removal to be dependent on the SOM quality and quantity, and that increases in soil C as a consequence of WTH is to be expected only in soils with deep organic layers and high soil C and N stocks.

5.1.5 Effects of SH

There is currently a lack of peer-reviewed literature on the effects of SH on soil C pools (Walmsley & Godbold, 2010) and Swedish studies on the effects of SH on soil C are basically lacking. However, that stumps are important C sinks were shown by Melin *et al.* (2009). They reported a decay rate of 4,6% annually for stump and root systems, with the subsequent time required for loss of 95% of the wood being 65 years. Between 1990 and 2003, the average annual net sink of stump systems was estimated to amount to 6,7 Mt CO_2-eq yr^{-1}, which according to Petersson & Melin (2010) may be compared to the reported net sink in 2008 of about 15 Mt CO_2-eq yr^{-1} from the whole land-use, land-use change and forestry sector, which excluded any C in stump systems. Furthermore, in 2003, the C stock of stumps and roots was estimated to be 495 Mt CO_2-eq yr^{-1}, which is approximately five times that of the dead-wood pool in Sweden (i.e. mainly boles; Petersson & Melin, 2010).

As for WTH, SH reduces the substrate availability. Furthermore, when stumps are removed from the forest, the major part of the soil organic layer is usually seriously disturbed (Walmsley & Godbold, 2010). In 15 Norway spruce stands in central Finland investigated by Kataja-Aho *et al.* (2011), the area of undamaged forest floor in the SH areas was only half of that in the traditionally managed areas. Intensive site preparation have generally resulted in losses of C (Jandl *et al.*, 2007; Walmsley & Godbold, 2010). In one of the few studies that do investigate effects of SH on soil C, significant decreases in both concentration and content of total C (by around 50% for the latter) in the forest floor layer of lodgepole pine (*P. contorta*) and hybrid spruce (*Pices glauca* (Moench) Voss x *Picea engelmanii* Parry) stands in Canada were found (Hope, 2007). Nine years later the differences in concentrations had disappeared, but the total content of C in the forest floor was still significantly lower and there was a significant decrease in the C content of the mineral soil between years 1 and 10. Furthermore, the C content in the forest floor was substantially lower in year 10 as compared with year 1, but the difference was not significant. According to Hope (2007), the lower soil C (and nutrient) stock is a consequence of elevated rates of decomposition of surface organic matter following SH, rather than direct removal of organic material, as indicated by the substantial decrease in forest floor depth with time since harvest. Zabowski *et al.* (2008), investigating five Douglas fir dominated stands across a range of conditions in the US, also found substantial decreases in the total content of C in the mineral soil 22-29 years after SH. The decline was on average 24%, a number that was also representative for the decrease in the forest floor depth. All sites had been fertilized with various amounts of N before planting.

6. CARBON LOSSES

CO_2 is returned from forest ecosystems to the atmosphere via a number of pathways that operate on various time scales: 1) autotrophic respiration by plants, 2) heterotrophic respiration, in which plant-derived organic matter is oxidized primarily by soil microbes, 3) leaching of dissolved inorganic C (DIC) and dissolved organic C (DOC) and 4) disturbances, such as fire, in which large amounts of organic matter are oxidized in very short periods of time. Here, we focus on the first three processes.

6.1 Autotrophic respiration

A large proportion of the carbohydrates that a plant assimilates each day are expended in respiration in the same period (Lambers *et al.*, 1998). The rate of respiration depends on three major energy-requiring processes: maintenance of biomass, growth and ion transport (Lambers *et al.*, 1998). Estimates of the cost for maintaining biomass range from 20 to 60% of the photosynthates produced per day in both herbaceous and woody plants (Lambers *et al.*, 1998). Root respiration generally accounts for approximately 10 to 50% of the total C assimilated each day (Lambers *et al.*, 1998). The higher values usually pertain to plants that grow very slowly (Lambers *et al.*, 1998). Respiration is thus a central process in the C budget of forest trees and small changes in the respiration process at tree level may significantly affect the C balance of the stand. According to Stockfors & Linder (1998), growth respiration is assumed to be directly related to growth, with a fixed respiratory cost for each unit of biomass produced. The magnitude of this cost is determined by the chemical composition of the tissue in question. The rate of maintenance respiration, on the other hand, is affected by a number of factors. With increasing age, growth and ion uptake slow down, and maintenance respiration generally accounts for an increasing proportion of total respiration (more than 85%; Lambers *et al.*, 1998).

6.1.1 Effects of temperature

That temperature influences C acquisition has been discussed above. However, the major influence of temperature on net C balance is probably through its effect on the rates of both autotrophic and heterotrophic respiration. In general, respiration rate more than doubles for each 10°C rise in temperature (Mahli *et al.*, 1999), a logical consequence of the temperature sensitivity of enzymatically catalysed reactions (Lambers *et al.*, 1998). The temperature stimulation of respiration also reflects the increased demand for energy to support increased rates of biosyntheses, transport and protein turnover that occur at higher temperatures. At higher temperatures, there is also an increased leakage and protein turnover, subsequently increasing maintenance respiration (Lambers *et al.*, 1998).

Stockfors & Linder (1998a,b) found strong seasonal variations in stem and leaf respiration in a Norway spruce stand (*P. abies* L. Karst) in northern Sweden. The pronounced seasonal variation in temperature dependence of respiration was more or less the inverse of the seasonal variation in air temperature. Similar results were found in model simulations of respiration in a Norway spruce stand in southern Norway (using the BIOMASS model). An elevated temperature of 4°C dramatically increased the maintenance respiration by an average of 31%, completely offsetting the increase in GPP (Zheng *et al.*, 2002). According to Stockfors & Linder (1998a,b), however, respiration has been shown to acclimate to changes in temperature, both in seedlings grown under controlled conditions and trees grown under natural conditions in the field.

6.1.2 Effects of moisture

According to Lambers *et al.* (1998), a sudden exposure of plants to water stress often enhances their respiration, while a long-term exposure often result in a gradual decrease in respiration, the latter being part of the general decline in C assimilation and overall metabolism associated with slow growth under drought conditions.

6.1.3 Effects of CO_2

According to Lambers *et al.* (1998), there are a vast number of papers on the inhibition of leaf respiration immediately upon exposure to elevated atmospheric CO_2 concentrations. However, most long-term studies seem to show an opposite trend.

When investigating the effects of elevated CO_2 and nutrition on needle respiration in a 30-year-old Norway spruce stand in northern Sweden during two growing seasons, Roberntz and Stockfors (1998) found that CO_2 enrichment increased the respiration rate by 18%. Several FACE experiments have also shown plant respiration increases at elevated concentrations of CO_2 (reviewed in Hyvönen *et al.*, 2007). According to Hyvönen *et al.* (2007), upper canopy leaves had significantly larger numbers of mitochondria, leaf mass per unit area and leaf starch than did lower canopy leaves in a FACE-stand in the US consisting of *Liquidambar styraciflua*, something that resulted in higher night-time respiration. In addition, stem respiration of the trees increased by 33% at elevated concentrations of CO_2. The increase was driven by an increase in the substrate supply from the leaves. Similar results have, according to Hyvönen *et al.* (2007), been reported from experiments with *Populus* spp.

However, Lambers *et al.* (1998), on the other hand, suggested that most long-term effects of elevated CO_2 are indirect, due to changes in allocation, plant growth rate, chemical composition of the biomass and so on, rather than accounted for by direct effects. Hamilton *et al.* (2002) came to a similar conclusion, when investigating the effects of elevated CO_2 in a FACE experiment with *P. taeda*. Elevated CO_2 had little direct effect on leaf tissue respiration of *P. taeda*. Instead, the influence was primarily through increased biomass.

6.1.4 Effects of N

Nutrient status, and especially N concentration, is likely to have an effect on respiration rates. It has even been suggested that N content may be used to predict maintenance respiration for all tissues in trees (Ryan 1991). Indeed, there is an observed positive correlation of respiration rate with N concentration (Lambers *et al.*, 1998). This correlation seems to be consistent with the prediction that maintenance respiration depends on protein concentration. Thus, leaves that have a high N investment in Rubisco and other photosynthetic enzymes have a correspondingly high maintenance respiration. However, Lambers *et al.* (1998) emphasized that it is unclear whether this is a general phenomenon, and points out that the higher respiration rates might also reflect a greater cost for loading of photosynthates in the phloem. Whatever the explanation for the higher leaf respiration rates is, it does according to Lambers *et al.* (1998) contribute to their higher light compensation point and therefore place an upper limit on the irradiance level at which these leaves can maintain a positive C balance. There is therefore a trade-off between high metabolic activity (requiring high protein concentrations and rapid loading of the phloem) and the associated increase in cost of maintenance and transport.

Stockfors & Linder (1998a), investigating a Norway spruce stand in northern Sweden subjected to nutrient fertilization, found no linear relationship between concentration of leaf N and leaf respiration during the growing season. In autumn, on the other hand, there was a significant correlation between the concentration of leaf N and the leaf respiration, but only if control and fertilized trees were treated separately. The regressions had different intercepts for the two treatments, meaning that even though fertilization increased average leaf N concentration, there was no significant difference in average respiration per needle structural dry mass. According to the authors, there is no obvious explanation for this result. During the winter period (October to April), the respiration in thawed needles from fertilised trees was significantly higher than respiration in control trees. The authors speculated that the difference might be due to the fact that needles from control trees were more frost damaged than needles from fertilised trees, something that was indicated by differences in chlorophyll fluorescence. In another study by Stockfors & Linder (1998b), this one examining stem respiration in the same stand, fertilization led to a significant increase in the absolute amount of total respiration. However, the respiration per unit of live cells did not differ between control trees and fertilized trees. Consequently, the increase in respiration was mainly an effect of increased live cell volumes and more growth in fertilized trees. N content and live cell volume were equally strong predictors of total respiration during the growth period. In April, however, when no growth respiration occurred, respiration was more closely correlated with live cell volume leading the authors to conclude that N content is a more useful predictor of growth and growth respiration than of maintenance respiration.

6.1.5 Effects of WTH

We are not aware of any studies looking at how WTH affect respiration rates in the subsequent forest stand.

6.1.6 Effects of SH

We are not aware of any studies looking at how SH affect respiration rates in the subsequent forest stand.

6.2 Heterotrophic respiration

Heterotrophic respiration is the respiration derived from oxidation of plant-derived organic matter by soil microbes. However, because of methodological difficulties in separating autotrophic root respiration from heterotrophic respiration, the majority of studies existing today have examined effects on the total efflux rather than separating the two components. The term soil respiration is commonly used, yet vague, since there is no single process that defines what is measured.

Recently, however, efforts have been made to separate the two. Högberg *et al.* (2001), performing a girdling experiment in a boreal pine forest in northern Sweden, showed that girdling reduced soil respiration by about 54% relative to respiration on ungirdled control plots within the first few months after girdling. They concluded that the use of current photosynthetic assimilates to roots is a key driver of soil respiration. Ruehr & Buchmann (2009) found that the contribution of root-rhizosphere respiration to soil respiration was higher during the growing season (50%) than during dormant periods (40%). Fine-root and root-rhizosphere respiration were strongly related to each other, with root-rhizosphere respiration contributing around 46% and fine-root respiration around 32% to total soil respiration.

6.2.1 Effects of temperature

Generally, higher soil temperatures increases the activities of roots and soil heterotrophs (Pendall *et al.*, 2004), resulting in enhanced soil respiration (Peterjohn *et al.*, 1994; Rustad *et al.*, 2001; Beier *et al.*, 2008). Rustad *et al.* (2001), performing a meta-analysis of 32 sites representing four biomes, found that across all sites and years, two to nine years of experimental warming in the range of 0.3-6.0°C significantly increased soil respiration rates by 20% (with a 95% confidence interval of 18-22%). According to Rustad *et al.* (2001), an annual increase of 20% corresponds to an extra release of 14-20 Pg C yr^{-1}, which is two to three times the estimated 7 Pg C yr^{-1} of CO_2 released to the atmosphere via combined fossil fuel combustion and land use changes. Rustad *et al.* (2001) cautions, however, that the increase may be an overestimation, since studies were conducted during a short period of time and it is possible that the observed increases in respiration rates are transient responses, reflecting the oxidation of the most labile soil C compounds. Once the labile soil C fractions are decomposed, the response of soil respiration to experimental warming might decline. That soil warming accelerates SOM decay and CO_2 fluxes to the atmosphere but that the responses are small and short-lived and values soon returns to pre-treatment levels have been found in several studies (Melillo *et al.*, 2002; Strömgren, 2001). Davidson & Janssens (2006) state that "Changes in enzymatic properties, commonly referred to as temperature acclimation, could offset temperature-induced increases in respiratory activity. However, although the existence of these processes is beyond doubt, their ecological importance remains to be tested".

In a review on the effects of climate change on microorganisms, Singh *et al.* (2010) concluded that increased temperature has been directly linked to increased soil respiration, and that a global average temperature increase of 2°C can be predicted to increase soil C release by 10 Pg, mainly owing to increases in microbial activity. However, Singh *et al.* (2010) emphasized that enhanced temperature does not always lead to enhanced C losses to the atmosphere. Recently Ruehr & Buchmann (2009), investigating the soil respiration fluxes in a temperate mixed forest, found that root respiration rates were correlated to temperature during the growing season, but that it depended heavily on seasonal changes of recent C supply from canopy photosynthesis to roots and via root exudates to the rhizosphere.

With regard to Swedish conditions, Jansson *et al.* (2008), simulating future changes in C pools in Sweden according to two IPCC scenarios using the COUP model, found a strong link between soil temperature and heterotrophic respiration. Lindroth *et al.* (1998), analysing the sensitivity of NEP of an old-growth Scots pine/Norway spruce forest in central Sweden, found that annual respiration would increase by 10% (74 g C m^{-2}) for a 1°C rise in temperature. Photosynthesis would need to increase by 12% to compensate for this increased respiration, something that according to the authors is not very likely since conifers have a relatively flat response curve with regard to photosynthesis. The net effect is thus for larger C losses in warm years. Furthermore, Lindroth *et al.* (2008), investigating net ecosystem exchange in three forests along a north-south climatic gradient in Sweden, found significant losses of C from forest soils of all three sites. The most plausible explanation was, according to the authors, that the studied years were much warmer than normal causing larger respiratory losses.

In coherence with the results of Lindroth *et al.* (1998; 2008), Goulden *et al.* (1996) found that smaller enhancements in fall, winter and spring respiration in a temperate deciduous forest were correlated with unusually warm soil temperatures. However, respiration rates in summer were extremely consistent over the years investigated despite a range of mean air temperatures. Goulden *et al.* (1996) explained this phenomenon with the occurrence of droughts in the summers. Severe drought affected respiration considerably more than it affected photosynthesis, probably because trees could access water remaining deep in the soil horizon when water near the soil surface was depleted. Consequently, C storage increased. Goulden *et al.* (1996) thus concluded that for this temperate deciduous forest, loss of C from the ecosystem through respiration was primarily determined by soil temperature in the dormant season (i.e. snow depth) and by drought in the summer, while being relatively insensitive to other aspects of climate, including growing season temperature. In accordance with the reasoning of Goulden *et al.* (1996), Ruehr & Buchmann (2010) showed that root-rhizosphere respiration and microbial respiration differed significantly in their temperature sensitivities. Root-rhizosphere respiration generally increased more strongly with temperature (Q_{10}=3.2) than did microbial respiration (Q_{10}=2.3). However, during the dormant season, microbial respiration was more strongly affected by temperature (Q_{10}=7.2), according to the authors highlighting that winter decomposition rates may be very sensitive to future increases in temperatures.

In contrast to most of the studies referred to above, Jarvis & Linder (2000) found no effect of temperature on respiration when comparing differences in CO_2 efflux from warmed and non-warmed Norway spruce plots in a long-term experiment in northern Sweden (a temperature increase of 5°C at 10 cm depth in soil). The lack of response was explained by there being a limitation with regard to the amount of readily metabolizable SOM and an acclimation in the temperature sensitivity of both autotrophic and heterotrophic respiration. A lack of sensitivity to temperature increases was also demonstrated by Mahecha *et al.* (2010), in an analysis comprising 60 sites. They found not only that Q_{10} was independent on mean annual temperature, but also that it did not differ among biomes. In addition, the Q_{10} value was lower (around 1,4) than the temperature sensitivities reported in other studies. The authors explained their results with the fact that measurements at ecosystem level always include multiple processes, and that ecosystem respiration is a mixed response of temperature-dependent and temperature-insensitive sub-processes. In the end, the rate-limiting step will determine the overall temperature response of the chemical reaction and the overall Q_{10} for the ecosystem is thus lower than for the individual processes. Mahecha *et al.* (2010) suggested that this universal and substantially lower Q_{10} value may partly explain recent findings by Frank *et al.* (2010), indicating a less pronounced climate-carbon cycle sensitivity than previously assumed by current climate-carbon cycle model parameterizations. Chapin *et al.* (2009) also emphasized other factors than temperature as determinants of heterotrophic activity. They give the example of European forest ecosystems, where much of the seasonal variation in soil respiration is explained by temperature, but GPP is a better predictor than temperature on an annual time scale.

Most of the studies investigating the influence of temperature on soil respiration are soil-only warming experiments. There are only a few examples of combined soil- and air-warming experiments, one of them being Bronson *et al.* (2008). They found that soil-only warming resulted in an increased respiration rate whereas soil plus air warming did not increase the soil respiration rate, suggesting that the mechanisms controlling respiration change with air warming. The authors suggested that the difference might be due to limitations imposed by greater stomatal conductance for the soil and air warming treatment. In contrast to Bronson *et al.* (2008), Vanhala *et al.* (2011), transplanting organic surface horizons of boreal soils into warmer regions (i.e. soil plus air warming experiment), found increased soil heterotrophic respiration rates.

6.2.2 Effects of moisture

It is generally acknowledged that changes in precipitation, evapotranspiration and soil water content are likely to affect microbial decay of SOM and soil respiration (Borken *et al.*, 2006). Several laboratory studies have shown that drying of soils can limit heterotrophic respiration when the water potential fall below a certain treshold (Orchard & Cook, 1983; Skopp *et al.*, 1990; Howard & Howard, 1993; Cook & Orchard, 2008). According to Borken *et al.* (2006), this treshold may vary from soil to soil and within the soil profile as soil organisms are differently adapted to water stress. For example, fungi are generally less affected by water stress than bacteria or soil fauna (Borken *et al.*, 2006).

There are relatively few field studies on the effects of soil water on soil respiration, a reason probably being the difficulties in isolating the response of soil respiration to summer drought and subsequent wetting, since moisture changes are often confounded with temperature variation. However, Borken *et al.* (2006) separated the effects of temperature and water content by conducting an experiment in which all plots experienced the same temperature regime, but throughfall was excluded in half of the plots. They found that throughfall exclusion significantly reduced mean soil respiration rates during two summers, particularly in the organic horizon. Furthermore, root respiration and respiration from "fresh" substrates in the rhizosphere made up a larger proportion of total soil respiration in plots where throughfall was excluded. The fraction tended to increase with increasing drought. In coherence with the results referred to in section 6.2.1, Borken *et al.* (2006) thus concluded that 1) drought can reduce soil respiration independently of temperature, 2) root respiration is less affected by drought than is decay of organic matter and 3) prolonged summer droughts may decrease primarily heterotrophic respiration, which can lead to increased storage of SOC in forests.

6.2.3 Effects of CO_2

Although the C flux below-ground is generally increased at elevated CO_2, as is below-ground biomass and fine root turnover (see section 4.3.3), results with regard to the effect of elevated CO_2 on soil respiration rates are variable. Lukac *et al.* (2009), investigating the effects of elevated CO_2 on the soil C cycle at four forested FACE experiments found that, at all sites, soil CO_2 efflux increased in excess of the increased root necromass inputs. The increase in respiration varied between 12 and 16% in older forests, and 22 and 46% in newly established forests (Lukac *et al.*, 2009). A mass balance calculation suggested that a large part of the stimulation of soil CO_2 efflux was likely due to increased root respiration. In accordance with Lukac *et al.* (2009), Heath *et al.* (2005), investigating the effects of CO_2 enrichment on soil microbial respiration using isotope techniques, found a marked decline in sequestration of root derived C in the soil as a consequence of increased levels of CO_2 (despite enhanced tree growth). After 15 months, soil C sequestration was reduced by as much as 40% at the highest CO_2 concentration. This reduction was clearly associated with increased soil microbial respiration rates. Addition of nutrients caused a slight increase in the amount of root derived C sequestered in the soil (a consequence of lower respiration rates). Changes in the quantity and quality of root-derived organic matter are, according to the authors, the main factors behind the increased respiration rates. Also Andrews & Schlesinger (2001) reported a marked increase in annual soil respiration (27%) as a consequence of elevated atmospheric CO_2 in a FACE experiment in a temperate loblolly pine (*P. taeda* L.) forest in the US.

In contrast to the studies mentioned above, Larson *et al.* (2002) did not find any effects of elevated CO_2 on microbial respiration and biomass in soils under trembling aspen, paper birch and sugar maple exposed to elevated CO_2 in a FACE experiment in the US. Gielen *et al.* (2005) did find a stimulation of microbial respiration in the EuroFACE experiment on poplar, but it was very small (on average 5%) and not significant. Furthermore, Bader & Körner (2010) found no overall stimulation of soil respiration in a mature hundred-year old deciduous forest in Switzerland after seven years of exposure to elevated CO_2. Instead, they suggested that elevated CO_2 affected Q_{10} mainly indirectly through changes in soil volumetric water content (VWC), since elevated CO_2 stimulated respiration only when VWC was ≤40% and concurrent soil temperature was high (>15°C). Zak *et al.* (2000), reviewing the effects of elevated CO_2 on microorganisms, found that the response of microbial respiration to elevated CO_2 was highly variable, ranging from a 4% decline to a 72% increase beneath woody plants.

Some of the variation in respiration rates may possibly be explained by variable soil properties. In an experiment on young spruce (*P. abies* (L.) Karst) and beech (*F. sylvatica* (L.)) trees grown under elevated CO_2, Spinnler *et al.* (2002) found that soil respiration rate was not increased in acidic soil. On calcareous soil, on the other hand, elevated CO_2 stimulated both fine root density and soil CO_2 efflux, suggesting that initial soil properties may sometimes be more important than C input for the fate of C in a forest ecosystem.

6.2.4 Effects of N

Root respiration generally increases when roots are suddenly exposed to increased ion concentrations in their environment (Lambers *et al.*, 1998). The stimulation of respiration is at least partly due to the increased demand for respiratory energy for ion transport, but may also reflect a replacement of osmotically active sugars by inorganic ions, thereby leaving a large amount of sugars to be respired via the alternative pathway (Lambers *et al.*, 1998). When plants are grown at a low supply of nutrients, their rate of root respiration is lower than that of plants that are well-supplied with mineral nutrients (Lambers *et al.*, 1998). According to Lambers *et al.* (1998), this is expected because their rates of growth and ion uptake are greatly reduced. However, rates of root respiration per ion absorbed or per unit root biomass produced at the low nitrate supply are relatively high if compared with those of plants which grow and take up ions at a much higher rate. This suggests, according to Lambers *et al.* (1998), that the specific costs of growth (i.e. cost per unit biomass produced), maintenance (cost per unit biomass to be maintained) and/or ion transport (cost per unit nutrient absorbed) must increase in plants grown at a limiting nutrient supply.

Nohrstedt *et al.* (1989) found that N fertilization of two pine forests in Sweden resulted in significant decreases in respiration rate, ATP content and microbial biomass C in all horizons when expressed per gram of C. However, since the amount of C per m^2 was higher in fertilized plots, there was no difference between fertilized and control treatments on an area basis. The calculated increase in litterfall in fertilized plots could not account for all of the increase in C per m^2 and Nohrstedt *et al.* (1989) thus concluded that the increase in C was at least partly due to a decrease in the microbial activity per gram of C, possibly as a consequence of changes in the quality of organic matter.

6.2.5 Effects of WTH

Pumpanen *et al.* (2004) examined soil CO_2 efflux from a podzolic forest soil after clear-cut and found that CO_2 efflux was higher from the sampling points where the logging residue was left on site and lower from points where the logging residue was removed. The higher CO_2 efflux from the points where the logging residue was left is not surprising, considering the rapid decomposition of fresh above-ground litter during the first years following harvest.

6.2.6 Effects of SH

Only a few studies exist where the effects of SH, or a disturbance comparable to SH, on soil respiration have been investigated. Pumpanen *et al.* (2004) examined the soil CO_2 efflux following different disturbances of forest soils. They found higher fluxes where the organic matter was mixed with the mineral soil, as compared to where the soil was left intact. However, the effect was rather short-lived. Recently, Strömgren *et al.* (2012) investigated soil CO_2 flux during the first two years after SH in two Swedish Norway spruce forests – one situated in the southern part and one in the centre of the country. Since there was no vegetation at the beginning of the study, the authors assumed that all CO_2 that was emitted came from heterotrophic respiration. At the southern site, respiration was increased on SH plots compared with undisturbed control plots. However, the difference was only apparent during the first few weeks and later disappeared. At the central site, SH was compared with mounding and no difference between treatments was observed. Strömgren *et al.* (2012) thus concluded that in a short-term perspective (months and years), the effect of SH on CO_2 fluxes and decomposition processes are small, or even absent, compared to site preparation such as mounding. However, long-term consequences are uncertain.

6.3 Leaching of dissolved C

Dissolved C plays an important role in the C cycle of terrestrial ecosystems and for the transfer of organic C from terrestrial to aquatic systems (Kindler *et al.*, 2011). However, the dynamics and origin of dissolved C in throughfall and soil solution are poorly understood (Kindler *et al.*, 2011; Schulze *et al.*, 2011) and there are relatively few studies of C leaching from various natural ecosystems. According to Kindler *et al.* (2011), leaching losses of dissolved C may be of great importance in grassland ecosystems. However, leaching losses from most forest ecosystems are relatively small and hardly affect actual net ecosystem C balances because of the small solubility of CO_2 in acidic forest soil solutions and their large NEE (Kindler *et al.*, 2011). Öquist *et al.* (2009) emphasized, however, that ignoring the C export through surface waters may lead to significantly over-estimated C-accumulation rates within terrestrial ecosystems.

An inventory of organic C pools in boreal forest soils in Scandinavia showed that around 70 to 80% of the organic C in the upper 100 centimeters of soil is normally found in the mineral soil (Callesen *et al.*, 2003). DOC is a major source of this C input to the mineral soil (Neff & Asner, 2001). In general, annual DOC fluxes in boreal and temperate forests follow a pattern, with low to moderate fluxes in bulk deposition and throughfall, high fluxes in O horizon leachates and low fluxes in leachates collected from the B horizon (Michalzik *et al.*, 2001; Fröberg *et al.*, 2006). According to Michalzik *et al.* (2001), typical concentrations in soil solution leaving the forest floor are in the range of 20-90 mg l^{-1}, whereas the concentration normally found in the mineral soil is around 2-35 mg l^{-1}. Schulze *et al.* (2011) found similar values, although in the upper range of the ones presented by Michalzik *et al.* (2001). There are no apparent differences between hardwood and coniferous forests (Michalzik *et al.*, 2001). Due to the lack of information on DIC and suspended C, the text below mainly refers to the influence of climate change and forest management practices on the production and transport of DOC.

6.3.1 Effects of temperature

Laboratory incubations have shown that DOC production rates increased with increasing temperature (Christ & David, 1996; Andersson *et al.*, 2000). Furthermore, Liechty *et al.* (1995) attributed differences in DOC concentrations between two northern hardwood stands in the USA to temperature, with the highest DOC concentration at the warmest site. Several biological temperature-dependent processes, apart from NPP and microbially mediated processes, are known to affect the production of DOC in the canopy (i.e. budding, pest-infection and pollination; Schulze *et al.*, 2011), supporting a temperature dependence of DOC production. Seasonal inter-annual variations of DOC concentrations, with the highest concentration of DOC in late summer/early autumn and the minimum in early spring, have been reported in the literature, indicating a temperature-sensitivity in the production of DOC that probably govern the within-year variation in DOC (Fröberg *et al.*, 2006).

However, Michalzik *et al.* (2001), reviewing 42 ecosystem studies in temperate forests in Europe and the US covering a wide range of mean annual temperatures (1-16°C), found no correlation between mean annual temperature and DOC concentrations or fluxes in soil leachates collected below the O horizon. Fröberg *et al.* (2006) thus suggested that care should be taken when extrapolating the findings in their study to other environmental conditions, since other factors may override the effect of temperature.

6.3.2 Effects of moisture

Fröberg *et al.* (2006) found no effect of soil moisture regime (dry, mesic or moist) or seasonal variation in soil mositure on DOC dynamics in three Norway spruce stands in Sweden. However, they suggested that drying and rewetting of the soil might influence the DOC flux. That drying and rewetting may have an influence on DOC production was shown by Tipping *et al.* (1999), and extended drought periods have been shown to exert a strong influence on the release and translocation of DOC from relatively old and stabilized SOM fractions (Schulze *et al.*, 2011). However, also water flux is regarded to be important in most studies. The transfer of DOC from terrestrial systems to aquatic ones is generally considered to be largely hydrological (Neff & Asner, 2001; Stanley *et al.*, 2012). Both Christ & David (1996) and Kalbitz & Knappe (1997) found that the amounts of DOM were enhanced by increased leaching rates. Their studies are supported by the results of Michalzik *et al.* (2001), who found that increasing annual precipitation increased the annual fluxes of DOC from forest floors and by Tipping *et al.* (1999) and Schulze *et al.* (2011) who found water flux to be an important driver of DOC fluxes from the organic layer into the mineral soil. With regard to DIC export from soil, Öquist *et al.* (2009) found that 90% of the variation in soil DIC export could be explained by variation in groundwater discharge.

6.3.3 Effects of CO_2

There are few studies on the effects of elevated CO_2 on dissolved C. Elevated CO_2 has been shown to increase soil pCO_2, and subsequently DIC, resulting in altered inorganic carbonate chemistry and thus system alkalinity (Andrew & Schlesinger; 2001; Karberg *et al.*, 2005). Andrew & Schlesinger (2001) found that the flux of DIC to groundwater increased by between 7 and 33% depending on year in one of the FACE experiments – a 15-year-old loblolly pine forest (*P. taeda* L.) in the US. However, the DIC flux represented only approximately 1% of annual NPP. As a comparison, the loss of C to the atmosphere via soil respiration was 56% of GPP.

With regard to DOC, King *et al.* (2001) found no significant effect of elevated CO_2 on DOC in a FACE experiment with trembling aspen and paper birch in Wisconsin, USA. Hagedorn & Machwitz (2007), on the other hand, found that elevated CO_2 increased DOC leaching in a 100-year-old broadleaf forest and a 30-year-old treeline ecosystem, both of them located in Switzerland. According to the authors, the increase was most likely a result of increased contents of non-structural carbohydrates and phenolics under elevated CO_2 (they both correlated with DOC leaching). Furthermore, DOC was found to be less biodegradable when the parent litter was grown under elevated CO_2. Although CO_2 enrichment increased DOC leaching from litter significantly, particularly during the initial phase, Hagedorn & Machwitz (2007) stressed that the differences between the species examined were much greater. For instance, *Carpinus* litter leached seven times more DOC than from *Fagus* litter. Hagedorn & Machwitz (2007) thus concluded that CO_2 enrichment of forests might stimulate DOC leaching from litter by altering its quality, but that these effects are likely to be short-term and much smaller than the effects of changes in species composition and forest management.

6.3.4 Effects of N

Pregitzer *et al.* (2004) found a three-fold elevation in the export of DOC from four northern hardwood forests subjected to eight years of fertilization with NO_3^- and situated along a geographic gradient in the US. The leaching losses increased over time, which according to the authors suggest that N fertilization had altered the availability of the substrates that led to the formation of DOC, or the processing of organic matter by soil microbial communities, or both. Fröberg *et al.* (2006), investigating DOC in three Norway spruce stands along a south-north climatic gradient in Sweden, found that the concentrations and fluxes of DOC in O horizon leachates were highest at the southern site (49 mg l^{-1}) and lowest (30 mg l^{-1}) at the northern. They suggested that the concentrations and fluxes of DOC in O-horizon leachates are primarily related to the net primary production of the ecosystem (i.e. more litter = more substrate for DOC), which arise from a combined effect of a gradient in mean annual temperature and N status, both of which are highest in the south. A similar south-north gradient, but on a European scale, was found by Mattsson *et al.* (2009). Their conclusion was that DOC concentrations are controlled by several factors, including wetland and forest cover, precipitation and hydrological processes.

In contrast to the studies mentioned above, a positive correlation between DOC production and C/N ratios of SOM have been observed in several laboratory experiments (Gödde *et al.*, 1996; Kalbitz & Knappe (1997). Furthermore, Kindler *et al.* (2011) investigated DOC and DIC leaching from forests, grasslands and croplands across Europe and found that the production of DOC in topsoil (upper 5-40 cm) was positively related to the C/N ratios. According to Kindler *et al.* (2011), studies with ^{13}C or ^{14}C have suggested that DOM mainly represents highly altered residues of organic matter processing. Processing of N-poor organic matter seems to result in production of more soluble residues, hence the positive correlation between soil C/N ratios and DOC concentrations. A hypothesis put forward by Gödde *et al.* (1996) was that microbial communities in soils with large C/N ratios have to process more organic matter to satisfy their N requirements than communities in soils with lower C/N ratios. Consequently, more DOC is produced as leftover of SOM degradation in N-poor soils. There are also some studies indicating no relationship between N addition and DOC concentration in the forest floor (Aandahl Raastad & Mulder, 1999; Sjöberg *et al.*, 2003; McDowell *et al.*, 2004).

Fröberg *et al.* (2006) suggested that the variable results could be due to the dual effect of N, on the one hand favouring net primary production in N limited ecosystems and on the other hand reducing SOM decomposition rates. Several studies have also suggested that the concentration and transport of DOC is mainly controlled by sorption-desorption processes and rather unaffected by environmental conditions and soil solution properties, particularly in the mineral soil (Michalzik *et al.*, 2001; Fröberg *et al.*, 2006; Kindler *et al.*, 2011). Considering the variable responses presented above and the lack of information on this topic, the summary of the state of knowledge presented by Fan *et al.* (2010) seems appropriate: "…the mechanisms that control DOC production and loss are complex, and future projections of climate impacts remain highly uncertain."

6.3.5 Effects of WTH

Although some early studies suggested that DOC could be affected by forestry practices, it was not until recently that forest harvesting was demonstrated to have a significant effect on the concentration and flux of DOC in boreal regions (Nieminen, 2004; Laudon *et al.*, 2009). Laudon *et al.* (2009) found, for example, that CH resulted in a 70% increase in DOC export to stream water, due to the combined effect of runoff and DOC concentration in a clear-cut catchment experiment in the north of Sweden. Such an effect is not surprising, considering that reduced evapotranspiration and increased annual and episodic runoff is a common consequence after forest harvesting (Sorensen *et al.*, 2009).

We are not aware of any studies that have investigated the impact of WTH on dissolved C.

6.3.6 Effects of SH

We are not aware of any studies that have investigated the impact of SH on dissolved C.

7. CARBON ACCUMULATION

7.1 Historical trends

Although there is uncertainty in the data on global C uptake by, storage in, and release from forests, they do without doubt contain enormous amounts of C. Globally, forests have been estimated to account for about 1 146 billion ton of C (Kimmins, 1997). According to Kimmins (1997), 37% of this C is in low latitude (tropical and subtropical forests), 14% in mid-latitude and 49% in high latitude forests. Over two-thirds is in soils and peat deposits (Kimmins, 1997). Similar numbers were presented by Mahli *et al.* (1999).

In general, the amount of C stored in forests in many parts of the world has increased during the last half-century (Kimmins, 1997) and when C losses from fires, harvests, erosion and export of DOC have been accounted for, NBP is estimated to have been -0.2 ± 0.7 Pg yr^{-1} during the 1980s and -1.4 ± 0.7 Pg yr^{-1} during the 1990s (Prentice *et al.*, 2001). Reforestation of abandoned farmland is one reason for the increase, while reduction of forest loss to wildfire is another (Kimmins, 1997). A third explanation may be increased growth as a consequence of increased N deposition (see section 3.3.1; Magnani *et al.*, 2007; Reay *et al.*, 2008; de Vries *et al.*, 2009). An increase in the C storage of northern forests is believed to account for much of the difference between the C released to the atmosphere by fossil fuel burning and the observed increase in atmospheric C.

Only 13% of the C in boreal forests is estimated to be in biomass (which can be compared to values around 50% for tropical and temperate forests; Mahli *et al.*, 1999). According to Mahli *et al.* (1999), the results are simplistic but nevertheless instructive: If boreal forest soils are loosing C, it seems unlikely that boreal forest biomass is sequestering sufficient amounts of C to compensate for it.

Calculations have shown that complete conversion of forests to climatically equivalent grasslands would add 400 to 800 Pg C to the atmosphere. Thus, global deforestation could theoretically add two to four times more CO_2 to the atmosphere than could be subtracted by reforestation of cleared areas (Prentice *et al.*, 2001).

7.1.1 C accumulation in Swedish forest soils

There have been several attempts to estimate the sequestration of C in Swedish forest soils. Akselsson *et al.* (2005) used the limit-value approach to conduct a scaling-up for forested land in Sweden and obtained a mean sequestration rate of 180 kg ha^{-1} yr^{-1} (range from 40 to 410 kg ha^{-1}), with a clear gradient across the country from south-west to north. Spruce (200 kg ha^{-1} yr^{-1}) sequestered more C than pine and birch (150 kg ha^{-1} yr^{-1}). The highest values (400 kg ha^{-1} yr^{-1}) were obtained for deciduous trees in the south of the country. Another approach, based on data for N retention and the C/N ratio in SOM, and where N retention could be calculated from N balances in a scaling-up procedure, gave similar C sequestration patterns but a lower mean C sequestration rate of 96 kg C ha^{-1} yr^{-1} (Akselsson *et al.*, 2007). However, Berg *et al.* (2009), estimating the C sequestration in the humus layer from direct measurements of podzolic soils, reached a considerably higher value of 251 kg C ha^{-1} yr^{-1}. Pine (283 kg ha^{-1} yr^{-1}) had a higher sequestration rate than spruce (239 kg C ha^{-1} yr^{-1}) and the sequestration rates were positively related to the temperature sum. According to Berg *et al.* (2009), their values are consistent with the literature on C accumulation in humus layers in northern Europe and show that the humus layer constitutes a significant C sink for Sweden, amounting to 6,7 Mt C yr^{-1} (which is more than half the estimated sink in trees due to increased stocking). Ågren *et al.* (2008), applying the Q-model (a model that use tree stocks to provide estimates on tree litter production, which is fed to a model of litter decomposition from which C stocks are then calculated), estimated that national C stocks had increased by 12-13 g C m^{-2} yr^{-1} in the period 1926 to 2000. They suggested that this increase will continue, because soil stocks are far from equilibrium with current litter inputs. That a higher litter input as a consequence of climate change will result in a larger accumulation of SOM in the future was also suggested by Ge *et al.* (2010), investigating the impacts of climate change on the productivity of Norway spruce dominated mixed stands in relation to water availability in southern and northern Finland using the process-based ecosystem model FinnFor (see also section 4.2.2).

However, Svensson *et al.* (2008), using the COUP model for analysing four sites located in different regions of Sweden, found that while soils in the southern region accumulated 9 and 23 g C m^{-2} yr^{-1}, soils in the central and northern regions lost 5 g C m^{-2} yr^{-1} and 2 g C m^{-2} yr^{-1}, respectively. The difference between the regions was suggested to be a consequence of the difference in growth between the north (not changed much from 1926 to 2000) and the south (increased during the same period; Olsson, 2008). Jansson *et al.* (2008), estimating the expected changes in C pools due to climate change according to the two IPCC climate scenarios A2 and B2 from Hadley Centre simulations from the period 1961-1990 to 2061-2090, found similar results. In southern Sweden, the future SOC accumulation rates were slightly increased, while for northern Sweden they decreased. That the soil C stocks will not simply increase in the future were also found by Schröter *et al.* (2005) in an analysis of the future impact of climate change on European ecosystems. They arrived at the conclusion that during the coming century, forest growth will increase more than decomposition, but at the end of the century the decomposition rates will become higher and the C sink will diminish.

7.2 Future trends

7.2.1 Effects of climate

Mahli *et al.* (1999), investigating the effect of temperature on the Norway spruce stand modelled by Bergh *et al.* (1998), found a three-week extension of the growing season and a 17% increase in NPP for a 2°C rise in temperature. For a 4°C rise in temperature there was a seven-week extension of the growing season but no further increase in NPP, because of the compensating effects of enhanced tissue respiration. In the review by Mahli *et al.* (1999), several other studies indicating increased vegetation activity as a result of warming temperatures at high latitudes are mentioned. What was unclear in the late 1990s, and what still is unclear, is the corresponding response of the soil C pools. According to Mahli *et al.* (1999), however, field evidence suggests that the opposing effects of photosynthesis and respiration are currently in approximate balance. As an example, they give NEE measurements at nine Canadian boreal forest sites, which indicated only small net sinks during the unusually warm years of the 1990s.

More recently, Piao *et al.* (2008) demonstrated that the atmospheric records from the past 20 years show a trend towards an earlier autumn-to-winter CO_2 build-up, suggesting a shorter net C uptake period. According to Piao *et al.* (2008), this trend cannot be explained by changes in atmospheric transport alone. Instead, it suggests, together with ecosystem flux data, increasing C losses in autumn. When using a process-based terrestrial biosphere model and satellite vegetation greenness index observations to further investigate the observed seasonal response of northern ecosystems to autumnal warming, Piao *et al.* (2008) found that both photosynthesis and respiration increased during autumn warming, but that the increase in respiration was greater. In contrast, warming increased photosynthesis more than respiration in spring. Their simulations and observations suggested that northern terrestrial ecosystems may currently loose CO_2 in response to autumn warming, with a sensitivity of about 0.2 Pg C per degree C, offsetting 90% of the increase in CO_2 uptake during spring. Piao *et al.* (2008) thus concluded that if future autumn warming occurs at a faster rate than spring warming, the ability of northern ecosystems to sequester C might be diminished earlier than previously suggested.

In accordance with the results of Piao *et al.* (2008), Lindroth *et al.* (2008) found significant C losses from soils of three different Norway spruce stands that were investigated using flux measurements along a north-south climatic gradient in Sweden. Lindroth *et al.* (2008) attributed the losses to the higher-than-normal temperatures, causing large respiratory losses. Dunn *et al.* (2007), recording the CO_2 flux between 1994 and 2004 in a 160-year old black spruce forest in Canada underlain by peat, found that the average net C balance for this forest was near zero, despite growing seasons turning longer as a consequence of increased annual mean temperatures (which resulted in increased net C uptake during the period). The authors emphasized the interactions between soil thaw and water table depth as important factors in providing critical controls on the C exchange in boreal forests of this kind. Also Melillo *et al.* (2011), investigating a deciduous forest stand in New England, US, found that soil warming resulted in C losses from the soil. However, in their study, the warming-enhanced decomposition of SOM released enough N to support increased plant growth and thus plant C storage. Although soil warming resulted in a cumulative net loss of C from the forest in comparison to the control, the annual net loss generally decreased over time as plant C storage increased. In the seventh year of warming, the soil C loss was almost completely compensated for by the increase in plant C.

Tree mortality as a consequence of increasing temperature and drought has not received much attention, possibly because it is very difficult to estimate considering the large number of factors generally involved in tree die-back. However, Allen *et al.* (2010) presented indications that at least some of the world's forested ecosystems may already be responding to climate change with episodic mortality, even in environments which are not normally considered to be water-limited. Lindroth *et al.* (2009) also emphasized the importance of tree mortality for C balances of forest ecosystems. Investigating the impact of the storm Gudrun that hit Sweden in January 2005 using the model BIOME-BGC, they found a reduction in the C sink capacity of 827-1407 g C m^{-2} yr^{-1} for the first year after the storm. Scaling up this reduction to the whole wind-thrown area, and adjusting for the net uptake of the same area (around 0.4 million tons C), resulted in a total change in the net C exchange of 2.6-3.8 million tons of C during the first year after the storm. These values can according to Lindroth *et al.* (2009) be compared with the net biome production of Swedish forests, which is around 14 million tons C annually, or with the total emission of anthropogenic CO_2 in Sweden, which is 18 million tons C. Although the uncertainties are very large in both of the above mentioned studies, they do show that elevated tree mortality as a consequence of climate change, storm events and associated factors (such as for example insect pests and diseases) has to be taken into account when estimating the potential C sink of future forests, something that is currently not often the case.

7.2.2 Effects of CO_2

Although several studies showed an increase in below-ground C allocation as a consequence of increased levels of CO_2 (see section 4.3.3), this increase does not necessarily translate into an increase in the C content of the soil. Schlesinger & Lichter (2001) reported that increased C accumulation in the litter layer as a consequence of elevated CO_2 did not increase the soil C content. Heath *et al.* (2005), investigating the effects of elevated CO_2 on sequestration of root derived C in the soil of several European tree species using isotope techniques, even found a decrease in soil C sequestration. After 15 months, soil C sequestration was reduced by more than 40% at the highest level of CO_2. The authors did not exclude, however, that the increased input of leaf litter (which was not included in this study) could counteract the effect of root-derived C on C sequestration over a longer period of time.

Such results were found by Hoosbeek *et al.* (2004). At the end of a three-year rotation of a poplar plantation, the C stock in soils exposed to elevated CO_2 was substantially lower than C stocks in soil exposed to ambient CO_2. This occurred despite larger litter inputs at elevated CO_2, and was explained as a priming effect of the native SOC. However, when the study continued for another two years, the decrease was turned into an increase (Hoosbeek *et al.*, 2006). An increase in SOC in the upper 5 cm of the soil as a consequence of elevated CO_2 was also found in a FACE experiment with sweetgum (*L. styraciflua*; Jastrow *et al.*, 2005). Furthermore, Jastrow *et al.* (2005) found, in a meta-analysis of outdoor experiments lasting for at least two years (including forests, grasslands and chaparral), that growth at elevated CO_2 had increased the soil C content with on average 5,6%.

Zak *et al.* (2000) suggested the variable response in soil C pools to elevated CO_2 to be dependent on soil characteristics and nutrient status (see section 5.1.2). That was supported by Van Groeningen *et al.* (2006). They reviewed 56 observations of C in mineral soils (mainly crop experiments) and concluded that unless more than 30 kg N ha^{-1} yr^{-1} was added as fertilizer, SOC did not change.

7.2.3 Effects of N

According to Schulze *et al.* (2010), evidence is accumulating that in the long term plant growth can only benefit from increased CO_2 when sufficient N is available. They emphasized that N interacts strongly with the C cycle, by affecting plant growth and by retarding the decomposition of organic matter. Despite an intense debate about the exact magnitude of the N-induced C sink in forests (Magnani *et al.*, 2007; De Vries *et al.*, 2008; Sutton *et al.*, 2008), it remains practically undisputed that N has been a major cause of variation in NEP of forests (Schulze *et al.*, 2010).

Although N appears to have had mainly beneficial effects on the C sequestration capacity of forests, the future relationship is not completely straightforward. A recent study by de Vries *et al.* (2009) reported that N deposition typically stimulated forest ecosystem C sequestration by 20-40 g C g^{-1} N deposited. However, the efficiency of C sequestration decreased at higher N deposition rates. Similar results were found by Eliasson & Ågren (2011) when investigating the feedback from increasing soil inorganic N-levels on N mineralization and tree growth in six boreal Scots pine stands in Sweden using the Q-model. Including the feedback resulted in a smaller increase in the soil C pool, because increased immobilisation of N in the soil restricted the increase in tree growth, and subsequently litter production, more than it restricted soil respiration. In a study by Hyvönen *et al.* (2008), where 600-1800 kg fertiliser N ha^{-1} was applied to 15 long-term fertilisation experiments of Norway spruce and Scots pine stands in Sweden and Finland for 14-30 years, a mean increase in the tree and soil (organic layer + 10 cm mineral soil) C stocks of 25 ± 5 and 11 ± 2 kg C sequestered per kg N added was found. However, the corresponding estimates for NPK addition were 38 ± 3 and 11 ± 2 kg C per kg N. According to Hyvönen *et al.* (2008), the difference in N-use efficiency between the two treatments indicates that P and K limits tree growth at these sites.

A recent review by Reay *et al.* (2008) also emphasized that the enhanced global CO_2 sequestration resulting from future changes in N deposition may not only be relatively low, but may also be compensated for by N_2O emissions. According to Dolman *et al.* (2010), a doubling of the year 2000 N emissions by 2030 may achieve 3 Pg of additional CO_2 sequestration in northern and tropical forests each year, but it would also induce global annual emissions of between 0,54 and 2,7 Pg of CO_2 equivalent, in the form of N_2O, via increased nitrification and denitrification on land and in the oceans. Dolman *et al.* (2010) thus concluded that the extra uptake of CO_2 as a consequence of N deposition is, from a greenhouse forcing perspective, counterbalanced by the related additional N_2O emissions and that such "pollution swapping" would greatly off-set any net climate change mitigation benefits.

Moreover, atmospheric N deposition is spatially correlated with other forms of air pollution. According to Denman *et al.* (2007), these pollutants may have detrimental effects on plant growth. As an example, a study estimated that surface ozone increases since 1950 may have reduced CO_2 sequestration in the US by 18 to 20 Tg C yr^{-1} (Denman *et al.*, 2007). The current generation of

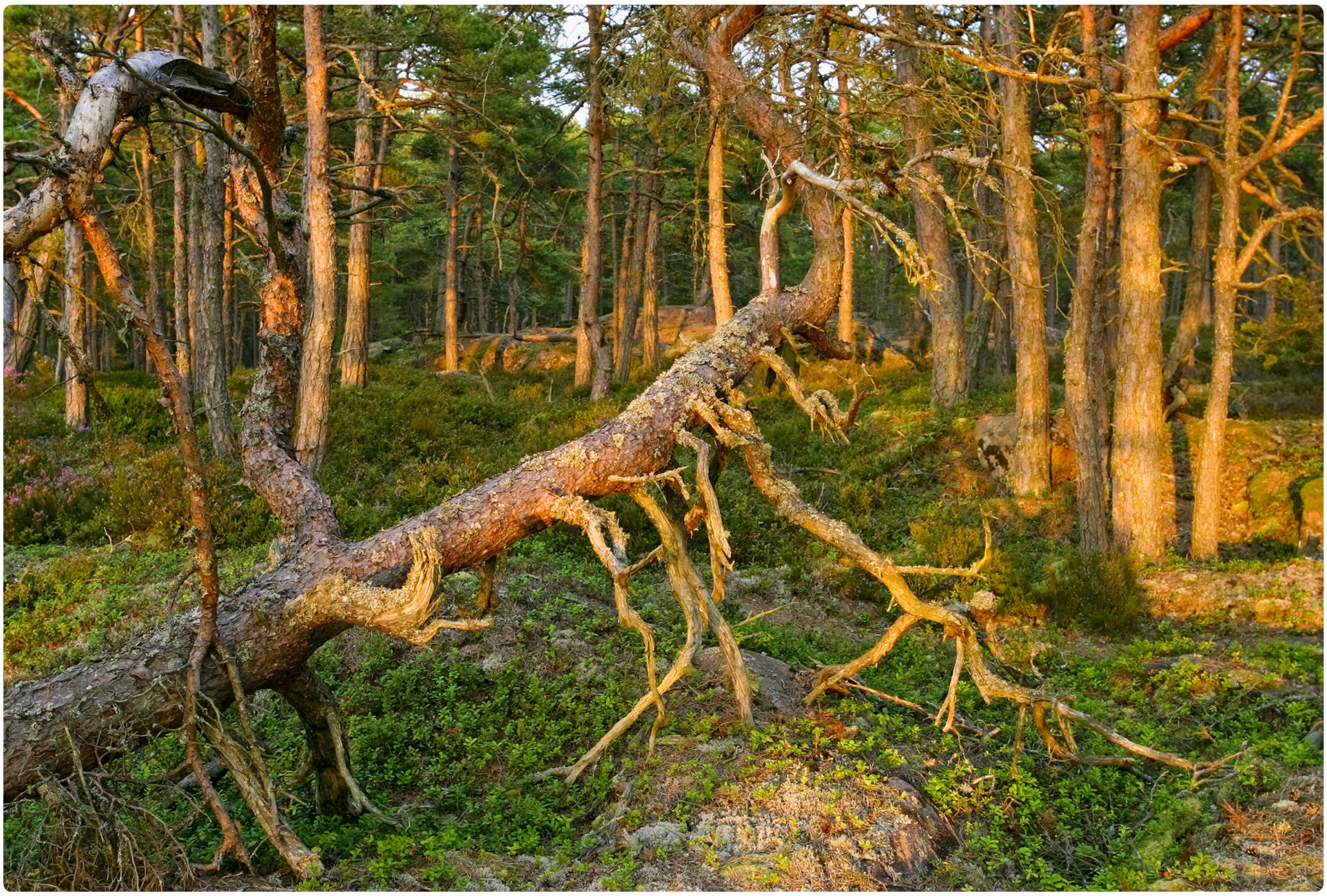


Table 1. Results from a life cycle assessment of forest fuel procurement chains of stumps and logging residues in southern and northern Sweden. The total emissions of greenhouse gases (GHG; g CO_2-eq MJ_{el}^{-1}) are related to MJ electricity produced and GHG savings when replacing electricity from natural gas and coal (negative values indicate savings and positive values no savings). Logging residues and stumps were assumed to be harvested from artificially regenerated stands dominated by spruce (Picea abies (L.) Karst.). Modified from Lindholm et al. (2011).

System[#]	Two or three rotations			One rotation			20 years		
		GHG savings when replacing power from:			GHG savings when replacing power from:			GHG savings when replacing power from:	
	Total emissions	Natural gas	Coal	Total emissions	Natural gas	Coal	Total emissions	Natural gas	Coal
1a	21	-85	-197	43	-63	-174	319	213	102
2a	22	-84	-196	44	-62	-173	320	214	102
2b	29	-77	-188	45	-60	-172	650	544	432
3a	20	-86	-197	43	-63	-175	318	212	101
3b	28	-78	-189	45	-61	-173	649	543	432
4a	34	-72	-184	79	-27	-138	568	462	351
4b	38	-68	-179	64	-42	-153	928	822	710

[#] 1= chipping of residues at the roadside, 2= bundling of residues, 3= handling of loose residues all the way to the end-use facility, 4= stumps; a= southern Sweden, b= northern Sweden. System 1 was not examined in northern Sweden.

coupled C-climate models does not include nutrient limitations or air pollution effects on tree growth (Denman *et al.*, 2007). Another possible impact of N on the C cycle was presented by Ollinger *et al.* (2008). They showed that both CO_2 uptake capacity and canopy N concentration are strongly and positively correlated with shortwave surface albedo, and suggested that this linkage may be an unrecognized feedback in the Earth's climate system. Their study was based on 12 forested research sites distributed across the US. Ollinger *et al.* (2008) concluded that the observation of the strong N-C-albedo linkages in forests add a new dimension to our understanding of the role played by ecosystems within the climate system, but that it would be premature to draw management implications from these results, or conclude that N fertilization would help offset climate warming induced by greenhouse gas emissions.

7.3 Sink capacity of old-growth forests

On the basis of the climax concept, largely undisturbed, old-growth forests have been assumed to be in a state of equilibrium, such that over a period of years they are C neutral with neither net gain nor loss of C. Sometimes, they have even been assumed to be C sources (Lambers *et al.*, 1998). Hyvönen *et al.* (2007) argued that, in general, young forest stands (<25 years old) are stronger C sinks than old stands and give as an example data collected over chronosequences in managed European forests. This data demonstrated that NEE peaks at an age of 10 to 60 years and generally declines thereafter. Several other studies have also shown that NEE reach neutral status in some old-growth boreal forests, or that the forests become C sources (see Hyvönen *et al.*, 2007 and references therein).

However, during recent years, the view of old-growth forests as C neutral or C sources has been challenged (see Luyssaert *et al.*, 2008 and references therein). Luyssaert *et al.* (2008) reviewed literature and databases of forest C-flux estimates and found that for forests between 15 and 800 years of age, NEP is usually positive, i.e. old-growth forests continue to accumulate C. According to Luyssaert *et al.* (2008), this applies to over 30% of the global forest area that is still unmanaged primary forest. Half of the primary forests (600 million hectare) are located in the boreal and temperate regions of the Northern Hemisphere. These forests alone sequester about 1.3 ± 0.5 Pg C yr^{-1}, suggesting that 15% of the global forest area previously considered to be non-contributing to net uptake provides at least 10% of the global NEP (Luyssaert *et al.*, 2008).

If the C content of harvested wood is put into long-term storage (e.g. long-lived houses, furniture etcetera) the total removal of C from the atmosphere over a 200-year period plus the C content of the second growth forest could exceed the C content of the old growth forest (Kimmins, 1997). Under these conditions, the managed forest would be a net C sink, even though the C stored in the second-growth forest at any one time would be substantially less than in the old growth forest. Mahli *et al.* (1999) emphasized that it may seem advantageous from a C sequestration perspective to harvest an old-growth stand with a NEE of around zero, put much of the timber into long-life timber products such as buildings, and replace the forest with a young fast-growing stand with a considerably higher NEE. However, with current practice, much of the biomass C is rapidly lost to the atmosphere via decomposition of waste products, fuel consumption and paper production. Harmon *et al.* (1990) estimated that only 42% of harvested timber in north-western US ended up as long-lived products and that it would take 200 years to replace stocks of C in living biomass by regrowth. They concluded that the conversion of 1.5 M ha of old-growth forest to plantations in western Oregon and Canada has resulted in the release of 1.6 Gt C to the atmosphere. According to Kimmins (1997), the proportion of tree biomass harvested, the proportion of harvested products manufactured into long-lived wood

products and the longevity of these products would all have to increase significantly from the levels of the 1980s to avoid a net release of C to the atmosphere as a consequence of logging.

7.4 Life cycle assessments

During the past five years, a number of life cycle assessment type studies have been published which attempt to evaluate the net C emissions of various forest management practices and forest utilization scenarios in Sweden. One of them is Eriksson *et al.* (2007). The scenarios in Eriksson *et al.* (2007) consisted of 1) forest management strategies (traditional, intensive, fertilization), 2) residue management regimes (no removal, slash removed, slash and stumps removed), 3) product uses (wood-based construction material replacing reinforced concrete and biofuel replacing fossil fuel) and 4) reference fossil fuels (coal and natural gas). In summary, Eriksson *et al.* (2007) found that the greatest reduction in net C emissions occurred when the forest was fertilized, slash and stumps were harvested, wood was used as construction material and the reference fossil fuel was coal. The lowest reduction in net C emissions occurred with traditional forest management, forest residues remained on site and harvested biomass was used as biofuel to replace natural gas. Product use had the greatest impact on net C emissions, whereas forest management regime, reference fossil fuel and residue usage as biofuel were less significant.

Another study was performed by Eriksson & Gustavsson (2008). They looked at the net energy balance and C emissions related to the harvest of stumps and small roundwood. Their results showed that production of stump wood fuel (harvesting, forwarding and processing) gave rise to greater C emissions than other forest fuels such as roundwood and forest residue bundles. However, this was more than off-set by its relatively high energy content and, accordingly, led to greater C reductions in terms of kg C avoided per hectare than other forest fuels, especially if compared with coal.

In later studies, Eriksson & Gustavsson (2010) showed that the recovery system, terrain class, forwarding distance, supply of nutrients and forest productivity had substantial impacts on costs, primary energy use and net C emissions of various forest fuel systems, while Gustavsson *et al.* (2011) showed that the CO_2 emissions per forest harvest area when logging residues replace fossil fuels depend more on the type of fossil fuel replaced than on type of transport system used and the total transport distance. Assessing the C balance trade-offs between bioenergy and C sequestration of stumps, Melin *et al.* (2010) found that in the short term, the choice of coal or stumps as an energy source had a minor effect on the gross emissions to the atmosphere, but that the most effective way of achieving net reduction in the long term is to burn stumps as an alternative to coal. Similar results, but including also slash removal, were found by Lindholm *et al.* (2011; Table 1). Intensive management, in terms of high stand density, fertilization and short rotation periods, was also found to be efficient in terms of CO_2 emissions per unit of energy gained (Routa *et al.*, 2011).

Although interesting, a major limitation of these studies, as emphasized by Walmsley & Godbold (2010), are that the models used generally assumes the decomposition of SOM to occur at the same rate for all forest management regimes. Furthermore, only SOM that originate from newly added litter is generally considered. Consequently, they do not attempt to include any potential change in C emissions from soils that may arise as a consequence of forest or residue management.

8. CONCLUSIONS

Although recent advances have resulted in a more comprehensive understanding of how climate change and forest management practices affect the processes controlling the C dynamics of boreal forest ecosystems, much information is still lacking, especially with regard to their impact on processes controlling soil C. Chapin *et al.* (2009) described our current knowledge about the effects of the soil microbial community structure on C storage and ecosystem C balances in forest ecosystems as a black box. Based on the fact that fungi favour C sequestration through their higher growth efficiency as compared with bacteria, and through the recalcitrance of the compounds they produce, microbial communities may, according to Chapin *et al.* (2009), have substantial impact on the C cycling in forest ecosystems. However, the importance of this impact and the link between microbial diversity and function is yet unknown.

The information with regard to plant responses is considerably more extensive. Yet, there is still insufficient evidence to predict with certainty what the plant responses in a changing climate will be and whether this will result in an increase or a decrease in the sequestration of new C in forest ecosystems (Heath *et al.*, 2005). Chapin *et al.* (2009) emphasized the fact that climate change may lead to changes in species composition that may radically and unexpectedly alter ecosystem C dynamics through changes in the functional types of plants, diseases, soil fauna, and soil microbes, something that is most often not included in current forest ecosystem scenarios and predictions about future C balances.

With regard to the forest management practices WTH and SH, there is currently not enough information available to draw any conclusions about their long-term impact on C cycling in boreal forest ecosystems. Initialising new studies, and follow-ups of existing studies to obtain long-term data, is vital to improve our understanding of their impact on C storage in soils and vegetation. Most importantly, life cycle assessments and modelling approaches need to include realistic information about the effects of forest management practices and climate change not only on tree C pools, but also on soil C pools. Without such information, the predictions arising from them regarding future changes in forest C balances are of limited use.

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