Forest Ecology and Management 256 (2008) 209–220

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Impact of bark beetle (*Ips typographus* L.) disturbance on timber production and carbon sequestration in different management strategies under climate change

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ARTICLE INFO

Keywords:
Forest management
Carbon storage
Natural disturbance
Bark beetle
Ips typographus
Climatic change
Secondary coniferous forests
Picea abies
PICUS
Simulation

ABSTRACT

The likely environmental changes throughout the next century have the potential to strongly alter forest disturbance regimes which may heavily affect forest functions as well as forest management. Forest stands already poorly adapted to current environmental conditions, such as secondary Norway spruce (*Picea abies* (L.) Karst.) forests outside their natural range, are expected to be particularly prone to such risks. By means of a simulation study, a secondary Norway spruce forest management unit in Austria was studied under conditions of climatic change with regard to effects of bark beetle disturbance on timber production and carbon sequestration over a time period of 100 years. The modified patch model PICUS v1.41, including a submodule of bark beetle-induced tree mortality, was employed to assess four alternative management strategies: (a) Norway spruce age-class forestry, (b) Norway spruce continuous cover forestry, (c) conversion to mixed species stands, and (d) no management. Two sets of simulations were investigated, one without the consideration of biotic disturbances, the other including possible bark beetle damages. Simulations were conducted for a de-trended baseline climate (1961–1990) as well as for two transient climate change scenarios featuring a distinct increase in temperature. The main objectives were to: (i) estimate the effects of bark beetle damage on timber production and carbon (C) sequestration under climate change; (ii) assess the effects of disregarding bark beetle disturbance in the analysis.

Results indicated a strong increase in bark beetle damage under climate change scenarios (up to +219% in terms of timber volume losses) compared to the baseline climate scenario. Furthermore, distinct differences were revealed between the studied management strategies, pointing at considerably lower amounts of salvage in the conversion strategy. In terms of C storage, increased biotic disturbances under climate change reduced C storage in the actively managed strategies (up to -41.0 tC ha^{-1}) over the 100-year simulation period, whereas in the unmanaged control variant some scenarios even resulted in increased C sequestration due to a stand density effect.

Comparing the simulation series with and without bark beetle disturbances the main findings were: (i) forest C storage was higher in all actively managed strategies under climate change, when biotic disturbances were disregarded (up to +31.6 tC ha^{-1} over 100 years); and (ii) in the undisturbed, unmanaged variant C sequestration was lower compared to the simulations with bark beetle disturbance (up to -69.9 tC ha^{-1} over 100 years). The study highlights the importance of including the full range of ecosystem-specific disturbances by isolating the effect of one important agent on timber production and C sequestration.

1. Introduction

Natural disturbances are inherent key processes of forest ecosystems and a major driver of forest development in various forest biomes (e.g., Peltzer et al., 2000; Gromtsev, 2002; Payette and Delwaide, 2003; Lorimer and White, 2003; Harcombe et al., 2004; Splechtna and Gratzer, 2005). Disturbances may affect forests over various spatial and temporal scales, from the level of plant functional elements to landscape scale (e.g., Ulanova, 2000; Lundquist and Beatty, 2002; Splechtna et al., 2005). Important processes in natural forest development, including regeneration dynamics or inter- and intra-species competition, are strongly affected by the prevailing disturbance regime.

Traditionally, forest management tries to minimize natural disturbances and related forest dynamics in favor of a deterministic sequence of regeneration, thinning and harvesting activities.

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doi:10.1016/j.foreco.2008.04.002

Schelhaas et al. (2003) in their review of historic disturbance events in European forestry clearly demonstrated the inability of forest management to completely control disturbances in forest ecosystems. According to their findings, on average over several decades, approximately 10% of the annual harvests in Europe have been salvage operations following natural disturbances. Recently, there has been a shift in management paradigms from sustainable timber production to sustainable forest management (SFM) in a much broader sense (e.g., Ministerial Conference on the Protection of Forests in Europe (MCPFE) 1993, 1998). This, together with an increased understanding of ecosystem processes, has promoted an alternative view on natural disturbances, and mimicking natural disturbance regimes is proposed as key component of an ecosystem oriented management approach (e.g., Niemelä, 1999; Franklin et al., 2002; Palik et al., 2002).

Both management approaches rely on a proper understanding of disturbance processes and the way these may interact with management. Thus, the development and application of new tools for risk assessment and forest management decision support have attracted substantial attention recently. While numerous risk assessment models are available which are designed to assess a particular state of the forest for its vulnerability to a disturbance agent in a static approach (e.g., Peltola et al., 1999; Gardiner and Quine, 2000; Gardiner et al., 2000; Gan, 2004; Achim et al., 2005; Netherer and Nopp-Mayr, 2005; Olofsson and Blennow, 2005), fewer examples exist (e.g., Lexer and Hönninger, 1998; Kurz et al., 2000; Mailly et al., 2000; Keane et al., 2004; Crookston and Dixon, 2005) where disturbance agents were explicitly included in dynamic forest ecosystem models. Discussions on a likely climate change increase the need to address climate dependencies of disturbance agents explicitly in decision support tools and models (Ayres and Lombardero, 2000; Peterson, 2000; Volney and Fleming, 2000; Harrington et al., 2001; Bale et al., 2002). Dale et al. (2000) conclude that a dynamic integrative approach explicitly addressing the multiple interactions between environmental changes, forest management and disturbance agents is urgently needed to support forest resource managers. Some of the few examples attempting to address these needs were reported by Keane et al. (1996), Chen et al. (2000) and Thornton et al. (2002).

Recently, increased interest has been paid to these questions, since countries can elect to account for forest management based carbon (C) sinks under the Kyoto Protocol (UNFCCC, 1997). Disturbance regimes, as influenced by a changing climate, may impair sink enhancement strategies in forestry (Breshears and Allen, 2002). So far several studies have addressed this issue, mainly focusing on the boreal zone: for fire disturbance, e.g., Seely et al. (2002), Thornley and Cannell (2004) and Ito (2005); for fire and insect disturbance, e.g., Kurz and Apps (1994), Kurz et al. (1998) and Li et al. (2003). Recently, Thürig et al. (2005) presented an analysis of windthrow effects on the C balance of Swiss forests. Most of these analyses assumed stand-replacing disturbances, which directly affect the age-class structure of the simulated forests. However, analyses including explicitly the inter-related effects of climate change and disturbances operating at low to intermediate intensity levels on timber production and the C budget of forest ecosystems have rarely been presented.

In Central Europe, Norway spruce (*Picea abies* (L.) Karst.) has been heavily promoted due to its superior productivity and ease of management outside its natural range, on sites naturally supporting broadleaved species compositions. These secondary coniferous forests are particularly prone to an array of insect and disease organisms (e.g., Klimo et al., 2000; Spiecker et al., 2004). Among these agents the spruce bark beetle *Ips typographus* (Scol. Col. L.) is regarded as the most important biotic risk agent for Norway spruce (Christiansen and Bakke, 1988; Schelhaas et al., 2003). Under a warmer and possibly drier climate the vulnerability of these forests to bark beetle infestations is expected to increase drastically. Possible forest management strategies to mitigate the risk of management are discussed intensively in forest practice as well as in the scientific literature (e.g., Klimo et al., 2000; von Teuffel et al., 2005) and include transformation of current age class Norway spruce forests to continuous cover forestry (e.g., Reininger, 2000; Pommerening and Murphy, 2004; Loewenstein, 2005) as well as conversion to mixed species stands which are better adapted to the prevailing site conditions (e.g., Spiecker et al., 2004). Currently, at the operational level of a forest management unit, there is no detailed analysis of how such proposed management strategies may affect timber production and C sequestration under conditions of climatic change that explicitly takes into account natural disturbances by bark beetles.

The objectives of this study were to: (i) investigate, by means of a simulation study (time horizon 100 years), the interaction of bark beetle (*I. typographus*) induced disturbances and alternative forest management strategies on C sequestration and timber production under conditions of climatic change; (ii) estimate the potential error of ignoring the biotic disturbance agent in the assessment, and thus contribute to the discussion on the influence of disturbances on forest functions under climate change. To this end, four alternative forest management strategies were investigated at the forest management unit level under a baseline climate scenario (de-trended climate 1961–1990) and two transient climate change scenarios with the model PICUS v1.41 (e.g., Seidl et al., 2005).

2. Materials and methods

2.1. Study material

2.1.1. The study site

The study was conducted for a 248.7 ha forest management unit (FMU) in the province of Carinthia in southern Austria (Lat. E14.37, Long. N46.78). The FMU is situated in the submontane vegetation belt at about 550 m above sea level. The climate regime is subcontinental. Soil conditions are characterized by mainly crystalline bedrock consisting of glacial residues with occasional calcite cliffs. The region has been managed intensively for centuries. Current forests are dominated by Norway spruce. The potential natural vegetation is dominated by deciduous species (mainly beech, *Fagus sylvatica* L. and oak, *Quercus robur* L.) with admixed Scots pine (*Pinus sylvestris* L.), and is mainly differentiated by soil water regime (see Mayer, 1985; Kilian et al., 1994). In general geomorphological conditions are smooth and allow for a fully mechanized harvesting technology.

2.1.2. Soil data

Soil conditions of the FMU are mainly characterized by fertile Cambisols with medium to good water holding properties. This soil type dominates 98.8% of the forest area (Steiner, 1998). For the simulations, two site types were distinguished within that soil type, differing with regard to water holding capacity (ST1 and ST2). The third site type is characterized by shallow rendzic Leptosols (ST3), which prevail in a limited area at the southern border of the FMU. Data for initialization of soil C and N pools were collected from soil samples in all three site types. Mineral soil properties (see Table 1) were kept constant within a site type, whereas stand-level forest floor C and N pools were derived from statistical relationships with stand characteristics (see Seidl et al., 2007a for details).

2.1.3. Stand data

Stand data were available for 103 compartments from a full inventory of the FMU (Unegg, 1999). Norway spruce is the

Table 1
Properties of the mineral soil for the site types (ST1-3) as derived from the laboratory analysis of 20 soil samples

	ST1	ST2	ST3
	Eutric Cambisol[a]	Eutric Cambisol[a]	Rendzic Leptosol[a]
pH (H_2O)	4.3	4.1	6.2
WHC (mm)	161	120	60
C (t ha^{-1})	82.0	95.8	66.3
N (t ha^{-1})	5.85	5.92	3.35
Soil depth (mm)	800	800	400

WHC: water holding capacity.
[a] Soil type.

dominant species (93% of basal area), followed by Scots pine (6%) and a minor share of deciduous species (*Q. robur*, *Acer* spp., *Salix* spp.). The age-class distribution is strongly skewed towards intermediate development stages with only a small number of stands over 70 years. For the simulation, stands were grouped by cluster analysis (method: partitioning around medoids, R Development Core Team, 2006) into 25 stand types according to stand age, inventory estimates of mean annual increment over 100 years (MAI_{100}), stocking density relative to yield table basal area (Marschall, 1975), share of Norway spruce, and basal area weighted mean diameter. A representative stand per cluster was chosen for simulation—i.e. 25 representative stand types were simulated for the FMU. Since deadwood stocks had not been recorded in the inventory they were initialized as zero. Main forest characteristics of the FMU are shown in Fig. 1 (see Seidl et al., 2007a for details).

2.2. Climate scenarios and management strategies

2.2.1. Climate scenarios

Three climate scenarios were employed. Climate scenario C1 is a synthetic climate baseline and features a de-trended 100-year climate series based on observed climate data of the period 1961–1990 (mean annual temperature 7.6 °C, mean annual precipitation 1013 mm) which had been interpolated from nearby weather stations of the Austrian weather service. This generic approach was chosen in order to obtain a baseline for the assessment of changes in bark beetle infestations not superimposed by trends in climate input. The other two climate scenarios implied a transient climate change and were based on global circulation model (GCM) simulations. Both scenarios refer to the IS92a scenario (“business as usual”) of the IPCC (1995), assuming a doubling of the atmospheric CO_2-concentration over the 21st century. Climate scenario C2 is based on the GCM ECHAM4-OPYC3 (European Center Hamburg, Germany) (cooling effect of sulphur particles not included), and climate scenario C3 on simulations of the GCM HadCM2 (Hadley Center, UK). Spatial interpolation of the GCM climate parameter anomalies to the study site was done using Delaunay triangulation. The climate data were provided by the Potsdam Institute for Climate Impact Research (see Kellomäki et al., 2005).

The climate change scenarios (C2 and C3) show steady warming until the end of the 21st century (+3.7 °C and +3.1 °C for C2 and C3, respectively for 2090–2100, relative to the first decade of the century, see Fig. 2). Precipitation patterns in the climate change scenarios show no clear trend: the scenarios predict an increase in precipitation for the first decades of the century with a decreasing trend towards the end of the 100-year period (Fig. 2). The last 20 years are particularly dry under scenario C3.

2.2.2. Silvicultural management strategies

All management interventions within the strategies were specified as percent volume removals in five relative diameter classes and were individually tailored to each simulated stand type (e.g., adopted to initial conditions of stand type). Merchantable dead trees (dbh >10 cm) were removed in the year of death, inter alia mimicking current forest protection routines. Pro-active forest

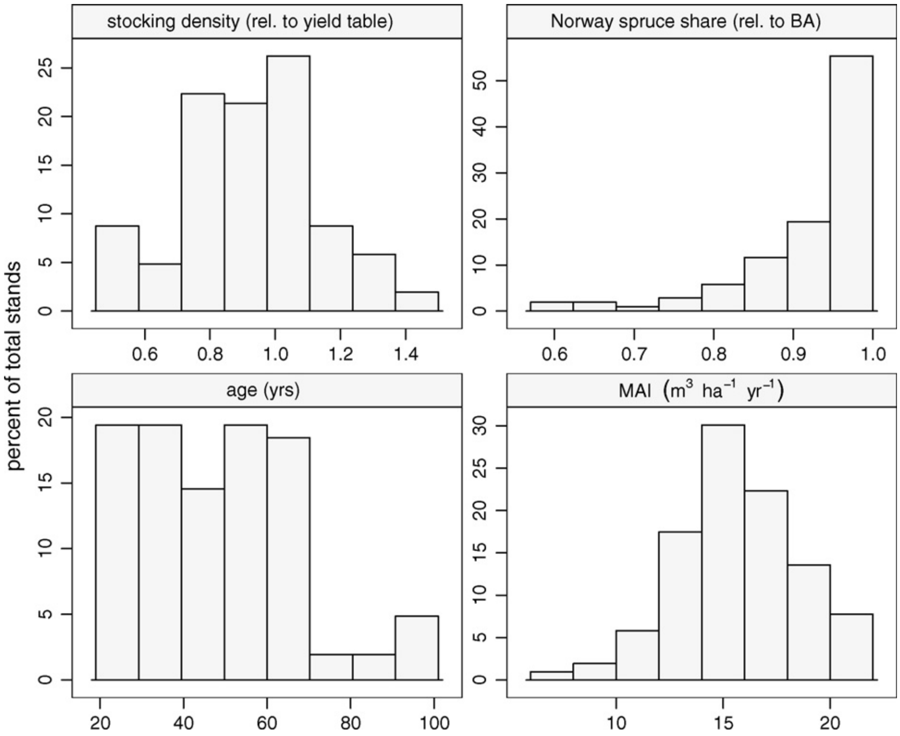

Fig. 1. Summary statistics of the 103 compartments of the FMU inventory. MAI refers to mean annual increment at age 100 (gross volume over bark, $m^3\ ha^{-1}\ a^{-1}$) and stocking density is relative to the yield tables of Marschall (1975). BA = stand basal area.

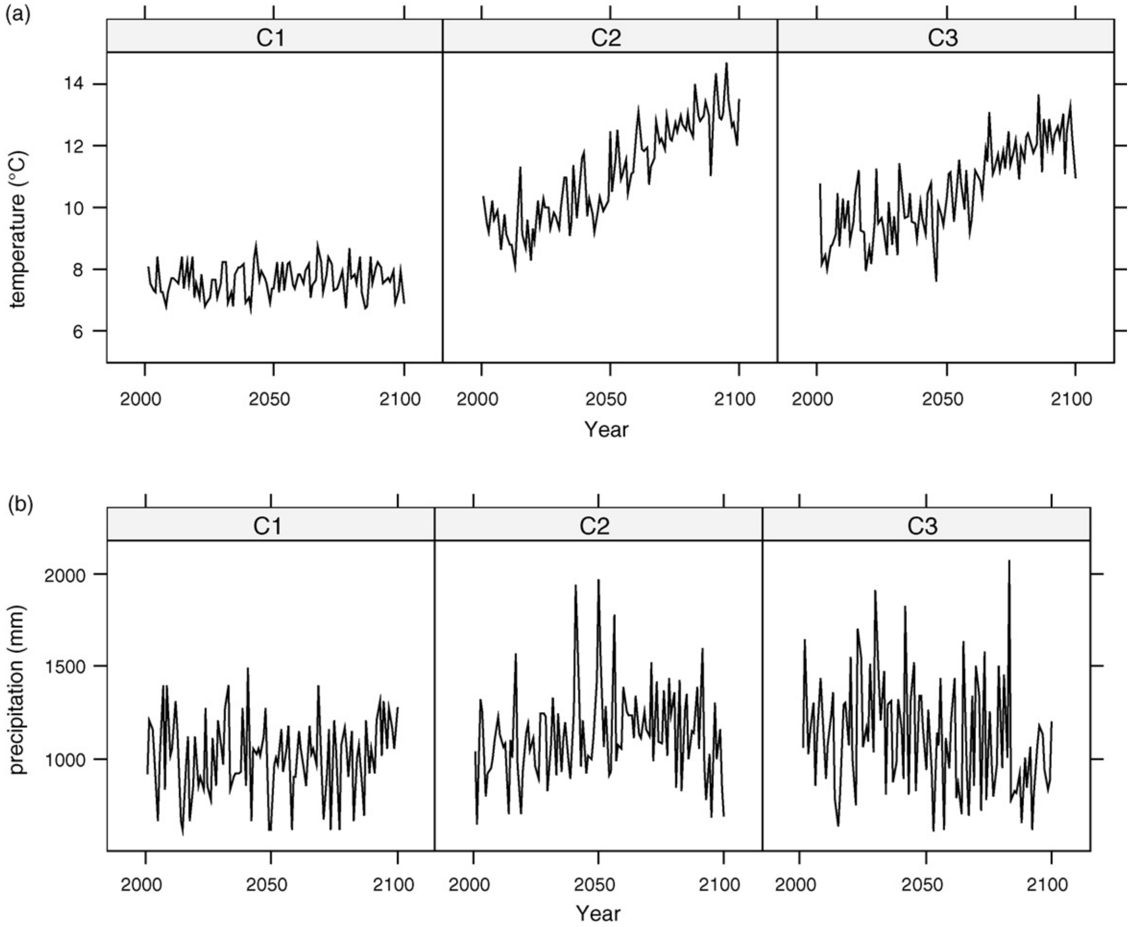

Fig. 2. Mean annual temperature (a) and precipitation (b) in the climate scenarios. C1: de-trended baseline climate based on the period 1961–1990. C2: climate change scenario for the IS92a storyline based on scenario output of ECHAM4-OPYC3. C3: climate change scenario for the IS92a storyline based on scenario output of HadCM2. See text for details.

protection measures were not simulated, but mortality-induced changes in stand characteristics had an impact on subsequent regular harvest removals, since harvest intensity was specified in percent of standing volume stock. Thus, a partial trade-off between regular harvests and salvage was considered with this study design.

Four silvicultural management options were investigated (see Table 2). Strategy MS1 is an age-class system and reflects business as usual management with a rotation period of 90 years. Norway spruce is regenerated naturally by a shelterwood approach (regeneration period approximately 10 years), followed by a pre-commercial thinning to control for stand density. The subsequent thinning regime is characterized by several selective thinnings (Schädelin, 1942; Johann, 1987). Alternative management strategies were based on recently discussed silvicultural alternatives for secondary Norway spruce forests in Central Europe (see Spiecker et al., 2004). Strategy MS2 is motivated by the discussion of potential benefits of improved vertical forest structure and represents a continuous cover management regime with natural regeneration of Norway spruce (see Reininger, 2000; Pommerening and Murphy, 2004). This strategy implies several thinnings from above ("structural thinnings") in early development phases to promote differentiation of stand structure, and a subsequent transition to a target diameter harvesting regime. Another recently discussed silvicultural option especially relevant for secondary coniferous forests is the conversion to mixed stands with broadleaved species better adapted to prevailing site conditions (MS3). In MS3 the rotation period for current Norway spruce stands is reduced to 80 years, and beech and oak are introduced. Within MS3 several conversion variants are distinguished according to initial stand and site conditions, ranging from conversion to pure oak (21.1% of FMU area) and beech (4.5% of FMU area) after clear-cutting of Norway spruce to mixed stands of

Table 2
Characterization of the applied management strategies (MS1–4)

Strategy	Management intervention	Scheduled removal (% of volume)
MS1	Pre-commercial thinning (20)	40–40–40–30–30
	Thinning from above (40, 50, 60)	00–10–10–25–15
	Thinning from below (70)	00–10–10–10–05
	Shelterwood cut (80)	00–25–30–35–10
	Clearcut (90)	100–100–100–100–100
MS2	Structural thinning (40, 50, 60)	00–10–15–30–20
	Target diameter harvest (15-year intervals starting at age 75)	00–00–00–10–75
MS3	Pre-commercial thinning (20)	40–40–40–30–30
	Thinning from above (40, 50, 60)	00–10–10–25–15
	Thinning from below (70)	00–10–10–10–05
	Clearcut (80)	100–100–100–100–100
MS4	None	

Numbers in parenthesis give the approximate stand age of the respective management intervention, removals are specified as percent volume removals in five relative diameter classes (lowest to highest diameter class from left to right). Values for MS3 relate to the current coniferous forests and are adapted accordingly to the successively changed species composition. See text for details.

Table 3
Stand conversion variants within management strategy MS3

Conversion variant	Target share of deciduous species (%)	Percent of forest area (%)	Silvicultural characteristics
Oak	100	21.1	Planting after clearcut
Beech	100	4.5	Planting after clearcut
Spruce-beech (1)	30	68.6	Underplanting of beech in groups/gaps under spruce canopy, natural regeneration of spruce
Spruce-beech (2)	20	5.8	Introduction of beech in groups in already existing natural regeneration of spruce

Spruce-beech variant (2) was applied in stands with existing natural regeneration of Norway spruce.

spruce and beech established by underplanting of beech under Norway spruce shelter and subsequent natural regeneration of spruce (74.4% of FMU area). A detailed description of the conversion variants can be found in Table 3. A “do nothing” (i.e., no active management) strategy (MS4) was simulated as a reference scenario with natural Norway spruce regeneration establishing spontaneously, and dead trees remaining in the forest.

2.3. Model approach and simulation design

2.3.1. PICUS v1.41

The model PICUS v1.41 used for the assessment builds on the hybrid forest patch model PICUS v1.31 (Seidl et al., 2005). The hybrid model approach aims at combining the strengths of both, patch models and process based production models, while circumventing the limitations of the individual approaches (see Mäkelä et al., 2000). Spatial basis of the simulation approach is a 10 m × 10 m patch array extended into the third dimension by 5 m crown cells. In contrast to classical patch models (compare Shugart, 1984; Botkin, 1993) spatial interactions between the patches are taken into account by simulating a detailed three-dimensional light regime and spatially explicit seed dispersal. Inter- and intra-species competition is modeled based on the patch model approach presented by Lexer and Hönninger (2001) whereas stand level net primary production is derived according to the simplified physiological principles of radiation use efficiency of the 3-PG model (Landsberg and Waring, 1997). The coupling of the two modeling approaches is accomplished inter alia via the stand level leaf area and is described in detail in Seidl et al. (2005). The model requires monthly input of temperature, precipitation, radiation and vapor pressure deficit.

In extension to model variant 1.31 two additional modules have been integrated. First, a process-based soil model of dynamic C and N cycling (Currie et al., 1999; Currie and Nadelhoffer, 1999) has been added (Seidl et al., 2007a). Interaction of aboveground production processes and belowground C and N dynamics are simulated on a monthly time-step. Soil organic C and N microbial-detrital pools, implicitly containing microbial biomass, are simulated for the forest floor and mineral soil. Fine litter enters detrital pools according to different C-classes and processes of nitrogen immobilization and mineralization are simulated. Furthermore, mass and N dynamics of fine and coarse woody debris are considered, including humification. The model explicitly simulates NH_4^+ and NO_3^- pools and fluxes and tracks leaching fluxes between the soil horizons. The general concept has been thoroughly tested in several studies (Currie et al., 1999; Currie and Nadelhoffer, 1999; Moorhead et al., 1999; Currie et al., 2004).

Motivated by the high relevance of biotic disturbances for forest management in Central Europe, an earlier approach to model bark beetle disturbances by Lexer and Hönninger (1998) was adopted and improved by new findings on the physiology and development of *I. typographus* (e.g., Netherer and Pennerstorfer, 2001; Netherer and Nopp-Mayr, 2005; Baier et al., 2007). The bark beetle disturbance module includes (i) the stochastic computation of the infestation risk for simulated forest stands, (ii) the estimation of damage intensity if an infestation occurs, and (iii) the spatial distribution of tree mortality in the stand.

Damage risk is derived from the number of potential beetle generations per year estimated using a thermo-energetic model approach (Coeln et al., 1996; Wermelinger and Seifert, 1999; Netherer and Pennerstorfer, 2001; Baier et al., 2007): annual potential beetle generations are calculated according to thermal requirements represented by a sum of degree-days (557) above a threshold temperature for beetle development (8.3 °C). Bark temperatures above the development optimum (30.4 °C) lead to a slowing and finally complete halt (>38.9 °C) of beetle development. Swarming requirements in terms of a combined day length and air temperature threshold are introduced for the start of a new generation. Currently, the simulation of potential generations does not account for a perennial bark beetle gradation – i.e. beetle development starts from zero every year. Annual potential generations are taken as a proxy of thermal environmental conditions for beetle development and are transformed into a stand level hazard rating introduced by (cf. Lexer (1995), Netherer and Nopp-Mayr (2005)).

In addition, a model of stand predisposition to *I. typographus* infestations is adopted from Lexer (1995) and Netherer and Nopp-Mayr (2005), including four stand level predisposition indicators (share of host trees in a stand, stand density (basal area), stand age, and Norway spruce drought index). Stand predisposition and thermal predisposition (potential generation score) are used to fit an empirical function to data on bark beetle infestations from Lexer (1995) to derive an annual probability for bark beetle damage (Eq. (1)). This simulated damage probability is assessed against a random number to derive whether damage from bark beetle occurs in a given year of the simulation.

$$\mathrm{pBB_{yr}} = 1 - \mathrm{e}^{(x1 * PI^{x2})^{\mathrm{GEN}}} \tag{1}$$

$\mathrm{pBB_{yr}}$ = annual probability for bark beetle damage;
PI = stand predisposition index to bark beetle damage [0, . . ., 1];
GEN = thermal predisposition scoring for potential generation number [0, . . ., 1];
x1 = empirical coefficient (−1.51);
x2 = empirical coefficient (1.65).

Damage intensity is calculated according to the empirical findings of Lexer (1995) using a stand hazard index combining a rating of south- and east-exposed stand edges, drought stress, and proportion of Norway spruce host trees in the stand (see Lexer, 1995) (Eq. (2)).

$$D_{\mathrm{rel}} = \frac{1}{1 + \mathrm{e}^{x3 - x4 \cdot \mathrm{SHI_{yr}}}} \tag{2}$$

D_{rel} = annually damaged stems in a stand [share of stem number];
SHI_{yr} = annual stand hazard index;
x3 = empirical coefficient (3.9725);
x4 = empirical coefficient (2.9673).

The spatial allocation of damage is derived from a predisposition ranking of the patches within the simulated stand and assumptions on the extent of an outbreak spot. A more detailed description alongside a thorough sensitivity analysis can be found in Seidl et al. (2007b): Model behavior along an elevation gradient in the Eastern Alps in Austria was found to be realistic and compared well with general observations of forest pest monitoring systems (Krehan et al., 2005).

PICUS v1.41 also contains a flexible management module allowing for spatially explicit harvesting and planting operations at the individual tree level. PICUS has been successfully evaluated with regard to the simulation of natural forest succession and equilibrium species composition over broad environmental gradients in the Eastern Alps. Furthermore, in a comparison with long-term growth and yield data the model was found capable of reproducing volume production and stand structure of managed, uneven-aged multi-species stands (Seidl et al., 2005).

Table 4 summarizes the main features of PICUS v1.41 following the scheme of Freeman et al. (2005), who compared the structure and function of six models applied for the simulation of forest management under climate change in Europe.

2.3.2. Simulations and analysis

Simulations were conducted over 100 years. To analyze the effect of biotic disturbances, two sets of simulations were performed, one including the effect of bark beetle infestations (BB), the second being the conservative, undisturbed baseline without the bark beetle submodule (UD). Model stochasticity (sources: random tree positions at initialization, random effect of non-stress related mortality) was considered negligible in the UD simulation series due to the 1.0-ha size of the simulated stands, but in the BB simulation series the stochastic nature of the bark beetle damage submodule was accounted for by replicating every stand simulation according to the number of stands represented by each stand type (total number: 103). This design granted comparability of the two simulation series UD and BB by applying the same 25 initial stand types, and also ensured a realistic consideration of disturbance risk, proportional to the number of stands represented by a stand type. The disturbance regime was characterized in terms of annual infestation frequency and damage intensity. Infestation frequency for the whole FMU was expressed as the proportion of stands with bark beetle infestation in a respective year. Damage intensity was presented as relative number of trees damaged annually per stand. A mean intensity over all damaged stands was calculated per year.

Timber production was assessed in terms of harvests, share of salvage from bark beetle infestations, and standing volume at the end of the simulation period. Timber volume is merchantable volume under bark, except where stated otherwise. C cycle effects were evaluated applying a net stock change approach, e.g. a summation of annual stock changes over the simulation period. Analyzed compartments were living tree C (including stem-, branch-, leaf- and root-carbon), C stored in deadwood (standing deadwood and downed woody debris of >10 cm in diameter), and soil C (consisting of soil organic carbon, litter, humified matter and fine woody debris <10 cm). Results on timber and C were aggregated to FMU level and presented on a per hectare basis.

3. Results

The results are structured into three sections. In Section 3.1, the simulated disturbance regime is characterized for business as usual management (MS1) in order to give a more detailed insight into the simulation results with regard to disturbance frequency and intensity under climatic change. The following two sections relate to the two main objectives of the study. Section 3.2 presents the simulated effects of bark beetle damage under climate change on timber production and C sequestration – i.e. results presented in this section stem from the simulation series with bark beetle damage. Section 3.3 focuses on isolating the effects of disregarding biotic disturbances (such as bark beetles) in such an analysis by

Table 4
The main features of PICUS v1.41 (see Freeman et al., 2005)

Properties	Description
Main model features	
Objectives	Dynamic forest succession, long-term simulations, climate change impacts, various management regimes, disturbances
Management options	Thinning, harvest, planting (all on individual tree level), natural regeneration, nitrogen fertilization
System structure (ecosystem)	
Stand structure	Multi-species systems, multi-layered systems
Tree structure	Crown, foliage, stem, roots
Soil structure	Two layers (forest floor and mineral soil)
Model structure (type, spatial and temporal resolution)	
Model type	Hybrid patch model, stochastic
Ecosystem	Central Europe, alpine
Spatial resolution	Patch/tree
Timestep	Year/month
Environment—atmosphere	Temperature, precipitation, radiation, vapor pressure deficit
Environment—soil	Soil water availability, nitrogen availability, carbon content, pH-value
Functioning of the model (description of main processes)	
Photosynthesis	3-PG approach (Landsberg and Waring, 1997)
Autotrophic respiration	Fixed ratio
Tree mortality	Dynamic (environment, density, age), bark beetle-induced (*Ips typographus*)
Soil—heterotrophic losses	Dynamic (actual evapotranspiration, litter quality)
Model parameters and evaluation	
Parameters	Literature, forest inventory
Evaluation	Lexer and Hönninger (2001) and Seidl et al. (2005)

comparing the two simulation series with (BB) and without (UD) bark beetle damage.

3.1. Bark beetle disturbance regime for business as usual management under climate change

Infestation frequency clearly reflected the temperature pattern of the corresponding climate scenario (Fig. 3). Whereas under the de-trended baseline climate (C1) the number of stands damaged per year remained relatively constant throughout the simulation period, a strong increase in disturbance events was simulated under the steadily warming scenarios C2 and C3 (Fig. 3). Mainly due to warmer climatic conditions, scenario C2 had a higher disturbance frequency than C3, although there was a high interannual variability, related to the underlying model formulation utilizing inter alia the threshold-driven completed bark beetle generations per year. Towards the end of the century, almost every stand was damaged annually by bark beetles in both climate change scenarios (mean for the years 2090–2100: C1 = 23.2%, C2 = 92.4%, C3 = 87.5% of simulated stands were infested). Disturbance intensity, which is strongly driven by drought stress and species composition, was found to vary relatively little for MS1 over the entire simulation period. However, the almost identical simulated damages (percent stems damaged) in the climate scenarios at the beginning of the study period (mean over all damaged stands for the decade 2000–2010: C1 = 1.56%, C2 = 1.58%, C3 = 1.62% of stems killed) diverged significantly, especially towards the drier end of the climate scenario C3 (mean over all damaged stands for the decade 2090–2100: C1 = 1.63%, C2 = 2.29%, C3 = 3.93%). The maximum annual damage of an individual stand was simulated under C3 and reached 18.1% of the stem number.

3.2. Effects of bark beetle damage on timber production and C storage under climate change

Climate change in all management strategies strongly increased the timber volume damaged by bark beetles, with a maximum increase of 219% under climate scenario C3 and management strategy MS4. Comparing the four strategies, the greatest damage was simulated in the “do nothing” strategy (MS4) under climate scenario C3, on average amounting to 4 $m^3\ ha^{-1}\ a^{-1}$ merchantable volume (under bark) (Table 5, disturbance series).

Both MS4 and MS2 increased timber stocks over the simulation period. In MS2 this was part of the strategy aiming at continuous cover forestry, and in MS4 the accumulation of stocks was due to the complete termination of harvest removals and subsequent natural forest development. Both strategies resulted in a distinct increase in bark beetle damage in relation to the business as usual management MS1 (increases between +8.6% and +48.3% in damaged volume over all three climate scenarios). In contrast, MS3 resulted in a considerably lower damaged timber volume compared to MS1, ranging from −9.0% to −20.3% over all climate scenarios. Salvage from bark beetle damage contributed considerably to total harvests at the FMU level: whereas under current

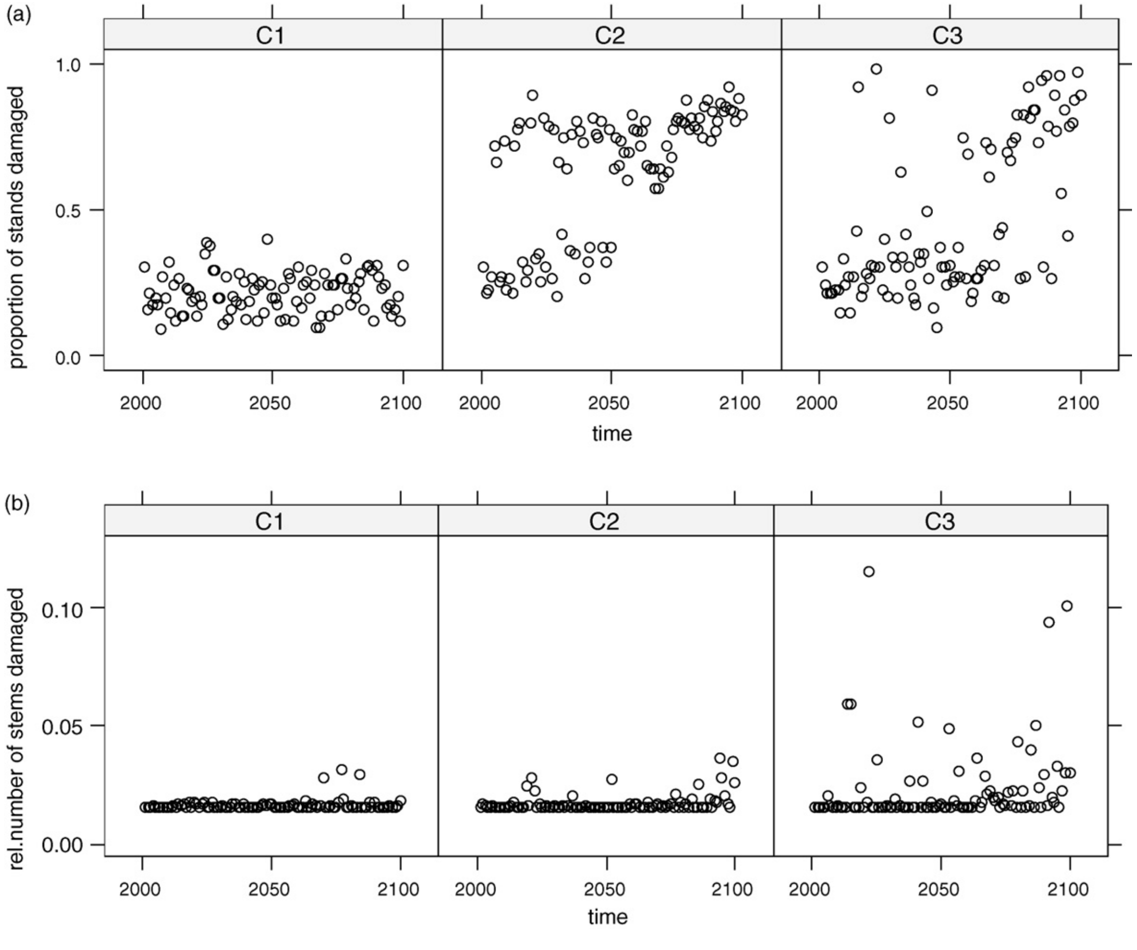

Fig. 3. Simulated infestation frequency (a) and damage intensity (b) for business as usual management (MS1) in the analyzed climate scenarios. Displayed damage intensities are averages over all damaged stands per year. C1: de-trended baseline climate (1961–1990). C2: climate change scenario for the IS92a storyline based on ECHAM4-OPYC3. C3: climate change scenario for the IS92a storyline based on HadCM2. See text for details.

Table 5
Mean annual cut and the included salvage from bark beetle damage given in parenthesis ($m^3\ ha^{-1}\ a^{-1}$ merchantable volume under bark) for management strategies MS1–3

	Disturbance series (BB)			Undisturbed series (UD)		
	C1	C2	C3	C1	C2	C3
MS1	11.3 (0.89)	12.9 (2.44)	12.4 (2.71)	10.6	12.8	13.0
MS2	10.4 (1.28)	12.0 (3.25)	11.7 (3.48)	9.3	10.1	9.4
MS3	11.0 (0.74)	12.9 (2.22)	12.2 (2.16)	10.1	11.3	10.8
MS4	– (1.26)	– (2.65)	– (4.02)	–	–	–

For the unmanaged strategy MS4 the bark beetle damage remaining in the stand is also given in parentheses. C1–3: climate scenarios; BB: simulation series with bark beetle module; UD: simulation series without bark beetle module.

climate, salvage shares ranged from 6.7% (MS3) to 12.3% (MS2) with intermediate values for MS1, they rose distinctly up to 17.7% for MS3 (minimal value) and 29.7% for MS2 (maximum value) in climate szenario C3. Under all simulated climatic conditions the continuous cover strategy MS2 showed higher, and the conversion strategy MS3 showed lower salvage shares than business as usual management MS1. Moreover the considerable increase of bark beetle damage under the climate change scenarios led to a rise in the FMU harvest level in all managed scenarios compared to cuts under current climate C1. Therefore, it is of particular interest to investigate the effect of the disturbance-driven increase in harvest levels on the FMU timber stocks. Fig. 4 shows that under both climate change scenarios timber stocks at the end of the simulation period were lower compared to C1. This effect was particularly strong under climate C3.

The general pattern of C sequestration in living tree biomass was closely correlated with the development of timber stocks. Under climate scenario C1 the strategies MS2 and MS4 had a positive C balance over the simulation period, whereas in MS1 and MS3 the balance was negative (Table 6, disturbance series). For MS2, which experienced the most severe bark beetle damage among the actively managed strategies (MS1–MS3), the living tree C balance turned negative under C3 (loss compared to C1: $-39.1\ tC\ ha^{-1}$ over 100 years). Whereas MS1 resulted in a comparable loss, in MS3 the negative effects of climate change and bark beetle damages under C3 were limited to $-16.6\ tC\ ha^{-1}$ over the entire simulation period (compared to the baseline climate C1).

As expected, deadwood C showed an increase in all simulations, since pools were initialized as empty. Increases were smallest under the continuous cover regime MS2, where, compared to the two clear-cut management systems MS1 and MS3, no pre-commercial thinning was performed. Highest net C stock increases in deadwood were simulated in the unmanaged strategy MS4. Here also the increase in bark beetle damage under climate change led to a pronounced rise in deadwood C stocks (2.5-fold under C3 compared to baseline climate).

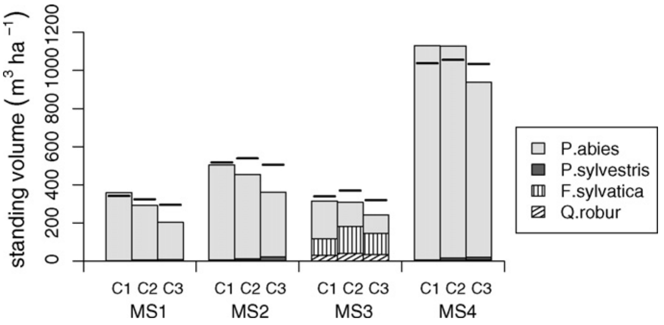

Fig. 4. Average timber stock for the FMU at the end of the study period for the simulation series including bark beetle damage. Horizontal lines indicate timber volume for corresponding simulations without biotic disturbance (UD). C1: detrended baseline climate (based on the period 1961–1990). C2: climate change scenario for the IS92a storyline based on ECHAM4-OPYC3 simulations. C3: climate change scenario for the IS92a storyline based on HadCM2 simulations. See text for details.

Belowground C pools were found to show a moderate positive C stock change in all scenarios. However, this increase was considerably lower under climate change conditions. MS3 had the highest positive soil C stock changes among the management strategies due to increased turnover of litter related to higher proportions of deciduous trees.

Total forest C stock changes integrate these findings. Especially under the climate scenario C3 with the most intense disturbance events considerable differences between the management alternatives can be seen: whereas MS1 and MS2 showed a substantial decline in C storage compared to C1 (-43.4 and $-41.0\ tC\ ha^{-1}$ over 100 years, respectively), in MS3 this loss amounted only to $-17.8\ tC\ ha^{-1}$. The results in terms of net C stock changes over 100 years are summarized in Table 6.

3.3. Effects of disregarding bark beetle disturbance

Disregarding biotic disturbances in the analysis (simulation series UD) resulted in lower harvest levels and higher mean timber stocks in the actively managed strategies (MS1–MS3), especially under the climate change scenarios (Table 5 and Fig. 4). In the simulations without bark beetle damage (UD), the climate change scenarios resulted in an increase in growth compared to results under C1, corresponding to higher harvesting levels as well as a moderate increase in standing stocks. Under active management, in all climate change scenarios the simulated timber stock levels after 100 years were lower when bark beetle disturbances were included (BB) compared to the UD simulations without consideration of disturbances (see Fig. 4). The simulated moderate damage under current climate (C1) resulted in a more complex interplay of factors, which is addressed in detail below.

In terms of C storage, C stock changes in living tree biomass in the actively managed strategies were significantly higher in UD than in the simulation set including biotic disturbance (BB), especially under climate change conditions. The only exception to this finding was the business as usual management MS1 under the baseline climate (C1). In the unmanaged control strategy MS4, living tree C stocks increased considerably less under UD compared to BB. In all management strategies deadwood C stock increases were substantially higher in the disturbed simulation series (BB) compared to the undisturbed runs (UD), an effect particularly pronounced under MS4. With regard to soil C, the comparison of the BB and UD simulation series revealed a moderately higher increase in net C-stocks in BB due to increased input to litter and woody debris pools (Table 6).

Overall, climate had a distinct influence on the difference between the two simulation series with (BB) and without (UD) bark beetle disturbance. For the actively managed strategies (MS1–MS3) the moderate damages in the BB experiment under C1 had only a limited effect on the total forest C balance compared to the

Table 6
Net C stock changes (tC ha^{-1}) over the 100-year simulation period

	Disturbance series (BB)			Undisturbed series (UD)		
	C1	C2	C3	C1	C2	C3
MS1						
Living tree C	−18.3	−36.6	−58.8	−27.7	−34.2	−38.2
Deadwood C	4.2	5.0	4.6	3.8	4.4	3.7
Soil C	16.9	11.5	13.6	16.0	10.2	11.7
Total C	2.8	−20.1	−40.6	−7.9	−19.6	−22.8
MS2						
Living tree C	37.2	29.1	−1.9	41.1	47.8	35.6
Deadwood C	2.9	3.5	3.2	2.6	2.9	2.5
Soil C	5.6	1.0	3.4	2.3	−3.0	−1.8
Total C	45.7	33.6	4.7	46.0	47.7	36.3
MS3						
Living tree C	−9.3	−6.1	−25.9	−6.7	1.1	−10.7
Deadwood C	4.5	5.2	4.7	4.1	4.5	4.1
Soil C	25.0	21.9	23.6	23.7	19.5	21.6
Total C	20.2	21.0	2.4	21.1	25.1	15.0
MS4						
Living tree C	280.6	303.5	246.0	235.1	248.5	234.3
Deadwood C	18.0	30.7	46.1	15.5	24.6	16.0
Soil C	8.4	7.6	14.3	3.5	−1.2	0.2
Total C	307.0	341.8	306.4	254.1	271.9	250.5

Living tree C: carbon in stems, branches, leafs and roots of living trees; deadwood C: carbon in standing and downed deadwood; soil C: carbon in soil; MS1–4: management strategies; C1–3: climate scenarios; BB: simulation series with bark beetle module; UD: simulation series without bark beetle module.

simulation without biotic damage (UD). However, considering climate change projections for the next century (C2 and C3), ignoring the increased beetle damage (UD) would result in pronounced overestimation of C sequestration compared to the simulations with biotic disturbance (BB) (up to 31.6 tC ha^{-1} over 100 years under MS2 × C3).

4. Discussion and conclusion

The current study explicitly approached the interactions and effects between climate change, biotic disturbances and forest management which are rarely tackled in an integrated approach. Interpretation of results focuses on three main elements: (i) a discussion of the chosen modeling approach (Section 4.1); (ii) an interpretation of the effects of bark beetle disturbance under climate change and its implications for sustainable forest management (Section 4.2); (iii) the effect of disregarding biotic disturbances (Section 4.3).

4.1. Evaluation of the methodology applied

Evaluating the ability of the model to simulate forest production we found good correspondence of estimated mean annual cut under business as usual management (MS1) and current climatic conditions (C1) to the allowable sustainable harvest level taken from management plans for the FMU (Anonymous, 1949, 1960). This good agreement, confirming the findings of Seidl et al. (2005) with regard to accuracy of simulated productivities, is particularly relevant since no FMU-level estimate for the allowable cut had been superimposed in the stand-level simulations. Corresponding simulated mean annual cuts for the FMU consisted of the sum of stand-level silvicultural prescriptions (i.e. "silvicultural harvest level"). In interpreting simulated timber production over the analysis period, it should be noted that the impact of browsing on establishment and development of regeneration was not taken into account in the simulations.

Besides simulation of forest productivity under a given management regime, the ability of the model to consistently simulate bark beetle damage in relation to environmental and stand conditions is a key element in the analysis. The bark beetle module has been tested in a separate study (Seidl et al., 2007b), including a detailed sensitivity analysis over an elevation gradient in the Alps. In the present study the simulated amount of bark beetle damage as well as infestation frequency under current conditions (i.e., baseline climate C1 and business as usual management MS1) corresponded well to the observations of the FMU owner (G. Kleinszig, personal communication) and average statistical values for the respective Austrian province (BMLFUW, 2004). Simulated annual damage intensities under current conditions appear low, but were in accordance with data from Lexer (1995) which had been gathered in the vicinity of the FMU during a bark beetle outbreak.

A limitation of the current approach is the restriction to annual beetle development, which does not allow for a build-up of the bark beetle population over several years. Furthermore, due to the still limited process knowledge on bark beetle infestation and damage (e.g., Wermelinger, 2004), several formulations in the computation of bark beetle damage are based on empirical data. Thus, extrapolation beyond conditions represented in the data base increases uncertainty. Finally, it is important to note that additional pro-active forest protection measures are not accounted for by the current approach due to knowledge gaps regarding the efficiency of protection measures. However, notwithstanding these limitations, PICUS v1.41 can be considered a suitable means to study the inter-related effects of forest management, bark beetle disturbances and climate change on forest production and C sequestration.

4.2. Effects of bark beetle damage on timber production and C storage under climate change

Consideration of the projected climate change for the 21st century in scenarios C2 and C3 resulted in increased disturbance frequency and severity of damage. Over all management strategies, bark beetle damages increased from doubling to a 3.2-fold increase compared to the de-trended climate of the period 1961–1990 (scenario C1). Moreover, the share of salvage cutting from bark beetle damage relative to regular harvests increased drastically under conditions of climate change (e.g., to 21.8% under MS1 and climate scenario C3), indicating strong limitations for regular forest management in the future. The large amounts of forced salvage cutting led to a considerable decrease of standing stock at the end of the simulation period in the managed strategies, being highest under MS1 (C3: −43.1%) and lowest under MS3 (C2: −2.3%). The conversion strategy MS3 had, despite its smooth gradual conversion progress, strong advantages in terms of avoidance of bark beetle damage, featuring the lowest absolute and relative damage amounts under all climate scenarios, and the smallest increase in damage when comparing climate change scenarios (C2 and C3) to C1.

The surprisingly high simulated damages for MS2 somehow contradict the common expectation of practitioners that structured stands should be at lower risk compared to age-class forests. However, several issues need to be considered in this respect. It has to be acknowledged that the empirical data base for the bark beetle model formulation did not include uneven-aged multi-layer stands (see Lexer, 1995). This is mainly due to the very limited extent of continuous cover forestry in secondary Norway spruce forests, which in turn made a comparison of the simulated damages for MS2 with practical experiences impossible. However, the simulated damages for MS2 were fully consistent with the applied model logic. The standing stock was considerably higher than in MS1 and MS3 which increased interception losses and reduced water availability, which in turn affected stand susceptibility. Additionally, according to the predisposition rating the large Norway spruce tree dimensions in MS2 also indicate high susceptibility to bark beetle infestations (see Netherer and Nopp-Mayr, 2005). Methods to reduce forest susceptibility within MS2 could include lowering biomass accumulation levels and the introduction of suitable species such as beech, maple (*Acer pseudoplatanus* L.) or silver fir (*Abies alba* L.). It is possible that the cooler stand micro-climate observed in multi-storied stands is currently not well reflected in the disturbance submodule. This indicates a need for additional tests of model sensitivity.

Regarding C sequestration, effects of increased bark beetle damages due to climate change were similar to those for timber production. Under all managed strategies, climate change led to a distinct decrease in above and belowground C-stocks over the simulation period. This is in good agreement with other studies on the impact of disturbances on forest C sequestration, which have generally found a decreased storage potential with increasing disturbance activity. For instance, Chen et al. (2000) found fire and biotic disturbances as the most influential factors on net biome production (NBP), both having negative short and mid-term effects on C sequestration in Canadian forests. In addition, the works of Kurz and Apps (1994, 1999) and Kurz et al. (1995) generally support the fact that increases in fire and insect disturbances result in a decrease in C sequestration or even in net C emissions from forest land. In contrast, the unmanaged variant MS4 in this study even showed an increase in C storage under the climate change scenario C2 compared to C1. The increase in C storage is mainly a result of the increased growth and advanced regeneration caused by the bark beetle induced tree mortality (stand density effect), and the storage and subsequent decomposition of considerable amounts of deadwood on site. However, increasing damage intensity, as experienced under C3, led to an offset of this effect, resulting in even slightly lower net C stock changes than the baseline climate C1. These findings are in agreement with the findings of Thornley and Cannell (2000), who report the highest C storage in stands subject to moderate disturbance levels. It is also in line with Assman's rule of maximum and optimum basal area (Assmann, 1961): based on thinning trials, Assmann found highest increments in basal areas lower than the maximum basal area, but also reported decreasing increments for stand densities considerably below this optimum basal area.

4.3. Effects of disregarding bark beetle disturbance

The debate on whether to elect forest management under the Kyoto Protocol has recently highlighted the possible adverse effects of disturbances on the C balance, and has led to a discussion of how to quantify these effects (e.g., Kurz and Apps, 1994; Li et al., 2003; Thornley and Cannell, 2004; Thürig et al., 2005). We conducted two sets of simulation runs for the studied FMU: (i) UD represented the common practice in assessments (e.g., without consideration of biotic disturbances); (ii) BB explicitly included the effect of bark beetle damage. A comparison allowed for a quantification of the effects of neglecting disturbances in the analysis.

In terms of timber production, salvage of bark beetle mortality in BB resulted in a higher harvest level than in the UD series. It should, however, be taken into account that scheduled regular harvest levels were implicitly adjusted to partly compensate for removals from salvage via the definition of removal as percentage of standing stock. In close relation to changes in harvest level, the standing timber stock in year 100 was significantly lower in the BB set. However, under the moderate damages of the current climate C1, strategy MS1 had even slightly higher timber stocks with the bark beetle module applied (BB). This also corresponded to net C stock changes, which under the baseline climate (C1) were slightly higher in the BB series than in the UD series. Detailed analysis resolved this result as a combination of increased growth through an enhanced light regime due to moderate canopy opening, and advance regeneration below canopy due to the improved light regime at the forest floor triggered by the moderate bark beetle damages in the BB-series. The latter effect accelerated the regeneration and contributed to the slightly higher living tree C stocks in MS1 under climate C1 in the BB-series. The strategy MS3, which in the BB experiment under C1 had only slightly lower bark beetle damage than MS1, could not benefit from this phenomenon to the same extent since here the focus was on introducing deciduous tree species which required different regeneration procedures compared to MS1. Such complex interactions between stand density, management and timber and C stocks are not observed for large-scale disturbances like wind or fire, affecting forests at the stand or even landscape scale (e.g., Kurz et al., 1998; Li et al., 2003) rather than at the level of individual trees or groups of trees. However, this limited positive effect of disturbances inversed under the climate scenarios C2 and C3 due to increasing levels of damage resulting in distinctly lower timber stocks and C storage in all managed strategies.

Simulating unmanaged forests disregarding natural disturbances (MS4, UD) resulted in considerably different forest dynamics compared to the BB series. Aging stands with decreasing growth rate and limited regeneration (due to closed canopies) in combination with lower standing and downed deadwood pools resulted in a lower net C stock increase in the UD than in the BB series in all climate scenarios. However, these findings need to be related to the particular initial state and time horizon of the study: it could be expected that considerably older (or less densely stocked) initial stand conditions would result in considerably different stand and deadwood dynamics (age-related mortality). Consequently, simulating the stand dynamics over an extended time horizon one could expect a diminishing influence of these factors.

Soil C storage was higher in the BB series compared to the UD series in all management strategies and climate scenarios, but only compensated for a small share of the eventual losses in aboveground C pools. This result is supported by recent findings concerning soil C dynamics after natural and human disturbances, pointing at the importance of slash input to the forest floor and finding even positive soil C effects from limited disturbances (Lal, 2005). However, several other effects associated with disturbances (e.g., changes in forest floor temperature, mixing of litter layer, erosion) are currently not captured in the decomposition model, and potentially hamper the reliability of the approach with respect to detailed soil processes. Thus, a future focus in model improvement needs to be given to soil C dynamics (Overby et al., 2003; Yanai et al., 2003).

Overall, the effect of disregarding biotic disturbances on C storage in the forest was considerable. This is clearly demonstrated for the strategies MS2 and MS3 under climate C3. Whereas in the simulations without bark beetle disturbances (UD) MS2 resulted in a surplus of +21.1 tC ha^{-1} over 100 years compared to MS3, this higher accumulation diminished to +2.3 tC ha^{-1} for the BB series where bark beetle disturbances were explicitly included.

4.4. Conclusion

The study agrees with others (e.g., Li et al., 2003) about the importance of biotic disturbances on forest functions in both managed and unmanaged forest ecosystems. Our findings support the general expectation that under climatic change damage frequency and intensity from poikilothermal insects may increase (e.g., Ayres and Lombardero, 2000, Bale et al., 2002). The high estimates for salvage removals (following bark-beetle induced mortality) under scenarios of climatic change strongly point at the need to mitigate the impact of climate change in secondary Norway spruce forests. To meet the multiple demands on Central European sustainable forest management, biotic disturbances should be included in impact assessments and adaptive management planning schemes. With regard to the climate mitigation function of forests our results show that effects of bark beetle infestations on the C budget may be considerable.

Acknowledgements

The work was partly funded by the Austrian Federal Ministry for Agriculture, Forestry, Environment and Water Management, Section Environment (grant GZ 54 3895/140-V/4/03) and the European Union project INSEA (“Integrated Sink Enhancement Assessment”, grant SSPI-CT-2003/503614). We are grateful to H. Kleinszig and G. Kleinszig for their long-term support of various research activities in their property “Wolschartwald”. Furthermore we would like to thank W.A. Kurz and an anonymous reviewer for valuable input and constructive criticism helping to improve an earlier version of the manuscript.

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