

Seminar series nr 215

# The Effect of Natural Disturbances on the Carbon Balance of Boreal Forests



**Amelie Lindgren**

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2011

Department of Earth and Ecosystem Sciences

Physical Geography and Ecosystems Analysis

Lund University

Sölvegatan 12

S-223 62 Lund

Sweden





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Amelie Lindgren

2011

Bachelor's thesis

in Physical Geography and Ecosystems Analysis,  
Department of Earth and Ecosystem Sciences, Lund University

Supervisor: Anders Lindroth

Department of Earth and Ecosystem Sciences,  
Division of Physical Geography and Ecosystems Analysis

**Cover Picture:** Fire in Grant Village during 1988 Yellowstone Fires. Image taken by Jeff Henry

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# The Effect of Natural Disturbance on the Carbon Balance in Boreal Forests

## **Abstract**

Natural disturbances such as fires, insect outbreaks and windthrows are able to influence the balance between the ecosystem gain and loss of carbon in the boreal forest. This effect of natural disturbances on the ecosystem carbon balance has been proposed as one of the reasons why the CO<sub>2</sub> concentration in the atmosphere varies between years. At present the boreal forest as a whole act to mitigate the high levels of CO<sub>2</sub> in the atmosphere but the future of this balance is far from certain. In a changed climate the frequency and severity of natural disturbances are projected to increase which will enhance the transfer of terrestrial carbon to the atmosphere. If this loss of carbon is not compensated by an increased accumulation of carbon, the boreal forest will transform from an important carbon sink into a carbon source. Natural disturbances thus have the potential to act as a positive feedback between the boreal forest and the climate system. On account of the importance of natural disturbances these must be included in estimations of the carbon budget of the boreal forest.

This review focuses on the effect of natural disturbances on the carbon balance in boreal forest in a current and future climate. Both direct and indirect emissions of CO<sub>2</sub> from different natural disturbances have been collected from various regions. Different natural disturbances affect the carbon balance in their own way, and at different time scales. They are also more or less important in some regions. To be able to fully account for the carbon balance of the boreal forest biome the effect of natural disturbances must be understood. Methods are available but there are still information gaps to be filled since data have not been collected with enough spatial and temporal coverage.

**Keywords:** Geography • Physical Geography • Natural Disturbance • Carbon Balance • Boreal Forest

# Naturliga störningars påverkan på den boreala skogens kolbalans

## Sammanfattning

Den boreala skogen, mer känd som taigan, breder ut sig på de nordliga delarna av norra halvklotet innan den trädlösa tundran tar över. I detta enorma skogsområde som sträcker sig genom Skandinavien, Ryssland och Nordamerika är störningar i form av bränder, insektsangrepp och stormar vanliga och en naturlig del av ekosystemet. Dessa störningar påverkar skogens kolbalans genom deras inverkan på både ekosystemets kolupptag och kolutsläpp. Detta medför konsekvenser för koldioxidhalten i atmosfären och har påtalats som en möjlig anledning till att halten koldioxid varierar i atmosfären från år till år. För närvarande agerar den boreala skogen som en kolsänka, vilket betyder att den tar upp mer kol från atmosfären genom fotosyntes än vad den släpper ut igen via respiration och direkt förbränning. Frekvensen och magnituden av dessa störningar tillsammans med skogens produktivitet avgör i stora drag hur kolbalansen beter sig. Det betyder att förändringar på någon sida av balansvågen kan tippa den åt ena eller andra hållet. I ett framtida varmare klimat kan naturliga störningar i den boreala skogen bli både fler och värre vilket betyder att kolutsläpp från den boreala skogen kan komma att bli större. Om inte detta ökade kolutsläpp kompenseras av ett ökat kolupptag kommer kolbalansen att skifta och det som nu är en viktig kolsänka kan förvandlas till en kolkälla. Eftersom den boreala skogen innehåller mycket kol samtidigt som störningar är vanliga är den en viktig pusselbit i den globala kolbudgeten. Samtidigt är det just störningars inverkan på kolbalansen som är viktiga att förstå och kvantifiera för att kunna uppskatta den boreala skogens roll i kolets kretslopp.

I denna litteraturstudie behandlas information om hur kolbalansen påverkas av naturliga störningar i den boreala skogen. Information om både direkta och indirekta kolutsläpp i samband med störningar sammanfattas för olika störningar från olika områden. Tyvärr finns det fortfarande informationsluckor i både geografisk och temporal omfattning som behöver åtgärdas för att fullt förstå hur den boreala skogens roll ser ut nu och i framtiden.

**Nyckelord:** Geografi • Naturgeografi • Naturliga störningar • Kolbalans • Boreal skog

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## Abbreviations

GPP – Gross primary production

GPP is the measure of the total uptake of CO<sub>2</sub> by plant photosynthesis in an ecosystem.

ER – Ecosystem respiration

Ecosystem respiration is the sum of both the autotrophic respiration (plant respiration) and the heterotrophic respiration (non-plant respiration, e.g. microbes, animals)

NPP – Net primary production

NPP is the measure of CO<sub>2</sub> uptake available for plant growth. It is the difference between GPP and autotrophic respiration.

NEP – Net ecosystem production

NEP is defined as the difference between gross primary production (GPP) and ecosystem respiration (ER). It is therefore a direct measure of the carbon status, if  $NEP > 0$  then the ecosystem is a carbon sink. It is also the difference between NPP and heterotrophic respiration.

NBP – Net biome production

Net biome production is the NEP minus the effect of disturbances on carbon fluxes

## **Acknowledgements**

Firstly I would like to thank Anders Lindroth for believing that my rather optimistic aim within this thesis was possible to pursue. Without this support I would probably have backed off, and the thesis would not have looked the same. I would also like to thank Anders for his interest in the project, and for valuable comments and questions. My second thanks go to my fellow students who by their persistent presence in school have been the best support imaginable when the sun have been shining outside and the computers have been buzzing. Lastly, as always the support from those closest have been as much valued as needed.



## 1 Introduction and Background

Natural disturbances are important and natural ingredients in terrestrial ecosystems (Sousa, 1984). Within forests, disturbances have always been an important driver of succession as well as essential to the existence of certain forest ecosystems. The frequency and severity of natural disturbances influence the carbon balance of ecosystems and if increased, disturbances may cause an increased transfer of terrestrial carbon to the atmosphere (Kasischke et al., 1995, Kurz and Apps, 1999). The boreal forest biome holds a large proportion of the terrestrial carbon pool and is at the same time frequently hit by large-scale disturbances (Dixon et al., 1994, Kasischke, 2000).

Rising levels of CO<sub>2</sub> in the atmosphere will have global consequences as the temperature will rise. As natural disturbances partly are driven by climatic factors, higher temperatures are believed to affect the boreal forest in such a way that it may give rise to positive feedbacks between the forest and the climate system (Blennow et al., 2010b, Flannigan et al., 2005, Stocks et al., 1998). This is because parts the boreal forest may become a carbon source instead of a carbon sink in response to a new disturbance regime in a changed climate. It is therefore important to study if the frequency and severity of disturbances are changing, if they will change in the future, to what extent, and what consequences that might have on the terrestrial carbon balance.

The aim of this review is to analyze the effect of natural disturbance on the carbon balance of the boreal forest in a current and future climate. In order to do this these questions are investigated:

- Which natural disturbances are having an important impact on the carbon balance in the boreal forest region?
- How do these disturbances affect the carbon balance and to what extent?
- How are the disturbances affected by climate?
- How is future disturbance frequency and severity likely to be affected by a changing climate?
- How do the disturbances interact with each other?
- Are there any large scale geographical differences concerning which disturbances that are dominating within a region?

Since this is a time limited study this review only manages to scratch on the surface of the subjects covered. Additionally certain interesting areas have been overlooked; peatfires, albedo changes, other natural disturbances than fire, insects and windthrow, and the boreal forest in China.

## **1.1 The carbon balance of ecosystems**

Emissions of CO<sub>2</sub> into the atmosphere are compensated partly by uptake by the ocean and the terrestrial biosphere. This uptake represents around 55% of the anthropogenic emissions (Baker et al., 2006). The uncertainty of the sink on land is very high ~35% but it is estimated to be larger than the ocean uptake (Le Quéré, 2010). Estimates of the northern land carbon sink range from 1.5 Gt to 2.9 Gt yr<sup>-1</sup> (Gurney et al., 2004, Jacobson et al., 2007, Stephens et al., 2007) and show large interannual variability (Baker et al., 2006, Bousquet et al., 2000). This variability may in part be due to forest disturbance (Schimel et al., 2001). The importance of this terrestrial sink has been recognized by scientists in various fields but the future of this sink is not yet clear.

The biosphere assimilates carbon from the atmosphere by photosynthesis. A net gain of carbon results if the amount of carbon assimilated into the ecosystem is larger than the amount going out through respiration, that is, a positive NEP. This flux between the ecosystem and the atmosphere can be measured using the eddy covariance technique. The description of the method is covered thoroughly in other studies (e.g. Aubinet et al., 1999). This net uptake or release of carbon may be substantially altered by disturbances, that may not be covered in these short-term measurements (Schulze et al., 1999). Therefore the NEP value acquired through this technique is not a long-term measure of the ecosystem carbon balance, but a measure of the carbon balance at a specific place and time. The long-term rate of carbon sequestration is still estimated from inventory data of carbon pools.

The boreal forest biome is vast and additionally the amount of carbon stored within it is large compared to other biomes (Gower et al., 2001). For these reasons alone the boreal forest is interesting to study, but there are other factors that make it even more important. The biome NEP is sensitive to small variations in climate. This is because gross primary production (GPP) and ecosystem respiration (ER) are large fluxes often nearly equally balanced by each other, however if one of the processes is favored or unflavored the result may be a changed carbon balance. Furthermore disturbances can quickly change a forest carbon sink into a carbon source as will be discussed in this review. Understanding the carbon balance in the boreal forest biome is important in order to fully appreciate the role it plays in the global carbon budget.

It has been proposed that the boreal forests may transform from net sinks of carbon to net sources (Kasischke, 2000). He proposes that there are two reasons for this, firstly deforestation is likely to increase and secondly a changing climate will likely cause an increase in natural disturbances which will cause a net release in carbon to the atmosphere.

## **1.2 The boreal forest**

On account of the fact that different authors use different definitions of the borders of the boreal forest, its extent is not presented with unity in the literature. Shvidenko and Apps (2006) report an area of 1160 million ha which is lower than estimates made by Dixon et al. (1994) and Apps et al. (1993) which was 1370 million ha and 1250 million ha respectively. About two thirds of this area of forest is located in Russia alone (Conard and Ivanova, 1997). The southern limit of

the forest ranges from 50° N in continental interiors and 60 – 65° N in maritime regions (Gower et al., 2001). The climate varies with latitude and at the southern limit the days with a temperature > 10° C are around 120 per year whereas they can be as few as 30 at the northern limit that borders to the tundra biome at approximately 70 ° N (Hari, 2008).



**Map 1** Extent of Boreal Forest. *UNEP/GRID-Arendal Maps and Graphics Library, Cartographers: Philippe Rekacewicz assisted by Cecile Marin, Agnes Stienne, Giulio Frigieri, Riccardo Pravettoni, Laura Margueritte and Marion Lecoquierre* <http://maps.grida.no/go/graphic/boreal-forest-extent>

The boreal region covers around 17% of the Earth's land surface, but contains around 30% of the carbon in terrestrial biomes (Kasischke, 2000). This includes the carbon in the forest itself, peat and tundra. Another estimate state that the boreal forest and their soils hold 49% of the carbon stored by all forested areas (Dixon et al., 1994). Finally, Gower et al. (2001) stated that the boreal forests and soils hold 300 Gt C which is equivalent to about 50% of the carbon in the atmosphere. This can be seen in relation to the temperate and tropical forests that together hold less carbon than the boreal forest. In fact the boreal forest holds 20% more carbon than the two others combined (Kasischke, 2000). The majority of the carbon within the boreal forest biome is held in the soil as a consequence of the cold conditions prevailing that slows down the decomposition of organic matter. Permafrost also impedes the soil drainage resulting in saturated soils that further slows down the process of decomposition. Although it is clear that the boreal forest contains a large amount of carbon it does not necessarily mean that the forest behaves as a carbon sink or a carbon source at present (Shvidenko and Apps, 2006). It is clear however that the carbon balance have been positive in the boreal forest since it has been able to accumulate its large pool of carbon within soil and biomass since the last ice age (Hari, 2008).

The boreal forest is dominated by conifer tree species that belong to the genera of Spruce (*Picea spp.*), Pine (*Pinus spp.*), Larch (*Larix spp.*), and Fir (*Abies spp.*) (Shvidenko and Apps, 2006). The two most important hardwood species are Birch (*Betula spp.*) and Aspen (*Populus tremuloides*).

The boreal forest in Russia accounts for 95% of the total forested area throughout the country (Shvidenko and Nilsson, 2000a). Larch is the absolutely most abundant species covering 37.3% of the forested area. Pine is the second largest group and cover 16.2%. The Siberian boreal forest covers around 600 million ha and here larch is even more dominating covering 54% of the forest (Schulze et al., 1999). Although the Siberian forest is vast the productivity is considerably lower than in European forests. Both Siberian larch and pine grow at a rate less than half of that measured for spruce stands (*Picea spp.*) growing in Western Europe. The most important reason for this is the length of the growing season which is shorter in Siberia. It is also considerably drier than the forests in North America and Fennoscandia which further inhibits forest growth. In fact, in the east parts of Siberia potential evapotranspiration may exceed precipitation. It is also evident that the forest growth is constrained by availability of nutrients.

The boreal forest of North America is dominating both Canada and Alaska and covers around 500 million ha (Schulze et al., 1999). The dominant coniferous species are black spruce (*Picea mariana*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), lodgepole pine (*Pinus contorta*) and alpine fir (*Abies lasiocarpa*) (Borgeau-Chavez et al., 2000). Among the deciduous species aspen (*Populus tremuloides*) and birch (*Betula spp.*) are common. Tamarack (*Larix laricina*) is the only deciduous conifer species.

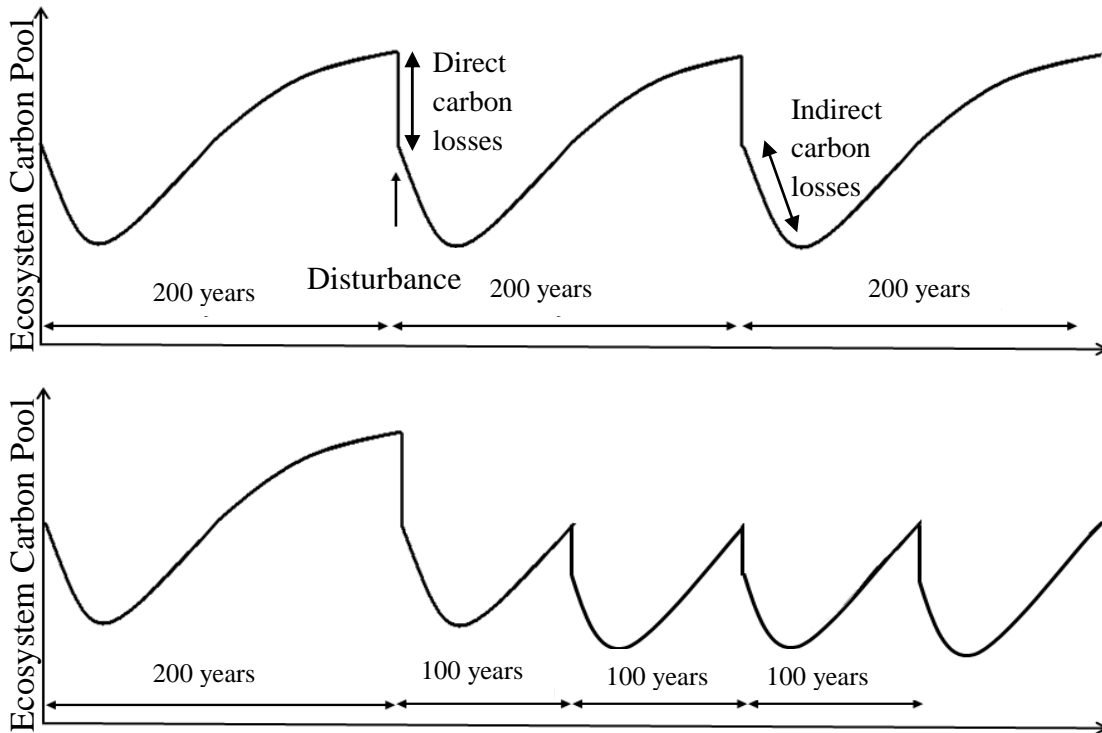
The boreal forests in the Fennoscandian region (Finland, Norway, Sweden) are intensively managed and forest succession is often no longer a result of natural disturbance but of management (Schelhaas et al., 2003). They are also relatively young forests with a potential to accumulate considerable amounts of carbon (Nabuurs et al., 2003). Thus, although the Fennoscandian and western Russia's boreal is considerably smaller than the Siberian forest estimations indicate that it in fact incorporate more carbon into its ecosystem through photosynthesis than the Siberian boreal forest (Schulze et al., 1999). The two most important species in the Fennoscandian forest is norway spruce (*Picea abies* (L.) Karst) and scots pine (*Pinus sylvestris* L.).

The boreal forest biome is likely to respond to a warmer climate by migrating north and unto higher elevations (Chapin and Danell, 2001). The southern margin is expected to be lost to other biomes. No change is expected in the overall area, but about one third of the boreal forest is projected to convert to other biomes, while one third is expected to migrate into tundra regions. The forest productivity is also projected to increase as a response to warmer temperatures, longer frost free periods, CO<sub>2</sub> fertilization, and increased nitrogen mineralization because of higher temperatures (Jarvis and Linder, 2000, Kellomäki and Kolström, 1994, Hyvönen et al., 2007).

### 1.3 The effect of natural disturbance

The degree of human activity in the boreal forest is limited to certain geographical areas (Shvidenko and Apps, 2006). In fact, these authors report that large parts of the boreal forest are still unmanaged in both Russia and Canada (about 50%). In these pristine forests natural disturbances influence the conditions and dynamics of the forest. In other areas natural disturbances are largely under control, such as the fire regime in Fennoscandia where fire return intervals are estimated to be several thousands of years because of extensive fire suppression (Zackrisson, 1977).

The most important aspect concerning natural disturbances is their ability to shape the forest structure. Disturbances can reduce the age class structure of the forest by forcing it to regenerate (Kurz and Apps, 1999). This has implications for the carbon balance since forests accumulate biomass as they age (Kasischke, 2000). A younger stand thus contains less carbon than an older one. Changes in the frequency of disturbances can thus have large effect on the carbon balance since this balance is related to the age class structure (Kurz and Apps, 1999). (See fig. 1 for a theoretical representation of this phenomenon) The same authors claim that changes in the carbon balance due to the disturbances effect on the age class distribution have begun at a large scale in Canada. Disturbance also affect the carbon balance by reducing the share in living biomass by moving it to the dead organic matter (DOM) pool in which carbon is lost through decomposition (Goulden et al., 2011).



**Figure 1** Simplified theoretical representation of what consequence increased stand replacing disturbance rates (doubled) may have on the carbon accumulation within a forest stand. Modified from Wirth et al. (2002)

Following a stand replacing disturbance decomposition of dead organic matter releases CO<sub>2</sub>, thus a disturbed stand is expected to lose carbon during the first years of recovery as long as the carbon assimilation through GPP is less than the ecosystem respiration (Goulden et al., 2011) (see figure 1,2,3). As succession proceeds carbon begin to accumulate within the ecosystem again and a positive NEP prevails until the stand approaches a steady state where carbon assimilation equals carbon losses and NEP ~ 0. However, old forests have been found to sequester carbon which poses the question if this general assumption that forest become carbon neutral or even sources as they age (see figure 2) is valid (Luyssaert et al., 2008). Figure 2 describe how the development of NEP relative the stand age is described in theory where old forests are not considered to be carbon sinks. In figure 3, the measured values of NEP from a previously burned chronosequence site in Manitoba, Canada is pictured. The fitted curve in figure 3 is consistent with how NEP is supposed to behave as a response to succession. It should be noted that this is a generalization for stand replacing disturbance since carbon balance response have different trajectories in stands with partial disturbance (Amiro et al., 2010). Chronosequences are used as an alternative to long term measurements (Wirth et al., 2002). The method is based on the assumption that carbon accumulation after a fire behave in similar ways if the forest is of the same type and the site conditions are similar. Therefore instead of measuring at the same site continuously for a number of years after a stand replacing disturbance, measurements are taken at many sites with different ages that are regenerating after the disturbance.

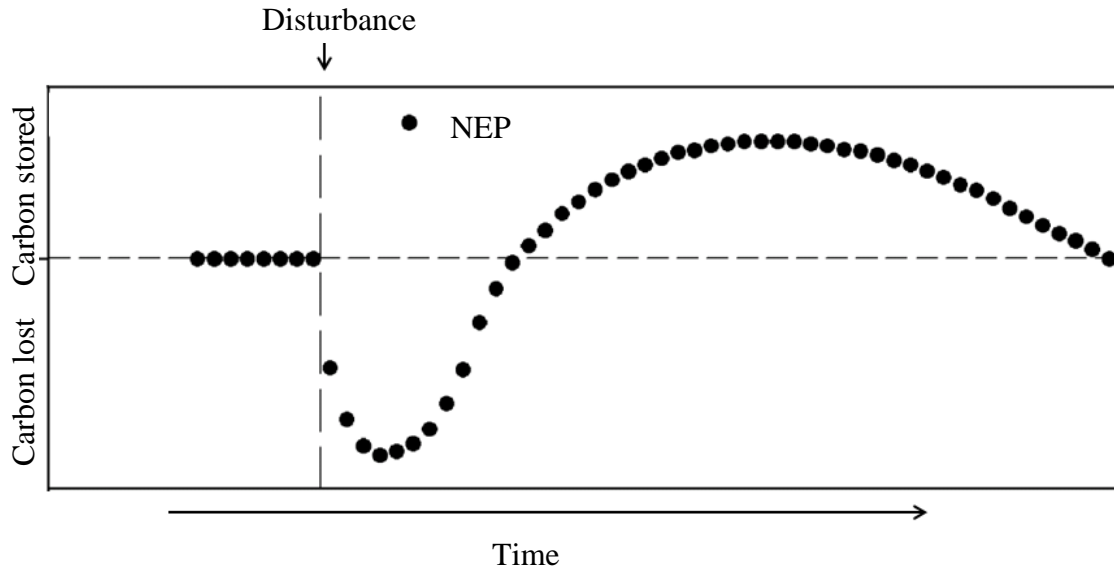


Figure 2 Hypothesized change in NEP in a stand after a stand replacing fire. Modified after Goulden et al. (2011).

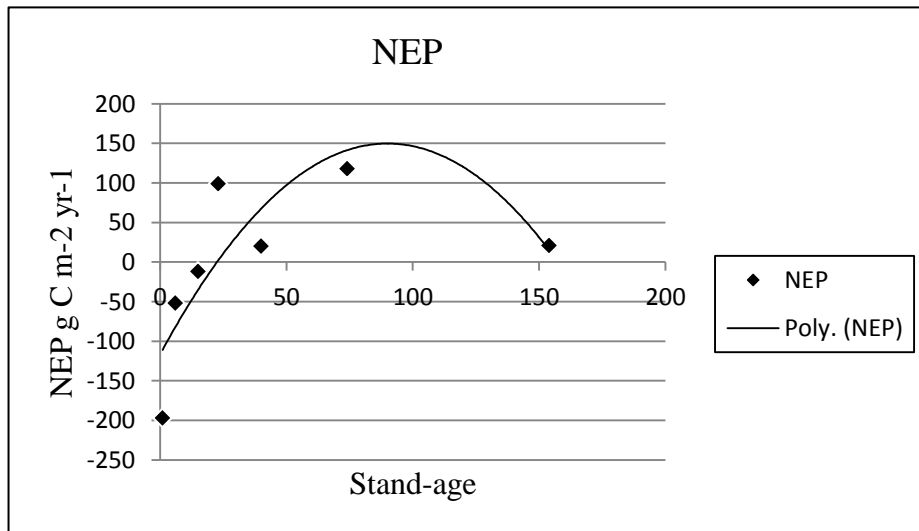


Figure 3 Measured NEP at a fire chronosequence (Goulden et al., 2011) and fitted curve.

## 2 Natural Disturbances

In this section, fire, insect outbreaks, and windthrow as natural disturbances are covered in turn. Each of these disturbances are introduced briefly before data on areal extent and the effect on the carbon balance from different regions are presented. There are additional important natural disturbances that are not covered here, but that may have large impact on the carbon balance of the boreal forest, examples of this are drought and fungus.

### 2.1 Fire

Fire is common in the boreal forest (Kasischke, 2000). There are several reasons for this, including dry conditions due to small amounts of precipitation, high summer temperatures, and the presence of fire prone species both in the understory vegetation and among the tree species. These species are easily ignited and burn as long as the conditions are right. Some species (e.g., spruce and pine) provide flammable fuel in the form of dead branches still attached to the trees. Fuel in the form of dead trees are also important, therefore tree mortality induced by other types of disturbances can aid in the development of fire prone forests (Grissom et al., 2000).

Fire plays an important role in the carbon cycling in the boreal forest as a result of its frequent occurrence (Kasischke, 2000). The effects on the carbon cycle and therefore carbon balance are both direct and indirect. The direct effect is attributed to the emissions of CO<sub>2</sub> released to the atmosphere during combustion of organic carbon. Indirect effects are mostly connected to lost photosynthetic capacity and increased decomposition. Forest soils tend to be drier after fires which influence soil respiration. In fact, the ground layer itself becomes a carbon source during the first years after a fire. It has been proposed that the ground layer may become 5-10°C warmer as a result of increased direct solar radiation, reduced surface albedo and the loss of insulation material in the form of mosses, lichens and organic soil. The increased temperature favors decomposition and the ecosystem is more likely to become a carbon source. This warmer condition in the soil may prevail for 20-30 years after the disturbance event in areas with underlying permafrost. In Alaska, elevated rates of decomposition have been found to remain for several years after a fire (Richter et al., 2000). Fires are also able to consume parts of the soil organic matter (Michalek et al., 2000) that may contain considerable amounts of carbon. In fact, Michalek et al. (2000) reported that the fraction of carbon consumed during fire were higher in the soil organic matter than in the above ground carbon at their study site in Alaska. Fire also speeds up nutrient cycling and can therefore have a positive effect on forest growth (Kasischke et al., 1995). Lastly, formation of charcoal as a consequence of burning acts as a long term carbon storage. However, the overall effect of fire on the actual carbon balance is to reduce the carbon stored in the ecosystem (Balshi et al., 2007).

Using eddy covariance measurements Amiro et al. (2010) found that burned stands act as carbon sources during the first ~10 years after the fire. After this the stands within the four different chronosequences studied began to sequester carbon again as new forests developed. This net release of carbon during the first years following a fire can be seen in figure 2 from a



chronosequence site in Manitoba, Canada (Goulden et al., 2011) and through a theoretical representation in figure 3.

Stand replacing fire is the most common type of fire in the boreal forest (Kasischke, 2000). In such a fire tree mortality is high and the stand must regenerate after the fire, resulting in the carbon balance curve described in theory in figure 2. Less extensive fires that allow some trees to survive are more common in some regions than others and should give a NEP curve a bit different from that described in figure 2 (Amiro et al., 2010). The role of these fires where many trees generally are able to survive may have been underestimated by Kasischke (2000). This is because the reported extent of Russian surface fires has risen substantially in the literature after the year 2000 (see section 2.1.1).

There are different kinds of fires that have different effects on the forest and the ecosystem as a whole. Generally, a burned area show signs of all the different fires that are mentioned in the following section (Borgeau-Chavez et al., 2000).

**Ground fires** or sub-surfaces fires are often low-intensity fires that spread slowly. They are smoldering fires often without any visible flames (Van Wagner, 1978). They burn the subsurface flues in organic soil layers (McCullough et al., 1998).



**Picture 1** Ground fire. Credits to National Park Service, U.S

**Surface fires** are more intense than ground fires and are able to spread more quickly (Borgeau-Chavez et al., 2000). Tree mortality induced by this type of fire is often depending on the species present and the stand age. As already stated; some trees are able to withstand fires of this kind as long as their crowns are unaffected. Surface fires consume the fuel present in the forest floor material such as shrubs and branches close to the ground.



**Picture 2** Surface fire. Credits to Oregon State University

**Crown fires** are the most severe and intense fires (Borgeau-Chavez et al., 2000). They can reach from the surface and up to three times the height of the canopy. These fires generally result in widespread tree mortality. As a result of their intensity, crown fires are almost impossible to stop once they have been initiated. Usually they dissipate once their fuel source is depleted or the winds subside.



**Picture 3** Crown fire with eddy covariance measurement equipment. Credits to USDA Forest Service

The different types of fire generate carbon emissions of different magnitudes. The average emissions per area can increase fourfold depending on what type of fire that is prevalent (Conard and Ivanova, 1997). A low-severity surface fire consumed 50% of the understory fuel and 10% of the litter layer. A high-severity surface fire was estimated to consume about 90% of the understory fuel and 50% of the litter layer in Russia. Crown fires consumed part of the canopy fuels in addition to the fuels mentioned.

### **2.1.1 Russia**

Throughout Eurasia there are evidence of forest fires since the glacial retreat (Goldammer and Stocks, 2000). It is therefore considered as a natural ingredient in the boreal ecosystem of Russia (Shvidenko and Nilsson, 2000a). Surface fires are the predominant type of fire representing 98% of all fires (Goldammer and Stocks, 2000). Some species (i.e. pines and larches) are able to withstand this kind of fire which means that these species become dominant in regions affected by surface fires. In fact, stands of pine and larches may have survived many fires during their lifetime. It is only during especially dry years that crown fires have been recorded in Russia. It happened during the years 1997 and 1998 which were severe fire years.

Surface fires may not always cause direct tree mortality but increased levels of mortality have been found to occur up to 10 years after the disturbance (Shvidenko and Nilsson, 2000a). This post-fire mortality varies greatly and depends on the type and intensity of the fire, species composition, age, weather conditions as well as many other factors. Generally, ground fires cause up to 20% postfire mortality, whereas other types of fires are more severe and cause higher mortality. In Siberian boreal forests, crown fires as well as peat fires often cause 100% mortality, which is typical for forests found on permafrost (Matveev, 1992). In actively monitored forests about 50-70% of forest mortality is attributed to fire (Krankina and Harmon, 1995).

The recorded average annual area burned in Russia have been reported to range from 1.5 million ha yr<sup>-1</sup> (Shvidenko and Nilsson, 2000a) to 12 million ha yr<sup>-1</sup> (Conard and Ivanova, 1997) in recent years. There are two reasons that contribute to the high uncertainty of current and historical estimates for area burned in Russia. The first is that around 40% of the land covered by the Russian Forest fund (all land managed by the federal government which is 64.4% of the total land area of Russia in the year 1993) have never received any fire protection nor any monitoring (Shvidenko and Nilsson, 2000a). The same authors also claim that a second reason is that the official data published prior the year 1988 were falsified. The reported annual area burned from this time is generally half of that reported after 1988.

The area burned in unprotected Russian forests have been estimated indirectly through the use of long term inventory data as well as information from reports, satellites and available statistics (Shvidenko and Nilsson, 2000a). Using these data estimates for average area burned in Russian forest ranges from 2.6 to 4.3 million ha annually during the period 1988 and 1992. About 1.5 million ha of this area is forest, the rest occur in non-forest landscapes (mires, tundra) as well as unforested areas (postfire areas, clear cuts etc.). Conard and Ivanova (1997) estimated from fire

return intervals that the annual area burned in Russia amounts to 12 million ha, this has been criticized as too high (see Shvidenko and Nilsson (2000a)). However, it is not far from the estimate made by Soja et al. (2004) that reported an average of 9 million ha yr<sup>-1</sup> burned between 1998 and 2002 in Siberia only. This estimate was derived from two satellite-based products that maps both active fires and fire scars.

During especially severe fire years as the year 1987, the area affected was estimated in eastern Asia (both Russia and northern China) to 14 million ha as derived from satellite imagery (Cahoon et al., 1994). To put the area 14 million ha in relation to something else one might compare it to Sweden which land surface covers around 45 million ha.

Estimations of direct and indirect emissions from the boreal forest in Russia differ between different studies. Balshi et al, (2007) found through the use of a terrestrial ecosystem model that the direct emissions of carbon from the Russia and Fennoscandia amounted to 208.8 Mt C yr<sup>-1</sup> between the years 1996 and 2000. Shvidenko and Nilsson (2000b) estimated that the direct fire emissions from Russia averaged over the years 1988 to 1992 were 58 Mt C yr<sup>-1</sup> and that the total emissions amounted to 127 Mt C yr<sup>-1</sup> showing that the indirect emissions are larger than the direct ones. Conard and Ivanova (1997) estimated annual direct emissions of 194 Mt C yr<sup>-1</sup> and indirect emissions of 484 to 1162 Mt C yr<sup>-1</sup> due to fire. Soja et al. (2004) estimated the direct carbon emissions in Siberia ranging from 152 Mt C yr<sup>-1</sup> for a low fire severity scenario, 252 Mt C yr<sup>-1</sup> for a medium to 412 Mt C yr<sup>-1</sup> for a high fire severity scenario between the years 1998 and 2002. Their use of different fire severities originate in the fact that fire events differ significantly in their fuel consumption. Zamolodchikov (2005) presented estimates on direct and indirect emissions from fire in the areas protected within the Russian Forest Fund. These averaged 0.9 Mt C yr<sup>-1</sup> and 11.8 Mt C yr<sup>-1</sup> respectively between the years 1992 and 2001. During the year 2001 Zhang et al. (2003) calculated that 39.3 to 55.4 Mt C was emitted to the atmosphere due to combustion of Russian forests. These emissions equaled 11-17% of that year's emission from the Russian Industry. Emissions measured from changes in carbon pools were estimated to 72-120 g C m<sup>-2</sup> yr<sup>-1</sup> after stand replacing crown fires in young (<40 years) Siberian scots pine stands at four chronosequence sites in Siberia (Wirth et al., 2002).

### **2.1.2 North America**

Fire is the most dominant natural disturbance in boreal North America and forests have developed under its influence (Murphy et al., 2000). The overall fire regime in North American boreal forests vary from short-interval crown fire/high-intensity surface fires to very long-interval crown fires. In Canada, fires are more common in the drier western boreal forest than in the moister eastern parts of the country (Campbell and Flannigan, 2000). As already mentioned, crown fires are common in North America. These fires cause widespread tree mortality and are thus an important regenerating factor within the forest (Amiro et al., 2003). After such fires, the probability for surface fires increase in the few years following in spruce and pine stands as the killed trees provide fuel (Johnson, 1992).



The annual area burned in North America amounted to 2.6 million ha yr<sup>-1</sup> between the years 1980 and 1994 (Murphy et al., 2000). Stocks et al. (2003) reported that the average area burned in Canada during the period 1959-1997 was about 1.8 million ha yr<sup>-1</sup> based on historical records. In severe fire years the reported areas covered more than 7 million ha showing the high variability between years. The average area burned is 0.7% of the forested area.

During the last 30 years of the 20<sup>th</sup> century the National statistics in Canada show that both the area burned and the number of fires have increased (Ward and Mawdsley, 2000). In fact, the annual area burned in North America has increased by a factor of 3 during the last two decades of the 20<sup>th</sup> century (Kasischke and Stocks, 2000). However, this increase may in part be due to inconsistencies in reporting and monitoring (Ward and Mawdsley, 2000). Fires in remote areas were often not reported in earlier years, and the accuracy of the documentation of fires has been questioned. To make it even more complicated, during recent years fires have been left unsuppressed deliberately, this because of the high costs for suppression and for ecological reasons.

In the boreal ecosystems in North America, fire is the driver of several important processes. It controls the distribution of plant species and also fuel accumulation (Borgeau-Chavez et al., 2000). If fires are suppressed this may lengthen the fire return interval (Ward and Mawdsley, 2000). Stands with flammable species such as pine and spruce are able to develop and grow older than normal. This has the consequence that those fires that cannot be contained will have access to more fuel and thus the potential to become more harmful (Grissom et al., 2000).

There is more fire activity in drier years which contributes to the fact that the area burned varies between the years (Flannigan and Harrington, 1988). Extreme fire years are highly episodic, and are most often a result of short-term weather situations favoring fire (Stocks et al., 1998). In these years it is common that several fires end up being one large fire that overwhelms the fire management resources. In fact, > 95% of the area burned in North America is the result of large fires > 2,000 ha and in severe fire years, fires greater than 1 million ha may occur (Flannigan and Harrington, 1998). These large fires are not thought to occur under natural conditions where small fires are not suppressed since fires may prevent large fires through the removal of fuel accumulations (Borgeau-Chavez et al., 2000).

Several studies have set out to quantify the effect of fire on the carbon balance in boreal North America. As mentioned the effects are both direct and indirect. The direct emissions have been estimated by Amiro et al. (2001) to 27 Mt C yr<sup>-1</sup> for Canada during the period 1959-1995. This is larger than the modeled emissions by Kurz and Apps (1999) that was reported as 15 Mt C yr<sup>-1</sup> for the period 1920-1989. Balshi et al. (2007) used a terrestrial ecosystem model to estimate the direct emissions of carbon lost to the atmosphere during a fire event. Presenting decadal averages they saw a doubling in the amount of carbon emitted between 1960 and 1980 in North America. After 1980 the simulated emissions decreased in Canada, but doubled again in Alaska. The mean annual emissions were estimated to 45.7 Mt C yr<sup>-1</sup> for North America between the

years 1959 and 2002. Although this estimate is much higher than that presented by Amiro et al. (2001) the interannual variability is correlated between the two and the discrepancy was thought to be due to the fact that Balshi et al. (2007) used a carbon consumption estimate that consumed larger amounts of soil organic matter.

Goulden et al. (2011) measured NEP at a chronosequence site in Manitoba, Canada. These data represent measurements of the indirect emissions. The net release of carbon lasted only for 11-12 years, which is very close to that reported by Amiro et al. (2010) (10 years). The net loss during these first years peaked at 50-150 g C m<sup>-2</sup> yr<sup>-1</sup> (Goulden et al., 2011). Amiro et al. (2006) measured a NEP release of 132 g C m<sup>-2</sup> yr<sup>-1</sup> at a site in Saskatchewan, Canada, 3 years after a severe crown fire and a release of 87 g C m<sup>-2</sup> yr<sup>-1</sup> the following year. This may be compared to maximum uptake that was measured by Amiro et al. (2010) amounting to 210 g C m<sup>-2</sup> yr<sup>-1</sup> for a mature boreal forest.

Kurz and Apps (1999) found that changes in the disturbance regimes had begun to affect the carbon balance during the last decades of the 20th century in Canada. The balance may have changed to the extent where the forest actually might have behaved as a carbon source instead of a carbon sink. Gurney et al. (2002) estimated that the boreal forest of North America was a source of CO<sub>2</sub> during the period 1992-1996 using transport- and atmospheric inversion models.

### **2.1.3 Fennoscandia**

It is not particularly interesting to study the effect of fire in the Fennoscandian boreal forest, and therefore neither its impact on the carbon balance. This is due to the fact that the annual areas burned are very small. The annual area burned in Finland (1975-2006) was 556 ha yr<sup>-1</sup>, thus fire can be considered to be of small importance in this region (Schelhaas et al., 2010). The same pattern is evident in Sweden where the fire return intervals have decreased substantially during the 20<sup>th</sup> century in response to extensive fire suppression (Niklasson and Granström, 2000) and in some areas fire return intervals are measured in thousands of years (Zackrisson, 1977). The annual area burned in Sweden currently ranges from a few hundred ha in wet years to a few thousand ha during dry years (Niklasson and Granström, 2004). In Norway the annual area burned between 1986 and 1996 was 564 ha yr<sup>-1</sup> (Bleken et al., 1997). The average size for these fires were only 1.3 ha suggesting that the problem of fire is minimal compared to North America and Russia. As such, it might be seen in relation to the compiled databases for large forest fires in Canada, where only fires larger than 200 ha are considered since these fires represent more than 96% of the area burned (Stocks et al., 2003).

### **2.1.4 Comparison**

The relative importance of fire in the different regions is evident. Fire as a disturbance is considered to be the most important natural disturbance in both Russia and North America (Gromtsev, 2002, Murphy et al., 2000). Fires in these regions cover large areas every year and the carbon emissions from these fires can be substantial. In contrast, fire is of little importance in

Fennoscandia. Although the countries are small the area burned in relation to their size is still small compared to both Russia and North America.

### **2.1.5 The impact of climate**

Climate have both direct and indirect controls on fire regimes (Campbell and Flannigan, 2000). Direct controls are those involved in ignition and spreading potential (lightning, fuel moisture and wind), while the indirect controls involve fuel availability and type of fuel present as climate influence the distribution of vegetation. Climatic controls over vegetation are occurring at decadal or longer timescales in contrast to the effect of weather on fire risk which can vary between days or weeks. It has been found that it is the fuel moisture that is the primary determining factor influencing fire behavior, not fuel accumulation (Johnson et al., 2001). Dry and warm conditions increase the risk of fire.

The annual area burned in Canada has increased during the latter part of the 20<sup>th</sup> century (Ward and Mawdsley, 2000). This increase was showed to be influenced by warmer summer temperatures experienced in this region (Gillett et al., 2004). The effect of climate on fire has thus already started to affect the annual area burned.

A warmer climate may also have an influence on the areas potentially subjected to fire because of migrating vegetation (Campbell and Flannigan, 2000). They propose that a future warmer climate may lead to decrease in conifers along the southern border of the boreal forest. As a consequence fires may decline as they are replaced by less fire prone species. At the other end, coniferous trees are likely to increase in density along the northern border, and thus increase the risk of fire. In areas where the distribution and species composition of the forest is likely to remain unchanged a warmer, drier climate will increase the risk of fire, while moister conditions might reduce the risk. Additionally, a rapidly changing climate may lead to short term disequilibrium between species distribution and favorable conditions in the boreal system. This may increase tree mortality and thus increase the availability of fuel. This in turn may enhance the risk of fire.

### **2.1.6 Future projections**

Stocks et al. (1998) modeled the future fire potential as a consequence of a doubled atmospheric CO<sub>2</sub> scenario in Russia and Canada. A warmer temperature increase the risk of fire, and therefore the fire potential was high in areas projected to experience warming. The increased risk was particularly evident in regions with a continental climate, Siberia and west-central Canada. The areas under high to extreme fire risk were generally increasing under a double CO<sub>2</sub> scenario. During the summer months, the results showed extreme fire risk in a vast area of Siberia, three times the size of the area experiencing the same risk in west-central Canada. This area in Russia is projected to increase two or three-fold in June and July in the future scenario. The results also showed that the start of the fire season may come earlier and that the end may come later across Canada and Russia as a whole, with regional variation. Stocks et al. (1998) conclude that the increased risk of fire will result in more frequent and severe fires. The shorter interval between

fires has the potential to change the stand age distribution towards younger stands and thus has the potential to decrease carbon storage.

Flannigan et al. (2005) made a future projection of area burned in Canada through the use of historical records and Global Circulation Models (GCMs). They found that the area burned in Canada will increase under a triple CO<sub>2</sub> scenario at the end of the 21<sup>st</sup> century. The increase from the annual area burned between the years 1959 and 1997 amounted to 74 – 118% until the end of the 21<sup>st</sup> century.

Macias Fauria and Johnson (2008) noted that temperature alone cannot be a determining factor of increased fire risk. The temperatures have been increasing during the last 150 years, but the increased fire frequency and area burned have only been recorded during the last decades of the 20<sup>th</sup> century. They highlight the importance of fuel moisture and state that the presence of mid-tropospheric (500hPa) blocking highs (present more than 10 days) is related to a large area burned in North America. Area burned explained by weather anomalies, such as persistent highs is generally a function of large scale climatic patterns such as ENSO (El Niño Southern Oscillation) and PDO (Pacific Decadal Oscillation) (Macias Fauria and Johnson, 2006). Thus the authors claim that the increased fire frequency and severity in North America, observed during the last decades of the 20<sup>th</sup> century, is a response to changes in these large scale climatic patterns. The future behaviors of these oscillations are still inconclusive.

Fire ignition is mainly divided between human sources and lightning. In Canada fires ignited by lightning produce the majority of the annual area burned (Weber and Stocks, 1998). In Russia, a majority of the number of fires are human-caused (Conard and Ivanova, 1997). In Canada, predictions of spatio-temporal patterns of lightning are not yet available from Global Circulation Models or Regional Circulation Models (Krawchuk et al., 2009). However, earlier studies have reported that lightning frequency is expected to increase in the Northern hemisphere under a double CO<sub>2</sub> scenario (Price and Rind, 1994).

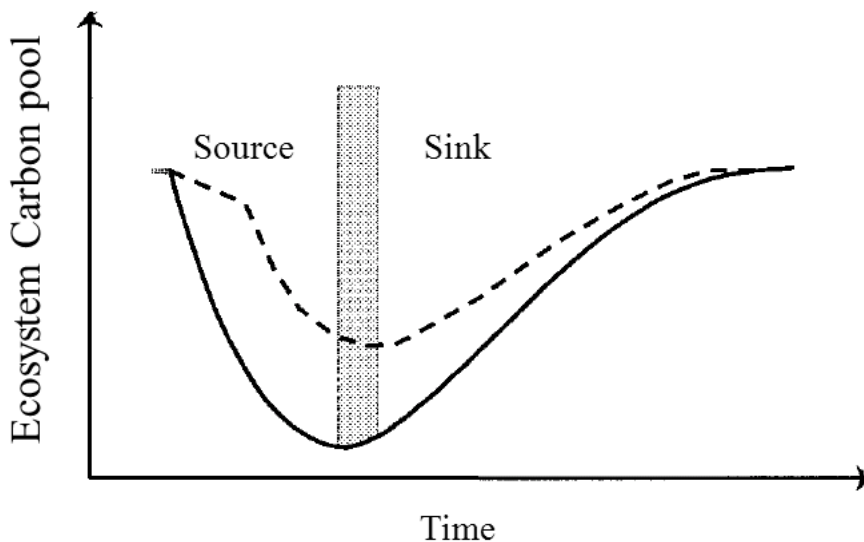
Even in Fennoscandia where fire is a minor trouble the risk of fire is likely to increase in a warmer dryer climate that is expected at least in southern Sweden (Chapin et al., 2007).

## **2.2 Insects**

Although insect outbreaks are not mentioned quite as frequently as fire as a dominant natural disturbance agent, their importance should not be neglected. An example of how severe insect outbreaks can become have been evident in the Province of British Columbia, Canada. In 2007 the ongoing outbreak of Mountain pine beetle (*Dendroctonus ponderosae*) had affected over 10.1 million ha of forest (Westfall and Ebata, 2010). The potential CO<sub>2</sub> emissions from this outbreak (year 2000 to 2020) was studied and modeled by Kurz et al. (2008a) and the result showed that it had the potential to emit as much CO<sub>2</sub> as the Canadian transport sector emits over a period of five years (emission level of 2005).



Insects affect the carbon balance through their impact on the NPP and the heterotrophic respiration (Kurz et al., 2008a). The reduction of NPP is caused by the decreased photosynthetic activity in affected areas. The enhanced heterotrophic respiration results from increased decomposition explained by a larger transfer of biomass to the dead organic matter pool. The effect of insect outbreaks on the carbon balance differs somewhat from other natural disturbances (Pfeifer et al., 2011). This is since the effect of decomposition on the carbon balance may not be instant, but instead spread over longer periods of time as the infested biomass dies and fall to the ground (figure 4) (Kurz et al., 2008a). For instance, bark beetle infestations (e.g. Mountain pine beetle, Spruce bark beetle) generally cause a minimal loss of carbon from the ecosystem initially but as the trees die they are subjected to decomposition which may shift the carbon balance into a negative phase if ecosystem respiration (ER) exceed photosynthesis (GPP) (Amiro et al., 2010). Often trees are left standing for a long while after an attack of insects, therefore elevated decomposition rates are expected to happen a few years after the attack. Defoliating insects consume the trees' foliage (leaves or needles) which has an instant effect on the photosynthetic capacity, but on the other hand the tree may survive if not defoliated many years in succession (Malmström and Raffa, 2000). Bark beetles attack the stems and feed on the trees' phloem (layer of cells that transport organic nutrients) which cause tree mortality. Not all bark beetles are able to attack living trees, but some of them may if they attack in sufficiently large numbers.



**Figure 4** Simplified expected relationship between disturbance and ecosystem carbon pool in relation to time since disturbance. The dashed line represents the effect by insect defoliation (Spruce budworm). The solid line represents the effect of fire. In the shaded area, the ecosystem is a sink after fire, but a source after insect outbreak. Modified after Fleming et al. (2002).

The effect of insect outbreaks on a forest stand and its carbon pool is somewhat different from other natural disturbances (Pfeifer et al., 2011). There is a wide range of different insect species that defoliate or infest their own preferred species of trees with various degree of severity (Fleming et al., 2002, Volney and Fleming, 2000). Some species kill their hosts at the first attack

while others must return to the same trees for more than a decade in order to cause tree mortality. It is also common that the insects prefer individual trees within a species such as already damaged ones or trees of a certain size. All of these factors play a role in how a stand will respond to an insect outbreak. Is the host tree abundant, are they of the right size, are they already damaged, how severely are they defoliated etc. Thus stand-age distribution and species composition are having an impact on the amount of carbon lost from the ecosystem during an insect attack (Pfeifer et al., 2011).

In contrast to the effect of fire on the carbon balance, the quantitative effect of insect outbreaks are not well documented (Kurz et al., 2008a). Those studies that have actually set out to measure the CO<sub>2</sub> fluxes are only a handful, and of these even fewer are measured within the boreal forest (e.g. Brown et al., 2010). Some studies have modeled the C loss from insect outbreaks (e.g. Dymond et al., 2010, Kurz et al., 2008, Kurz and Apps, 1999). Even so, although the importance of insects is evident their impact on the boreal carbon budget have generally been ignored in large-scale carbon budget modeling studies (Kurz et al., 2008a). The reason for this is thought to be economical as well as difficulties to model their impact as well as lack of data on the actual effects on ecosystem carbon. For this reason the boreal forest's ability to sequester carbon may have been overestimated.

In the following sections a few but important insect species are covered from each region, Russia, North America and Fennoscandia.

### **2.2.1 Russia**

Insects are considered to be of minor importance in the European part of Russia, while Siberia is more severely affected (Shorohova et al., 2009). The insect that is considered the most damaging agent in Siberia is the siberian silk moth (*Dendrolimus sibiricus*), this insect will be covered further in this section. Other insects that are able to cause forest dieback in Siberia are the dingy larch bell (*Zeiraphera dinania*) and the saddleback looper (*Ectropis crepuscularia*) as well as some bark beetle species that often only are able to infest already damaged trees (Shorohova et al., 2009). Bark beetles will be covered more extensively in both the section Insects – North America (section 2.2.2) and Insects – Fennoscandia (section 2.2.3).

#### **Siberian silk moth *Dendrolimus sibiricus***

The insect considered to be the most important defoliator in Siberia is the siberian silk moth (picture 4 and 5) (Gninenko and Orlinskii, 2002). It has slowly been spreading westward and northward during the 20<sup>th</sup> century. In the year 2001 it was widespread in a region only 500 km east of Moscow far from the area where it is indigenous (China and south-east Siberia). The authors believe that this moth may be a threat not only to the boreal forests in western Russia, but also to the remaining Fennoscandian coniferous forests. The insect is rated a high pest danger in Russia because of its level of defoliation, its ability to defoliate large areas and the fact that it attack tree species that are sensitive to defoliation (coniferous species) (Kharuk et al., 2004).

The siberian silk moth is able to develop on practically all coniferous species but they prefer siberian pine, siberian larch, stone pine, fir, and spruce (Kirichenko et al., 2009). The moth seldom kills the siberian larch as this is deciduous and may regenerate its needles, whereas the other species generally are more severely affected (Gustafson et al., 2010). Outbreaks of the insect normally occur every 15-30 years (Kondakov, 1974).



**Picture 4** Larvae of the Siberian silk moth. Credits to John H. Ghent, USDA Forest Service, Bugwood.org



**Picture 5** Adult specimen of the Siberian silk moth. Credits to Natalia Kirichenko, Bugwood.org



**Picture 6** Siberian larch forest attacked by Siberian silk moth. Credits to John H. Ghent, USDA, Forest Service, Bugwood.org

It is the larvae that feed upon the trees' needles that cause defoliation (see picture 4 and 6) (Kharuk et al., 2004). The larvae need to feed during two summer seasons before they develop into pupae in the following early summer (EPPO, 2005). It is during these months before they develop into pupae that they cause the most extensive damage. During outbreaks it is common that the same tree is defoliated 2 to 3 years in succession many trees are unable to withstand. Damaged trees are also more susceptible to outbreaks of other insect species, such as the European bark beetle (*Ips typographus*), a species which will be covered more thoroughly in the section of insects – Fennoscandia (section 2.2.3).

The siberian silk moth has a history of large outbreaks. During the period from 1870 to 1963 around 1.06 million ha of siberian pine forest died in the Irkutsk region (Shorohova et al., 2009). Later data covering the last 40 years reported outbreaks covering 1.4 million ha in the same region (Vaschuk and Shvidenko, 2006). Shvidenko and Apps (2006) relayed that areas attacked by the siberian silk moth extended over around 10 million ha in both 2001 and 2002. More than half of this area was observed in the north where outbreaks of this magnitude never have been reported before.

Shvidenko and Nilsson (2003) used inventory data of carbon pools and fluxes from 1988-1990 to assess the importance of natural disturbance agents and their impact on the carbon balance in Russia. They mention the total effect of insect and the carbon flux amounted to around 78 Mt C yr<sup>-1</sup> in 1990, which is close to the flux reported for fire (84 Mt C yr<sup>-1</sup> in the same year). The areal extent of insect disturbance was reported as 1.91 million ha yr<sup>-1</sup> on average for the period 1988-1992. The reported area is smaller than the area burned (2.23 million ha) but larger than the area harvested (1.65 million ha) averaged over the same time period.

### **2.2.2 North America**

The effect of insects on the carbon balance may not be well documented but the severity of the outbreaks in North America speaks for themselves. In 2007 the ongoing outbreak of Mountain pine beetle (*Dendroctonus ponderosae*) in British Columbia, Canada, had affected over 10.1 million ha of forest (Westfall and Ebata, 2010). After this peak the area affected have begun to decline and was reported to 6.3 million ha in 2010. During its peak the area affected amounted to 17% of the forested area in British Columbia (59 million ha). The outbreak is of unprecedented size and can be compared to the reported annual area burned in Canada of 1.8 million ha (Stocks et al., 2003). Outbreaks of spruce budworm (*Choristoneura fumiferana* (Clem.)) are even larger, and they can cover millions of square kilometers (Williams and Birdsey, 2003).

Using a carbon stock model to simulate the carbon stock for the Canadian boreal forest Kurz and Apps (1999) found that the impact of insects had a negative effect on the Canadian carbon balance. Together with the effect of fire these disturbances caused the Canadian forest to shift from a carbon source to a carbon sink in the 1980s. More recent data have supported this large impact of insects on the carbon balance (e.g. Brown et al., 2010, Dymond et al., 2010, Kurz et al., 2008a).

Two species of insects stand out in the literature concerning insect attacks in the North American boreal forest. It is the spruce budworm and the mountain pine beetle. They attack their hosts very differently since one of them feed on the foliage while the other feed on the tree phloem. Both species are important disturbance agents and are described further below. There are additional important species that are not covered in here, i.e. spruce beetle (*Dendroctonus rufipennis*), jack pine budworm (*Choristoneura pinus* (Free)), and forest tent caterpillar (*Malacosoma disstria* (Hübner)).

**Spruce budworm** *Choristoneura fumiferana* (Clem.)

Fleming et al. (2002) concluded that the spruce budworm together with fire were the dominant disturbance factors in Canada. The insect was estimated to have a depleted on average 35.1 million  $\text{m}^3 \text{yr}^{-1}$  forest in Canada during the period 1977-1987. Another example is that the areal extent of outbreaks causing tree mortality amounted to 38.9 million ha in Ontario, Canada, between the years 1941 and 1996. In the same area fires were reported on 6.5 million ha during the same period. Historically, outbreaks of spruce budworm have occurred across millions of square kilometers in the North American boreal forests several times during the last century (Williams and Birdsey, 2003).

The insect species belong to the boreal fauna and preferably attack white spruce and balsam fir (Volney and Fleming, 2000). They produce one generation per year and their current northern limit seems to be 400 km south of the white spruce limit. This has not yet been explained, and the authors have suggested that they due to their adaptability may outrun this boundary, thus threatening the remaining parts of the now unaffected white spruce forest. In order to cause wide-spread tree mortality the spruce budworm must defoliate the same trees about 5-15 years in succession (Fleming et al., 2002). High density populations of this insect often last 5-15 years, and may after this period become rare for 20-60 years (Fleming and Volney, 1995).

It is the larvae of spruce budworm that preferably feed on the current-year foliage of the conifer host trees (picture 7) (Dymond et al., 2010). This is one of the reasons why consecutive years of defoliation are needed to cause tree mortality.



**Picture 7** Left, tree attacked by spruce budworm. Right, larvae of spruce budworm. Credits to Steven Munson, USDA Forest Service, Bugwood.org and Jerald E. Dewey, USDA Forest Service, Bugwood.org

The one study that exists concerning the effect of defoliating insects on the ecosystem carbon was made within the temperate forest i.e. Clark et al.(2010). The studied insect was gypsy moth, and the location was New Jersey, USA during the years 2005 to 2007. Their results are included here as a reference although the forest studied lies outside of the boreal zone. They found that the gypsy moth converted some stands into carbon sources. The stand with highest net release of carbon was an oak/pine stand that released  $293 \text{ g C m}^{-2} \text{ yr}^{-1}$  during the year 2007.



Dymond et al. (2010) anticipated that outbreaks of spruce budworm could have significant effects on the forest carbon in the boreal forest due to their extensive and severe defoliations. They modeled the potential carbon loss within a large area in Canada between the year 2000 and 2024 and found that the spruce budworm started to influence the biomass carbon stock negatively after four years of defoliation. Carbon gains were then observed in the DOM pool and in the soil carbon. Three years after the start of the outbreak the ecosystem had turned into a carbon source instead of a carbon sink with net loss of carbon to the atmosphere. This carbon source lasted for 10 years before it became a carbon sink again. At the end of their simulation the ecosystem carbon pool had decreased with 2-10%.

### **Mountain pine beetle** *Dendroctonus ponderosae* (Hopk.)

The mountain pine beetle is a bark beetle that is native to North America. Its range covers the western North America and within the boreal zone the Province of British Columbia, Canada is most severely affected (Gibson et al., 2009). The insects spend their entire lifecycle (1 year) under the bark of trees (picture 9) except during a few days of summer when adults (picture 8) emerge and fly to new hosts. Its preferred host in the boreal zone is the lodgepole pine but it can infest all pine species within its range.



**Picture 8** Adult mountain pine beetle. Credits to USDA Forest Service - Ogden Archive, USDA Forest Service, Bugwood.org



**Picture 9** Mountain pine beetle galleries within stem. Credits to Scott Tunnock, USDA Forest Service, Bugwood.org

Bark beetles must breed in dead tissue therefore they primarily attacks stressed or damaged trees (Rudinsky, 1962). Mountain pine beetle is also able to overcome the defensive system of live trees if they attack in sufficiently large numbers (Malmström and Raffa, 2000). By this trait populations of mountain pine beetle may become self-sustaining and even spread as they are able to kill trees themselves. To its help the mountain pine beetle carries with it a fungi that aid in the tree killing. When the beetles attack lodgepole pine the trees' foliage becomes discolored. The needles change from green to yellow-green to red and finally brown (picture 10). The discoloration often starts several months after the actual infestation and the trees may retain their needles up to 5 years after an attack (Safranyik and Wilson, 2006).

The mountain pine beetle normally produce one generation every year which means that they are univoltine (Safranyik and Wilson, 2006). In exceptionally warm years they may be able to breed a second generation (bivoltine) whereas they during cool years may need two years to mature and finish their lifecycle. The first generation of mountain pine beetle often causes tree mortality since the trees ability to use the phloem is hampered (Gibson et al., 2009). During epidemic outbreaks tree mortality is often high within infested stands and it can reach 30-45% on average. However, the volume of trees killed is often much higher as the beetle prefer to attack older trees (Safranyik and Wilson, 2006). These large outbreaks occur at irregular intervals and may persist for 5 to 20 years. They can also change stand age, density and species composition within a stand, which may have consequences for the carbon balance. Between these larger outbreaks the insect populations are small and infestations generally only occur in few already damaged trees.

During the epidemic stages the outbreaks can cover vast areas but none during the last century have been as large as the ongoing outbreak in British Columbia. As mentioned, the ongoing outbreak reached its climax in 2007 when it covered over 10.1 million ha of forest. This exceptionally large outbreak is attributed to a combination of factors including; the abundance of mature lodgepole pine in the area and milder winters (Safranyik and Wilson, 2006).



**Picture 10** View of area with lodgepole pines attacked by mountain pine beetle (red colored trees are attacked). Copyright © Province of British Columbia. All rights reserved. Reprinted with permission of the Province of British Columbia. [www.ipp.gov.bc.ca](http://www.ipp.gov.bc.ca)

The effect of Mountain pine beetle outbreaks on the carbon balance is somewhat more complicated than the effect of other disturbances since the beetle prefer to attack older trees (Pfeifer et al., 2011). The response of the carbon stock and fluxes of a forested area is then driven both by the number of trees prone to attack, such as the percentage of the preferred lodgepole pine, the tree size and also the readiness of other species to take advantage of the lost competition.

One effect that the insects have on the infested stands is reduced photosynthetic activity. Using satellite data to estimate the photosynthetic activity Coops and Wulder (2010) found that the reduction of carbon accumulation due to reduced GPP amounted to  $5.21 \text{ Mt C yr}^{-1}$  or  $75 \text{ g C m}^{-2} \text{ yr}^{-1}$  less in the infested area in 2005 as compared to a long term average of GPP.

Brown et al. (2010) used eddy covariance technique to examine the impact of the beetle on the carbon balance in two attacked lodgepole pine stands in central British Columbia. One stand was attacked in 2006 and by 2008 only 21% of the trees were still healthy. The other stand had been attacked in 2003 and >95% of the stand was affected by canopy mortality. Measurements showed that both stands were carbon sources during 2007, with a NEP of  $-82$  and  $-56 \text{ g C m}^{-2}$  respectively. In 2008 the first stand was still a carbon source of  $33 \text{ g C m}^{-2}$  while the second stand that had been attacked in 2003 had become a carbon sink of  $4 \text{ g C m}^{-2}$ . However, the trees at the two sites were still standing and the authors expected that the respiratory release of carbon would increase when the trees eventually fall. Thus, the stands may become larger carbon sources than measured.

Kurz et al. (2008a) modeled the effect on the carbon balance by simulating the ongoing outbreak of mountain pine beetle between the years 2000 and 2020. They found that the cumulative impact on the ecosystem carbon during these years amounted to a loss of  $270 \text{ Mt C}$  or  $36 \text{ g C m}^{-2} \text{ yr}^{-1}$  over an area of  $374,000 \text{ km}^2$  forest. The simulated outbreak was projected to peak between 2006 and 2008 which it actually did (Westfall and Ebata, 2010). The maximum area infested in the simulation ranged from 7.4 to 9.4 million ha. This is actually less than the maximum area observed in 2007 by Westfall and Ebata (2010) (10.1 million ha).

The loss of carbon induced by the insect outbreak resulted from a loss of photosynthetic capacity during and after the outbreak and increased respiration due to large transfers of biomass to the DOM pool (Kurz et al., 2008a). The losses are substantial and for comparison; the maximum carbon loss modeled during one year ( $20 \text{ Mt C}$ ) in British Columbia is of the same magnitude as the direct emissions from forest fires throughout Canada averaged over the years 1959 to 1999 ( $27 \text{ Mt C yr}^{-1}$ ) (Amiro et al., 2001).

Although their study was made outside of the boreal zone some results from Pfeifer et al. (2011) is included here. Their study area was located in central Idaho, where mountain pine beetle had attacked the forest between 2001 and 2004. They found some relationships that are worth mentioning. They saw different responses of post-outbreak carbon fluxes and time of recovery to



pre-outbreak levels of carbon stock, these were; 1) The size of the carbon flux depended on the severity of the attack and the percentage of small trees ready to compensate the carbon loss by increased growth. 2) The percent of trees killed during an attack was a strong driver for how fast the carbon stock recovered. 3) The percent of carbon in the killed trees compared to those not killed was important. Thus, if the beetle would kill all large trees with substantially more carbon content than other trees in the area the time of carbon stock recovery would take a considerable *longer* time. The effect on the carbon budget is then largely driven by the stand age distribution as well as species composition.

Pfeifer et al. (2011) also found that the average time for the carbon flux to return to pre-outbreak levels was 30-60 years for the measured and modeled plots. The carbon stock returned to pre-outbreak levels in 1-25 years. However, by modeling the potential carbon stock if the stand was unaffected from the beginning the carbon stock would take 50-160 years to catch up to these levels, and some plots did not manage to recover to that simulated value within the simulation time.

### **2.2.3 Fennoscandia**

Averaged over all of Europe insects was responsible for 16% of all the damaged inflicted on the European forests by natural disturbance during 1850 to 2000 (Schelhaas et al., 2003). That is the same fraction that was found to be affected by fire. Even if this result encompass forests outside of the boreal region it is interesting to relate for comparison. Half of this damage was caused by bark beetles. One especially damaging bark beetle is the european spruce bark beetle (*Ips typographus*). It is considered the most damaging insect in Swedish coniferous forests (Jönsson et al., 2009) and will be covered in brief below.

#### **European spruce bark beetle *Ips typographus***

The european spruce bark beetle is native to both Europe and Siberia (Wermelinger, 2004). It attacks mature norway spruce (*Picea abies* (L.) Karst) which is a very common coniferous species in the boreal forest of Sweden, Norway and Finland. The beetle produce galleries under the bark just as the mountain pine beetle where their larvae feed and pupate before they emerge as adults (picture 11 right and middle). The larvae feed on the phloem and by this they cause tree mortality (picture 11 left). As the mountain pine beetle, the european spruce bark beetle is a vector for a fungi that aid in the process of killing the host tree.

Outbreaks of the european spruce bark beetle are generally connected to forest damage induced by extreme weather conditions such as drought or wind (Wermelinger, 2004). This is because of that although the bark beetle normally reproduce in already damaged or otherwise stressed trees they are able to infest healthy trees when they swarm in sufficiently large numbers (Schroeder, 2001). Thus, when many damaged trees are available the risk of damage to healthy trees increase since the population of beetles is likely to grow. Large scale windthrows are almost always subjected to attack (Wermelinger, 2004). Once an attack has started it usually lasts between 3 to 6 years. The damage caused by spruce bark beetle has increased during the last 15 years

(Schelhaas et al., 2003). This increase has been attributed to storm damage and favorable warm temperatures but also increase of forest volume, area and age.



**Picture 11** Left picture, Norway spruce attacked by European bark beetle. Middle picture, adult beetle. Right picture, galleries in stem, white larvae visible. Credits to Jan Liska, Forestry and Game Management Research Institute, Bugwood.org, Maja Jurc, University of Ljubljana, Bugwood.org and Louis-Michel Nageleisen, Département de la Santé des Forêts, Bugwood.org

Schroeder (2001) found that tree mortality induced by spruce bark beetle after a windthrow was low during the first two summers after the storm in the area observed. This was attributed to the fact that the insect initially colonize damaged trees instead of healthy ones. How long this period of low tree mortality last was found to be related to how many damaged trees that were available in relation to the size of the beetle population. The peak in tree mortality was found to happen the second or third summer after the storm. This result was explained by relating that the population had grown larger and the damaged trees were no longer suitable hosts for reproduction. When this happens the population usually starts to decline again as a response to the less successful reproduction in standing trees. Another factor may be that they leave the area. Schroeder (2001) found very good positive correlation between the number of killed trees and the number of windthrown trees colonized by spruce bark beetle. This indicates that the size of the beetle population is affecting the magnitude of tree mortality. This relationship was valid also if not only counting the infested windthrown trees but also those not infested. This means that the number of windthrown trees was correlated to the number of trees killed by the beetle. Lastly, the same kind of relationship between the number of killed trees and the area of storm disturbed stands was also found. A larger area thus meant that more trees were killed.

January 2005, Sweden was struck by a severe storm that led to extensive windthrow in southern Sweden. In 2007, a second storm hit approximately the same area again, although this storm was less severe. These two storms favored development of the European spruce bark beetle, and larger populations were observed between 2005 and 2008 (Långström et al., 2009). The average number of beetles trapped in their equipment were ~ 2,500 in 2005, ~10,000 in 2006, ~13,000 in 2007 and ~30,000 in 2008. During 2005, virtually no attacks were observed in healthy trees and only a small fraction of the fallen trees were attacked. This fraction increased in 2006 when more than half of the fallen trees were under attack. Later that summer season the beetle began to attack healthy trees and in fact attacked more volume of living trees than dead. In 2007 the attack on fallen trees declined as well as the number of living trees attacked. By 2008 the beetle had to switch their main habitat from fallen to living trees but by this time the attack had lessened in severity and only about half of that volume of living trees attacked in 2006 were attacked in 2008. Altogether about 800,000 m<sup>3</sup> of wood was killed by beetles from 2005 to 2008.

The insect is considered the most destructive insect species in Swedish forests (Jönsson et al., 2009). In the Swedish climate, which is similar to that of Norway and Finland, the insect is able to grow one mature generation per year except in the Northern mountainous areas where the conditions are still too harsh (Jönsson et al., 2009). However, during the warm summer of 2006 the spruce bark beetle managed to develop two generations in Southern Sweden (Långström et al., 2009). This second generation was thought to affect the amount of living trees infested in late summer 2006.

The European spruce bark beetle have not yet developed large populations in Finland (Eriksson et al., 2007)

So far, there are no studies available that have tried to measure the impact of bark beetles on the forest carbon balance in Fennoscandia.

#### **2.2.4 Comparison**

In the case of insects, the differences between the regions that are most evident are the insect species present. In Russia, the Siberian silk moth is an important disturbance factor and since it is migrating into new areas further west and north it may become a larger problem. Insects in the European Russia do not seem to be such of a problem as in Siberia (Shorohova et al., 2009). In North America, insects are an important disturbance factor but there are regional differences. The only province experiencing severe attack from mountain pine beetle is British Columbia, but its range is projected to expand. Spruce budworm is present over all of Canada. In Fennoscandia the European spruce bark beetle is the most important insect, but it has so far not shown the same severe damage to large regions as the outbreaks of mountain pine beetle in Canada.

### 2.2.5 The impact of climate

Insects are cold blooded which means that they are very sensitive to changes in climate. Warmer temperatures is likely to affect the timing of development from one stage in their lifecycle to the next (Fleming and Candau, 1998). The rates at which the insects develop have increased during recent years, and a warmer climate is likely to be the reason for this. These shifts can possibly disrupt trophic relationships that in the end might affect species composition and through that ecosystem stability. Insects are also able to expand their range and exploit new habitats faster than their hosts can migrate (Logan et al., 2003).

The siberian silk moth have managed to migrate into areas previously outside of their range during the beginning of the 21<sup>st</sup> century (Gninenko and Orlinskii, 2002, Shvidenko and Nilsson, 2003). Whether this is climatically driven or not is left unsaid. Outbreaks of the siberian silk moth is favored by certain climatic conditions; low summer precipitation, mild winters with snow cover and the absence of frost in early autumn and late spring (Kharuk et al., 2009). Unusually large outbreaks have been recorded during the 21<sup>st</sup> century, but no reason for this was given (Shvidenko and Nilsson, 2003).

The spruce budworm is thought to respond with higher population densities in a warmer, dryer climate (Fleming and Volney, 1995). A warmer climate may also have a potential effect on the outbreak cycle of the spruce budworm, this is expected to increase the average population densities and therefore worsen the chronic attacks between large outbreaks (Fleming and Candau, 1998). However, ecosystems are complex and climatically induced changes may disrupt interactions between different trophic levels which may reduce the population growth. For instance, tree foliage may grow faster which reduces the time when preferred young foliage is available. Also, predators may help to reduce the potential population growth if they are also favored by the climatic conditions.

The mountain pine beetle is currently not limited by its hosts' range, but of climate (Carroll et al., 2004). It is limited by elevation as well as both in the north and east direction. During the last part of 20<sup>th</sup> century the beetle has expanded its range into former unsuitable habitats as these have transformed into climatically suitable ones. The colonization of these areas has been rapid and continued warming is likely to aid the beetle to further expand their habitat into new areas. The insect range expansion can only be explained by changes in climate. However, in former suitable habitats the mountain pine beetle infestations have declined because of warmer temperatures. This is because the insect may have to become bivoltine which makes it more sensitive during the winter months as it overwinters in the wrong phase of their lifecycle. This may reduce the mass-attacks in these areas.

The european spruce bark beetle as well as other insects is sensitive to changes in climate (Volney and Fleming, 2000). The effects are both direct and indirect. A direct effect is that their metabolic rate is temperature dependent which means that a higher temperature influence both the insect's activity and development. This may have far-reaching consequences as the spruce



bark beetle may become bivoltine instead of univoltine further north than before (Jönsson et al., 2009). Indirect effects are those that are related to tree damage or stress like drought or wind damage, forest conditions that favor larger beetle populations (Malmström and Raffa, 2000, Schelhaas et al., 2003).

### **2.2.6 Future projections**

The range expansion of the mountain pine beetle is thought to continue in a warmer climate (Carroll et al., 2004). If this expansion continues it might not only lead to new areas affected, but also that the beetle will have a steady supply of new hosts to infest. This may result in that a population collapse due to shortage of food is prevented to some degree. Movement into higher elevations may also cause the beetle to overcome former natural barriers (the Rocky Mountains). This barrier have constrained the beetles to British Columbia, (west of Rocky Mountains) but a persistent mountain beetle population is now present in Alberta at the northeastern slopes of the mountains indicating that the barrier might be overcome already.

In their study Jönsson et al. (2009) sought to answer if a warmer climate in accordance with different projected scenarios for the future climate would favor the development of a second generation of spruce bark beetle in Sweden. They found that the beetle would succeed to develop a second generation in Southern Sweden in up to 10% of the years modeled for the period 2011-2040. This aided by a temperature increase projected as 0.4 – 1.5 degrees during the same period. After 2040 the temperature is projected to be 1.4-2.2 degrees higher corresponding to an increasing risk of spruce bark beetle development during this period (2040-2070). A second generation is then believed to develop in 30-49% of the summers. During this period it is also possible that a second generation will develop in mid-Sweden and along the north-eastern coast if the temperature increase is in the higher part of the interval (scenario A2, IPCC).

In a study from Austria Seidl et al. (2008) modeled how a warmer climate would affect the degree of damage from the European spruce bark beetle. The study area is outside of the boreal region where Norway spruce is more susceptible to damage, however the results are presented as an example. Assuming a double CO<sub>2</sub> concentration they ran two different GCMs (Global Circulation Models) with predicted temperature increase of +3.7 °C and +3.1 °C for 2090-2100 compared to 1961-1990. They also ran one baseline scenario without any future CO<sub>2</sub> change. They found a strong increase in the number of disturbance events induced by the bark beetle in both scenarios with a doubled CO<sub>2</sub>. Toward the end of the century almost every stand (92.4% and 87.5% of the stands) within their study was damaged by bark beetle except in the baseline scenario which showed less damage (23.2%). They also found that climate change increased the timber volume damaged by bark beetles. The increase in carbon storage over 100 years within the ecosystem did not increase as much if the beetle was included in the model (+21.1 t C ha<sup>-1</sup> without beetle, +2.3 t C ha<sup>-1</sup> with beetle), indicating that the beetle had an important effect on the carbon balance. They concluded their study by saying that damage intensity and frequency by the European spruce bark beetle is likely to increase in the future as a response to a warmer climate and that the effect on the carbon balance may be considerable.

## 2.3 Windthrow

Strong winds have the potential to cause physical damage to forests by breaking stems, roots, branches or even up-rooting whole trees (Mayer et al., 1989). This has implications for the forest stand structure and windthrow is considered an important factor in shaping the boreal forests (Ulanova, 2000). The scale of windthrows are important, it can range from catastrophic windthrows at the landscape level that actually cause widespread secondary succession to individual trees falling within a forest. It is only the catastrophic events that are generally covered in the literature, but dead wood within the forest has been suggested to be a vast flux of carbon (at least as large as fossil fuel burning) that should be considered (Krankina and Harmon, 1995). In this section of windthrow it is only the large scale events that are covered.

Wind as a disturbance regime is more similar to insects than fire in the sense that it is partly discriminating in what species it affects. Its effect on the landscape is thus more heterogeneous and it may play an important role in accelerating succession (Rich et al., 2007). Early successional species with low shade intolerance have been found more susceptible to windthrow than shade-tolerant species. This is because shade-intolerant species are thought to allocate more of their resources to improve their height at the expense of their structural strength. In a study from Minnesota balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*) were more prone to wind damage than for example jack pine (*Pinus banksiana*) and red pine (*Pinus resinosa*). In the same study Rich et al. (2007) found that larger trees were more susceptible than smaller ones. This relationship was valid across all species they considered. Mature stands (90 years) were more susceptible than old stands (> 130 years). This may be because of the presence of less susceptible shade-tolerant late successional species in older stands.

Trees can also be more susceptible to windthrow if they are already damaged (Schlyter et al., 2006). Drought and frost damages are presented as important factors affecting tree vitality. In addition to the tree species and characteristics the conditions at the site is also important. Site characteristics such as soil type, soil moisture, and topography partly determine how susceptible a forest is to windthrow (Seidl et al., 2011). Also, Talkkari et al. (2000) pressed that trees are more susceptible to wind damage at forest margins due to higher wind speeds. Trees that are used to stronger winds are less vulnerable, therefore trees at the margins of clear-cuts or windthrows are the most threatened (Pellikka and Järvenpää, 2003). For this reason, once a windthrow has occurred, it is more probable that the area will grow further in size due to less resistance in the standing trees surrounding it (Vygodskaya et al., 2007). Lastly, the wind intensity itself is a crucial factor determining the severity of the disturbance (Rich et al., 2007).

In contrast to the rather immediate effect on the carbon balance caused by fire disturbance the effect of windthrow is a rather slow process. Nearly all of the carbon remains on site and is left to decompose (Köster et al., in press). Whether or not this biomass should be removed from the ecosystem is debated since it on one hand provides a long term carbon storage but on the other

hand result in an increased respiration. Leaving the wood also increase the risk of bark beetle populations growing into levels large enough to damage living trees (Jönsson et al., 2007).

Storms severe enough to cause windthrows affect the carbon balance through the loss of photosynthetic capacity in the forest. Additionally soil disturbance by windthrow is another factor that contributes to increased losses of carbon from the ecosystem (Kramer et al., 2004)

### **2.3.1 Russia**

In Russia windthrow is considered a less severe natural disturbance than fire and insects (Shorohova et al., 2009). The annual areal extent of windthrow is largely missing from the literature reviewed but one article from the Ural Mountains is presented. Also, Schulze et al. (1999) and Knohl et al. (2002) have measured changes in the carbon fluxes after a windthrow in European Russia.

The risk of windthrow in Russia is higher in coastal and mountainous areas (Lässig and Mocalov, 2000). In the Ural Mountains extensive windthrows generally occur every 50-75 years. Less severe windthrows in this area have returned every 8-10 years between 1965 and 1996. The recorded area damaged between the years 1965 and 1996 in the Ural region amounted to ~46,000 ha which is less than 1% of the measured area (0.17-0.62%). However, the area contains large unforested areas where no windthrow occurred (Lässig, 2011 pers. com.). The storms generally occurred during summer when thunderstorms form strong gusts in the area (Lässig and Mocalov, 2000).

Schulze et al. (1999) used eddy covariance measurements to investigate the carbon balance of a 2 year old windthrow in European Russia. The measured fluxes showed a loss that amounted to 192 g C m<sup>-2</sup> during a 3 month period (June to September). All the trees at the site had been felled by the storm and secondary succession was still sparse. The windthrow did take up some carbon during daytime, but large nighttime fluxes overcame this uptake and the net effect was a net loss of carbon.

Knohl et al. (2002) investigated the effect of windthrow on the carbon balance in a site located in European Russia 300 km west of Moscow. The area had been dominated by spruce with some additional birches and aspen. They measured the exchange of CO<sub>2</sub> with eddy covariance technique two years after a stand replacing windthrow. None of the dead wood had been removed from the site but was left to decompose. During the tree month measurement between July and October the area lost 180 g C m<sup>-2</sup> to the atmosphere. This flux was thought to be a conservative estimation of the carbon released from the site because of measurement flaws. For comparison they also measured the carbon flux from a nearby undisturbed old (110 year) forest. Differences between the two sites were mostly discerned during daytime fluxes, indicating that the disturbed area acted as this type of undisturbed forest during the night. During daytime the disturbed site did gain some carbon, but the small amounts could be compared to the carbon uptake of a young forest.

### 2.3.2 North America

The extent of windthrown areas in boreal North America is largely missing from the literature reviewed. Windthrow seems to be of smaller importance than fire and insects both because it is absent from literature and that windthrows are not mentioned as one of the dominant disturbance regimes. However, reports from Quebec, Canada damage from fire and insects amount to only 25% of that induced by wind (Achim et al., 2005). Hence, geographical differences may be important. In British Columbia the importance of windthrow, fire and insects was fairly the same in 1992, each damaging 4% of the annual allowable cut every year (Mitchell, 1995).

Bouchard et al. (2008) studied the extent of stand replacing windthrows in Quebec. In the 3.1 million ha area investigated stand replacing windthrows affected 0.0255% annually averaged over the period 1971-2000. Their definition of a stand replacing windthrow was stands with > 75% mortality and only areas > 5 ha were included. About 46% of the windthrown area was due to a storm (1964) that damaged around 10,000 ha.

### 2.3.3 Fennoscandia

In contrast to the other large boreal regions windthrow is an important type of disturbance across Fennoscandia and Europe (Lindroth et al., 2009). Across all of Europe including the non-boreal forest it accounts for 53% of the total damage annually averaged over the period 1950-2000 (Schelhaas et al., 2003). Studies have tried to find out whether the frequency of severe storms in Europe has increased in recent decades as a response to global warming (Barring and von Storch, 2004, Carretero et al., 1998, Heino et al., 1999). These studies have not been able to show any persistent increasing trend. However the damages these winds are causing seem to become more severe at the end of the 20<sup>th</sup> century (Nilsson et al., 2004). This discrepancy may be due to the fact that many other factors than just wind intensity affect how susceptible the forest is to damage.

Records of wind damaged forests in Sweden were compiled for the period 1901-2000 (Nilsson et al., 2004). These records showed the storm damage has increased in Sweden during the last century. Furthermore the records stated that 49% of the volume losses during that century were caused by five severe storms occurring in the years 1954 and 1969. The total volume losses during the century were estimated to 110.7 million m<sup>3</sup>. Unfortunately this study had the bad luck of being published one year too early since the worst windthrow recorded in Sweden happened in 2005 affecting more than half of the volume of trees (66 million m<sup>3</sup>) as had been recorded for the entire previous century (Lindroth et al., 2009).

The increased storm damage recorded for Sweden during the last century and especially the second half has been suggested to partly depend on the altered forest management practices applied (Nilsson et al., 2004). Also the total volume of trees has increased during recent years as well as the forest age. The amount of forest older than 41 years has doubled in some parts of Sweden during the 20<sup>th</sup> century. Additionally the reporting system applied is another factor that may contribute to the increased reported damage during later years.



The effect on the carbon balance instigated by the particularly severe storm affecting Sweden in 2005 has been subjected to study by Lindroth et al. (2009). They found that the carbon lost during the first year after the storm in their study area in southern Sweden was in the range of 897 to 1259 g C m<sup>-2</sup> yr<sup>-1</sup>. If this number is extrapolated for the entire windthrown area (272,000 ha (Valinger et al., 2006)) the loss of carbon would amount to 3 million ton (Mt) during the first year. They also noted that the enhanced respiration from the windthrown site was double to that measured at a clear-cut site the first year after harvest.

### **2.3.4 Comparison**

There seem to be large geographical differences concerning where windthrows occur, especially as large scale events. Fennoscandia is situated in a region often receiving storms during winter (Carlson, 1998). Storms severe enough to cause widespread windthrow are rather rare events, but the damage induced may be considerable as was the case during the severe storm hitting Sweden in 2005. Reports from Russia stated that damaging storms often occurs during thunderstorms in summer, at least in the Ural Mountain area (Lässig and Mocalov, 2000). Studies from North America are scarce which in itself tells that windthrow is of smaller concern than disturbances like fire and insect outbreaks. Windthrow disturbance seems to be worst in Fennoscandia.

### **2.3.5 The impact of climate**

Windthrow is directly related to climate in that aspect that wind intensity is a crucial factor determining the severity of the disturbance (Rich et al., 2007). When wind speed exceed a certain threshold, which is different depending on species, location, etc. trees begin to fall or break (Nilsson, 2008). Wind direction is also of importance since trees are more resistant in the prevailing wind direction. There are also additional responses to climate that are not related to the wind itself. Precipitation may reduce root anchorage by water logging and snow can put heavy loads on the trees making them more susceptible to breakage. Snow covered ground also reduce ground frost which may be one important factor that influence the forest's susceptibility since it act as an additional anchorage together with the tree roots (Blennow et al., 2010b). Ground frost is important during those periods generally affected by severe winds, is during the winter months in northern Europe (Nilsson et al., 2004). If storms reoccur over an area trees may be more susceptible if they are damaged successively.

Fennoscandia lies in a region often hit by mid-latitude cyclones therefore it more likely that the boreal forests here are damaged on a large scale by severe winds. Although analysis of historical measurements of wind climate are problematic (Nilsson, 2008) it has been concluded that the number of storms during the last 200 years in southern Scandinavia have been very stable (Bärring and von Storch, 2004) although decadal variations have been found (Alexandersson et al., 2000). The number of storms may have been rather constant but the frequency of winds from the northwest has increased (Nilsson, 2008). When geostrophic winds come from this direction the surface winds have caused the worst storm damage. It should be noted that the geostrophic wind direction does not need to correspond fully with the surface wind direction.

### **2.3.6 Future projections**

Future scenarios for the wind regime are still somewhat inconclusive for the extratropical cyclones in the mid-latitudes (Kattsov and Källén, 2010). However, if the storminess should increase it is likely that some regions will be more subjected to wind disturbance. Rich et al. (2007) reported that the importance of windthrow may increase in North American boreal forests as a response to a changed climate.

Although the future wind regime still is quite unsure, the projection of a temperature increase is not (Kattsov and Källén, 2010). Reduced or absent ground frost expected in a warmer climate may be one important factor that increase the forest's susceptibility to windthrow (Blennow et al., 2010b). Also, by simulating how a warmer climate might affect future forest growth in Sweden Blennow et al. (2010b) found that the probability for increased wind damage became higher. This increased sensitivity to wind damage posed by higher growth rates were a result of increased NPP (15-40% increase until 2071-2100) and present management methods (Blennow et al., 2010a). This result was explained by enhanced sensitivity to wind damage for the young trees previously too small to be affected. Their increased growth allows them to become sensitive at a younger age and consequently sensitive during a longer period of their lifetime. If the rotation periods are not shortened in response to this the forest becomes more vulnerable. Also, a warmer climate may affect forest vitality through increased risk of drought and climate extremes (Schlyter et al., 2006). Decreased forest vitality makes the trees more vulnerable.

Blennow et al. (2010b) investigated how the risk of damage by wind responded to changes in temperature as well as the wind itself. They found that the risk of damage increased further if the future wind regime was accounted for. Overall, the probability of wind damage in the period 2071-2100 was significantly increased for the two sites investigated.

### **2.4 Interactions**

Natural disturbances do interact with each other to some degree. Most prominent is perhaps the effect of windthrow on bark beetle populations (Jönsson et al., 2007). The abundance of breeding ground leads to larger populations of european bark beetle, the insects may then start to attack living trees.

The risk of fire may become more common in Canada if the damage from insects increase since fuel load in the forest may increase as a result of enhanced tree mortality (Fleming and Candau, 1998). Fleming et al. (2002) found that, even though it could not be verified by statistics, evidence pointed toward the fact that fires occurred disproportionately often 3-9 years after an outbreak of spruce budworm indicating an interaction between defoliating insects and fire (Fleming et al., 2002). However, this relationship between spruce budworm and increased area burned was not found in a more recent study (i.e. James et al., 2011) even though the defoliated areas were more flammable. The authors noted that this result may have been different if they had used shorter time scales in their model since the effect of spruce budworm is temporary.

Instead they found that area defoliated by spruce budworm lessened in the presence of fire as their host trees burned.

Insects may also be indirectly aided by fire and the subsequent suppression of it. The large outbreak of mountain pine beetle in British Columbia is thought to have connections with the fact that large fires in the late 1800s and early 1900s have provided the beetle with homogenous mature lodgepole pine stands (Safranyik and Wilson, 2006). The area burned in this region has declined during the 20<sup>th</sup> century because of fire suppression and the trees have been able to mature into suitable ages for beetle attacks.

Neither fire nor insects were mentioned in Nilsson (2008) as factors influencing the risk of windthrow.

## 2.5 Sink or Source

Although the carbon balance in the boreal forest is disrupted by various disturbances, the forest as a whole may still behave as a carbon sink. It is here the term NBP (net biome production) is commonly used as a description of the long term carbon sink in an ecosystem. This estimate includes the effect of disturbance ( $NBP = NEP - \text{ecosystem disturbance}$ ). NBP is also referred to as the measure of CO<sub>2</sub> sequestered within ecosystems that represents the direct contribution of ecosystems to climate change mitigation (Luysaert et al., 2010). Over long time scales with stable environmental conditions NBP is thought to be near zero (in balance) for the global forests but in our changing environment this balance is thought to behave differently. Overall the global forests are thought to have a positive NBP, which means that they sequester more carbon from the atmosphere than they lose during disturbances.

Inventory based studies made by Shvidenko and Nilsson (2003), Kurz and Apps (1999) and Myneni et al. (2001) showed that the carbon balance have been positive during the latter part of the 20<sup>th</sup> century throughout the boreal region. This means that the ecosystem have continued to sequester carbon. Russia was thought to have a positive NBP of 322 Mt C yr<sup>-1</sup> between the years 1961 and 1998 (Shvidenko and Nilsson, 2003). Myneni et al. (2001) found that the carbon sink in woody biomass for Canada was 73 Mt C yr<sup>-1</sup> and 470 Mt C yr<sup>-1</sup> for Eurasia between the years 1995 and 1999. Kurz and Apps (1999) found that the mean from 1970-1989 was a sequestration of 52 Mt C yr<sup>-1</sup> in Canada. However, during the study's last years (1985-1989) the balance became negative and instead released 69 Mt C yr<sup>-1</sup> into the atmosphere due to increased disturbance rates. Myneni et al. (2001) found that some parts of the Canadian forest acted as carbon source between the years 1982 and 1999, but that it as a whole was a carbon sink. Kurz et al. (2008b) reported that the managed Canadian forest will behave as a net carbon source at least until 2022, the end year in their projection.

In a model based study Quegan et al. (2011) found that the NBP in central Siberia amounted to 27.5 g C m<sup>-2</sup> yr<sup>-1</sup>. If this could be considered representative for entire boreal Asia the NBP would be 352 Mt C yr<sup>-2</sup>. This may be compared with the fossil fuel emissions from the Russian

Federation that amounted to  $427 \text{ Mt C yr}^{-1}$  in the year 2010. They noted that boreal Asia might not play any major role in the northern hemisphere land sink on account of its low NBP relative to its size.

Balshi et al. (2007) found that the boreal forest in North America was a sink of  $18.7 \text{ Mt C yr}^{-1}$  on average between the years 1959 and 2002, which is equivalent to  $1.5 \text{ g C m}^{-2} \text{ yr}^{-1}$ . By adding the effect of  $\text{CO}_2$  fertilization, meaning that a higher concentration of  $\text{CO}_2$  in the atmosphere boosts the photosynthesis, the sink was estimated to be  $81.7 \text{ Mt C yr}^{-1}$ , equivalent to  $7.5 \text{ g C m}^{-2} \text{ yr}^{-1}$ . Balshi et al. (2007) believed that the sink may have been lower if they had included disturbances other than fire. On account of this, North America should be an even smaller contributor to the northern hemisphere land sink. Balshi et al, (2007) also made the same estimations for the pan-boreal region and found that it was a sink of  $405.6 \text{ Mt C yr}^{-1}$  on average between the years 1996 and 2002, equivalent to  $10.6 \text{ g C m}^{-2} \text{ yr}^{-1}$ . This estimate includes the effect of  $\text{CO}_2$  fertilization.

### 3 Discussion

The effect of natural disturbances on the carbon balance of boreal ecosystems is important to understand in order to account for its ability to mitigate anthropogenic CO<sub>2</sub> emissions. There exists a large interannual variability in the terrestrial land sink in the northern hemisphere and the reasons for this should be understood. It has been proposed that forest disturbances can explain part of this variability which should be a possible explanation on account of their ability to shift the carbon balance in large areas and their irregular occurrence. Whether it is fire, insects or windthrow the effect is to change the carbon balance through reduced GPP and increased ER. The decreased NEP on account of this does not mean that the NEP must become negative. However, those measurements that are available have so far provided data that tells of negative carbon balances at least a few years after a disturbance. Hidden within these two previous sentences is the tale of partial disturbances (non-stand replacing) and their effect on the carbon balance, which is not covered in the literature reviewed nor found when looked for.

The natural disturbances with important impacts on the carbon balance of the boreal forest are the ones covered within this review, fire, insect outbreaks and windthrow. An additional factor is drought that affects tree vitality and of course fuel moisture, thus drought can work to enhance the risk of other disturbances even if it in itself does not cause widespread tree mortality.

How important each natural disturbance is proved to be somewhat difficult to answer since the range of results is quite wide. Below follows some comments on the data from each region;

#### **Russia**

The importance of fire in Russia is difficult to discern on account of the wide range of estimations on annual area burned (1.5 – 12 million ha yr<sup>-1</sup>), this also influence the amount of annual direct emissions reported (58 – 484 Mt C yr<sup>-1</sup>). The one thing that the different authors do agree on is that the indirect emissions after a fire are larger than the direct ones. The authors used different methods to arrive at their answers that further complicate any comparison. The time scales used to calculate the annual average area burned are also different between the authors.

Insect outbreaks in Siberia are extensive and emissions in 1990 were estimated to 78 Mt C and the areal extent reported as 1.91 million ha yr<sup>-1</sup> between 1988 and 1992. This is however a very limited time period and should perhaps not be considered as a long time average neither for the emissions nor the areal extent.

The areal extent of windthrow in Russia on the other hand is not reported in any of those studies reviewed and perhaps it is difficult to monitor in the vast boreal forest of Russia. Measurements of emissions from windthrown sites have been taken at 2-year old windthrows for 3 months during summer at two sites in European Russia. These emissions were reported to 180 g C m<sup>-2</sup> and 192 g C m<sup>-2</sup>. Even if these sites lost carbon to the atmosphere the measurements are only

taken during one season and general conclusions for windthrows in Russia are difficult to draw from this limited data.

### **North America**

Fires are common and severe in North America as well as important to their forests' carbon balance. Reported estimated direct emissions range from 15 Mt C yr<sup>-1</sup> to 45.7 Mt C yr<sup>-1</sup> and the methods used vary. The indirect emissions are measured with eddy covariance technique but they are difficult to compare from articles since they are reported differently (integrated, maximum or selected values). Annual areal extent of fires in North America is more certain since long term records are available.

Insect outbreaks are another major concern and the reported outbreaks are well monitored. Areal extent has been recorded for a long time, and measurements and modeling of NEP have been made for the mountain pine beetle outbreak in British Columbia. These measurements showed that the attacked stands were carbon sources a couple of years after the attack. The modeled release of carbon during the outbreak period was estimated to 270 Mt C during 20 years which is equivalent to a release of 36 g C m<sup>-2</sup> yr<sup>-1</sup> in the affected area. This modeled annual average was not so far from the measured values using eddy covariance technique. However, the measured values were taken before the majority of killed trees had started to fall and larger respiratory releases were expected at these sites. On account of the time lag between insect attack and peak of respiratory release from decomposition, measurements of insect outbreaks should be carried out for several years or through the use of chronosequences in order to fully account for all the carbon lost because of an insect attack. In the case of defoliating insects like the spruce budworm, their effect on the carbon balance may be a bit different than the effect of mountain pine beetle since the trees may survive the attack. No eddy covariance measurements taken within the boreal region are available. However, spruce budworm outbreaks are able to convert forests into carbon sources.

Data on windthrow are scarce from North America within the literature reviewed. No data was found concerning extent over the whole area, nor any estimation of emissions connected to windthrow disturbance.

### **Fennoscandia**

Fire seems to be of little consequence in the extensively managed forests of Fennoscandia as a consequence of effective fire suppression. No estimations of direct or indirect emissions connected to fires have been reviewed.

Insect outbreaks of the European spruce bark beetle are important disturbances often connected with windthrows. However, the average annual areal extent could not be found for the whole region and measurements of the CO<sub>2</sub> emissions are yet to be recorded. Future increased populations of European spruce bark beetle in Sweden have been projected and may have



negative consequences for the carbon balance but it should also be combined with data of how much carbon that might be lost.

Windthrow is an important natural disturbance in Sweden. The damage caused by severe storms has increased during the last decades even though the wind climate has been rather steady. The reason for this may be many and some of those mentioned are plausible. The effect of windthrow on the carbon balance was measured the first year after a severe storm in Sweden 2005. The results showed a very large release of carbon from the ecosystem in the range of 897 to 1259 g C m<sup>-2</sup> that year. Compared to other results from other disturbances and other regions the carbon flux is very large. However, the studies from Russia only reported the release during the summer months. Extrapolated for the whole windthrow area these emissions from the Swedish windthrows amounted to a release of 3 Mt C during the first year after the storm.

One problem with the review of Fennoscandia is that almost all of the data are collected within Sweden. No data have been reviewed that concentrate on natural disturbance in Norwegian forests except for fire, which is considered to be of small consequence. Very little data have been reviewed concerning the Finnish forests.

Each individual type of disturbance is driven partly by climatic parameters. Because of this, it is likely that a changing climate will affect the disturbance regimes. This was the initial question that was asked during the planning for this literature study and in the end the answer is that an effect can already be seen. What the future might bring is always uncertain, but projections do tell us that the effect of natural disturbance may indeed become even more important. Fires are expected to increase both in frequency and severity. Insects are projected to expand their range and possibly produce more generations per year. Windthrows may become more damaging if trees grow into susceptible sizes faster than before and if management strategies are not adapted accordingly. Projections of future storms are still inconclusive but if they were to increase in severity and/or frequency, windthrows may become even more important. Evidently natural disturbance is a potential positive feedback within the climate system.

How the boreal forests may behave in the future is not only due to the changed disturbance regimes. There might be gains in the form of warmer temperatures, CO<sub>2</sub> fertilization, more nutrients due to higher mineralization rates etc. Increased forest productivity is projected and this gives a higher NPP which is one parameter in the NBP equation. On the other hand, a temperature increase may cause disequilibrium between species range and favorable conditions that in turn may affect tree vitality negatively and thus the trees may become more susceptible to disturbance.

There are important interactions between the different kinds of natural disturbances mentioned in this review. Some interactions work to exacerbate the disturbance, such as the European spruce bark beetle attack on windthrow or the possible connection between fire and mountain pine beetle suggested. Others might work to prevent each other, such as fire suppressing insect attacks

by spruce bark beetle. Interactions are important to understand in order to predict disturbance behavior and perhaps the carbon balance may behave differently if two disturbances interact to release carbon.

The NBP of ecosystems is supposedly the long term carbon balance as it includes the effect of disturbance. This balance would in a stable environment become near zero, that is not the case today as it is still positive in the boreal region. That is, our boreal forests are still acting to partly smooth over our release of fossil carbon to the atmosphere. The question is whether this will continue, or if the forests may transform into carbon sources, adding to the anthropogenic emissions of CO<sub>2</sub> in our near future. A net release of CO<sub>2</sub> from boreal forests is already occurring in Canada at present and other boreal forests throughout the boreal region might follow. Overall the NBP is still positive and help to mitigate the high concentrations of CO<sub>2</sub> in the atmosphere.

If one were to try solving the NBP equation in the boreal region one would need not only an estimate of the NEP but also sufficient data on the areal extent of each disturbance as well as the carbon balance behavior during some years after the disturbance within a particular kind of forest. It is evident that some factors of this equation are missing. The areal extent should be easy enough to explore using remote sensing, but even so the reported annual area burned in Russia have increased substantially during the last decade. Whether this is because of differences in reporting and monitoring or increased area burned is not clear. As to the carbon balance response to disturbance it is evident that it differs from place to place and between different disturbances. Also, carbon emission measurements are yet to be made for insect outbreaks in Fennoscandia, data on windthrow effect and areal extent are missing from North America, and the extent of measurements both spatially and temporally are somewhat lacking in Russia. The effect of partial disturbance should also be studied since not all disturbance events are stand replacing. Additionally, the effect of drought may be another important factor, although not covered in this review.

## 4 Conclusion

The NBP equation for the entire boreal forest still misses important components in order to fully describe the long term carbon balance. Future projections are worrisome since they are indicating that natural disturbances may become more severe and frequent in a future climate. If they do they may enhance the level of CO<sub>2</sub> in the atmosphere and have thus become a positive feedback between the boreal forest and the climate system. If natural disturbances increase in severity and/or frequency in the boreal forest one of the Earth's most important sinks of CO<sub>2</sub> may become a source in itself. Perhaps this is not likely over the entire boreal forest in an immediate future but a lessened sink potential could be enough to aggravate the levels of CO<sub>2</sub> in the atmosphere. Processes governing the carbon cycle are well understood, models are available and measurement techniques to estimate fluxes of CO<sub>2</sub> are in use, thus all the ingredients needed for a good understanding of the effect of natural disturbance already exist. However, it seems that more data is needed with better spatial and temporal coverage to fully quantify the importance of natural disturbance on the carbon balance of boreal forests.

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