

Climatic Change (2008) 87:91–106
DOI 10.1007/s10584-007-9340-6

Impact of non-outbreak insect damage on vegetation in northern Europe will be greater than expected during a changing climate

Annett Wolf • Mikhail V. Kozlov • Terry V. Callaghan

Received: 6 July 2006 / Accepted: 3 October 2007 / Published online: 16 November 2007
© Springer Science + Business Media B.V. 2007

Abstract Background insect herbivory, in addition to insect outbreaks, can have an important long term influence on the performance of tree species. Since a projected warmer climate may favour insect herbivores, we use a dynamic ecosystem model to investigate the impacts of background herbivory on vegetation growth and productivity, as well as distribution and associated changes in terrestrial ecosystems of northern Europe. We used the GUESS ecosystem modelling framework and a simple linear model for including the leaf area loss of *Betula pubescens* in relation to mean July temperature. We tested the sensitivity of the responses of the simulated ecosystems to different, but realistic, degrees of insect damage. Predicted temperature increases are likely to enhance the potential insect impacts on vegetation. The impacts are strongest in the eastern areas, where potential insect damage to *B. pubescens* can increase by 4–5%. The increase in insect damage to *B. pubescens* results in a reduction of total birch leaf area (LAI), total birch biomass and birch productivity (Net Primary Production). This effect is stronger than the insect damage to leaf area alone would suggest, due to its second order effect on the competition between tree species. The model's demonstration that background herbivory may cause changes in vegetation structure suggests that insect damage, generally neglected by vegetation models,

A. Wolf (✉)
Forest Ecology, Universitätstrasse 16, ETH-Zentrum,
CHN, G 77, CH-8092 Zürich, Switzerland
e-mail: annett.wolf@env.ethz.ch

M. V. Kozlov
Section of Ecology, University of Turku,
20014 Turku, Finland

T. V. Callaghan
Abisko Scientific Research Station,
SE-981 07 Abisko, Sweden

T. V. Callaghan
Department of Animal and Plant Sciences,
University of Sheffield, Sheffield S10 2TN, UK

can change predictions of future forest composition. Carbon fluxes and albedo are only slightly influenced by background insect herbivory, indicating that background insect damage is of minor importance for estimating the feedback of terrestrial ecosystems to climate change.

1 Introduction

Insect herbivores play important roles in terrestrial ecosystems, especially forests. Mass outbreaks of insects and their devastating impact on vegetation are well documented (Hogg 1999; Malmström and Raffa 1999; Neuvonen et al. 2001; Tenow et al. 2001; Logan et al. 2003; Wager and Baker 2003; Wermelinger 2004), and possible effects of climatic change on forest pests are considered in several phenomenological models (Kittel et al. 2000; Price et al. 2001; Clein et al. 2002; Logan et al. 2003). However, little is known about background insect damage (sometimes termed endemic herbivory) and its importance for vegetation (Schowalter et al. 1986). The few available estimates of the amount of foliage routinely removed by insect herbivores (not accounting for the loss of biomass due to sap feeders) vary between 2–16% for trees (Bray 1964; Gosz et al. 1972; Whittaker and Woodwell 1968) and less than 1% for dwarf shrubs in the sub-Arctic (Richardson et al. 2002). Although these figures suggest minor importance, even slight damage of top-canopy plants allows more light to reach the ground, reducing competition for light and potentially leading to changes in composition of plant communities (Schowalter et al. 1986; Blatt et al. 2005).

Climate change is expected to have strong impacts, both direct and indirect, on insect herbivores. Changes in temperature in temperate regions influence the winter survival of insects, including the principal outbreaking pest of northern birch forests, the autumnal moth *Epirrita autumnata* (Virtanen and Neuvonen 1999); at more northerly latitudes, the thermal budget influences growth and reproduction of insects (Bale et al. 2002). For the outbreak species, *E. autumnata*, the frequency of outbreak might not change in a future warmer climate, but many areas, which are presently protected by low winter temperatures, will be susceptible to outbreaks (Virtanen et al. 1998). Increasing CO₂ and UV-B change the palatability and digestibility of leaves (Dury et al. 1998; Lavola et al. 1998; Buck and Callaghan 1999; Johns and Hughes 2002; Hamilton et al. 2004; Julkunen-Tiitto et al. 2005; Knepp et al. 2005), whereas simultaneous increases in both temperature and CO₂ are likely to have smaller effects on herbivory than predicted from studies involving each of these factors alone (Zvereva and Kozlov 2006). Still, there is no doubt that climate change will modify the population dynamics of insect herbivores and hence their impact on vegetation. Moreover, many insects are good dispersers, and there is a growing pool of evidence that recent changes in climate have resulted in a northward spread of insects in Europe (Parmesan et al. 1999; Conrad et al. 2004); therefore northern forests are likely to suffer from an additional increased herbivory due to their exposure to new pests arriving from more southern regions.

The importance of climate change on background herbivory is usually not considered in studies of climate change impacts on ecosystems. However, in a study of latitudinal gradients of background insect herbivory, Kozlov (this issue) found a strong correlation of insect damage with mean July temperature for *Betula pubescens* in northern Europe. Kozlov (this issue) estimated that the insect damage to *B. pubescens* leaves in Scandinavia will increase by 0.91% for 1° increase in mean July temperature.

There is agreement that it is important to consider outbreaks of herbivorous insects when modelling arctic–boreal vegetation dynamics (Kittel et al. 2000; Price et al. 2001; Clein et al. 2002; Logan et al. 2003) but still, only few models are available that emphasise, for example, the importance of insect outbreaks for carbon fluxes and storage (Kurz and Apps 1999), tree growth variations (Pothier et al. 2005) and vegetation distribution in the transition zone between forest and tundra (Starfield and Chapin 1996). However, we are not aware of any ecosystem model that considers background herbivory, and this gap in knowledge decreases reliability of the predicted vegetation structure and productivity.

In this study, we use a dynamic ecosystem model (GUESS) to investigate whether expected changes in background herbivory have detectable impacts on birch biomass and productivity, and subsequently influence vegetation structure and several ecosystem parameters such as carbon fluxes and albedo.

2 Materials and methods

2.1 The ecosystem model

We used the GUESS (General Ecosystem Simulator; Smith et al. 2001), which combines the mechanistic representation of plant physiological and biogeochemical processes of the LPJ-DGVM (Lund-Potsdam-Jena dynamic global vegetation model, Sitch et al. 2003) with detailed representation of vegetation dynamic processes (Smith et al. 2001). The growth of cohorts of plant functional types (PFTs) is simulated in a number of replicated patches. The cohorts possess different dynamics, depending on their characteristics (e.g. biomass, age, height) and the influence of the other vegetation in the gridcell (e.g. light extinction by vegetation growing above the cohort). Thus the floristic composition of each grid cell was unique and grid cells were spatially independent of each other. The PFTs are either trees or herbaceous (non-woody) vegetation and are characterised by a number of parameters controlling establishment, growth, metabolic rates and the limits of the climate space that the PFT can occupy. The version of the model and parameterisation used in this study are described in Wolf et al. (this issue) who modified the model to better represent northern plant functional types.

2.2 Specifications

We used two different tree PFTs: boreal needle leafed evergreen trees, which represents Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) in our study region; shade intolerant deciduous trees, which represents *Betula pendula* Roth. and *B. pubescens* Ehrh.

The background damage for Scots pine and Norway spruce in our study region is negligible (Kozlov pers. obs. and P. Niemelä pers. comm.) and it is therefore not considered in the model runs. For *B. pubescens*, we used the empirical relationship between the total loss of leaf area ($Loss_{LA}$) dependent on mean July temperature (T_{July}) as found in a field study of foliar damage along transects in Finland and Karelia: $Loss_{LA} = b_1 + b_2 \times T_{July}$, ($R^2=0.42$, $b_1=-11.05 \pm 2.16$, $b_2=0.91 \pm 0.14$, Kozlov this issue). We assumed that these estimations are valid for the entire modelling region, which is larger than the area actually surveyed for insect damage. The estimations are only dependent on mean July temperature and do not consider the amount of *B. pubescens* in the gridcell.

To test the sensitivity of the model, we varied the parameters b_1 and b_2 (Table 1), which resulted in different strengths of insect impact. The parameters were varied to cover a broad range of different responses, but not exceeding the observed values of insect damage. As a control, we used the model simulation without any insect damage, as this is used as a standard assumption in ecosystem models. In the model simulations, each year, the amount of leaf of a PFT was reduced by the proportion damaged by the insects.

2.3 Climate and CO₂ data

The model is driven by monthly averages of temperature, precipitation, percentage of sunshine hours, annual atmospheric CO₂ concentration and soil type, the latter derived from the FAO global soil data set (FAO 1991).

For the 1,000 year spin-up and the historical period 1901–1960, we used the Global Climate Dataset from the Climate Research Unit (CRU), which gridded monthly surface climate variables for the period 1901–2000 (http://ipcc-ddc.cru.uea.ac.uk/obs/cru_climatologies.html). The CRU data point closest in distance (in longitude-latitude degrees) to the REMO-grid point (see below) was used to derive driving data for the spin-up and 1901–1960 periods. For the period 1961–2099, we used the output data from the regional climate model REMO (Jacob 2001) with a 0.5 degree resolution driven by ECHAM4 data (Roeckner et al. 1996) as a boundary condition. The Barents Sea was laid in the centre of the regional climate model, using the grid cell coordinates from the REMO model. The climate prediction for 1961–2099 was based on the SRES-B2-CO₂ scenario (IPCC 2001).

Global atmospheric CO₂ concentrations derived from ice-core measurements and atmospheric observations (c.f. Sitch et al. 2003) were used for the 1901–2000 period. The CO₂ concentration for the future projection is based on the SRES-B2-CO₂ scenario

Table 1 Potential leaf area loss (LA_{loss}, percent) of birch trees due to insect damage in four time periods

		Parameters		Potential leaf area loss (%)			
		b_1	b_2	1981–2000	2011–2030	2041–2060	2071–2090
Russia	Simulation 1	-11.05	1.82	13.2	17.9	19.0	19.7
	Simulation 2	-6.73	1.19	9.2	12.2	12.9	13.4
	Simulation 3	-5.53	0.91	6.6	8.9	9.5	9.8
	Simulation 4	-8.89	1.05	5.1	7.8	8.5	8.8
	Simulation 5	-11.05	0.91	1.4	3.5	4.1	4.4
	Simulation 6	-13.21	0.77	0.0 [#]	0.1	0.3	0.4
	control	No damage			0.0 [#]	0.0 [#]	0.0 [#]
Scandes	Simulation 1	-11.05	1.82	9.4	10.4	12.4	12.7
	Simulation 2	-6.73	1.19	6.7	7.3	8.6	8.8
	Simulation 3	-5.53	0.91	4.7	5.2	6.2	6.3
	Simulation 4	-8.89	1.05	2.9	3.5	4.6	4.8
	Simulation 5	-11.05	0.91	0.2	0.4	0.9	1.1
	Simulation 6	-13.21	0.77	0.0 [#]	0.0	0.0	0.0
	Control	No damage			0.0 [#]	0.0 [#]	0.0 [#]

The damage is calculated from expected mean July temperature (T_{July}) according to the REMO climate model. $LA_{\text{loss}} = b_1 + b_2 \times T_{\text{July}}$ where b_1 and b_2 are presented in the table. In order to test the sensitivity of the outputs, we varied b_1 and b_2 in six simulations. For all years and all simulations, Russia has a significantly higher potential damage than the Scandes ($p < 0.001$): the only exception is marked with [#], where there is no significant difference.

(IPCC 2001). For the spin-up period we used a constant CO₂ concentration of 296 ppmv (the concentration in 1901).

2.4 The focal areas

We have chosen two study areas, each currently forested by *B. pubescens* (Bohn et al. 2004). One area is situated in northern Russia and one in the Scandes mountains of northern Sweden and Norway (Fig. 1), each about 2.2×10^5 km². The two focal areas differ in their predicted climates: mean July temperatures are expected to increase by 3.5°C (from 13.4 in 1981–2000 to 16.9 by the 2071–2090) in the Russian study area, but only by 1.7°C (from 11.3 in 1981–2000 to 13.0 in 2071–2090) in the Scandes.

2.5 Albedo estimation

As we did not find albedo measurements for the Barents region, we used various methods to estimate changes in albedo. Model estimations of fractional projected cover were used as a measure of what fraction of the gridcell was covered by the different PFTs, and the rest of the gridcell was assumed to be bare ground. Albedo values for vegetation were taken from

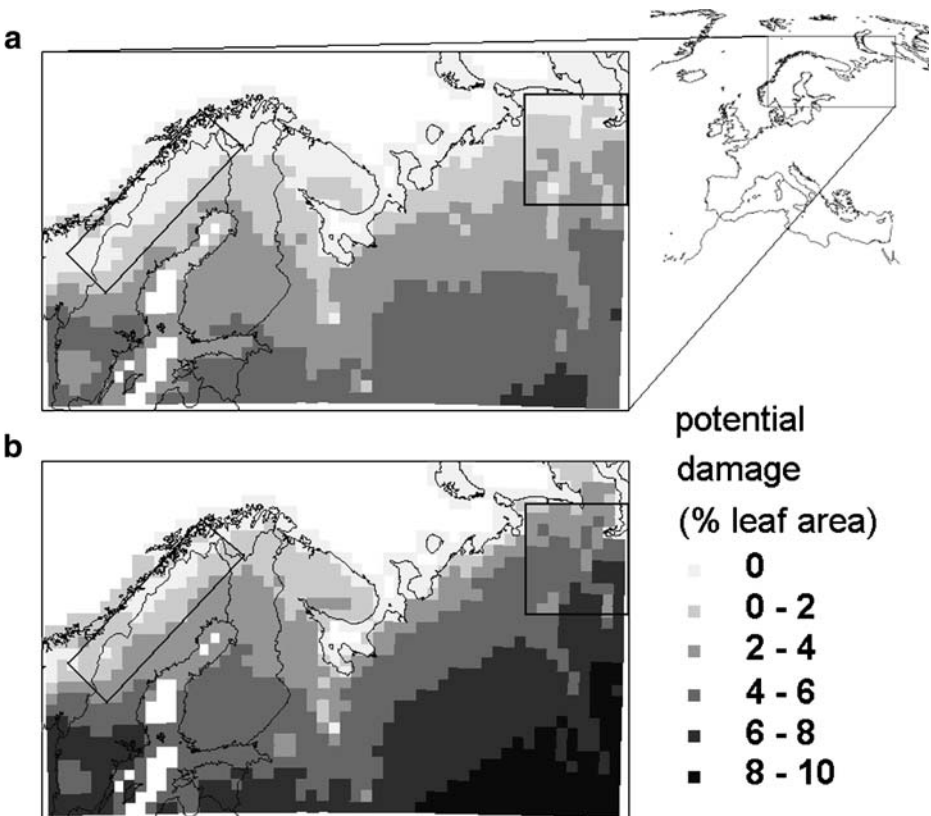


Fig. 1 Potential insect damage to *Betula pubescens* according to estimates from mean July temperatures (T_{July}): leaf area loss (%) (estimates from Kozlov [this issue](#)). The average reduction in leaf area is presented for **a** 1981–2000, **b** 2071–2090. The two outlined regions are the focal areas (see text)

data on boreal forests (Betts and Ball 1997) as follows: average summer albedo for spruce/poplar mixed forest=0.081, for aspen=0.156 and for grass=0.197; average winter albedo for spruce/poplar mixed forest=0.108, for aspen=0.150 and for grass=0.75. Average summer albedo of bare ground was estimated as 0.19 (Oguntunde and van de Giesen 2004) and average winter albedo as 0.75 (taken from data on snow-covered grass from Betts and Ball 1997). As an alternative estimate of albedo, we used values from the Biosphere-Atmosphere-Transfer Scheme (BATS, Version 1e) as follows: wavelengths <0.7 μm for evergreen needle leaf trees=0.05, deciduous broadleaf trees=0.08, tundra=0.10 and semi-desert (equivalent to bare ground)=0.17. For wavelengths >0.7 μm the values were 0.23, 0.28, 0.30 and 0.34 respectively. To calculate the total albedo of a gridcell, we weighted these albedo estimates by the fractional cover of each PFT.

2.6 Statistical analyses

Mean values of leaf area loss, LAI (Leaf Area Index, m^2 leaf area per m^2 ground) and birch biomass were calculated for four time periods: 1981–2000, 2011–2030, 2041–2060 and 2071–2090 (Tables 1, 2 and 3) and used for the analyses.

The significance of the correlation between the output variables and the degree of insect damage was tested using the Spearman rank correlation as the assumption of a normal distribution was not fulfilled. We used the relative change compared to the control run with no insect damage and analysed each time slice and each focal area (Russia: 90 gridcells, Scandes: 88 gridcells; 6 simulations for each focal area) separately. In the figures, we present the average values for each simulation.

To test for the difference between the two focal areas, we used a General Linear Model (GLM) of biomass change by insect damage and focal area, in order to account for the variation already explained by the amount of insect damage.

The change in PFT distribution was calculated as the difference in the proportion of gridcells that predicted a different dominant PFT in the simulation compared to the control run for the year 2080. This was correlated with the potential insect damage for each simulation, whereby we combined the results for both areas and the six simulations ($N=12$).

We also calculated the change in birch biomass (or NPP) from 1981–2000 to each of the time slices (2011–2030, 2041–2060, 2071–2090) for the control run and for simulation 1. We then used the non-parametric, paired Wilcoxon Signed Ranks Test to check whether the increase in biomass (or NPP) differed between the simulation with and without insect damage.

3 Results

3.1 Potential impact of insects

In agreement with the field-collected data (Kozlov [this issue](#)) and for the recent climate, our model demonstrated a clear geographical pattern in the potential amount of foliar damage to *B. pubescens* (Fig. 1), with a decrease of insect impact towards the north and higher up in the mountains. The model that uses empirically estimated parameters (Simulation 5, Table 1) for the future warmer climate predicts similar geographical gradients, although with higher absolute values of foliar losses (Fig. 1). The predicted changes are strongest in the eastern areas, where insect damage on *B. pubescens* can increase by 4–5%.

Table 2 Average projected LAI for birch (leaf area index: m² leaf area per m² ground) under varying levels of background herbivory

		LAI (m ² *m ⁻²)			
		1981–2000	2011–2030	2041–2060	2071–2090
Russia	Simulation 1	0.68 (-31.7)****	0.79 (-38.4)****	1.08 (-35.1)****	0.84 (-36.9)****
	Simulation 2	0.74 (-25.8)****	0.91 (-29.8)****	1.27 (-24.0)****	1.00 (-24.7)****
	Simulation 3	0.82 (-17.0)****	1.05 (-18.6)****	1.46 (-12.5)****	1.16 (-12.4)****
	Simulation 4	0.83 (-16.3)****	1.03 (-19.9)****	1.40 (-15.9)****	1.11 (-16.2)****
	Simulation 5	0.91 (-7.9)****	1.14 (-11.5)****	1.56 (-6.7)****	1.25 (-6.1)****
	Simulation 6	0.97 (-2.5) ^{ns}	1.24 (-3.9)***	1.67 (0.1) ^{ns}	1.36 (2.6) ^{ns}
	control	0.99	1.29	1.67	1.33
Scandes	Simulation 1	0.91 (-24.7)****	1.08 (-25.6)****	1.21 (-26.9)****	0.97 (-29.7)****
	Simulation 2	1.00 (-17.5)****	1.20 (-17.3)****	1.33 (-19.3)****	1.07 (-21.8)****
	Simulation 3	1.07 (-11.7)****	1.31 (-9.7)****	1.48 (-10.2)****	1.22 (-11.6)****
	Simulation 4	1.09 (-10.2)****	1.31 (-9.8)****	1.46 (-11.2)****	1.20 (-12.5)****
	Simulation 5	1.19 (-1.8) ^{ns}	1.46 (0.3) ^{ns}	1.61 (-2.3)*	1.34 (-2.6)**
	Simulation 6	1.20 (-1.5) ^{ns}	1.46 (0.2) ^{ns}	1.63 (-1.1) ^{ns}	1.38 (0.5) ^{ns}
	control	1.22	1.45	1.65	1.37

In parenthesis: change of LAI compared to no insect damage (%). Significant values indicate difference in LAI compared to control run without insect damage. *ns* not significant; * *p*<0.1; ** *p*<0.05; *** *p*<0.01 **** *p*<0.001

The prediction of background damage differed for the two areas (Fig. 1, Table 1). The reduction in leaf area increases from 1 to 4% in the next 100 years in northern Russia, when we used the parameters estimate by Kozlov ([this issue](#)) (Simulation 5, Table 1). In the Scandes, the damage is lower, reaching up to 1% by the end of this century (Table 1). For the most extreme parameterisation of the dependence of insect damage on mean July

Table 3 Biomass of birch (kg C*m⁻²) projected for varying degrees of background herbivory

		Biomass of birch (kg C*m ⁻²)			
		1981–2000	2011–2030	2041–2060	2071–2090
Russia	Simulation 1	1.7 (-20.4)****	2.1 (-23.2)****	3.0 (-22.6)****	3.3 (-21.2)****
	Simulation 2	1.7 (-18.0)****	2.2 (-18.2)****	3.3 (-14.2)****	3.7 (-13.2)****
	Simulation 3	1.9 (-10.46)****	2.3 (-13.0)****	3.5 (-9.2)****	3.9 (-7.5)****
	Simulation 4	1.8 (-11.3)****	2.3 (-12.8)****	3.5 (-9.2)****	4.0 (-6.3)**
	Simulation 5	2.0 (-2.8) ^{ns}	2.4 (-9.0)****	3.6 (-5.0)**	4.1 (-1.5) ^{ns}
	Simulation 6	2.0 (-2.3) ^{ns}	2.6 (-2.7) ^{ns}	3.9 (2.2) ^{ns}	4.5 (7.1)**
	control	2.1	2.7	3.8	4.2
Scandes	Simulation 1	2.3 (-14.8)****	2.9 (-13.8)****	3.6 (-13.8)****	3.6 (-17.2)****
	Simulation 2	2.4 (-12.1)****	3.1 (-9.1)****	3.9 (-8.2)****	3.9 (-10.8)****
	Simulation 3	2.5 (-8.3)****	3.2 (-5.3)****	4.0 (-4.0)**	4.2 (-3.9) ^{ns}
	Simulation 4	2.5 (-7.4)****	3.2 (-6.9)****	4.0 (-5.8)****	4.1 (-5.5)****
	Simulation 5	2.6 (-3.9)*	3.4 (-1.6) ^{ns}	4.2 (0.4) ^{ns}	4.4 (1.2) ^{ns}
	Simulation 6	2.8 (-2.8) ^{ns}	3.5 (-1.6) ^{ns}	4.2 (-1.4) ^{ns}	4.4 (1.0) ^{ns}
	control	2.7	3.4	4.2	4.3

In parenthesis: change in biomass compared to no insect damage (%). Significant values indicate difference in biomass compared to control run without insect damage. *ns* not significant; * *p*<0.1; ** *p*<0.05; *** *p*<0.01; **** *p*<0.001

temperature (Simulation 1), the potential reduction in leaf area reaches 20% in northern Russia and 13% in the Scandes (Table 1).

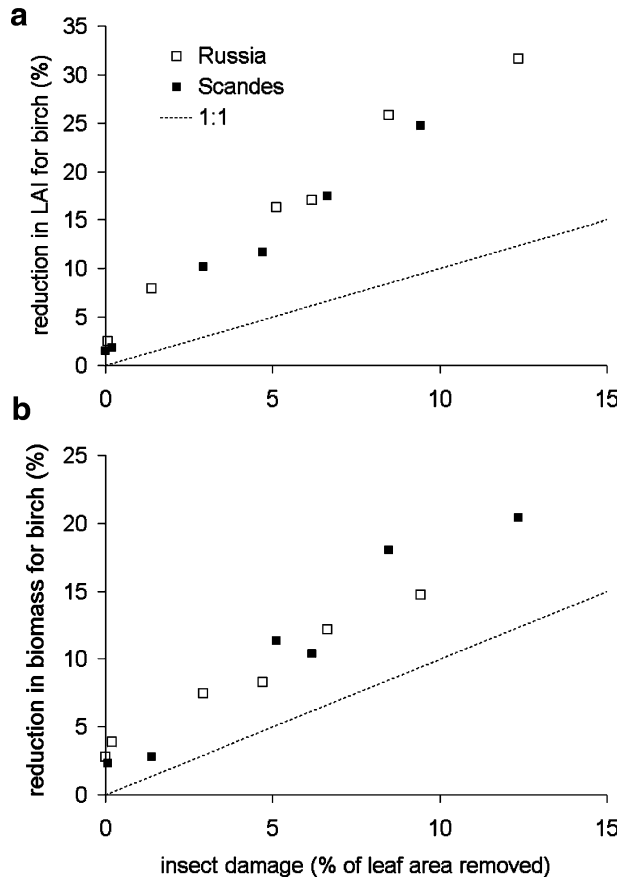
3.2 LAI

As expected, LAI for birch strongly declined with increase in the potential removal of leaf area (Russia: $r=-0.59$; $p<0.001$, Scandes: $r=-0.52$, $p<0.001$, in the 1981–2000 period). However, the modelled reduction in LAI is much greater than the consumption of leaves by insects (Table 2). If the reduction in leaf area could be explained simply by the amount removed by insects, the plot of predicted LAI values against potential leaf area consumed should be found on the 1:1 line. Instead, the reduction in LAI is about 2–3 times greater than expected in 1981–2000, and similar differences occur at other time periods (Fig. 2).

3.3 Biomass

The modelled change in birch biomass (total biomass, including roots, stems and leaves in $\text{kg C}\cdot\text{m}^{-2}$) significantly correlated with the potential leaf consumption by insects (Fig. 2, Russia: $r=-0.40$, $p<0.001$, Scandes: $r=-0.31$, $p<0.001$, in 1981–2000). Similar to LAI

Fig. 2 Reduction in **a** leaf area index (LAI), and **b** biomass of birch in relation to insect damage for the period 1981–2000 estimated with the control run (no insect damage) as reference. Each point represents the average value of one simulation (parameters in Table 1.)



reduction, losses in birch biomass are around 1.8 greater than the removal of foliage by insect herbivores. When we accounted for the change in biomass due to insect damage, the increase in birch biomass in the Scandes was significantly smaller than in Russia for 1981–2000 (GLM of biomass change by insect damage and focal area, focal area: $p=0.013$), but not in other time periods (effect of focal area: $p>0.1$).

The change in total plant biomass of the ecosystem is also weakly correlated with insect damage in Russia ($r=-0.11$, $p=0.01$, for 1981–2000), but not in the Scandes ($r=-0.04$, $p=0.34$, for 1981–2000). However, the mean reduction in total biomass for Russia is on average only 2%, hence of minor importance (data not shown).

The biomass of boreal conifers increases when birch biomass decreases (Fig. 3) and hence compensates for the loss in birch biomass. There is a significant correlation between the change of biomass in shade-intolerant broad leafed trees and change of biomass in needle leafed evergreen trees (Russia: $r=-0.24$ $p=0.001$, Scandes $r=-0.33$ $p<0.001$, for 1981–2000).

Birch biomass in the study region is expected to increase with time, as the climate becomes warmer (Fig. 4). However, when insect damage is taken into account, the increase in biomass is significantly lower compared to the control run. This difference is significant for all time slices for Russia (Wilcoxon Signed Ranks Test: 2011–2030: $Z=-4.0$, $p<0.001$, 2041–2060: $Z=-4.1$, $p<0.001$, 2071–2090: $Z=-3.7$, $p<0.001$). For the Scandes, the effect of insects become stronger in the warmer future climate and is only significant at the last time slice (2011–2030: $Z=-1.4$, $p=0.16$, 2041–2060: $Z=-1.4$, $p=0.16$, 2071–2090: $Z=-2.0$, $p=0.039$).

3.4 PFT distribution

The changes in biomass (reported above) resulted in changes in the distribution of forest types: 6–16% of the gridcells had a different dominant tree species in 2080 when insect

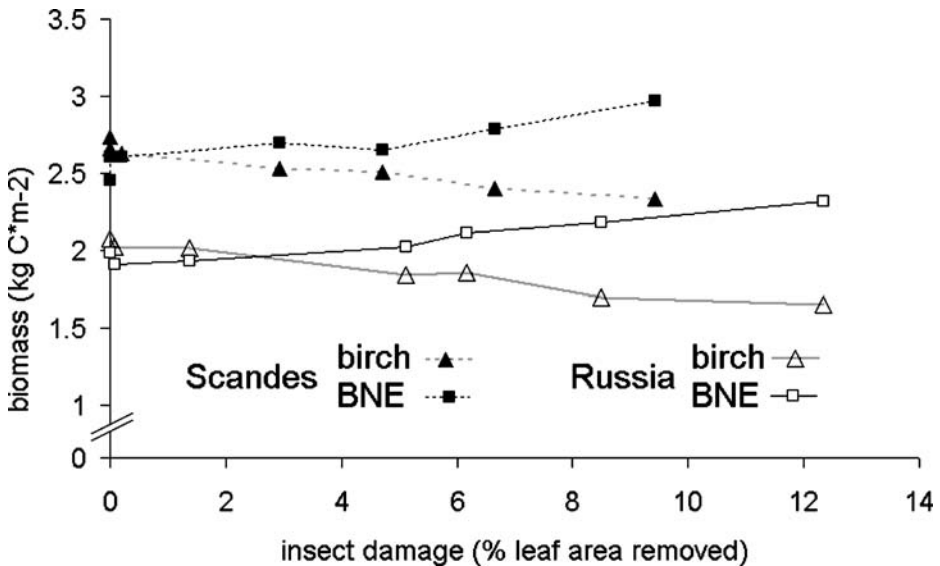
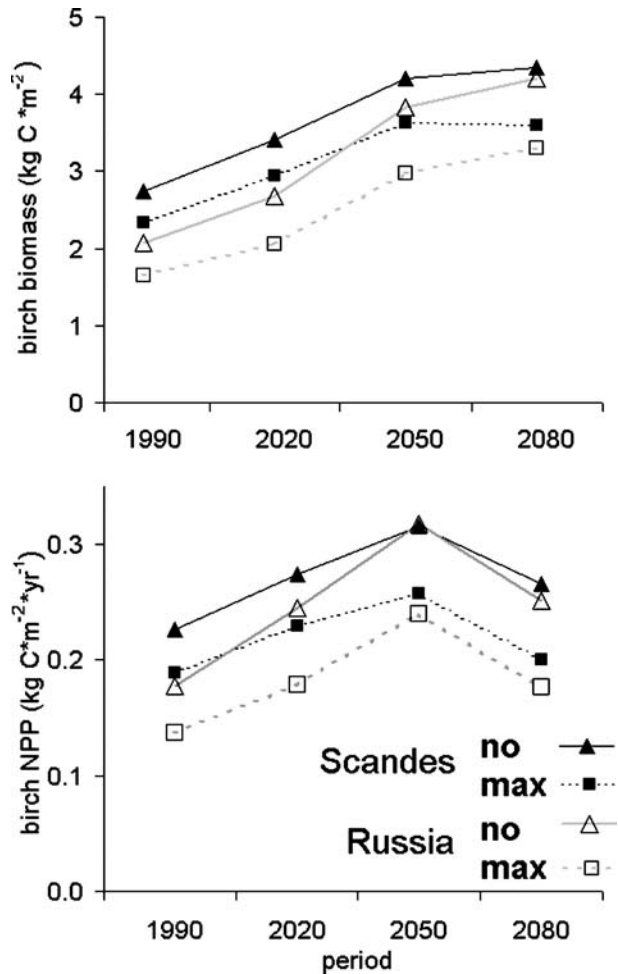


Fig. 3 Importance of insect removal of biomass on the biomass of the different PFTs. *Black symbols*: Scandes, *open symbols*: Russia. *Triangle*: IBS (shade-intolerant broad leafed deciduous tree), *square*: BNE (boreal needle leafed evergreen trees). The values are for the 1981–2000 period

Fig. 4 Change in birch biomass and NPP over four time periods. The biomass is predicted for maximum insect damage (dotted lines, Table 1, Simulation 1) compared to no insect damage (solid line) for the two study regions. Grey lines: Russia, black lines: Scandes



damage was included, compared to the run where no insect damage was considered. Furthermore, the stronger the insect damage, the greater the difference in dominant PFT ($r=0.79$, $p=0.002$). This clearly suggests that PFT distribution can be influenced by background herbivory.

3.5 NPP

Birch NPP decreased with increasing insect damage (Russia: $r=-0.49$, $p<0.001$, Scandes: $r=-0.40$, $p<0.001$, in 1981–2000, Fig. 4). Similar to the reduction of biomass, it is not only the removal of foliage which explains the loss in NPP, as NPP is reduced 1.6–1.7 times more than we would expect from the reduction in leaf biomass alone. Also similar to the biomass changes, effects of leaf consumption by insects increase in the future changing climate (Wilcoxon Signed Ranks Test, Russia 2011–2030, $Z=-5.7$, $p<0.001$, 2041–2050, $Z=-5.3$, $p<0.001$, 2071–2090: $Z=-4.8$, $p<0.001$, Scandes: 2011–2030, $Z=-1.7$, $p=0.091$, 2041–2050, $Z=-5.2$, $p=0.002$, 2071–2090: $Z=-3.6$, $p<0.001$). Hence, insect damage is predicted to reduce productivity more in a warmer future than today.

3.6 Carbon fluxes

At the ecosystem level, the vegetation uptake and soil respiration of carbon are significantly reduced only when the heaviest insect damage to birch is considered (Simulation 1). As the insect damage becomes stronger, the change in fluxes also becomes stronger (vegetation uptake, Russia: $r=-0.22$, $p<0.001$, Scandes: $r=-0.20$, $p<0.001$; soil respiration, Russia: $r=-0.24$, $p<0.001$, Scandes: $r=-0.33$, $p<0.001$). The simulated reduction of leaf area of 5–7% will, on average, only result in a 1–2% change in vegetation fluxes. This is mainly due to the improved growth of boreal conifers which take advantage of the reduced birch competition and compensate for the loss in biomass and productivity.

3.7 Albedo

Independently of the type of albedo estimations we used, the change in albedo is small, less than 2% on an average. For Russia and the Scandes, there is however, a significant decrease in albedo of wavelength $>0.7 \mu\text{m}$ with increasing insect damage (Table 4). Furthermore, the Scandes showed a decrease in winter albedo with increasing insect damage (Table 4), but none of the other estimations of albedo correlated with the increasing insect damage. The small and/or not significant responses might result from compensation of losses in birch leaf area by other plants, mainly conifers. Since differences in albedo between PFTs are relatively small, total albedo remains nearly the same.

4 Discussion

It is usually assumed that low levels of background herbivory do not affect biomass of trees (Schowalter et al. 1986, Kaitaniemi et al. 1999). However, our simulations clearly suggest that background defoliation even at a low level can change the biomass distribution of the affected plants in the longer term and alter the relative contributions of different plant types to the total biomass and productivity of an area.

The simulated defoliation, even in the worst insect defoliation scenario (simulation 1) and the warmest climate, did not exceed 20%. For the other simulations (2–6), the estimated herbivory does not exceed the recent range (2–16%) of background insect damage (Bray 1964; Gosz et al. 1972; Whittaker and Woodwell 1968), which is usually considered of low importance for ecosystem structure and functioning (Schowalter et al. 1986; Kaitaniemi et al. 1999). Nevertheless, the GUESS dynamic vegetation model, which simulates plant growth in response to their abiotic and biotic environments over the course of time, shows that the removal of even small amounts of leaves over many years results in

Table 4 Correlation of change in the amount of insect damage with the change in albedo for the different albedo estimates

	Russia	Scandes
Change in summer albedo	0.04 ^{ns}	-0.03 ^{ns}
Change in winter albedo	0.05 ^{ns}	-0.09 ^{**}
Change in albedo of wavelength $>0.7 \mu\text{m}$	-0.14 ^{***}	-0.11 ^{**}
Change in albedo of wavelength $<0.7 \mu\text{m}$	-0.04 ^{ns}	0.10 ^{ns}

ns not significant; * $p<0.1$; ** $p<0.05$; *** $p<0.01$; **** $p<0.001$

an accumulated effect on the performance and competitiveness of *B. pubescens*. The model also shows that even low levels of background insect damage can change PFT composition in the future.

The effects of background leaf herbivory on total birch biomass or LAI are greater than expected from the loss of leaf biomass alone. In our model runs, the biomass of boreal needle leaf trees increases when the birch biomass decreases, and hence compensates for the loss in birch biomass. This replacement is not simply explained by the successional advantage that spruce has over birch. As we run all simulations with the same climate input data, any difference between the runs is totally attributed to the amount of insect damage. So, a small increase in background damage of birch can turn birch-dominated forest into coniferous forest in a longer time perspective. This is in agreement with studies on abandoned fields (Blatt et al. 2005) and the review by Schowalter et al. (1986) that herbivory of susceptible tree species accelerates changes in forest structure and community development.

Although low levels of background herbivory have the potential to change PFT distribution and abundance, their effects on feedbacks from northern ecosystems to the climate system were small. Only projected increases in long wave albedo ($>0.7 \mu\text{m}$, BATS 1993) and winter albedo in the Scandes, although less than 2%, reached statistical significance. Similarly, fluxes of carbon were only significantly reduced in the simulation with high herbivory levels. The GUESS model is a state-of-the-art dynamic vegetation model that has performed well with modelling Swedish forest growth (Koca et al. 2006) and vegetation of the Barents Region (Wolf et al. [this issue](#)) but there are some uncertainties in the overall modelling process presented here.

We used only one emission scenario; however, it is one that assumes moderate changes in CO_2 emissions, and therefore the climate model has underestimated rather than overestimated the resulting climate change. We used results from only one climate model (REMO) and are aware that there is a range of predictions for future climate change. However, our conclusion on the importance of background insect damage would not have changed had we used another climate model, as the REMO model shows the generally accepted warming trend in arctic and subarctic regions.

Our estimates of the potential impact of insects are only dependent on mean July temperature and do not consider the amount of *B. pubescens* in the gridcell. Also, increasing CO_2 and UV-B change the palatability and digestibility of leaves (Fajer et al. 1989; Dury et al. 1998; Lavola et al. 1998; Buck and Callaghan 1999; Johns and Hughes 2002; Hamilton et al. 2004; Julkunen-Tiitto et al. 2005; Knepp et al. 2005) and might therefore counteract increased herbivory due to increased temperatures (Zvereva and Kozlov 2006). However, many of these studies are short term and do not consider the possible adaptation of insects to altered nutritional status of their host plants. Impacts on herbivory due to changes in plant tissue chemistry resulting from changes in CO_2 , UV-B and induced plant defenses are not considered within this modeling study. Furthermore, we do not account for any adaptation of trees to increase herbivory.

As regards parametrization of our model, the values provided by Kozlov ([this issue](#)) on the basis of the field data of 2004 may underestimate rather than overestimate the foliar losses: repeated sampling of *B. pubescens* in ten study sites between Murmansk and Luga demonstrated, that in 2005 an average loss of leaf area was three times higher than in 2004 (Kozlov [this issue](#)). Furthermore, our modelling results are valid not only for *B. pubescens*, but for the entire PFT, because foliar damage of another birch species, *B. pendula*, in 2005 was ca. 70% of the foliar damage observed in *B. pubescens*, and both species showed similar a geographical pattern along the Murmansk–Luga gradient.

Mammalian herbivores, not included in our model, can influence future PFT composition by selectively browsing on certain species (Smirnov and Sudnitsyna 2003; Weisberg and Bugmann 2003; Olofsson et al. 2004, Stolter et al. 2005). However, only 2% of total loss of birch leaves at Kevo in northern Finland was attributed to reindeer browsing, as most leaf loss was due to various leaf consuming insects (Haukioja and Koponen 1975). Nevertheless, interactions between browsing mammals and insects can have important effects on plant species distribution in a future warmer climate (Niemelä et al. 2001).

Periodic outbreaks of insect herbivores in the north of the study region are also not accounted for by our model. The distribution of *E. autumnata* populations, that sometimes cause complete defoliation of birches, is controlled by minimum winter temperatures in the north (Tenow and Nilsson 1990; Virtanen and Neuvonen 1999). Although this species is present further south, no outbreaks occur, mainly because of the controls by predation and parasitism (Ruohomäki et al. 2000; Tanhuanpää et al. 1999, 2003; Klemola et al. 2002). Assuming a return interval of severe outbreaks of about 60–70 years (Tenow et al. 2005), and that 100% of the leaves are removed, those severe outbreaks are more dramatic than low background damage in the short-term, but the latter might have a larger impact in the long-term. Tree mortality is expected to increase drastically due to repeated insect outbreaks in a future climate with fewer cold winters (Virtanen et al. 1998) and this could lead to step changes in forest composition (Chapin et al. 2004) rather than the gradual change resulting from climate change and increases in background herbivory modeled here. Also, background insect damage might lead to different predictions of the composition and restructuring of ecosystems in the transition zone between forest and tundra (Starfield and Chapin 1996). Other changes in biodiversity resulting from increased background herbivory are likely to arise, because the projected larger numbers of herbivores will increase food resources for insectivorous fish, birds and mammals which might lead to an increase in diversity. The long-term contribution of herbivory to stand productivity and heterogeneity will also influence habitat availability and therefore biodiversity (Schowalter et al. 1986; Ayres and Lombardero 2000).

5 Conclusions

To our knowledge, our ecosystem model is the first attempt to consider the impact of background herbivory on vegetation and its dependence on climatic change. This model clearly shows that, in a future warmer climate, background insect herbivory may increase over the Barents Region with wide ranging implications for productivity, forest composition and distribution, forest management, and biodiversity. Furthermore, consequences of background herbivory over the long term might well exceed impacts from the more frequently considered outbreaks of insect herbivores. We conclude that insect damage, both background and outbreak, should not be ignored in assessing responses of ecosystems to climate change, and that it should be included in vegetation modelling.

Acknowledgements The study was funded by the EC through the BALANCE project carried out under contract EVK2-2002-00169. We wish to thank colleagues from the LPJ-GUESS modelling group at Lund University for support and inspiring discussions. We thank Elena Zvereva for useful comments on the manuscript. We also thank Margareta Johansson for administrative help and Anders Lindroth and Torben Christensen who made it possible for A. Wolf to take part in the productive atmosphere of the GeoBiosphere Science Centre of Lund University. We also thank the staff from ANS for help and support and the REMO modelling group at the MPI in Hamburg for providing the climate data.

References

- Ayres MP, Lombardero MJ (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Sci Total Environ* 262:263–286
- Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, Butterfield J, Buse A, Coulson JC, Farrar J, Good JEG, Harrington R, Hartley S, Jones TH, Lindroth RL, Press MC, Symrnioudis I, Watt AD, Whittaker JB (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Glob Chang Biol* 8:1–16
- BATS (1993) Biosphere-Atmosphere-Transfer Scheme (BATS, Version 1e). Climate and global dynamics division. National Center for Atmospheric Research, Boulder Colorado
- Betts A, Ball JH (1997) Albedo over the boreal forest. *J Geophys Res* 102:28901–28909
- Blatt SE, Crowder A, Harmsen R (2005) Secondary succession in two South-eastern Ontario old-fields. *Plant Ecol* 177:25–41
- Bohn U, Gollub G, Hettwer C, Neuhauslova Z, Raus T, Schlüter H, Weber H (2004) Map of the natural vegetation of Europe (Karte der natürlichen Vegetation Europas). CD-ROM. Bundesamt für Naturschutz, Germany
- Bray JR (1964) Primary consumption in three forest canopies. *Ecology* 45:165–167
- Buck N, Callaghan TV (1999) The direct and indirect effects of enhanced UV-B on the moth caterpillar *Epirrita autumnata*. *Ecol Bull* 47:68–76
- Chapin FS III, Bergeron Y, Callaghan TV, Fukuda M, Johnstone JF, Juday G, Zimov SA (2004) Global change and the boreal forest: thresholds, shifting states or gradual change? *Ambio* 33:361–365
- Clein JS, McGuire AD, Zhang X, Kicklighter DW, Melillo JM, Wofsy SC, Jarvis PG, Massheder JM (2002) Historical and projected carbon balance of mature black spruce ecosystems across North America: the role of carbon–nitrogen interactions. *Plant Soil* 242:15–32
- Conrad KF, Woiwod IP, Parsons M, Fox R, Warren MS (2004) Long-term population trends in widespread British moths. *J Insect Conserv* 8:119–136
- Dury SJ, Good JEG, Perrins CM, Buse A, Kaye T (1998) The effects of increasing CO₂ and temperature on oak leaf palatability and the implications for herbivorous insects. *Glob Chang Biol* 4:55–61
- Fajer ED, Bowers MD, Bazzaz FA (1989) The effect of enriched carbon dioxide atmospheres on plant–insect herbivore interactions. *Science* 243:1198–1200
- FAO, and (Food_and_Agricultural_Organisation) (1991) The digitized soil map of the World (Release 1.0). FAO, Rome
- Gosz JR, Likens GE, Bormann FH (1972) Nutrient content of litter fall on the Hubbard Brook experimental forest, New Hampshire. *Ecology* 53:769–784
- Hamilton JG, Zangerl AR, Berenbaum MR, Phippen J, Aldea M, DeLucia EH (2004) Insect herbivory in an intact forest understory under experimental CO₂ enrichment. *Oecologia* 138:566–573
- Haukioja E, Koponen S (1975) Birch herbivores and herbivory at Kevo. In: Wielgolaski FE, Rosswall T (eds) Fennoscandian tundra ecosystems. Springer, Berlin, pp 181–188
- Hogg EH (1999) Simulation of inter-annual responses of trembling aspen stands to climatic variation and insect defoliation in western Canada. *Ecol Model* 114:175–193
- IPCC (2001) Climate change 2001: The scientific basis. Contribution working group I to the Third assessment report of the IPCC. Cambridge University Press, Cambridge
- Jacob D (2001) A note to the simulation of the annual and inter-annual variability of the water budget over the Baltic Sea drainage basin. *Meteorol Atmos Phys* 77:61–73
- Johns CV, Hughes L (2002) Interactive effects of elevated CO₂ and temperature on the leaf-miner *Dialectica scariella* Zeller (Lepidoptera: Gracillariidae) in Paterson's Curse, *Echium plantagineum* (Boraginaceae). *Glob Chang Biol* 8:142–152
- Julkunen-Tiitto R, Haggman H, Aphalo PJ, Lavola A, Tegelberg R, Veteli T (2005) Growth and defense in deciduous trees and shrubs under UV-B. *Environ Pollut* 137:404–414
- Koca D, Smith B, Sykes MT (2006) Modelling regional climate change effects on potential natural ecosystems in Sweden. *Clim Change* 78:381–406
- Kaitaniemi P, Neuvonen S, Nyssönen T (1999) Effects of cumulative defoliations on growth, reproduction, and insect resistance in mountain birch. *Ecology* 80:524–532
- Kittel TGF, Steffen WL, Chapin FS III (2000) Global and regional modelling of Arctic–boreal vegetation distribution and its sensitivity to altered forcing. *Glob Chang Biol* 6(S1):1–18
- Klemola T, Tanhuanpaa M, Korpimäki E, Ruohomäki K (2002) Specialist and generalist natural enemies as an explanation for geographical gradients in population cycles of northern herbivores. *Oikos* 99:83–94
- Knepp RG, Hamilton JG, Mohan JE, Zangerl AR, Berenbaum MR, DeLucia EH (2005) Elevated CO₂ reduces leaf damage by insect herbivores in a forest community. *New Phytol* 167:207–218

- Kozlov MV (this issue) Losses of birch foliage along geographical gradients in northern and central Europe: A climate-driven pattern? *Clim Change*
- Kurz WA, Apps MJ (1999) A 70-year retrospective analysis of carbon fluxes in the canadian forest sector. *Ecol Appl* 9:526–547
- Lavola A, Julkunen-Tiitto R, Roininen H, Aphalo P (1998) Host-plant preference of an insect herbivore mediated by UV-B and CO₂ in relation to plant secondary metabolites—contrasting effects of (specialist and generalist) herbivores and natural enemies. *Biochem Syst Ecol* 26:1–12
- Logan JA, Régnière J, Powell JA (2003) Assessing the impacts of global warming on forest pest dynamics. *Front Ecol Environ* 1:130–137
- Malmström CM, Raffa KF (1999) Biotic disturbance agents in the boreal forest: considerations for vegetation change models. *Glob Chang Biol* 6(S1):35–48
- Neuvonen S, Ruohomäki K, Bylund H, Kaitaniemi P (2001) Insect herbivores and herbivory effects on mountain birch dynamics. In: Wielgolaski FE (ed) *Nordic mountain birch ecosystems*. Parthenon Publishing, New York, pp 207–222
- Niemelä P, Chapin FS, Danell K, Bryant JP (2001) Herbivory-mediated responses of selected boreal forests to climatic change. *Clim Change* 48:427–440
- Oguntunde PG, van de Giesen N (2004) Crop growth and development effects on surface albedo for maize and cowpea fields in Ghana, West Africa. *Int J Biometeorol* 49:106–112
- Olofsson J, Hulme PE, Oksanen L, Suominen O (2004) Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. *Oikos* 106:324–334
- Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA, Warren M (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399:579–583
- Pothier D, Mailly D, Tremblay S (2005) Predicting balsam fir growth reduction caused by spruce budworm using large-scale historical records of defoliation. *Ann For Sci* 62:261–267
- Price DT, Zimmermann NE, van der Meer PJ, Lexer MJ, Leadley P, Jorritsma ITM, Schaber J, Clark DF, Lasch P, McNulty S, Wu J, Smith B (2001) Regeneration in gap models: priority issues for studying forest responses to climate change. *Clim Change* 51:475–508
- Richardson SJ, Press MC, Parson AN, Hartley SE (2002) How do nutrients and warming impact on plant communities and their insect herbivores? A 9-year study from a sub-Arctic heath. *J Ecol* 90:544–556
- Roeckner E, Arpe K, Bengtsson L, Christoph M, Claussen M, Dümenil L, Esch M, Giorgetta M, Schlese U, Schulzweida U (1996) The atmospheric general circulation model ECHAM-4: Model description and simulation of present-day climate. Max–Planck–Institut für Meteorologie Report No. 218
- Ruohomäki K, Tanhuanpää M, Ayres MP, Kaitaniemi P, Tammaru T, Haukioja E (2000) Causes of cyclicality of *Epirrita autumnata* (Lepidoptera, Geometridae): grandiose theory and tedious practice. *Population Ecology* 42:211–223
- Schowalter TD, Hargrove WW, Crossley DA (1986) Herbivory in forested ecosystems. *Ann Rev Entomol* 31:177–196
- Sitch S, Smith B, Prentice IC, Arneeth A, Bondeau A, Cramer W, Kaplan JO, Levis S, Lucht W, Sykes MT, Thonicke K, Venevsky S (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Glob Chang Biol* 9:161–185
- Smirnov KA, Sudnitsyna TN (2003) Changes of structural and physicochemical parameters of spruce forest ecosystem under the effect of moose (*Alces alces* L.). *Russ J Ecol* 34:175–180
- Smith B, Prentice IC, Sykes MT (2001) Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. *Glob Ecol Biogeogr* 10:621–637
- Starfield AM, Chapin FSI (1996) Model of transient changes in arctic and boreal vegetation in response to climate and land use change. *Ecol Appl* 6:842–864
- Stolter C, Ball JP, Julkunen-Tiitto R, Lieberei R, Ganzhorn JU (2005) Winter browsing of moose on two different willow species: food selection in relation to plant chemistry and plant response. *Can J Zool* 83:807–819
- Tanhuanpää M, Ruohomäki K, Kaitaniemi P (2003) Influence of adult and egg predation on reproductive success of *Epirrita autumnata* (Lepidoptera: Geometridae). *Oikos* 102:263–272
- Tanhuanpää M, Ruohomäki K, Kaitaniemi P, Klemola T (1999) Different impact of pupal predation on populations of *Epirrita autumnata* (Lepidoptera: Geometridae) within and outside the outbreak range. *J Anim Ecol* 68:562–570
- Tenow O, Nilsson A (1990) Egg cold hardiness and topoclimatic limitations to outbreaks of *Epirrita autumnata* in northern Fenoscandia. *J Appl Ecol* 27:723–734

- Tenow O, Bylund H, Holmgren B (2001) Impact on mountain birch forests in the past and the future of outbreaks of two geometrid insects. In: Wielgolaski FE (ed) Nordic mountain birch ecosystems. Parthenon Publishing, New York, pp 223–239
- Tenow O, Nilssen AC, Karlsson PS (2005) Long-term influence of herbivores on northern birch forests. *Ecol Stud* 180:165–181
- Virtanen T, Neuvonen S (1999) Performance of moth larvae on birch in relation to altitude, climate, host quality and parasitoids. *Oecologia* 120:92–101
- Virtanen T, Neuvonen S, Nikula A (1998) Modelling topoclimatic patterns of egg mortality of *Epirrita autumnata* (Lepidoptera: Geometridae) with a Geographical Information System: predictions for current climate and warmer climate scenarios. *J Appl Ecol* 35:311–322
- Wager DJ, Baker FA (2003) Potential effects of ozone, climate, and spruce budworm on Douglas-fir growth in the Wasatch Mountains. *Can J For Res* 33:910–921
- Weisberg PJ, Bugmann H (2003) Forest dynamics and ungulate herbivory: from leaf to landscape. *For Ecol Manag* 181:1–12
- Wermelinger B (2004) Ecology and management of the spruce bark beetle *Ips typographus*—a review of recent research. *For Ecol Manag* 202:67–82
- Whittaker RH, Woodwell GM (1968) Dimension and production relations of trees and shrubs in the Brookhaven forest, New York. *J Ecol* 56:1–25
- Wolf A, Larsen K, Callaghan TV (this issue) Future changes in vegetation and ecosystem function of the Barents Region. *Clim Change*, doi:10.1007/s10584-007-9342-4
- Zvereva EL, Kozlov MV (2006) Consequences of simultaneous elevation of carbon dioxide and temperature for plant–herbivore interactions: a meta-analysis. *Glob Chang Biol* 12:27–41