Vulnerability assessment of ecosystem services for climate change impacts and adaptation (Vaccia)

ACTION 9: Assessment of impacts and adaptation measures for forest production; Case study at Northern Häme and Lapland *(Short name: Forest Production)*

Process based model analysis of pine and spruce growth to predict climate change impacts

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Process based model analysis of pine and spruce growth to predict climate change impacts

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Contents

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1. Introduction

1.1 Ecosystem processes and forest development

Forests undergo continuous change that is characterized by the increase in plant size, consequent competition of space and growth resources, suppression and dominance of individuals and mortality of individuals. Mortality of individuals or group of individuals results either directly from competition or from biotic or abiotic factors leading to plant senescence. These biotic or abiotic factors, often also called disturbances, may be dependent on climatic factors, such as storms or drought that promotes fires, or they may be linked to development phase of vegetation. The latter together with appropriate climatic conditions and existence of biotic factors may predispose the vegetation to biotic disturbances. The scale of disturbance vary between these two phenomena. While the abiotic disturbances may lead to large scale openings of tree canopies, the biotic disturbances often concern only individual trees or groups of trees. The continuous change of the forests is called succession and in natural conditions it leads to variable forest structure which is characterized at spatial scale of patches of widely different dimensions. At local scale it results into tree canopies that can be dominated by single cohorts or canopies with different size trees or multiple tree cohorts.

Increasingly, the forest structure results from man-made management where the biomass production of trees in a certain forest area is harvested and brought to human use instead of it being burned in forest fires or slowly decomposed at the site after trees fall. These practices alter mainly the disturbance process, influencing the size and quality of openings formed in the tree canopy and the age of the dominant trees. The other processes of succession i.e. establishment, competition, differentiation and mortality leading to succession of species and self thinning have remained relatively less altered. Silvicultural practices of soil scarification and artificial regeneration through sowing or planting aim at favoring the selected species but this happens within the context of vegetation competition that is more difficult to control than the disturbance pattern that has naturally longer repetitiveness than the desired managed rotation (Kuuluvainen 2002).

Climate change influences practically all of the above processes. In the boreal Fenno- Scandia temperature will rise faster than the global average, precipitation will increase somewhat along with the global increase in the CO_2 concentration. These

changes will have impact on the frequency of natural disturbance factors, such as fires and biotic causes that spreading of new species of animals and fungi and changes in the behavior of the existing ones will cause. However, as Finnish forests are predominantly managed, it is expected that the role of natural disturbance factors will also remain small in the future. Natural vegetation change with climate is buffered as existing established populations tend to be able to resist out competition even in suboptimal conditions (Chapin et al. 2004). Forestry operations could actively introduce both new provenances and entirely new species as adaptive forestry (e.g. Kellomäki et al. 2005). From the forest management point of view the most important changes will be those related to the change and establishment of vegetation upon the liberation of space after the disturbance and the consequent competition between species, first between grasses, herbs and the trees, then between trees of different species and lastly the growth and development of established tree population.

1.2 The approach of the analysis

In this document we will use our biological understanding of the processes that govern the plant growth in order to estimate how the situation of forest management of even-aged forests is likely to change under the predicted climate change. The analysis will concentrate on: a) productivity and growth changes of pine and spruce stands in changing climate, b) changes in severity of herb layer competition after clear-cutting and c) changes in competitive status between conifer and broad leaved trees in sapling stands. We will use both literature analysis (b and c) and a number of different process based models in the analysis of stand growth changes in changing climate. For the relative changes in the initial development of conifer vs. broadleaved growth we use the functional- structural tree model LIGNUM (Perttunen et al. 1998), for the tree crown and canopy productivity changes we use SPP model (Mäkelä et al. 2006) and for the stand growth changes we utilize process based stand growth models PipeQual (Mäkelä and Mäkinen 2003) and MicroForest (Hari et al. 2008). These models will be supported by soil hydrology models to analyze the occurrence of drought under different climate assumption and recently developed mechanistic stem growth model to estimate the drought impact on stem growth.

2. Process-based analysis of climate change impacts on forest growth

2.1 Growth and development of vegetation

The vegetation succession after disturbance depends first on its establishment and then its growth. Physiologically these two processes are related to separate traits in plants life cycles. The establishment results from flowering, pollination, seed

maturation and dispersal and subsequent seed germination and early growth. The growth results from photosynthesis and nutrient uptake and their allocation to permanent structures. There is normally a trade-off between vegetative growth and reproduction. Annual plants invest only a part of their seasonal resource capture to increase the vegetative size (i.e. leaves and roots that are able to take up resources) and direct the rest to reproductive organs and seed production. In contrast, some trees, like for example Norway spruce, need to gain rather large size and age before they start flowering.

Vegetation growth is best understood as a sequential process in which plants harvest growth resources from their environment and utilize those to increase their size. The harvesting of the growth resources depends on the resource density in the surroundings of plants. This is dependent on the surrounding vegetation structure. The change in the size of plants will influence the resource density and has a feedback to resource capture and subsequent growth (see Figure 1).
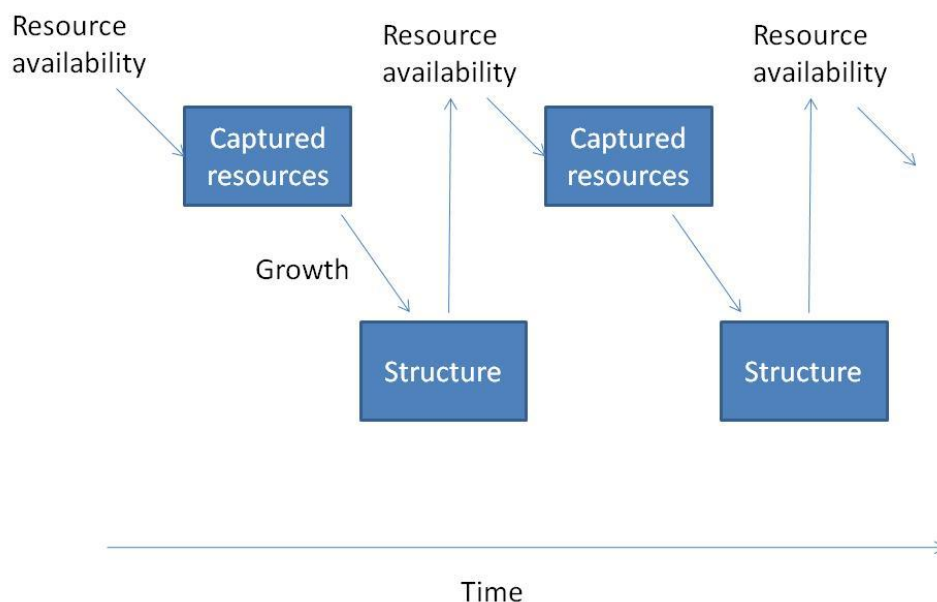
Figure 1. Schematic presentation of vegetation growth process

The individual plant development depends on the resource capture, allocation to growth and senescence rate of plant organs. This is illustrated with respect to plant carbon balance in Figure 2. Efficient resource uptake facilitates rapid growth but it also requires a good access to high resource flux density. The latter require either low competing vegetation or good position within the competing vegetation. Fast growth rate will gain a good resource supply. However, also allocation to height development will give access to better light conditions (and also root system spread

below ground for nutrients). Investment to extension growth requires allocation of resources to supporting structures and consequently less resource availability to organs capturing resources. In the short run this means losing out in resource uptake but in the long run may signify gain in the competition if new growth is taking place on top of the previously built structures.
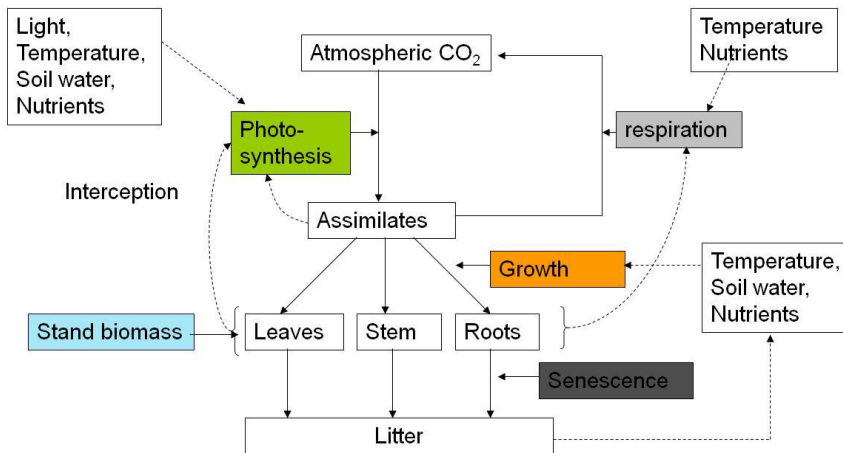

Figure 2 Schematic presentation of carbon flows in plants and influencing factors

When analyzing the climate change impact on vegetation we need to study what happens to resource uptake and losses e.g. in photosynthesis, respiration, allocation to growth and senescence of different plant biomass compartments. The responses in different types of species from annual herbs to different pioneer and tree species require that we first analyze what kind of changes can be expected within species of given functional and structural traits and how they compare with each other. The latter is needed to be able to predict changes at plant community level.

In the following we first study the impacts of climate change on tree productivity and growth and subsequently estimate how competitive status between trees and ground vegetation will change after clear cutting and also how the conifer vs. broadleaved growth is influenced by climate change.

2.2 Photosynthetic production of trees

We estimated the potential increase in photosynthetic productivity in Scots pine (*Pinus sylvestris*) and silver birch (*Betula pendula*) due to direct effects of increasing temperature and CO_2. The model of photosynthesis calculates the light driven biochemical processes that bind CO_2 into sugars and the diffusive influx of carbon dioxide into the leaf from the atmosphere resulting from the concentration gradient that photosynthesis establishes. The biochemical activity of leaves depend on the radiation that they receive, the leaf nutrient status (here estimated with nitrogen (and

6

thus protein) concentration) and the temperature and the seasonal cycle in it. The carbon dioxide influx depends on the steepness of the concentration gradient and the conductivity of the diffusive pathway from atmosphere into internal air spaces in leaves. The former depend on the net rate by which photosynthesis minus respiratory processes consume CO_2 in leaf and the atmospheric CO_2 concentration. The conductivity of the diffusive pathway is mainly controlled by the degree of opening of the leaf stomata. Between species important changes in the leaf boundary layer and within leaf diffusive pathway conductivity exist as well. The stomatal conductivity depend on rate of leaf CO_2 gain and leaf water loss, that inevitably takes place.

Depending on the growing conditions the photosynthetic production of leaves responds in a predictable manner to variations in the atmospheric and soil conditions. This response can be estimated from field observations. Once established as a model, it can be used to calculate how photosynthetic production varies with measured or predicted changes in these driving conditions. We calculated photosynthetic production of a single leaf in half-hourly time steps with leaf intercepted radiation, temperature, atmospheric vapor pressure deficit and CO_2 concentration and soil water status as variables driving the photosynthetic rate using a biochemical model of photosynthesis (Farquhar et al., 1980) along with a model of stomatal conductance (Leuning (1990). The seasonality of photosynthetic capacity and quantum yield in conifer pine were described as delayed temperature response (Mäkelä et al., 2004). The model parameters were estimated from multiannual time series of shoot and leaf gas exchange in pine shoots in Hyytiälä, Southern Finland (Kolari et al., 2007). For deciduous birch, the annual cycle model was replaced by simple temperature-driven model of leaf unfolding and day-length-triggered leaf senescence that determined the seasonal development of the leaf area index of the stand. The parameters of the photosynthesis model were estimated from gas exchange of birch leaves (Juurola 2003).

Photosynthetic production of the trees was determined by integrating the instantaneous photosynthetic rate at shoot (pine) or leaf (birch) level over the whole stand. The integration was done with SPP (Stand Photosynthesis Program, Mäkelä et al., 2006) that combines a model of shoot photosynthetic production with the model of light interception in the canopy (Stenberg 1996) and soil water limitation to gas exchange (Duursma et al., 2007). In the model the soil water starts to limit the transpiration rate as soil water content drops below 40% level of the total potential plant available water in the soil (which is defined as the difference in soil water content at field capacity (i.e. when freely draining water has drained from soil pores) minus that at the plant wilting point) and decreases henceforth rather linearly with decrease in the plant available water. In SPP, photosynthetic production is modelled

at tree level. Trees of different species, size, leaf area density or physiology are represented as size classes. Each size class may have its own photosynthetic parameters, canopy shape and dimensions. The individual crowns consist of a homogeneous medium. The trees are assumed to be randomly distributed in the stand. When calculating the light environment inside the crowns, shading by the neighboring trees is taken into account in addition to within-crown shading.

In the present climate the model can explain the seasonal pattern of photosynthetic production very well, including drought-induced decline (Figure 3).
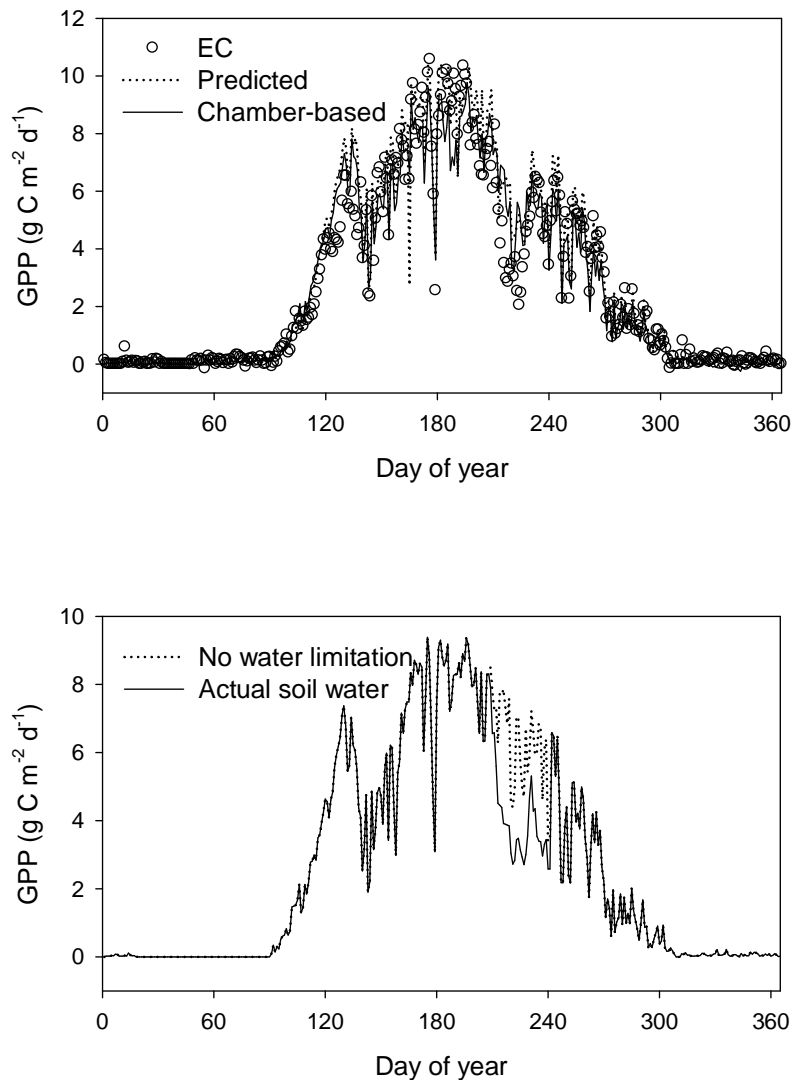

Figure 3. Daily photosynthetic production (GPP) of the stand during year 2006: a) GPP extracted from eddy covariance, upscaling directly from chamber measurements, and prediction with SPP (Kolari et al. 2009), b) predicted stand GPP with no soil water limitation on tree gas exchange and GPP with the actual soil water status

8

In the simulations tree dimensions, leaf area index and tree density were typical for an established tree stand in a self-thinning phase well after canopy closure. The model was run with a climate change scenario (Jylhä et al., 2009) that corresponds to approx. 50% increase in the emissions of CO_2 from fossil fuel combustion by 2050 and a slow decline after that (scenario A1b, Table 1). Climate change modified weather data from Hyytiälä was used as the model input. All half-hourly records of air temperature and atmospheric CO_2 were increased by the mean annual temperature rise and CO_2 increase, respectively. Water vapor concentration in the air was altered so as to keep relative humidity of air unchanged (Dessler and Sherwood 2009; Kimmo Ruosteenoja, personal communication).

Table 1. Projected increase in atmospheric CO_2 and mean annual temperature in Finland according to Jylhä *et al.* (2009).

Year	CO_2 (ppm)	T increase (deg C)
2025	430	1
2055	540	2
2085	650	3

Annual photosynthetic production will increase more in birch due to steeper instantaneous temperature response and higher temperature optimum of photosynthesis than in pine (Figure 4). Most of the increase can be attributed to longer growing season, in midsummer the simulated momentary photosynthetic rates in 2085 are only 10–15% higher than in the present climate. The summertime enhancement in photosynthetic production is almost exclusively caused by the increase in atmospheric CO2.
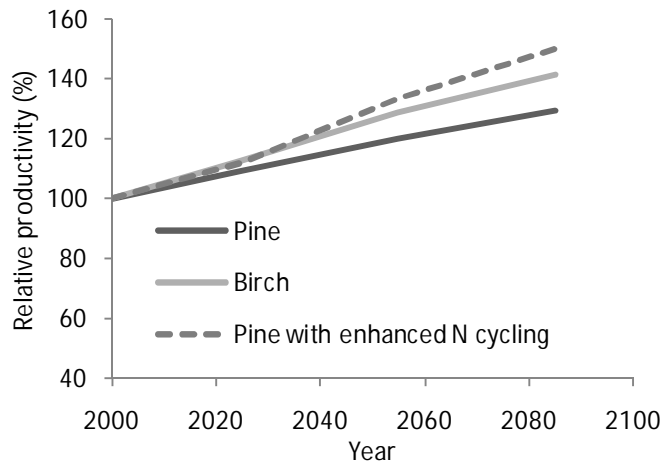
Figure 4. Predicted relative (year 2000 = 100) annual photosynthetic production in middle-aged pine and birch stands (only direct effect of temperature and CO_2 considered) and in the stemwood production of pine (enhanced N cycling and changed allocation patterns taken into account) until year 2085.

The model predicts a decline in instantaneous transpiration rates in both pine and birch. Due to the longer growing season in the future, however, the annual cumulative transpiration will remain approximately at the present level. Increasing CO_2 enhances water-use efficiency as the stomata tend to open less at elevated CO_2 than in present CO_2 (Figure 5). The free-air CO2 enrichment studies have shown no significant change in the stomatal responses to CO2 (Medlyn et al., 2001). Increasing stand foliage area, however, may partly offset the enhanced water-use efficiency.
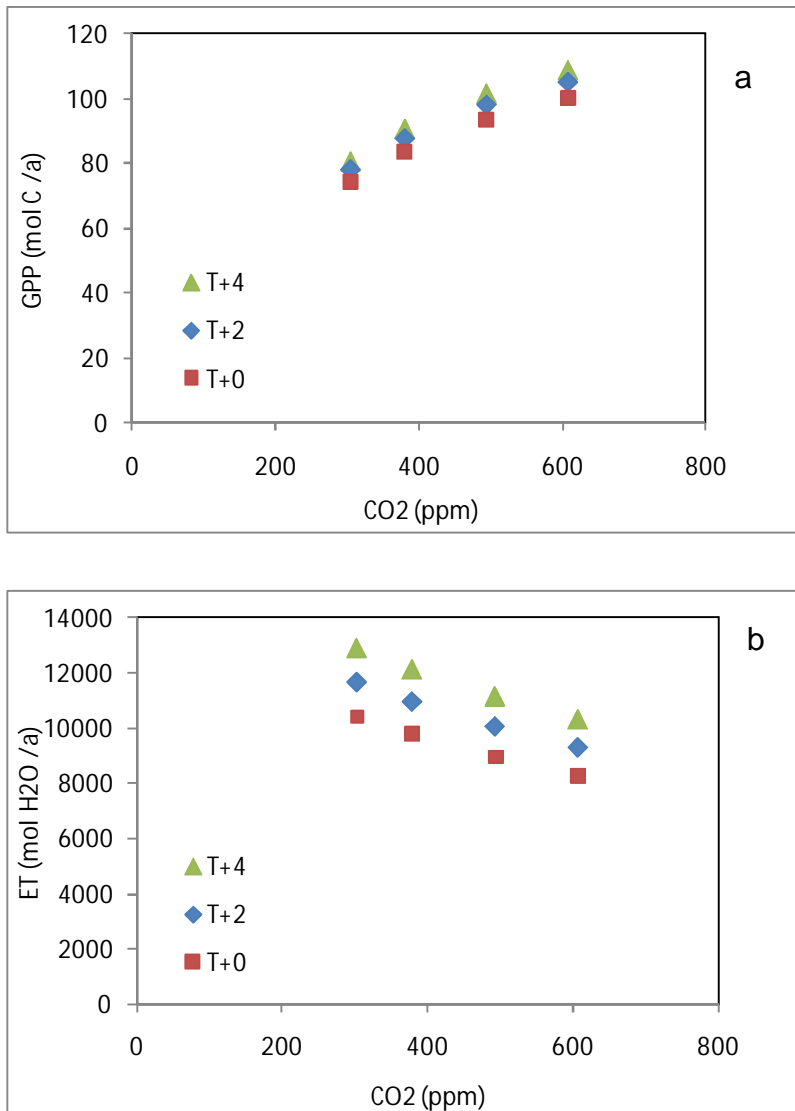
Figure 5. Variation in a) photosynthetic productivity and b) transpiration at different atmospheric CO_2-concentrations and average temperature rises.

Overall, drought will probably remain a minor risk for forest productivity in Finnish conditions in the future if the temporal distribution of precipitation over the growing season remains similar to the present conditions. The predictions done with SPP model assuming climate change scenarios and using known soil properties showed that the number of drought days (i.e. days when photosynthetic production drops below 50% of the potential) will slightly increase on average towards the end of the century, but the increase is just two to five days from the present (Mäkelä et al., 2010). The increase is slightly larger on drier site in the south-western part of the

country while on moist sites in most of the country would not be suffering from drought even in the future climate on average (see Figure 6)
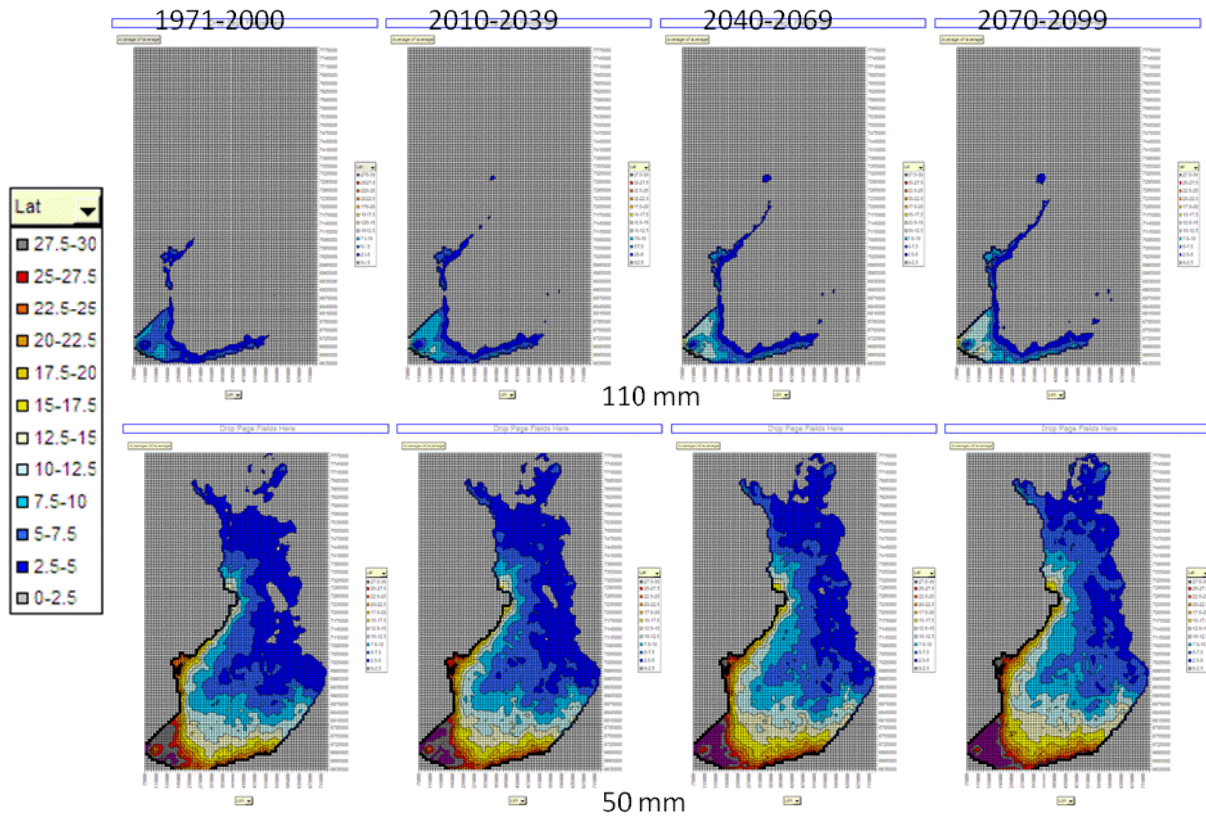

Figure 6. The development of the average number of drought days under climate change scenario (A1b) on medium fertile (110 mm) and poor (50mm) site (Mäkelä et al. 2010)

2.3 Acclimation of photosynthetic processes

Figure 3 illustrates that analysis is able to predict the variation of photosynthetic production in present climate. However CO_2 and temperature increase will directly influence leaf properties that may change the CO2 and water vapor fluxes at leaf – atmosphere boundary and also indirectly influence the situation through possible enhanced nitrogen availability and deeper canopy shading that may result from increased foliage growth. While the expected temperature variation is not changing during growing season dramatically from the present there is considerable change in the expected ambient CO_2. This will change the balance between the energy, water and CO_2 fluxes at leaves. In particular angiosperms are efficient in adjusting their leaf proteins to correspond to changing conditions (Evans 1991). A number of experiments have shown that if CO_2 alone is increased, in the long run the leaf

nitrogen content decreases and photosynthetic capacity down-regulates (Tjoelker et al., 1998, Juurola 2003, Elsworth et al., 2004). Normally this decrease is associated with increasing leaf biomass at canopy scale. Similar down-regulation of photosynthesis is not reported or is not as strong in conifers (Tjoelker et al., 1998, Juurola 2003) that generally have much lower variation in leaf nutrient content and that are much more limited by the CO_2 diffusion pathway in their productivity than broadleaved trees (Manter and Kerrigan 2004). So at leaf level, conifer productivity is expected to rise more but at the canopy scale the differences are partially compensated by the relatively higher leaf area to present that the broad leaved trees are able to produce. However, acclimation to elevated CO_2 may decrease the difference between these tree groups from the predicted trends (Figure 4)

Although temperature during growing season will most likely not cause directly acclimation in trees that would influence the predictions it has indirect influence on growing season length and other ecosystem processes influencing the net productivity. The models used are able to predict accurately seasonal variation of photosynthesis from southern France to Lapland, so that influence should be accounted for quite well in the predictions (Mäkelä et al 2008). However, as the climate change in the winter time is large enough, there may be some problems for tree acclimations that could result into either spring time frost damage and accelerated needle mortality, in particular with spruce (e.g. Koca et al., 2006).

Another possible factor that may be influencing the productivity is enhanced nitrogen availability for trees that follows from accelerated nutrient turnover in the soil. This will potentially have a stronger influence on broadleaved than conifer trees (Ripullone et al., 2003). Higher nitrogen availability may increase the maximum photosynthetic rate particularly in broadleaved trees. However, the additional nitrogen may also increase leaf growth. The results from long term CO2 enrichment experiments would tend to suggest that in forests with rather low leaf areas the increased leaf area may be the dominating influence (Norby et al., 2005). Elevated CO2 and nitrogen availability increase the leaf area duration (McCarthy et al., 2006). At higher leaf areas there also seems to be an enhancement in the light use efficiency of the leaves (Norby et al., 2005, McCarthy et al., 2006). Overall, the vegetation acclimation to new growing conditions will influence the predictions that are done assuming current response pattern to changing conditions. The elevated CO2 concentration will most likely decrease the predicted difference between the conifer and broadleaved species but simultaneously the predicted increase in the nitrogen availability has an opposite effect. Bearing in mind the uncertainty involved in the scenarios and possible other factors concerning the vegetation response the scenario result of about 25% higher productivity in pine and about 40% higher productivity in birch gives a fairly good representation of the expected change.

2.4 Tree Growth

Changes in photosynthetic productivity(GPP) is but one of the responses to changing climate and long term response includes changes in net productivity (NPP) as changes will also influence the respiration rate, changes in resource allocation to different biomass compartments, changes in their size that will have feedback to productivity as shown before and changes in the senescence (see Figure 2). Experiments with long term exposure to elevated CO_2 in temperate climate have shown considerable increase in both net primary production (NPP,i.e. phosynthetic production minus respiratory losses) and growth allocation between leaves, wood and fineroots (Franklin et al., 2009). Temperature increase will instantaneously influence respiration rate (eg. Kolari et al., 2009) but there is a lot of evidence that it will tend to balance with the production rate (Malhi et al., 1999, Saxe et al., 2001, Körner 2006) so that increased GPP will also be associated with proportional increase in the net productivity.

Biomass production changes of pine was further studied with MicroForest (Hari *et al.*, 2008) that incorporates soil nitrogen (N) cycling and changing allocation into foliage, wood and roots. It calculates the allocation between the leaves, wood and fine-roots from determined structural regularities between the wood dimensions and amount of foliage and from the requirement that the resource uptake and the resource use for growth will match each other (Hari *et al.*, 2008). The key parameters of the model that change with climate are annual photosynthetic production in unshaded conditions, decomposition rate of proteins in the soil, and nitrogen deposition. For the productivity simulations the annual photosynthesis was obtained from the previously presented simulations with increased CO_2 and temperature. The rate of decomposition was increased by 6% per °C rise in temperature. Nitrogen deposition was assumed to remain at the present level. Simulations with just warmer climate scenario and elevated CO_2 did not bring about growth enhancement. However, enhanced N cycling and change in within-tree biomass allocation allowed, along with productivity changes, for additional increment of approximately 20% in pine stemwood production. This mainly results from lower allocation below ground. The experimental results from the large scale CO2 enhancement experiments have produced similar results (Oren et al., 2001) in terms of elevated CO2 while soil warming experiments produced similar outcome in terms of enhanced nitrogen availability (Strömgren and Linder 2002). The fate of nitrogen quantitatively upon the enhanced decomposition is not certain as part of it may be immobilized within the soil microbial communities. However, combined influence of continuous nitrogen deposition and elevated temperatures and CO_2 are certain to produce growth acceleration as predicted (Magnani et al. 2007)

Tree species seem to have different response pattern in growth allocation as regards to the enhanced production in elevated CO_2. The nutrient use efficient conifers seem to allocate relatively more to stem while the broadleaved species had much higher allocation to fine root under elevated CO_2 (Delucia et al. 2005). Franklin et al. (2009) attributed these changes to different turnover rates of the fine roots which imposes large differences in the nitrogen usage for root growth. Due to this difference the broadleaved species that have generally more rapid root turnover rate would be more susceptible to low soil nitrogen availability than pines. However, if indeed the nitrogen availability increases in soil due to climatic warming and enhanced decomposition, it may be that the broadleaved trees may invest more of their growth to stems than pines (McCarthy et al. 2006). This is also seen in the Finnish growth and yield tables of Scots pine with saturating stem yield with the highest soil fertilities (Koivisto 1959). Some of those allocation changes are considered in the modeled response but they may be slight overestimations as not all the changes in branchiness that are associated with higher productivity. We could thus suspect that the gain in stem growth may be slightly lower than predicted in the simulation for Scots pine and about the same or higher for birch.

Increase of drought days was not predicted to cause any significant reduction in the plant productivity but it may have direct influence to growth. In the long term historical growth data there was a decrease in both pine and spruce growth during dry years (Yrjönen 2008). The growth influence of drought results from the growth process itself. Trees use water pressure to expand the newly differentiated cells to the size of mature cells that are then lignified in the cell wall formation process. The water pressure is created osmotically and trees use sugars for that. If they are under water stress more sugars are needed to just maintain the cell turgor not to mention the cell expansion. If drought is persistent, the achievable final cell size remains smaller. However, if the drought is reversed also growth may resume and rather rapid expansion may follow. This naturally depends if the phase of the annual cycle still allows it. Figure 7 shows how much earlier the growth starts to react to decrease in soil moisture compared to photosynthetic productivity.
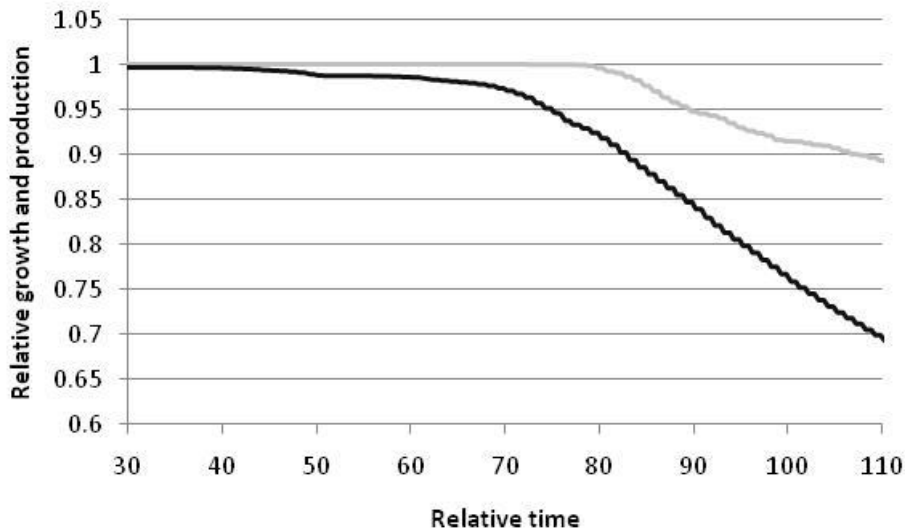
Figure 7. Relative decrease in modeled cumulative photosynthetic production (grey line) and modeled cumulative stem diameter growth (black line) during 2006 drought year vs. no drought conditions.

Although the average number of drought day does not increase considerably, the climate change may imply occasional more severe drought periods that may severely influence growth and enhance leaf turnover and increased mortality. Figure 8 shows the extent of drought periods during the last 50 years and how their length would change in the climate of elevated temperature. It is clear that almost doubling the number of drought days from 2006 drought to otherwise similar rainfall pattern in the new climate would be extremely stressful for trees and almost certainly lead to increased tree mortality. As Figures 6 showed, the severity and extension of the drought period depend on the soil water storing capacity. The main problem in the future may follow from the combination of favorable growth years that may allow establishment of trees with too large foliage fine-root ratio for possible soil- drought combinations and occasional severe drought that will then kill the ill suited trees.
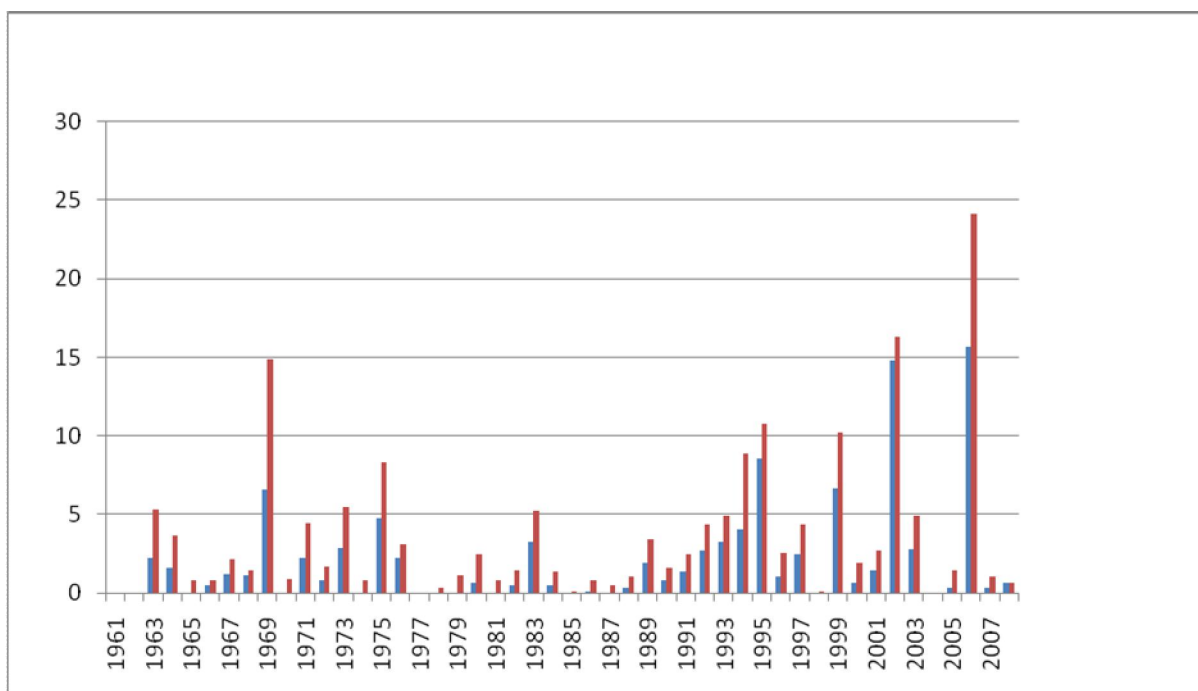
Figure 8 Simulated number of drought days under current (blue bars) and changed (A1b, 2070-2099) climate (Mäkelä et al., 2010)

2.5 Post disturbance competition

Creation of canopy gap or enhances availability of radiation and nutrients that favors initially efficient species over the species adapted to scarcity of resources under the closed canopy. Grasses and herbs that allocate their production predominantly to productive and reproductive organs quickly conquer the space. Perennials and trees that use substantial proportion of their production to development of permanent support structures only gradually gain better access to resources and over the time can shade out the annual plants.

Elevated temperature, CO_2 concentration and more rapid turnover rate of soil organic matter that releases more nitrogen to plant use will lead to eutrofication of the sites. This will favor more rapid post disturbance development of grasses and herbs (Theurilat and Guisan 2001, Manninen et al. (in print)). Also comparable size seedlings of present broadleaved species such as birches are better competitors for resource capture in high resource availability during early development in comparison to our conifers (e.g. Dehlin et al., 2004). The difference is manifested through the spouting capability that places the broadleaved species in a superior

competitive position relative to conifers during the early years after clear cutting and due to contrasting broadleaved growth pattern that is able to gain much higher sapling height per invested resource than in conifers during the early growth.

Muukkonen and Mäkipää (2006) published models for ground vegetation biomass based on the large forest inventory database. Figure 9 presents the calculated variation of grass and herb biomass both as a function of fertility class and annual temperature sum acoording to Muukkonen and Mäkipää (2006). The current temperature sum variation between 500 to 1300 dd is predicted to change to be between 900 to 2400 dd. The upper limit corresponds to current weather in Southern UK. There Ford and Newbound (1970) observed about triple the biomass of herbs and grasses 2 years after clear-cutting the tree stand compared to the values of the most fertile sites in South Finland currently. According to Palviainen et al. (2005) the maximum ground vegetation biomass occurs 5 years after clear cutting in the current 1000 dd climate conditions.
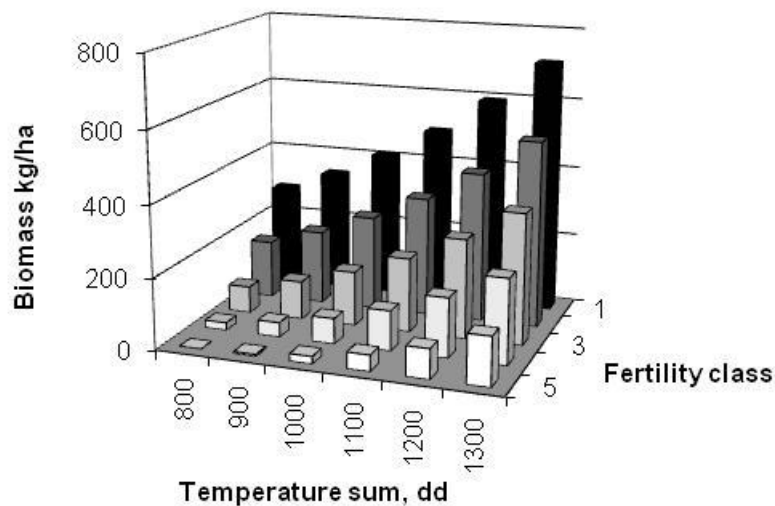

Figure 9. The post harvest biomass of herbs and grasses as a function of site temperature sum and fertility class (1 rich, 5 poor) according to Muukkonen and Mäkipää (2006)

3. Climate change impacts on forest management

We use the stand growth simulator Pipe Qual (Mäkelä and Mäkinen 2003) to analyse the impact of higher productivity on the pine stand growth. The model assumes monoculture without between species competition. We increase the forest productivity to correspond to the situation at 2090 in Figure 4 and compare the

situation to present growth on medium fertile Myrtillus type forest. This value assumes increased productivity due to elevated temperature and CO2 plus enhanced nutrient turnover in the soil organic matter and considers the impacts of drought on the production. However, it does not include possible impacts that extreme drought years may have on the survival and leaf senescence nor any increase in the biotic stress factors. In that sense the simulations can be considered as examples of the highest potential growth that may be attainable.

The rate of stand development is greatly enhanced in the changed climate. The stand closure takes place about 5 years earlier than currently and the stand reach the phase of first commercial thinning about 15 years earlier than currently. The rotation length that maximizes timber yield is about 45 years and the stand volume then is about 500 m^3/ha that corresponds to volumes at final cut also currently; only the rotation that yields the same production is currently about double the length.

As the simulations assume no competition from other species, we need to consider also the silvicultural treatments necessary to reach such a situation. Stand establishment requires planting immediately after clear-cutting with rather intensive management of herb layer. Soil scarification will not be sufficient to control the ground vegetation but special treatment of herbs need to be done during the second year after planting. Also at least two treatments of the competing broadleaved trees are required. Alternatively pre-harvesting treatment of the broadleaved trees may be necessary to control the sprouting.

The quality control of the trees most likely becomes very important as the fast growth rate tends to lower the wood quality in pines. Maintaining sufficient stand density is important but with the very fast growth rate there is the possibility that canopy becomes too dense and individual crowns prune too high. Another factor that needs to be considered are the possible severe drought years. Although pines are well adapted to withstand drought, large scale mortality may follow if stands are allowed to grow very dense during a favorable period that is followed by a drought. Targeted thinning before the extreme drought may alleviate the problem as the transpiring leaf area is decreased and the leaf area of the below canopy ground vegetation is small due to earlier shading by the canopy trees.

It is clear that climate change will both increase the productivity and production costs of pine growing. Careful economical analyses are needed to clarify the net influence in terms of the economy of pine growing. Birch growth in South Finland may be even more enhanced and it has much less problems in terms of early competition or wood quality as pine has. Climate change will thus influence the relative economic returns of silviculture with different tree species on different growing sites.

Similar analyses as done here for pine vs. birch productivity needs to be done for all the present and potential tree species. Previous analysis has suggested that spruce might be declining in the warmer climate. Both increased drought (Kellomäki et al. 2005) and warmer winters (Koca et al. 2006) have been suggested as potential reasons for the decline. In our analysis we also studied spruce behavior but did not find any drastic difference from the behavior of pine. However, slight changes in various values might together lead to decreased productivity. Spruce has a highly economic growth habit. Per leaf lifetime it requires less nutrients and less wood and root growth than our other species. That allows spruce saplings to survive in deeper shade than those of other species in Scandinavian boreal forests. On the other hand, when resources are plentiful, it can develop very large foliage and crown that casts deep shade to competing trees. If water stress or warm winter induced accelerated defoliation prevent it from developing large foliage mass, it will lose in its competitive ability. Overall, the climate change impacts for spruce management can be expected similar to pine. We may expect shorter rotation but more difficulties in stand establishment. However, similar problem with wood quality as there is for pine should not concern spruce. The drought problem will be stronger than for pine and attention should be paid not to establish spruces on too coarse soils with inadequate water holding capacity. The adequate timing of thinning will be equally or more important than for pine relative to drought years.

In the beginning we limited the impact of climate change on the disturbance frequency outside the scope of this paper. However, both increased wind and insect damage (Parviainen et al. 2010) and extreme drought years may influence the length of maximal possible rotation length. This would naturally favor trees with more rapid early development. However, the expected shorter rotation length for both of our conifer species will partially compensate for the problem. Currently unevenaged forest management has gained wide popularity among the forest owners. The higher frequency of natural disturbances most likely will influence the relative productivity of this management scheme, however, the net outcome is difficult to predict. Unevenaged forests can favor establishment of new saplings but their ability to resist drought, windthrows and biotic stress factors need to be studied.

As we limited our analysis for managed forest, the flowering, seed dispersal and germination and initial seedling growth was left out of the analysis. However, in forest management chain the management of regeneration material i.e. seeds and seedlings is an important bottleneck. Also natural regeneration of sites will depend on the natural seed production. Overall, the temperature increase will influence favorably to seed production of all the considered species. The only risk may be involved with phenotypic acclimation to new temperature pattern that may cause problems in phenotypic acclimation and associated risks of e.g. spring frost damage.

Both our conifer species are quite conservative with their flowering temperature requirement, so large scale frost damage is not likely. Provenance selection would be a tool to better adjust our trees with the changing climate and it would partially help to adjust the vegetation properties to match the climatic conditions (Kellomäki et al., 2005). The change would take place naturally, but due to different disturbance barriers it is a buffered process (Chapin et al., 2004).

4. Conclusions

Climate change will have profound impact to forest productivity and silviculture. Growth increase can be expected but also modifications to silvicultural practices can be foreseen. The economic productivity between species and site types will change as the presently growing broadleaved trees are both more responsive to the climate change and they are also able to cope with post clear-cutting conditions better than our conifers. However, also the production potential of the presently dominating conifers seems to increase.

5. Cited literature

Chapin, III, F.S., Callaghan, T.V., Bergeron, Y., Fukuda, M., Johnstone, J.F., Juday, G and S. A. Zimov. 2004. Global Change and the Borea Forest: Thresholds, Shifting States or Gradula Change? *Ambio* Vol. 33 No. 6:361-365.

Dehlin, H., Nilsson, M-C., Wardle, D.A. and A. Shevtsova. 2004. Effects of shading and humus fertility on growth,competition, and ectomycorrhizal colonization of boreal forest tree seedlings. *Can. J. For. Res.* 34: 2573–2586

DeLucia EH, Moore DJ, Norby RJ. 2005. Contrasting responses of forest ecosystems to rising atmospheric CO_2: implications for the global C cycle. *Global Biogeochemical Cycles,* 19, 1–9.

Dessler A.E. & Sherwood S.C. 2009. A matter of humidity. *Science* 323:1020–1021.

Duursma R.A., Kolari P., Perämäki M., Nikinmaa E., Hari P., Delzon S., Loustau D., Ilvesniemi H., Pumpanen J., Mäkelä A. 2008. Predicting the decline in daily maximum transpiration rate of two pine stands during drought based on constant minimum leaf water potential and plant hydraulic conductance. *Tree Physiology* 28, 265-276.

Ellsworth DS, Reich PB, Naumburg ES, Koch GW, Kubiske ME, Smith SD. 2004. Photosynthesis, carboxylation and leaf nitrogen responses of 16 species to elevated

pCO_2 across four free-air CO_2 enrichment experiments in forest, grassland and desert *Global Change Biology 10: 2121–2138*.

Evans, J. R. 1991. Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78:9-19.

Farquhar, G.D., S. von Caemmerer and J.A. Berry (1980). A biochemical model of photosynthetic CO2 assimilation in leaves of C3 species. *Planta* 149, 78.

Ford, E-D. and P.J. Newbould. 1977. The Biomass and Production of Ground Vegetation and Its Relation to Tree Cover Through a Deciduous Woodland Cycle. *Journal of Ecology*, 65(1):201-212

Franklin, O., McMurtrie, R.E., Iversen, C.M., Crous, K.Y., Finzi, A.C., Tissue, D.T., Ellsworth, D.S., Oren, R. and R.J. Norby. 2009. Forest fine-root production and nitrogen use under elevated CO2: contrasting responses in evergreen and deciduous trees explained by a common principle. *Global Change Biology* 15:132-144.

Hari, P., M. Salkinoja-Salonen, J. Liski, A. Simojoki, P. Kolari, J. Pumpanen, M. Kähkönen, T. Aakala, M. Havimo, R. Kivekäs and E. Nikinmaa (2008). Growth and development of forest ecosystems; The MicroForest Model. In: Hari, P. and L. Kulmala (eds.) Boreal forest and climate change. Advances in Global Change Research, Vol. 34 (Springer Verlag), 433.

Juurola, E. 2003. Biochemical acclimation patterns of Betula pendula Roth. and Pinus sylvestris L. seedlings to elevated carbon dioxide concentrations. Tree Physiology, 23: 85-95.

Jylhä, K., K. Ruosteenoja, J. Räisänen, A. Venäläinen, H. Tuomenvirta, L. Ruokolainen, S. Saku and T. Seitola (2009). Changing climate in Finland: estimates for adaptation studies. Finnish Meteorological Institute, Reports 2009: 4.

Kellomäki, S., Strandman, H., Nuutinen, T., Peltola, H., Korhonen, K.T. and Väisänen, H. 2005. Adaptation of forest ecosystems, forests and forestry to climate change. FINADAPT Working Paper 4, *Finnish Environment Institute Mimeographs 334*, Helsinki, 50 pp.

Koca, D., Smith, B. and M.T. Sykes. 2006. Modelling regional climate change effects on potential natural ecosystems in sweden. *Climatic Change* 78: 381–406

Koivisto, P. 1959. Kasvu- ja tuottotaulukoita. Summary: Growth and yield tables. *Communicationes Instituti Forestalis Fenniae* 51.8. 1–49 s.

Kolari P, Kulmala L, Pumpanen J, Launiainen S, Ilvesniemi H, Hari P, Nikinmaa E 2009. CO_2 exchange and component CO_2 fluxes of a boreal Scots pine forest. Boreal Environment Research 14, 761-783.

Kolari, P., Lappalainen, H.K., Hänninen, H. & Hari, P. 2007. Relationship between temperature and the seasonal course of photosynthesis in Scots pine at northern timberline and in southern boreal zone. *Tellus* 59B, 542–552.

Körner C. 2006. The significance of temperature in plant life. In: Morison J.I.L. & Morecroft M.D. (eds.) Plant growth and climate change. Wiley-Blackwell.

Kuuluvainen, T. 2002. Natural variability of forests as a reference for restoring and managing biological diversity in Boreal Fennoscandia. *Silva Fennica* 36: 97–125.

Leuning, R. 1995. A critical appraisal of a combined stomatal-photosynthesis model for C3 plants. *Plant, Cell and Environment* 18, 339-355.

Magnani, F., Mencuccini, M., Borghetti, M., Berbigier, P., Berninger, F., Delzon, S., Grelle, A., Hari, P., Jarvis, P.G., Kolari, P., Kowalski, A.S., Lankreijer, H., Law, B.E., Lindroth, A., Loustau, D., Manca, G., Moncrieff, J.B., Rayment, M., Tedeschi, V., Valentini, R., and Grace, J. 2007. The human footprint in the carbon cycle of temperate and boreal forests. *Nature* 447: 848–850.

Mäkelä A and Mäkinen H. 2003. Generating 3D sawlogs with a process-based growth model. *Forest Ecology and Management* 184:337-354

Mäkelä, A., P. Hari, F. Berninger, H. Hänninen and E. Nikinmaa 2004. Acclimation of photosynthetic capacity in Scots pine to the annual cycle temperature. *Tree Physiology* 24, 369.

Mäkelä, A, P. Kolari, J. Karimäki, E. Nikinmaa, M. Perämäki and P. Hari 2006. Modelling five years of weather-driven variation of GPP in a boreal forest. *Agricultural and Forest Meterology* 139, 382.

Mäkelä A, Pulkkinen M, Kolari P, Lagergren F, Berbigier P, Lindroth A, Loustau D, Nikinmaa E, Vesala T, Hari P 2008. Developing an empirical model of stand GPP

with the LUE approach: analysis of eddy covariance data at five contrasting conifer sites in Europe. *Global Change Biology* 14:92-108

Mäkelä, A., Linkosalo, T., Kolari, P., Grönlund, L., Härkönen, S., Pulkkinen, M., Peltoniemi, M., Höltta, T., Duursma, R., Mäkipää, R. ja E. Nikinmaa 2010. Metsikön kasvu muuttuvassa ilmastossa – yleisen mallisysteemin kehittäminen. *ISTO-hankkeen loppuraportti.*

Malhi Y., Baldocchi D.D. & Jarvis P.G. 1999. The carbon balance of tropical, temperate and boreal forests. *Plant, Cell and Environment* 22:715–740.

Manninen, S., Forss, S. and S. Venn. (in print). Management mitigates the impact of urbanization on meadow vegetation. *Urban Ecosystems.*

Manter, D.K. and J. Kerrigan. 2004. A/Ci curve analysis across a range of woody plant species: influence of regression analysis parameters and mesophyll conductance. *Journal of Experimental Botany* 55(408):2581-2588.

McCarthy HR, Oren R, Finzi AC, Johnsen KH. 2006. Canopy leaf area constrains [CO_2]-induced enhancement of productivity partitioning among aboveground carbon pools. *Proceedings of the National Academy of Sciences, USA* **103**: 19356–19361.

Medlyn BE, Barton CVM, Broadmeadow MSJ, Ceulemans R, de Angelis P, Forstreuter M, Freeman M, Jackson SB, Kellomäki S, Laitat E, Rey A, Roberntz P, Sigurdsson BD, Strassemeyer J, Wang K, Curtis PS, Jarvis PG. 2001. Stomatal conductance of European forest species after long-term exposure to elevated [CO2]: a synthesis of experimental data. *New Phytologist* 149: 247–264.

Muukkonen, P. and R. Mäkipää. 2006. Empirical biomass models of understorey vegetation in boreal forests according to stand and site attributes. *Boreal Environmental Research* 11:355-369.

Norby RJ, DeLucia EH, Gielen B, Calfapietra C, Giardina CP, King JS, Ledford J, McCarthy HR, Moore DJP, Ceulemans R, De Angelis P, Finzi AC, Karnosky DF, Kubiske ME, Lukac M, Pregitzer KS, Scarascia-Mugnozza GE, Schlesinger WH, Oren R. 2005. Forest response to elevated CO2 is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences*, USA 102: 18052–18056.

Oren, R., Ellsworth, D.S., Johnsen K.H., Phillips N., Ewers B.E., Maier C., Schäfer K.V.R., McCarthy H., Hendrey G., McNulty S.G. & G.G. Katul. 2001. Soil fertility limits carbon sequestration by forest ecosystems in CO2 –enriched atmopshere. *Nature* 411:470-472.

Palviainen, M., Finer, L., Mannerkoski, H., Piirainen, S. and M. Starr. 2005. Responses of ground vegetation species to clear-cutting in a boreal forest: aboveground biomass and nutrient contents during the first 7 years. *Ecol. Res.* 20:652-660.

Parviainen, J., Vapaavuori, E. and A. Mäkelä. 2010. Finland's Forests in Changing Climate. *Working Papers of the Finnish Forest Research Institute* 159.

Perttunen, J., Sievänen, R. and Nikinmaa, E. 1998. Lignum: A model combining the structure and functioning of trees. *Ecological Modelling 108:189-198.*

Ripullone, F., Grassi, G., Lauteri, M. and M. Borghetti. 2003. Photosynthesis–nitrogen relationships: interpretation of different patterns between *Pseudotsuga menziesii* and *Populus* × *euroamericana* in a mini-stand experiment. *Tree Physiology* 23:137-144

Saxe H., Cannell M.G.R., Johnsen Ø., Ryan M.G. & Vourlitis G. 2001. Tree and forest functioning in response to global warming. *New Phytologist* 149: 369–400.

Strömgren M, Linder S. 2002. Effects of nutrition and soil warming on stemwood production in a boreal Norway spruce stand. *Global Change Biology* 8: 1194–1204.

Tjoelker, M.G., Oleksyn, J. and P.B. Reich. 1998. Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO_2 and temperature. *Tree Physiology* 18:715-726.

Theurrilat, J-P. and A. Guisan. 2001. Potential impact of climate change on vegetation in the european alps: a review. *Climatic Change* 50:77-109.

Yrjönen J. 2008. Mitä provenienssikokeet kertovat puiden sopeutumisesta ilmastonmuutokseen? Pro gradu -tutkielma. Helsingin yliopisto, metsäekologian laitos. (MSc-Thesis, Department of Forest Ecology, University of Helsinki).