MODELLING FOREST DYNAMICS IN VIRGIN AND MANAGED FOREST STANDS

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ABSTRACT

Modelling forest dynamics in virgin and managed forest stands

The main goal of the presented work was to evaluate if a biogeochemical modelling environment is an appropriate tool to assess the sustainability of forest ecosystems and forest management. In the study we used a species-specific adaptation of the biogeochemical model BIOME-BGC. The validation of the self-initialisation spinup procedure was performed using the data from two virgin forests (Rothwald in Austria, and Babia hora in Slovakia). The results showed, that the original self-initialisation of the model produced an unrealistic steady state of the forest ecosystem for the conditions in Central Europe, unless the fire mortality was switched on. As a reason for the unrealistic performance we identified the shortcoming of the model to account for the succession dynamics of natural forests. Therefore, we incorporated a new dynamic mortality model that mimics a simple succession cycle defined by its length, minimum and maximum mortality within one cycle. After the implementation of the dynamic mortality, the spinup procedure produces the steady state that corresponds with the equilibrium observable in Central European virgin forests.

In the second part of the work we tested and evaluated the applicability of a species-specific biogeochemical mechanistic model to assess the impact of different harvesting scenarios after thinning. For this task we used the data from three management sites (Hartberg, Wilhelmsburg and Bad Zell), on which three harvesting scenarios were applied: (1) whole tree harvest, (2) whole tree harvest after one vegetation period, i.e. without needles, and (3) commercial stem wood harvest. The analyses revealed that the long-term modelled responses of the forest ecosystem on applied forest management mirror field observations, but for correct reproduction of the short-term responses to external influences further research is needed.

Keywords: biogeochemical modelling, forest dynamics, mortality, virgin forest, sustainability, biomass removal

ABSTRAKT

Modellierung der Walddynamik in Urwäldern und bewirtschafteten Wäldern

Hauptziel der vorliegenden Arbeit war es zu evaluieren, ob die biogeochemische (BGC) Modellierungsumgebung ein geeignetes Instrument für die Bestimmung der Nachhaltigkeit des Forstökosystems und des Forstmanagements ist. Für die Arbeit benutzten wir die baumartenspezifische Anpassung des biogeochemischen Modells BIOME-BGC. Die Validierung der Selbstinitialisierungsprozedur (Spinup) wurde mit den Daten aus zwei Urwäldern (Rothwald in Österreich und Babia hora in der Slowakei) durchgeführt. Die Modellberechnungen haben gezeigt, dass das Modell einen für mitteleuropäische Bedingungen unrealistischen Gleichgewichtszustand des Waldökosystems hervorbringt, wenn die Feuermortalität bei der Simulation auf Null gesetzt ist. Den Grund für dieses unrealistische Verhalten sahen wir in dem Umstand, dass das Modell die Sukzessionsdynamik in Naturwäldern nicht berücksichtigt. Deshalb haben wir in das bestehende Modell ein neues dynamisches Mortalitätsmodell implementiert. Dieses Mortalitätsmodell bildet den einfachen Sukzessionzyklus nach, der durch die Länge, die minimale und die maximale Mortalitätsrate definiert ist. Nach der Einführung der dynamischen Mortalität in das Modell entspricht der simulierte Gleichgewichtszustand, der durch die Selbstinitialisierungsprozedur erreicht wurde, jenem Zustand, der auf einem Waldstandort in Mitteleuropa ohne menschlichen Einfluß möglich ist.

Im zweiten Teil der Arbeit haben wir die Benutzung des biogeochemisch-mechanistischen Modells für die Evaluierung des langfristigen Einflusses von Biomassenentzug nach der Durchforstung auf das Waldökosystem überprüft. Für diese Aufgabe haben wir die Daten von drei bewirtschafteten Waldstandorten in Österreich benutzt (Hartberg, Bad Zell und Wilhelmsburg), an denen drei Behandlungsvarianten zur Anwendung gebracht wurden: (1) Entnahme der ganzen Bäume inklusive Äste und Nadeln unmittelbar nach dem Fällen, (2) Entnahme der ganzen Bäume ein Jahr nach der Schlägerung, so-dass die Nadeln im Bestand verblieben, und (3) Entnahme des Schaftholzes. Die Analysen haben gezeigt, dass die modellierten langfristigen Reaktionen des Waldökosystems auf den menschlichen Eingriff mit den Beobachtungen übereinstimmen, aber für die korrekte Wiedergabe der unmittelbaren Reaktionen weitere Forschungsarbeit notwendig ist.

Schlagworte: biogeochemische Modellierung, Walddynamik, Mortalität, Urwald, Nachhaltigkeit, Biomassenentzug

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1. INTRODUCTION

Forestry is currently changing from a pure wood production oriented field to multi-functional area, which should satisfy various demands of society. This kind of multiple use forestry requires a so called sustainable forest management, that ensures the sustainable production of woody and non-woody products as well as the wide range of environmental services including protection of natural resources, conservation of biodiversity, recreation and tourism etc. (FAO 1994). To meet all these requirements, the continuity of the forest life needs to be secured. According to Berlyn and Ashton (1996), this can be achieved by a management, that is based on a continued functionality of the crucial natural processes that drive forest ecosystems. Such a continuity is in nature represented by virgin forests.

1.1 VIRGIN FORESTS

The term virgin (old-growth, primeval, pristine) forests encompasses forest ecosystems, that were developed untouched by human under natural conditions (Parviainen 2003), i.e. such forests, that have not been influenced by any direct human activities. Therefore, these forests are original in terms of their species composition and structure (Peterken 1996). The community is composed of those species for which the combination of ecological factors (climate, site and soil conditions etc.) is suitable in a particular time and space.

The largest and the most precious virgin forests to life on earth are undoubtedly rainforests. However, virgin forests exist also in other parts of the world. Unfortunately, in Western and Central Europe only few remnants of virgin forests can be found since these areas were largely colonised from early years of human civilisation (Průša 1990, Bastian and Bernhardt 1993, Peterken 1996). Some of the current European virgin forests were preserved as hunting areas, e.g. Fontainebleau in France (Schuck et al. 1994), but most of them survived because of their inaccessibility (Peterken 1996). Therefore, the majority of central European virgin forests are located on remote areas and steep slopes (Korpeľ 1995, Parviainen 2003), that were neither interesting for cultivation nor for wood production (Peterken 1996). The current area of the compact virgin forest ecosystems in Central Europe varies from several hundreds square meters to nearly one thousand hectares. Most of them are however of smaller size; approximately 100 to 500 hectares.

Virgin forests represent the climax stadium of ecosystems in Central Europe (Vacek 2003). The climax is characterised as a dynamic equilibrium, where the amount of fixed energy equals the amount of consumed energy, whereby the equilibrium is determined by the climate conditions (Križová et al. 1992). According to Korpeľ (1995), a climax forest is a self-sustaining ecosystem with regard to its biology, production and long-term development. The climax forest stand is hence characterised by long-term average growing stock, "zero" increment and occurrence of all developmental stages (Vacek 2003). Korpeľ concludes that in Central European conditions such an equilibrium can be observed on an area of 30 - 60 hectares depending on the geographic area and the forest type.

A forest is a dynamic living system that develops as each living organism over time. The temporal development of a forest stand or a stand dynamics is usually interpreted as a sequence of several developmental or succession stages (Peterken 1996). Natural stand dynamic of virgin forests was studied by several authors, e.g. Leibundgut (1959), Zukrigl et al. (1963), Mayer et al. (1972), Korpeľ (1989), Oliver and Larson (1996), etc. Based on the research studies each author created its own classification scheme of the natural development.

In general, two types of development cycles can be distinguished: a large and a small cycle

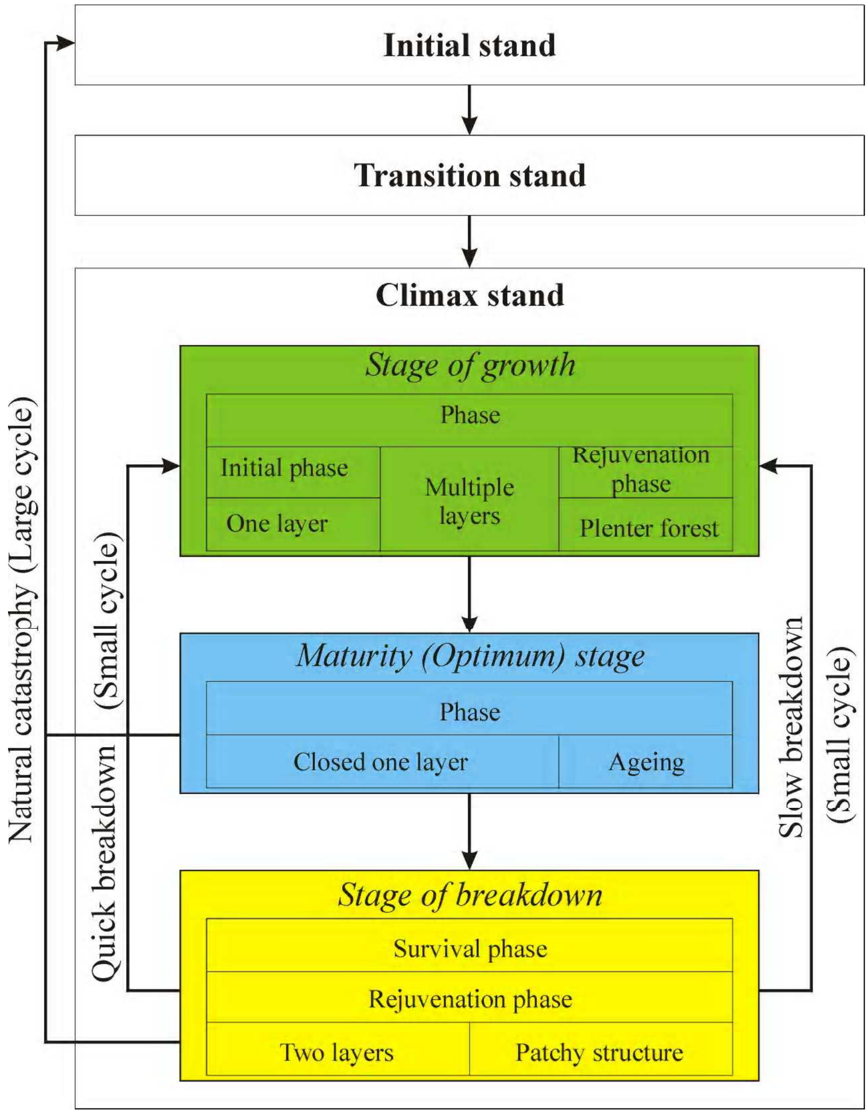

Figure 1: Development of a climax forest as defined by Korpeľ (1995).

(Figure 1, Schuck et al. 1994, Korpeľ 1995, Oliver and Larson 1996, Peterken 1996). An ecosystem follows the large cycle after large-scale (major, catastrophic) disturbances, e.g. fire, wind throw, etc., whereas we talk about the small cycle, when the ecosystem dynamic is driven by intrinsic characteristics, such as competition or senescence, or only minor external disturbances.

A major disturbance radically changes the situation on the site, whereby the kind and the intensity of changes depends on the disturbance factor and its severity. Usually, the upper tree layer is completely destroyed, which creates a space for the initiation of new generation. If the disturbance was too severe, the whole succession cycle starts with the pioneer vegetation, which is followed by subsequent development stages until the climax stage is achieved (Figure 1).

On the other hand, within the small cycle only a small number of trees die or are killed at the same time. After such events smaller or larger gaps occur within the stand, where the new generation has suitable conditions for its growth. This type of the developmental cycle was mostly observed in the Central European virgin forests (Zukrigl et al. 1963, Mayer et al. 1972, Průša 1990, Veblen 1992, Korpeľ 1995, Emborg et al. 2000 and others) and is sometimes described as a mosaic cycle (Remmert 1991). As already mentioned, each scientific group created its own description of natural forest stand development derived from the results from particular forest stands. Based on the earlier studies as well as own observations, Korpeľ (1989) distinguishes three main development stages (Figures 1 and 2):

1. growing-up stage (stage of growth), during which the stand is composed of three vertical tree layers. Young trees grow rapidly and are very vital. The crown closure is considerable. The number of trees and stand volume is moderate and the mortality rate is low. The gaps after the death of larger trees are quickly reoccupied with the new generation.
2. optimal stage (stage of maturity), defined by the maximum stand volume and a small number of trees per unit area. Due to the decreasing vitality of the trees, height increment is almost zero and volume growth is considerably decelerated. The mortality rate is the lowest, the multiple vertical layers vanish and one-layered vertical structure is developed, which resembles an even-aged management stand.
3. stage of breakdown (disintegration, destruction) described as the stage when the stand volume decreases rapidly due to the high mortality of large trees, which cannot be balanced by the higher increments of remaining old trees and individuals of the new generation. The stand has a patchy structure with groups of old trees, newly created gaps and patches with new regeneration.

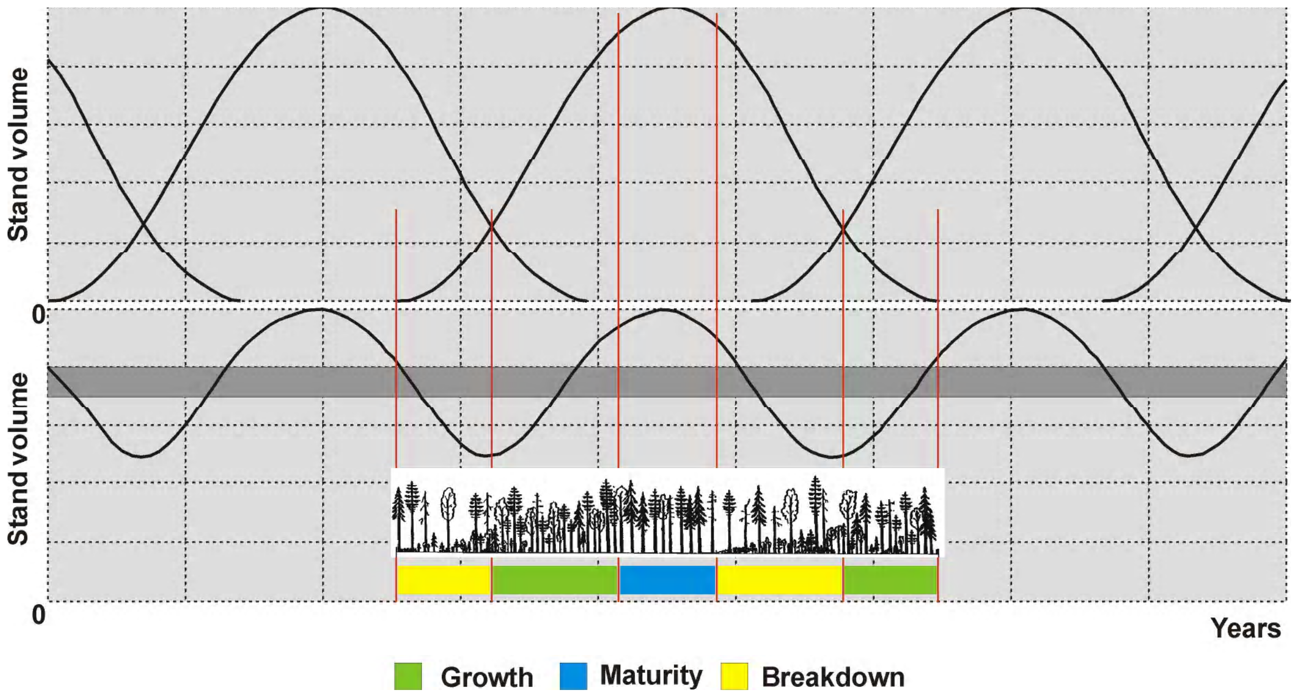

Figure 2: The temporal development of stand volume in a virgin forest following the small development cycle with the identification and the sequence of the three development stages (taken from Korpeľ 1995). The dark grey strip represents the average long-term stand volume of the climax forest.

Within each development stage Korpeľ recognises several development phases (Figure 1). Although other authors define the development cycle and the stages/phases differently, all the systems try to describe the changes of a forest ecosystem over time. In this study, we decided to use the given classification by Korpeľ.

Virgin forests provide us with valuable information about the natural potential for the long-term continuity of the forest life, or in other words about a biological sustainability that can be achieved without a human interference.

However, regarding active forestry, where apart from biological and ecological issues also the economic aspects play a major role (Landsberg 2003), the sustainability needs to be understood in a much broader sense than just the preservation of the forest life. The principal objective of sustainable forest management is hence to ensure a sustainable growth and yield of several forestry products, e.g. timber, game, recreation etc., simultaneously (Berlyn and Ashton 1996). This complexity raises new questions in assessing what is sustainable. Already the quantification of sustainable harvesting, which foresters until recently understood as “sustainability” (Oswald 1997), using various indices or ratios of successive harvests was found to be limiting for the evaluation of the long-term effect of the applied harvesting operation (Vanclay 1996). Botkin (1993) stated that for the correct assessment of sustainability the studies covering a time span of 400 years are needed.

Such long-term data are, however, not available. The longest time series come from Germany and encompass approximately 100 years (Pretzsch 2002). Due to the lack of long-term measurements, the sustainability of forest management practices is in most classical forestry studies assessed by applying different management scenarios to nearby forest stands and comparing their effect on these forest ecosystems. Although such works can provide us with important information about the responses of a given ecosystem to applied management, the conclusions do not necessarily have to be correct, since the collected data are influenced by various sources of error that cannot be excluded in field trials, e.g. different microsite conditions. Therefore, the results of comparable studies are often diverging or even controversial due to differences in geographic locations, sampling design, methodology etc.. For example, there exists a number of works dealing with the influence of different harvesting scenarios, usually stem wood harvest versus whole tree harvests and their variants, on the remaining or the future forest stands. While one group of scientists did not reveal any significant differences between the forests subjected to different harvesting scenarios (e.g. Hendrickson 1988, Egnell and Leijon 1997, Mård 1998), others reported that the applied harvesting scenario has a significant effect on future stand development (e.g. Sterba 1988, Dyck et al. 1994, Proe and Dutch 1994, Jacobson et al. 2000, Nord-Larsen 2002).

Moreover, the data collected for such studies usually comprise only the values of stand volume with no information about other ecosystem parameters, e.g. litter or soil, that are known to be particularly sensitive to changes in the ecosystem structures (White 1974, Binkley 1984, Olsson et al. 1996). Thus, the comparison of these kinds of data does not thoroughly address the sustainability of an ecosystem under a specific forest management.

Although additional data collection can compensate for the shortage of such information, field measurements are often very time consuming and expensive. Therefore, forest growth and yield models are more and more used as diagnostic tools to assess the impact of natural or human induced changes on a forest ecosystem (Aber et al. 1978, Morris et al. 1997, Rolff and Ågren 1999, Peng et al. 2002, Raulier et al. 2003).

1.2 MODELLING

Forest growth and yield modelling has a long history that dates back to the last century, when the first yield tables were constructed. Since then, this field has developed rapidly. Expanding computer technology, recent advancements in physiological and ecological research has allowed modellers to construct more complex models that account for species composition, inner stand structure, underlying processes, species specific demands etc. Furthermore, modelling objectives have shifted from creating forest management support by estimation of future yields towards the explanation of natural dynamics and processes ongoing in forest ecosystems. Thus, we can now distinguish three major groups within forest ecosystem modelling (Hasenauer et al. 2000): (1) empirical (management) models, (2) successional (gap) models and (3) mechanistic (biogeochemical, process-based) models (Figure 3).

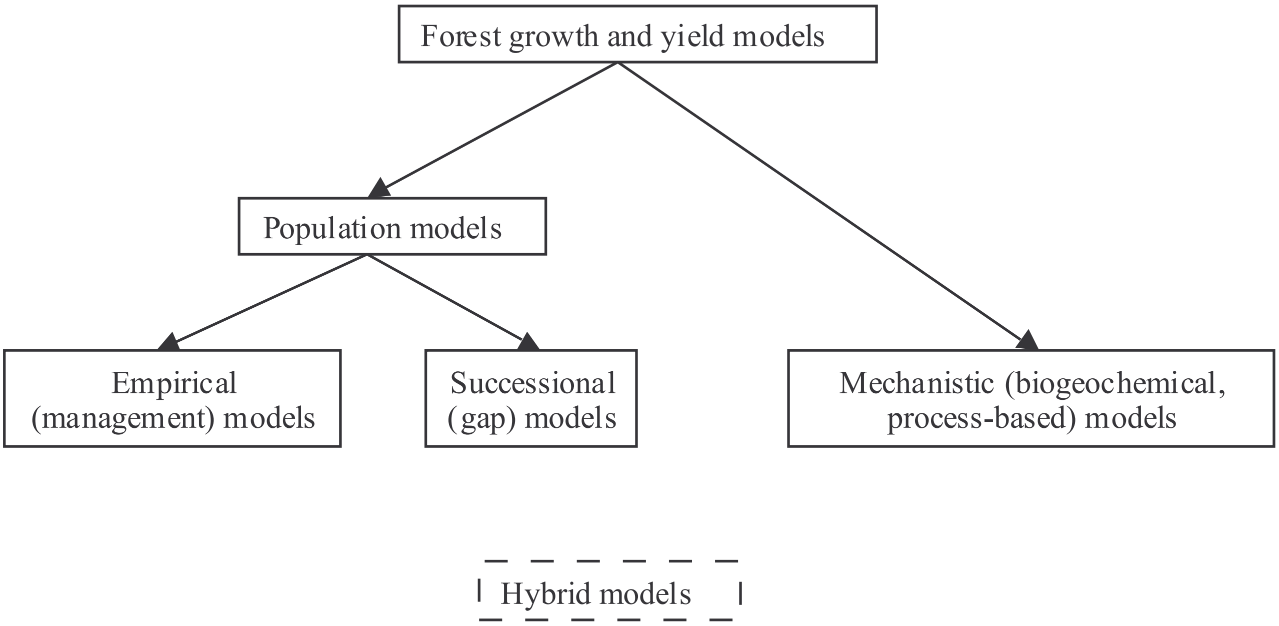

Figure 3: Classification of forest growth and yield models (according to Hasenauer et al. 2000).

1.2.1 Empirical models

Empirical models have been widely used for growth and yield predictions under different silvicultural treatments to assist forest managers in decision-making. Their construction is based on statistical regression techniques, which requires exceeding data sets usually coming from forest inventories or permanent inventory plots. The main goal of this modelling approach is to develop height and diameter increment functions and mortality functions for each species assuming that they depend on tree and/or stand characteristics.

According to the required input data and produced output, this category can be further divided into whole stand models, size-class distribution models and individual tree models (see Vanclay 1994). The simplest ones are the whole stand models, of which the most well-known are yield tables (e.g. Schwappach 1890, Assmann and Franz 1965, Halaj 1987). However, their use is restricted to pure, fully-stocked and even-aged stands. On the contrary, individual tree models are able to simulate the growth of mixed and uneven-aged stands. In addition, these models enable the user to compare the impact of different silvicultural treatments on forest growth and hence help him in management decisions. Examples of such models are SILVA (Pretzsch 1992, Pretzsch et al. 2002), MOSES (Hasenauer 1994), B-WERT (Nagel 1995) or PROGNAUS (Sterba et al. 1995, Monserud et al. 1997, Hasenauer 2000).

1.2.2 Gap models

Successional models simulate the natural development of forest stands in terms of species composition. Unlike empirical management models, the growth of the trees in the succcessional models depends on the physiological amplitude of a particular tree species defined by site specific factors, such as light, temperature, water and nutrients (Botkin et al. 1972, Hasenauer et al. 2000). They are often called gap models, because they simulate the stand dynamics through the "gaps" that occur when a tree or a group of trees dies. The models usually simulate the development of individual trees, although an alternative approach simulating small groups of trees, so called cohort-based models, also exists (Reed 1980). One of the main difficulties to apply gap models for forest management studies is their assumption of constant height/diameter relationship regardless of forest stand density.

The first gap model was JABOWA developed by Botkin et al. (1972). All the subsequent gap models (e.g. FORET (Shugart and West 1977), FORSKA (Prentice et al. 1993), PICUS (Lexer 2001) etc.) use largely its logic and are therefore often named as JABOWA models. For further details concerning this category see e.g. Hasenauer et al. (2000).

1.2.3 Biogeochemical models

Mechanistic or biogeochemical (BGC) models were primarily directed at understanding the biological, physical and chemical (from this the term biogeochemical) relationships within ecosystems. They are considered mechanistic because they are designed to calculate the flux of energy, water and nutrients (above all carbon and nitrogen) through an ecosystem. Therefore, their development closely follows the improvements of knowledge about the underlying processes, such as photosynthesis, respiration, litter fall, decomposition etc.

BGC-models incorporate a mechanistic description of the interactions between plants and the surrounding environment based on the current understanding of the key mechanisms (Waring and Running 1998). Consequently, they are explicitly designed to be responsive to changes in environmental conditions including soil and hydrological processes (VEMAP Members 1995), which explains why they are sometimes called process-based models (Korzukhin et al. 1996).

Usually such models operate on a daily (Running and Coughlan 1988) or monthly basis (Landsberg and Waring 1997). They require daily meteorological input data including minimum and maximum temperatures, precipitation, dew point and incident solar radiation. Furthermore, leaf area index (LAI) and soil water holding capacity have to be initialised for calculating canopy interception and evaporation, transpiration, drainage and runoff of water, photosynthesis, growth and maintenance respiration, allocation, litter decomposition, deposition, uptake, litterfall and mineralization of nitrogen.

The main simulation output of BGC-models is the Net Primary Production (NPP) expressed in grams of carbon per m^2 [gC/m^2]. In addition, they may produce up to 500 different output parameters describing the water and nutrient cycles in a given ecosystem at different time levels (day, month, year) and the amount of carbon stored in the different compartments (e.g. stem, roots, leaves) of an ecosystem.

Examples of the mechanistic models are FOREST-BGC (Running and Coughlan 1988), BIOME-BGC (Thornton 1998, White et al. 2000), 3-PGC (Landsberg and Waring 1997), LPJ (Bonan et al. 2003, Sitch et al. 2003) etc. Within the category of BGC-models there are also subgroups working at the tree, stand or ecosystem level (Korzukhin et al. 1996). However, the most common approach is to simulate ecosystem processes on a per unit area basis.

Mechanistic models were long considered as scientific tools because of their high complexity. However, many authors nowadays believe that possible implementation of BGC models into practical forest management either as models working individually (Bartelink 2000) or linked with empirical (e.g. Amateis 1994, Korol et al. 1996, Korzukhin et al. 1996, Battaglia and Sands 1998, Mäkelä et al. 2000, Peng 2000) or gap models (Lindner et al. 1997, Talkkari et al. 1999) may improve growth predictions. The most common argument in the favour of their practical use is that BGC-models explicitly address changing climatic and site conditions, whereas empirical and successional models treat them as constant characteristics.

An example of a management-oriented BGC-model is the individual tree growth model COMMIX (COMpetition in MIXtures) developed by Bartelink (2000). The model simulates the growth of individual trees in stands mechanistically considering the availability of resources, whereby radiation is considered to be the crucial factor influencing the growth rate of trees and stand development. Including three thinning scenarios (systematic thinning, thinning from below and above), the model also offers a user a possibility to investigate the effects of different silvicultural treatments. The practical applicability of this model is, however, limited because apart from the usually available tree characteristics (e.g. species, tree height, crown base height), it also requires information about the position of the trees within the stand (stem co-ordinates), its crown shape and its leaf area.

Large data requirements are thought to be the most serious drawback of BGC-models. On the other hand, because of their nature they are not restricted to specific site conditions of parameterisation data sets as is the case with empirical tree growth models. Those have, however, the advantage of taking into account stand structure and different management regimes.

1.2.4 Hybrid models

Considering the modelling opportunities of the three above mentioned approaches, their coupling and creating so called hybrid models (Figure 3) has become of increasing interest. It is assumed that this approach may allow us to efficiently utilise the best features of different modelling types (Battaglia and Sands 1998). The produced output of such models may serve forest managers as well as ecologists, as it provides the user not only with the information about the stand production (produced wood biomass), but also with the levels of nutrients stored in different compartments of ecosystem including soil. Models such as TREE-BGC (Korol et al. 1995, 1996), FORSANA (Grote and Erhard 1999), PROMOD (Battaglia et al. 1999), can be named as examples of the hybrid models.

1.3 OBJECTIVES OF THE STUDY

Although the utilisation of the models as diagnostic tools seems to be very challenging, one should always be aware of their limitations. Models are in general defined as "a simplified description of reality" (Shugart 1998) meaning that not all ecosystem processes are included in the model, or that the processes are often simplified. Their simplification can reach such an extent that in some cases models can produce unrealistic output. Moreover, models inevitably involve many assumptions, which were not formally stated and have not been explicitly tested (Vanclay 2003).

Thus, before a certain model is used for a specific task, its behaviour should be first evaluated to ensure that the model is able to answer the questions of interest. Based on this comprehension, the goals of the presented study, in which we use a biogeochemical mechanistic model, were defined.

The work follows two major aims. First, using the data collected in two Central European virgin forests we evaluate the steady state that is simulated in the biogeochemical environment. This analysis should answer the following questions:

(1) if the model steady state is comparable with the equilibrium that can be observed in nature and thus,

(2) if the steady state obtained from the model can be regarded as the natural potential of the particular site under given climate conditions, that can be achieved without human interference, and

(3) if the model can reproduce the main processes in such a complex ecosystem as a virgin forest correctly.

In the second part, we test the applicability of the selected biogeochemical model for assessing the effects of biomass removal on a forest ecosystem. For this purpose we use the data from three locations in Austria, on which three different harvesting scenarios were applied after thinning operations. Within this analysis we are particularly interested

(1) if the formal model implementation adequately addresses the reactions of the forest ecosystem after a human interference and hence,

(2) if the model can be used as a diagnostic tool to analyse the impact of different harvesting scenarios on the forest growth and thus, as a support in future decision making.

2. METHODS

2.1 MODEL DESCRIPTION

In this study we use a species-specific adaptation (Pietsch and Hasenauer 2002, see Section 2.1.4 for details) of the model BIOME-BGC (BioGeoChemistry, Thornton 1998). This model belongs to the category of biogeochemical models (see Section 1.2.3), that simulate main biogeochemical and hydrologic processes in the ecosystem. The model has been developed by the Numerical Terradynamic Simulation Group at the University of Montana, U.S.A. (Thornton 1998, White 1999) from its predecessor FOREST-BGC (Running and Gower 1991). In contrast to the model FOREST-BGC, which was able to simulate only the forest ecosystems, BIOME-BGC can model seven different forest and non-forest terrestrial vegetation types: deciduous broadleaf forest, deciduous needle-leaf forest, evergreen broadleaf forest (subtropical and tropical) and evergreen needle-leaf forest, C3 grasses and C4 grasses, and evergreen shrubs (White et al. 2000). Moreover, the algorithms implemented in BIOME-BGC have been refined in comparison to those used in FOREST-BGC.

The model BIOME-BGC was used with success in many studies, e.g. for the assessment of ecosystem productivity (Kimball et al. 1997, Kimball et al. 2000), for studying the causes of climate change (White et al. 1999, Jager et al. 2000, Churkina and Running 2000), analysing the carbon dynamics in the ecosystems (Churkina et al. 2003), coupling with remote sensing data (Kimball et al. 2000), comparison with other models (Coops et al. 2001) etc.

BIOME-BGC estimates the cycles of carbon, nitrogen, water and energy in the ecosystem based on the interactions between the atmosphere, plant and soil (Thornton et al. 2002). The processes that are modelled include: interception, evaporation, transpiration, water drainage and outflow, radiation absorption, photosynthesis, respiration, nitrogen uptake and loss from the soil, growth and mortality, litter fall, decomposition of organic material. Figure 4 presents a simplified scheme of the carbon and nitrogen dynamics as implemented in the model. Since the detailed description of individual processes can be found elsewhere (e.g. Kimball et al. 1997, Kimball et al. 2000, Coops et al. 2001, Thornton et al. 2002), we present here only those that are of a special interest to our work.

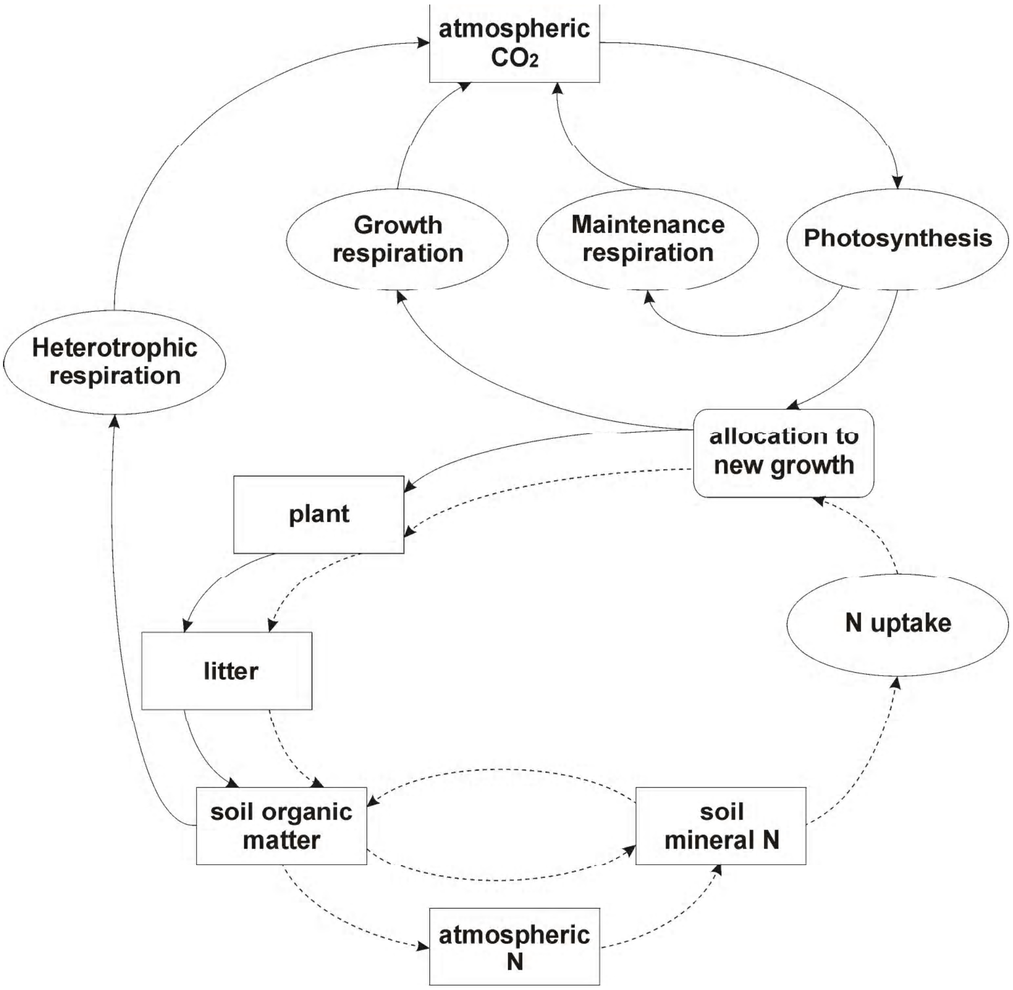

Figure 4: Carbon (solid lines) and nitrogen (dashed lines) cycle as simulated by the model BIOME-BGC (taken from Thornton et al. 2002).

Gross primary production (GPP) represents the total gain of carbon to the system by net photosynthesis. Photosynthesis is calculated using the Farquhar photosynthesis routine (Farquhar et al. 1980). Principal factors controlling photosynthetic assimilation are canopy conductance to CO_2, leaf maintenance respiration, and daily meteorological conditions (air pressure, air temperature, solar irradiance. Total respiration from the system is given as the carbon loss due to autotrophic and heterotrophic respiration. Autotrophic respiration consists of the maintenance and growth respiration (see Ryan 1991). Maintenance respiration is calculated from mean daily air temperature and prescribed leaf, root and sapwood carbon pools using an exponentially increasing function of respiration with temperature (Kimball et al. 1997). Growth respiration is assumed to be a constant proportion (30%) of daily allocated carbon. Heterotrophic respiration in the model represents the respiration of soil microorganisms. It is estimated as a proportion of prescribed litter and soil pools and depends on soil temperature and soil water potential. GPP reduced for the autotrophic respiration gives the net primary production (NPP), which is dynamically partitioned into the different plant compartments (Figure 5) in dependence on the availability of soil mineral nitrogen for plant uptake.

In the model, several sources of soil mineral nitrogen exist: atmospheric deposition, nitrogen fixation and decomposition fluxes. On the other hand, plant uptake, microbial immobilisation and volatile and leaching losses resemble the sinks of mineral nitrogen. Plant nitrogen demand is defined by NPP. The immobilisation demand is given by the amount of decomposable material and the decomposition rates. Decomposition rates of litter and soil pools are regulated by C:N ratios of litter components (which depend on the inputs from plants), soil temperature (Lloyd and Taylor 1994) and soil moisture (Andren and Paustian 1987). They determine the magnitude of heterotrophic respiration and nitrogen mineralisation. Coarse woody debris can be in the model only physically degraded, whereby the rate of its defragmentation is also driven by soil temperature and soil moisture. The defragmented coarse woody debris is assigned to the litter pools, where it undergoes chemical degradation.

During mineralisation, 1% of the nitrogen is released into the atmosphere by the denitrification processes. The second option for nitrogen release results from the denitrification processes of excessive mineral nitrogen and depends on the amount of nitrogen needed for plant and microorganism uptake. In the model it is assumed that 50% of the excessive mineral nitrogen is released into the atmosphere while the rest (50%) remains in the soil. In addition, excessive mineral nitrogen can be lost from the system due to leaching. Leaching is regulated by the presumed proportion of the soil mineral nitrogen which is soluble, the soil water content, and the outflow.

If the sum of microbial and plant uptake demand is equal to the amount of available soil mineral nitrogen, no additional denitrification losses occur. In situations, where the available soil mineral nitrogen is lower than the total demand, plants and microorganisms compete for soil mineral nitrogen according to the following principles: Plant demand depends on NPP. Microbial demand depends on the amount of material available for decomposition as well as the decomposition rate, which is driven by temperature and soil moisture. Summarising both numbers and comparing it with the available mineral nitrogen allows us to calculate a supply/demand ratio, which is used for weighting the final available nitrogen for plant uptake and the microorganisms. Note that in the model the population density of microorganisms is defined by the amount of decomposition material, which then defines the microbial nitrogen demand.

The only input source of water in the model is precipitation. Based on air temperature threshold of 0°C it is categorised either as rain or snow. Rainfall is intercepted by the canopy using a prescribed interception coefficient based on leaf area, which is defined by leaf area index LAI. All snowfall and remaining rainfall is passed directly to surface. Evapotranspiration is calculated as the sum of transpiration and evaporation from surface, snowpack and canopy. Both evaporation and transpiration processes are estimated using a modified Penman-Monteith equation (Running and Hunt 1993). A one-dimensional bucket model defines the soil water holding capacity. If the capacity is exceeded, outflow occurs. Soil water storage capacity is a function of soil type and the depth of the rooting zone.

Mortality

Mortality is a complex phenomenon, that occurs as a result of stress factors and their interactions (Franklin et al. 1987). According to the effect that causes dying and its consequences, two types of mortality are usually distinguished: regular and catastrophic (irregular) mortality (Lee 1971, Monserud 1976, Dobbertin 1992, Vanclay 1994, Oliver and Larson 1996). Regular mortality is the result of senescence and competition for sources, such as light, water and nutrients. Ecological perturbations, e.g. fire, wind-throws, great outbreaks of insects or germes, induce a catastrophic mortality.

BIOME-BGC accounts for the regular mortality due to competition and aging, and fire mortality, which in the model is also assumed to occur on a regular basis rather than as a catastrophic event. Both regular and fire mortality rates are given within the list of ecophysiological parameters (Figure 6, Appendix 2). Regular mortality is defined as the fraction of the whole plant that dies or is consumed in one year. The predefined value of the annual mortality rate in the forest ecosystems is set to 0.005 in the model, i.e. 0.5% of the above- and the below-ground carbon content of vegetation is lost per year due to branch and tree mortality. This value is based on the single field experiment (White 1999, White et al. 2000). Dead parts of the plant are assigned to the pools of coarse woody debris or litter.

Since the model BIOME-BGC was developed in America, where fire is an important driving factor of the natural dynamics, fire mortality is also included in the simulations. Despite the catastrophic character of fire in nature, fire induced mortality is modelled as a regular event taking place every year. Model fire mortality rate is defined as the ratio of the whole plant that is burnt per year. This ratio specifies also the amount of coarse woody debris and litter lost in a fire. Unlike regular mortality, carbon and nutrient losses due to fire are permanent losses from the ecosystem. The rates of fire mortality were estimated for each biome from the data published by Aber and Melillo 1991 (in White et al. 2000). The fire mortality in evergreen needle leaf and deciduous broadleaf forests is set to 0.50% and 0.25% per year, respectively.

The model simulates a spatial unit (of a size of one square meter), which assigns it into the category of stand-level models. A stand is a simplified big tree divided into the several compartments: leaf, stem, coarse root and fine root (Figure 5). The canopy represented as a big leaf

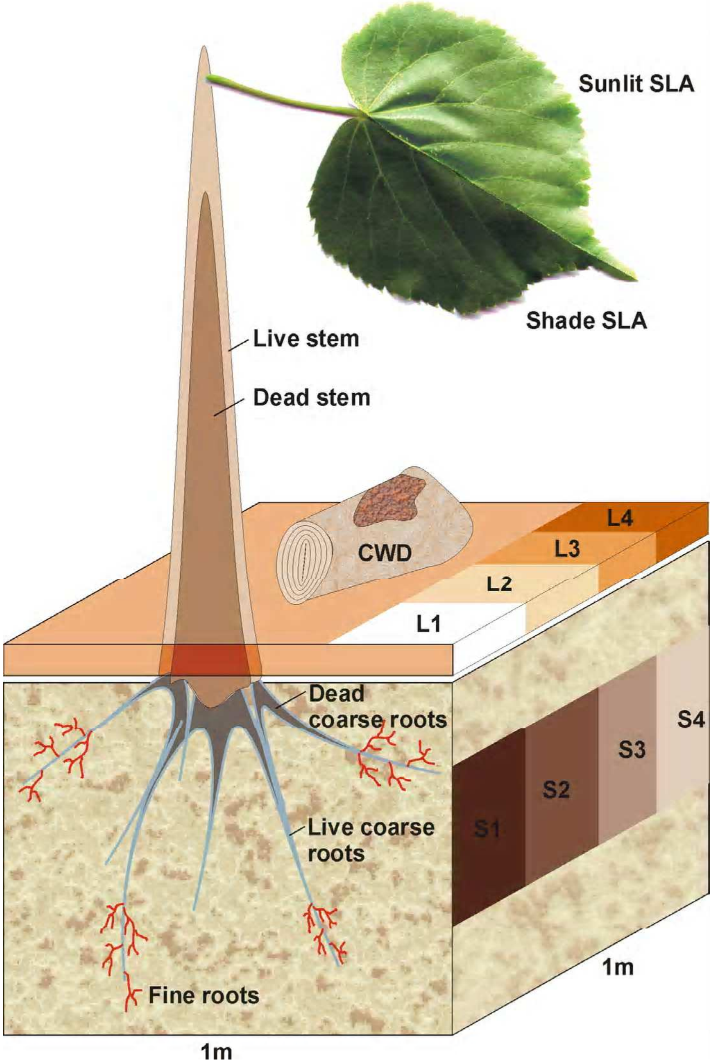

Figure 5: Forest ecosystem in the model BIOME-BGC, where CWD is coarse woody debris, L1-L4 litter and S1-S4 soil pools.

is assumed to be singular and homogeneous in that all units of canopy leaf area are characterised by canopy-averaged flux and state variables. Similarly, the belowground area is assessed and modelled as a single unit of homogeneous soil with a specified depth and uniform rooting density. The pool coarse woody debris (CWD) is composed of the dead aboveground woody material and the belowground dead coarse roots. Forest floor, in the model referred to as litter, and soil are divided into four different pools (L1-L4 and S1-S4) according to the chemical structure that pre-defines their decomposition rate. L1 and S1 represent the fastest decomposable material (so called labile pool). L2 and L3 are cellulose litter pools and L4 is lignin litter. S2 is a medium recycling pool, S3 slow microbial decomposable material and S4 represents the recalcitrant soil organic mass (SOM).

The model operates on a daily time step, which was proved to be suitable for applications with a medium to high spatial resolution because of the moderate demand on input data and computation (Chen et al. 1999).

2.1.1 Input data

The fundamental environmental drivers of ecological processes in the model are the daily meteorological data: air minimum and maximum temperature, daily total precipitation, humidity defined as daytime average vapour pressure deficit, daytime average incident solar radiation and day length, and site descriptive characteristics: geographic coordinates, elevation, soil depth, soil texture determined as the proportions of sand, silt and clay, atmospheric nitrogen deposition and CO_2 concentration (Figure 6, Appendix 1). Daily climate data are rarely available for a particular location. Therefore, they are either approximated with the data from a nearby climate station or estimated from one or more surrounding climate stations using the interpolation models, e.g. MT-CLIM (Running et al. 1987) or DAYMET (Thornton et al. 1997) (see Chapter 2.2 for details). Soil depth is defined as an effective depth that determines the depth of rooting.

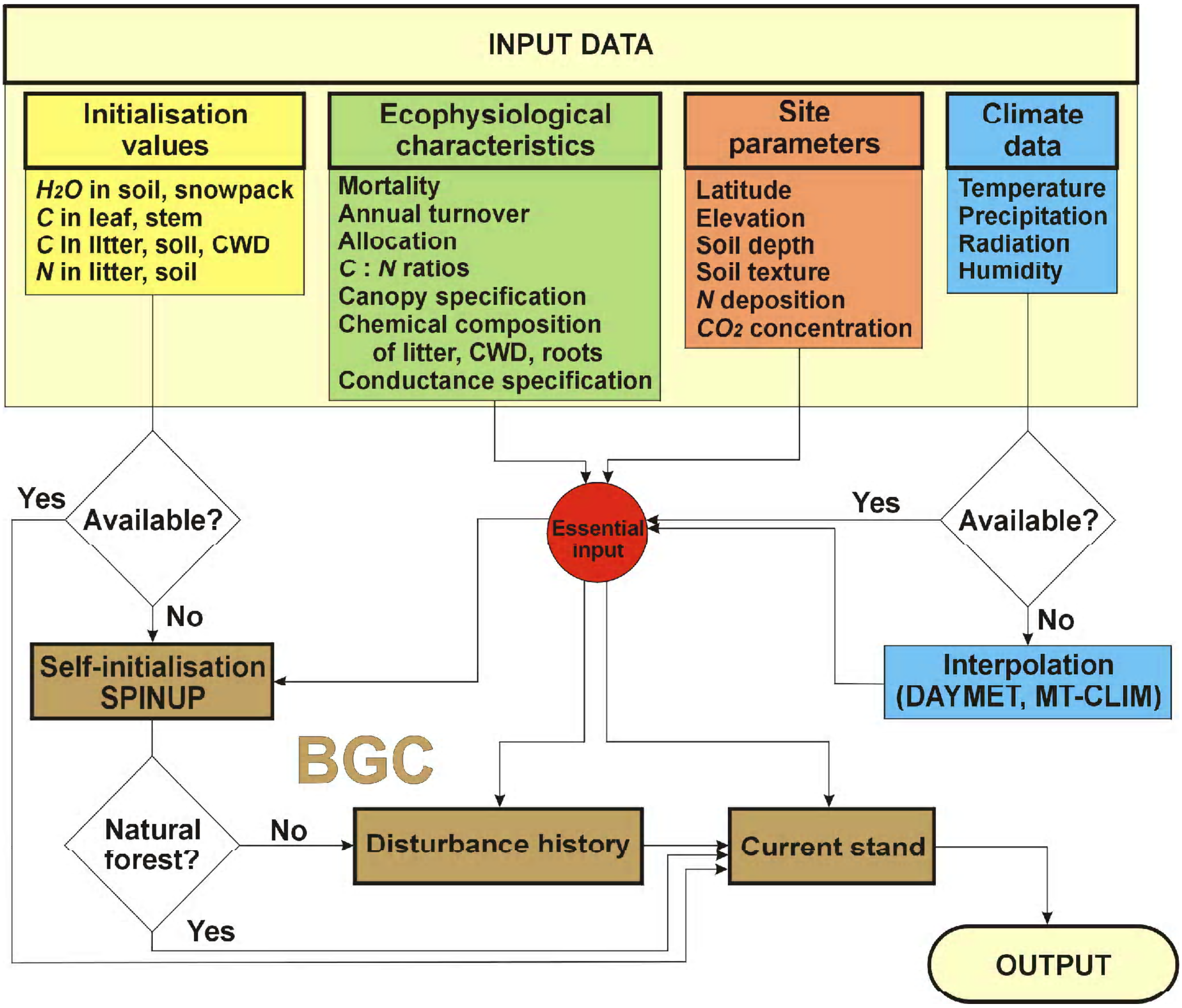

Figure 6: The simulation of the forest ecosystem using the model BIOME-BGC with the identification of required input data. The brown boxes represent the individual simulation steps.

Apart from the meteorological and site characteristics, BIOME-BGC requires as input a set of the prescribed ecophysiological characteristics describing the vegetation at a particular site (see Figure 6 and Appendix 2). The given parameters are held constant throughout the simulation. The model distinguishes the above given biomes by the values of these characteristics, which were estimated after a thorough survey of literature (White 1999, White et al. 2000). If available, it is desired to use the values from the direct measurements in the field for the applications at a particular site.

The three above mentioned groups of data are an essential input for BIOME-BGC (see Figure 6). However, in Figure 6 there is one more group of input data that are required for simulations. This group comprises 15 state variables describing the initial water, carbon and nitrogen status in the ecosystem (see Appendix 3 for the whole list). However, these data are usually not collected during the regular forest inventory. In cases, where no initial forest stand data are available, a self-initialisation procedure (so called spinup) is a useful arbitrary initialisation procedure that brings the model state variables, e.g. carbon amount in soil, into a dynamic equilibrium (climax), a state used as a starting point for further simulations. For details see Section 2.1.2.1.

2.1.2 Model simulations

According to the amount of available input information and the type of ecosystem that is to be modelled, there are three possible ways how to perform the particular simulation: (1) In the case where all the input data are available, it is possible to simulate the current forest stand directly. If, however, the initial information (Appendix 3) about the forest ecosystem is missing, the simulation of the particular stand has to start with the spinup procedure. (2) In the case an undisturbed forest ecosystem is to be simulated, the spinup procedure needs to be followed by the step "current stand simulation". (3) The simulation of managed forests consists of three steps: "spinup" followed by the "site history simulation", after which the "current stand" is modelled (Figure 6). In the following sections, we describe the three simulation steps: spinup, site history, and current stand.

2.1.2.1 Spinup

In situations, when the initial data (Appendix 3) are missing, a preliminary run has to be used to obtain the starting values for further simulations. Spinup, sometimes called a precursor run (Thornton et al. 2002), begins with no soil organic matter (SOM), very small initial carbon amount in leaves (0.001 kgC/m^2) and 50% soil water saturation. During the ongoing simulation, the organic mass is accumulated. The spinup process stops after the soil organic matter, the pool that is stabilised in an ecosystem most slowly, reaches a steady state. The model presumes that the steady state is reached when the difference in SOM between two successive climate periods does not exceed the value 0.0005 kgC/m^2/year.

The achieved equilibrium is dynamic with large inter-annual variability caused by variation in weather records (Law et al. 2001). For the simulations, available climate records are used covering a certain time period, e.g. from 1961 to 2000. These records are repeated as necessary to create weather records for model runs of longer duration. (Thornton et al. 2002). Hence, if the simulation lasts for example 4,000 years and our climate records cover a 40-year period, during the simulation the whole time series of the weather data will be repeated 100 times.

At the end of the spinup simulation a list with the initial values of the necessary variables is produced:

- Water stored in soil, snowpack and crown,
- Carbon and nitrogen amount in particular plant organs (leaf, stem, coarse and fine roots), in coarse woody debris, in four litter pools, in four soil pools,
- Amount of mineral nitrogen in soil,
- Nitrogen amount for re-translocation,
- Maximum amount of carbon in leaves, stem, fine and coarse roots during the year,
- Number of days per year without precipitation.

The typical spinup run lasts approximately 20,000 years depending on the simulated vegetation type (Thornton et al. 2002). Although this period seems to be long from the perspective of evolutionary development, it is important to note that the spinup run does not attempt to simulate the evolution of an ecosystem. It only provides the modeller with the initial values of the model state variables. In other words, the aim of the spinup run is to correctly reproduce the steady state as observed in the current forest ecosystems and not the succession that led to the current situation, as it is in the case of gap models (see Botkin et al. 1972). Moreover, the simulation starts with bare soil, a state that does not correspond with the situation on Earth 20,000 years ago.

To shorten the simulation time, the competition for mineral nitrogen between microbes and plants is switched off by the mechanism that adds the necessary amount of mineral nitrogen if their total demand exceeds its available amount. This procedure accelerates the spinup process by about a factor 10, and produces the same output as without nitrogen additions (Thornton et al. 2002).

Apart from BIOME-BGC a similar spinup procedure is also incorporated in other models, e.g. Lund-Potsdam-Jena Dynamic Global Vegetation Model LPJ (Sitch et al. 2003).

2.1.2.2 Site history

Forest management and other human induced actions, e.g. litter ranking, grazing, slash burning, as well as natural disturbances, such as wildfire, affect the status of the ecosystem. Pietsch and Hasenauer (2002) found that ignoring management site history within the model simulations leads to systematic overestimations of the carbon amount in litter and soil when compared to the field observations. Therefore, if a non-virgin forest is to be simulated, it is necessary to account for the land-use history to ensure unbiased and consistent simulation results of the actual run (Pietsch and Hasenauer 2002).

The disturbances should be simulated according to the available historical information for each site. For example, if from the historical documents it is known that in a certain forest site litter raking took place in the past, the simulations should account for it by reducing the modelled litter pools. However, in Central European conditions, where intensive forest management began in some areas approximately 600 years ago (Güde 1960), an exact description of site history is often lacking. Therefore, based on the available general information (Mayer 1974, Kral 1980, Peterken 1996), Pietsch and Hasenauer (2002) suggested simulating a certain number of successive rotations assuming clear-cutting and the replanting of the forest stand to account for management impact. The length of the rotation period depends on the tree species growing in a particular site. The number and the length of the rotation periods is optional, since this simulation of land-use history is controlled by the user himself.

Apart from the direct human impacts on forest vegetation, modern human society influences nature also indirectly through industrialisation, which started approximately 250 years ago and has resulted in an increasing atmospheric CO_2 concentration and higher deposition rates of e.g. nitrogen. The model allows the user to take these temporal changes of atmospheric chemistry into account during the simulations. The changes of CO_2 concentrations follow the IPCC scenario (IPCC WGI 1996). Nitrogen deposition is raised from pre-industrial levels to its current levels at a particular site following the same pattern as CO_2 (Thornton et al. 2002).

Similarly to spinup procedure, as daily weather data available climate records are used repeatedly throughout the whole simulated period.

2.1.2.3 Current stand

The simulation procedure of the current forest stand depends on the type of the forest (natural or managed) and the amount of input data. In the case where all the input data are on hand, it is possible to simulate the current forest stand directly and skip the first two steps (Figure 6). If, however, no initial information (Appendix 3) about the forest ecosystem is available, the simulation of the current stand can be performed only after the first two procedures, i.e. spinup (Section 2.1.2.1) and for managed stands also site history (Section 2.1.2.2). The simulation of the managed forest stand begins with the planting of the forest at the time of its establishment. The forest has to be planted also when it in reality developed from natural regeneration, since this mechanism is not covered in the model. Afterwards, the forest is left to grow until the present time, whereby the increase of CO_2 concentration and nitrogen deposition is considered. The available weather records should be used in such a way, that the period in the model coincides with the measured period.

If the forest stand was during its development a subject to different management operations, e.g. thinnings or fertilisation, these impacts have to be driven by the user manually, i.e. the simulation has to be stopped at a certain time and the state of the ecosystem has to be changed accordingly, before the simulation is continued.

Since in the virgin forests no management was applied, the simulation of the current stand starts immediately after the steady state is reached in the spinup procedure, and involves only the effect of indirect human impact on vegetation, i.e. the increase of CO_2 concentration and nitrogen deposition since 1765.

2.1.3 Model output

BIOME-BGC can produce approximately 500 different output variables describing the actual state of the simulated ecosystem. The output encompasses both state and flux variables. The model allows the user to choose which variables should be written in the output file as well as which time horizons, i.e. day, month or year, they should represent. The variables can be divided into several major groups according to the type of information they represent:

- variables describing the meteorological conditions of the site. This group includes the basic climate data that enter the model at the beginning of the simulation, such as temperature or precipitation, as well as variables derived from them, e.g. soil temperature, photosynthetically active radiation etc.
- variables defining the water status of the ecosystem, e.g. amount of soil water, amount of transpired water, and water fluxes in the ecosystem, e.g. transpiration, evaporation etc.
- variables representing carbon status and carbon fluxes in the ecosystem. The state variables provide us with information about how much carbon is stored in the individual ecosystem compartments (Figure 5), how much carbon was fixed with the photosynthesis, how much was respired by vegetation and microorganisms. Flux variables describe the movements of carbon within an ecosystem due to the processes that take place there, e.g. respiration, mortality, decomposition.

- variables reporting nitrogen status and movement in the ecosystem. Most of these variables make pairs with carbon variables, e.g. the amount of nitrogen stored in the stem matches with the amount of stem carbon. Apart from such paired variables, this group consists also of parameters describing nitrogen fixation, deposition, leaching and volatilisation.
- variables describing phenology, i.e. the length of the growing period and the time of the litterfall.
- variables providing information about ecophysiology comprising values of leaf area, assimilation, water potential, stomatal conductance, decomposition ratios etc.
- variables necessary for the estimation of photosynthesis, e.g. ratio of leaf nitrogen in rubisco enzyme, for sunlit and shade leaves separately.
- summary variables including NPP, GPP, respiration, amount of carbon fixed in the whole vegetation, litter, soil and the whole ecosystem.

2.1.4 Model extensions

The model BIOME-BGC was primarily developed for the applications on a regional or a global scale (Pietsch et al. 2000). Its usage on a stand level requires the refinement of the model parameters and eventually also of the model structure. Model testing and necessary model adaptations for stand-level applications have been the main research goals of Hasenauer and Pietsch since 2000. The authors published a number of papers (e.g. Pietsch et al. 2000, Pietsch and Hasenauer 2002, Pietsch et al. 2003 etc.), in which they presented the results of their ongoing research. Their basic assumption was that the main ecophysiological processes are correctly described in the model. Hence, the essential constraint in using the model on a small-scale level was the fact, that the current version of the model distinguishes only between seven global vegetation types – biomes, from which only four represent forests. This distinction was proved to be too coarse for the simulations of individual forest stands (Pietsch and Hasenauer 2004).

Therefore, species-specific parameterisations for the main tree species in Central Europe have been developed: lowland and highland Norway spruce (Pietsch and Hasenauer 2002, 2004), common beech (Pietsch and Hasenauer 2002), oak (Pietsch et al. 2003), Scots pine (Pietsch and Hasenauer 2004), Cembran pine (Pietsch and Hasenauaer 2003), and European larch (Pietsch and Hasenauer 2004). The parameterisation for a particular tree species is based on the refinement of model ecophysiology and/or the adaptation of key ecophysiological parameters. From the whole set of the ecophysiological constants (see Appendix 2), the following parameters were found to be particularly species sensitive: allocation ratios, C:N ratios of individual plant organs (e.g. leaves, roots) etc. The improvements in the model behaviour achieved due to the species-sensitive parameterisation are presented in Pietsch and Hasenauer (2004).

Apart from the changes of the ecophysiological parameters, the authors made some other changes in the model. For example, the evaluation of the model in the oak stands revealed that floods need to be accounted for in the model, if the model is to produce correct simulation results. Therefore, a new submodel simulating floods was included in the model structure (Pietsch et al. 2003).

2.2 CLIMATE INTERPOLATION

Daily climate characteristics, e.g. temperature, precipitation, solar radiation etc., are necessary input and important driving variables in the biogeochemical models. These variables are however usually not available for a site or a forest stand of our interest. In such cases, the modellers have to find an appropriate alternative to approximate the actual climate situation of the site.

The simplest approach is to use the data from a nearby climatic station. This approximation of site climate is suitable in homogeneous areas with high density of stations, but in mountainous regions or areas with low density of climate stations this attitude may lead to very inaccurate results. Therefore, different interpolation and extrapolation techniques have been developed. An overview of these methods is given in e.g. Xia et al. (2001) or Hasenauer et al. (2003).

On the basis of these techniques, a number of computer models were created. In our work we used two models: DAYMET (Thornton et al. 1997) and MT-CLIM (Running et al. 1987). Both models were developed by the Numerical Terradynamic Simulation Group at University of Montana, which also constructed the biogeochemical model BIOME-BGC.

2.2.1 DAYMET

DAYMET is a climate interpolation model (Thornton et al. 1997) that was developed for generating daily surfaces of climate characteristics over large regions of a complex terrain. The model simulates daily precipitation, minimum and maximum temperature from the surrounding stations using truncated Gaussian weighting filter. Air humidity and incoming shortwave solar radiation are derived from the simulated values of precipitation and air temperature. Required inputs include daily observations of minimum and maximum temperature and precipitation of the surrounding stations and a digital elevation model or the characteristics defining the location. The influence of the surrounding station decreases as the distance between the station and the point of interest increases. The model also accounts for the elevation gradient of climate characteristics, which is calculated for each day separately. More details about the inner structure of the model can be found in Thornton et al. (1997), Petritsch (2002) and Hasenauer et al. (2003).

The model DAYMET was originally used and tested across the U.S.A. (Thornton et al. 1997). Only recently the model was applied outside the U.S.A., too. Hasenauer et al. (2003) validated the model for the applications in Austria. The sensitivity study based on the cross-validation procedure and the model validation using an independent data set did not reveal any significant temporal or spatial trends in model results. This suggests that the model is an appropriate tool for the interpolation of daily air temperature, precipitation, solar radiation and air humidity over such a complex mountainous terrain as the Austrian Alps.

The original version of the model DAYMET interpolates climate parameters on a systematic grid 1x1 km using the digital elevation model of a particular interpolated area. Petritsch (2002) developed a point version of DAYMET for Austria that allows a user to simulate daily climate data for any location within the country, which is defined by its geographic co-ordinates (longitude and latitude), elevation, slope and aspect. The point interpolation is important for forest ecosystem modelling, because using this method we can obtain the necessary weather data for a specific location (forest stand). In addition, this adaptation of the model gives us the possibility to link the existing field observations, of e.g. stand volume, with the missing information about climate.

2.2.2 MT-CLIM

In cases, when only data from one nearby climatic station are available, the previous model is of no use since it requires information about multiple surrounding stations. In such cases, the model MT-CLIM can be used to extrapolate the climate variables from the base station to the site of our interest. This model was developed for mountainous terrain. Since climate stations are usually situated in valleys, whereas the forest stands are often on the adjacent mountain slopes, the model makes corrections for differences between the two locations in elevation, slope and aspect. Similarly to DAYMET, the essential input data for MT-CLIM are daily minimum and maximum air temperature and precipitation, and site descriptive characteristics of the site of interest (elevation, slope, aspect). The routines for estimating air humidity and incoming shortwave solar radiation are in both models the same. A detailed description of the model is given in Running et al. (1987).

2.3 DATA DESCRIPTION

Data used in this study come from different Austrian and Slovak sites as indicated in Figure 7. They may be divided into (1) data from virgin forests, which were applied for the validation of the model steady state, and (2) the data from managed stands used for testing the model applicability for the assessment of the impacts of different harvesting scenarios.

Figure 7: Location of the sites used in this study. The sites written in red colour represent virgin forests, whereas managed stands are indicated by black colour.

2.3.1 Data from virgin forests

The steady state achieved in the model using the spinup simulations was evaluated with the data collected in the virgin forests Rothwald, Austria and Babia Hora, Slovakia. Both sites are nature reserves, where no forest management was performed in the past because of their inaccessibility. Therefore, these regions are appropriate for this kind of analysis, since they represent stable natural ecosystems with natural dynamics undisturbed by man.

2.3.1.1 Rothwald

Rothwald (Rotwald) is a virgin forest situated in the eastern part of the Northern Limestone Alps, on the border of Lower Austria and Styria between upper Ybbstal and Lassingbach. It is situated at an elevation ranging from 950 to 1,600 m above sea level and covers almost 250 ha. The brook Moderbach divides the virgin forest into two parts named Small and Great Rothwald (in

German Großer and Kleiner Urwald, see Figure 8). Parent rock material is represented mainly by limestone and dolomite. From soil types, lithic leptosols, rendzic leptosols and chronic cambisols occur in this region (Neumann 1978, Schrempf 1986). The forest stands are in prevailing degree mixed, composed of European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* L./Karst.) and silver fir (*Abies alba* Mill.). Sporadically, sycamore (*Acer pseudoplatanus* L.), Norway maple (*Acer platanoides* L.) and Scotch elm (*Ulmus grabra* Huds.) are admixed. Table 1 presents an average species composition obtained from the data collected on the permanent sample plots (described in the following text).

Table 1: Tree species composition in Rothwald calculated from permanent sample plots.

Species composition	**Development stage**			
	Growth	**Maturity**	**Breakdown**	**All**
Spruce %	23.96	20.45	16.56	20.33
Beech %	14.20	20.09	12.65	15.65
Fir %	61.84	58.21	69.56	63.20
Other %	0.00	1.25	1.23	0.82

For our analysis we used the data collected on 7 permanent sample plots in 2002 and 2003. Three sample plots (Schrempf = S, Josef = J, Ripl = R) of a size 1 ha (100 x 100 m) are located in Great Rothwald (Großer Urwald), whereas in Small Rothwald (Kleiner Urwald) one 1 ha plot (Mayer-Wegelin = MW) and 3 plots (I, II, III) in the form of transect with a size 20 x 100 m are located. Their position within the virgin forest is shown in Figure 8.

On each permanent sample plot all standing trees (both alive and dead) with the height above 1.3 m were measured. For each tree the following characteristics were recorded:

- Tree species,
- Position on the plot (described as X and Y coordinates from one corner of the plot with coordinates 0,0),
- Diameter at breast height (d.b.h.) measured with band dendrometer or with slide calliper for the trees with diameter lower than 4 cm,
- Tree height and height to crown base measured with Vertex or a measuring pole for all trees smaller than 5 m,

- Sociological position (three categories: D=dominant, CD=co-dominant, S=suppressed)
- Occurrence of gaps around the tree (YES or NO description)
- Determination if the tree is alive or dead (1=alive, 0=dead).

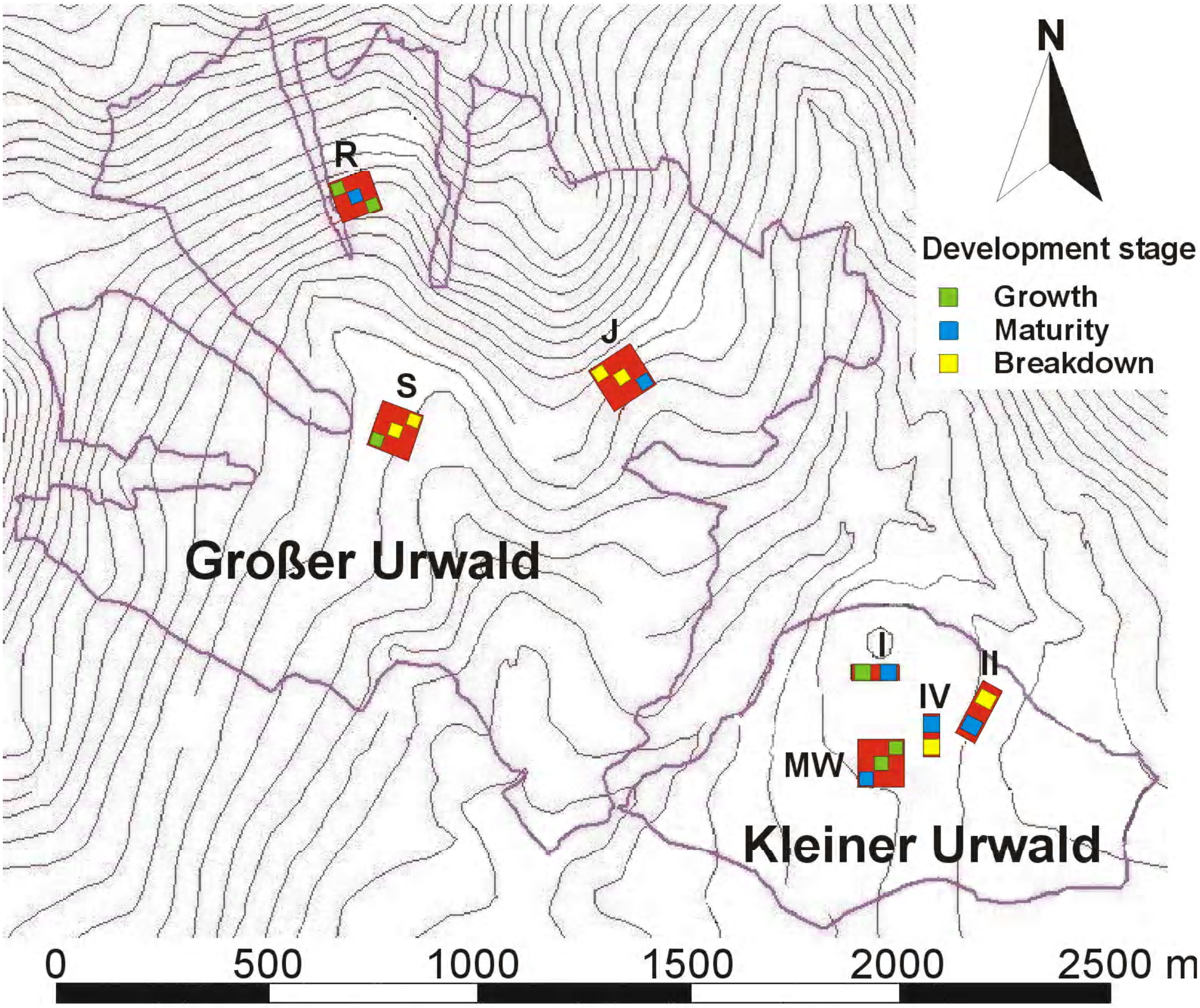

Figure 8: Location of permanent sample plots in Rothwald.

In addition, lying dead wood was recorded if the diameter at one place along its length exceeded 20 cm. The following characteristics were determined:

- Total length of the dead wood measured with band;
- Diameter at both ends and in the middle measured with calliper with an accuracy of 1 cm;
- Degree of deterioration (decay class) estimated according to the scale proposed by Maser et al. (1979) (see Table 2).

Table 2: Description of decay classes according to the scale of Maser et al. (1979).

Decay class (Maser et al. 1979)	Description
0	living trees
1	bark intact, twigs present, round shape, texture intact, log elevated on support points
2	bark intact, twigs absent, texture partly intact, round shape, log elevated on support points
3	bark trace to absent, solid interior, possible exterior decay, round shape, log near or on ground
4	bark absent, texture soft, blocky pieces, round to oval shape, log on ground
5	bark absent, texture soft and powdery, oval shape, log on ground

For the soil description, 20 x 20 m sub-plots were selected on each permanent sample plot. On the 4 one ha plots, three 20 x 20 m areas were chosen, whereas on the three transects only two such sub-plots according to the scheme in Figure 9 were used. All these subplots were further divided by 5 x 5 m grid as it is shown in Figure 9. The nine central intersection points indicate the points of litter and soil sampling. On each of the collection points, litter samples were taken using 30 x 30 cm frame and soil cores using the soil auger with a diameter of 70 mm and a length of 50 cm.

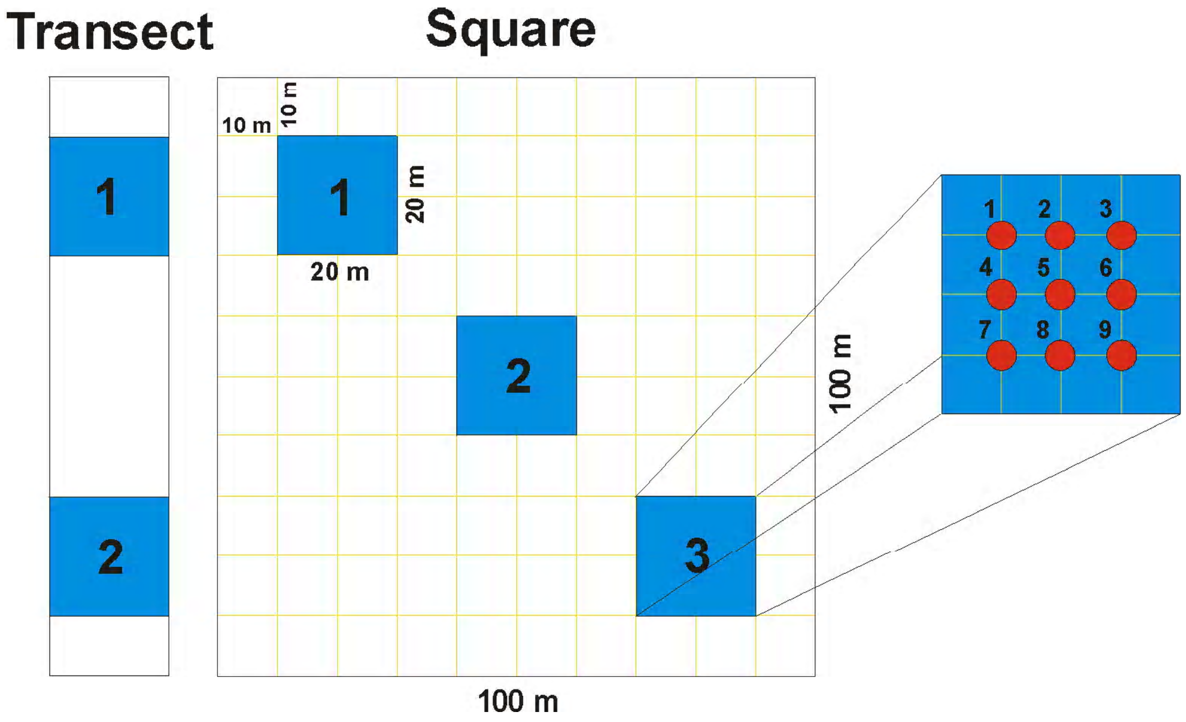

Figure 9: Applied design of soil sampling in Rothwald. Red circles indicate the points, from which the soil samples were collected.

The following characteristics were recorded in the field:

1. forest floor (hereafter referred to as litter):
    - type of litter,
    - genetic horizons L, F, H and their width,
    - transition between the horizons (4 types of boundaries: 1=straight, 2=wavy, 3=in slots, 4=discontinuous)
    - texture (material and its amount in percent, e.g. spruce needles 85%),
    - structure and consistence (6 groups from loose to compact),
    - fungus penetration (3 groups: no, mild, strong),
    - smeariness (no=0, yes=1),
    - rooting density (6 groups: 0=no, 1=mild, 2=middle, 3=strong, 4=very strong, 5=root tomentum).
2. mineral soil:
    - type of mineral soil,
    - genetic horizons, their width and soil texture by the "Feel" method,
    - type of boundaries between the horizons (4 groups: straight, wavy, etc.),
    - soil colour, mottling,
    - amount of soil skeleton, its type (round or angular) and size,
    - structure,
    - rooting density.

The collected litter and soil samples were deep-frozen transported to the laboratory for further analyses. Each soil core was divided into the genetic horizons, that were analysed separately. Litter was analysed as one unit regardless of its horizons. The number of horizons per soil core varied between 1 and 5 according to the soil type and the depth of coring. The analysis was performed either on each litter or soil core separately or in case the samples were small to be analysed separately, a mixed sample was prepared from several cores. All together, 95 litter and 259 soil horizon samples were analysed.

Litter samples were first cleaned from skeleton and live organic material (plant roots) and then dried in oven at temperature 105°C to determine their dry mass amount. The chemical analysis included the estimation of carbon and nitrogen amount. Carbon content in 1 gram of soil was determined from the oven-dried mass (ÖNORM L 1080) by the combustion in O_2-flow and consequent measurement of CO_2 using the infrared-spectrometer (LECO S/C 444), whereas nitrogen content was estimated according to Kjeldahl (ÖNORM L 1082).

Likewise litter, soil samples were first sieved with 2 mm sieves to separate fine earth (i.e. grain size classes with diameter below 2 mm) from skeleton, roots and other coarse organic material. The sub-samples of fine earth were air- and oven-dried (at temperature 105°C) to assess the amount of dry mass. The chemical analyses were performed on fine earth material only. The acidity (pH value) was determined from the fresh samples electrometrically in $H_2O_{deion.}$ (actual acidity) and 0.01M $CaCl_2$ (potential acidity) suspensions. The content of carbon and nitrogen in the soil was estimated using the same methods as for litter.

The main descriptive characteristics of the forest status derived from the collected data according to the principles given in Section 2.4 are given in Table 3. Table 9 presents average site characteristics for the virgin forest Rothwald.

Table 3: Basic stand and soil characteristics of the virgin forest Rothwald, where *h* is the mean tree height, *DBH* the mean quadratic diameter at breast height, *V* the stand volume per hectare, *N* the number of trees per hectare, *SDI* the stand density index according to Reineke (1933), V_{CWD} and C_{CWD} the volume and the amount of carbon of coarse woody debris, respectively, C_{litter} and N_{litter} are carbon and nitrogen amount in litter, and C_{soil} and N_{soil} carbon and nitrogen amount in soil.

Characteristics	**Development stage**			
	Growth	**Maturity**	**Breakdown**	**All**
h [m]	6.07	9.58	8.98	8.21
DBH [cm]	15.4	31.25	19.26	21.09
V [m^3/ha]	454.13	771.29	505.04	559.20
N [ha^{-1}]	2,575	820	1,587.5	1,758.33
SDI	966.45	1,053.42	946.29	983.89
V_{CWD} [m^3/ha]	603	582	693	626
C_{CWD} [kgC/ha]	84,032	74,870	97,989	86,139
C_{litter}[kgC/m^2]	1.0146	0.9420	0.9003	0.9523
N_{litter}[kgN/m^2]	0.0332	0.0337	0.0286	0.0319
C_{soil} [kgC/m^2]	7.9377	9.2906	7.5615	8.2633
N_{soil} [kgN/m^2]	0.5001	0.5066	0.4463	0.4843

2.3.1.2 Babia hora

Babia hora (1,725 m) is an isolated mountain massif belonging to the outer Western Carpathian mountain range. It is located in the northern part of Slovakia at the border with Poland (Figure 7). In 1926, a nature reserve was established to preserve the forest ecosystems. Although originally the nature reserve encompassed only 117.6 ha, in 1974 the reserve was enlarged and currently it covers an area of 503.94 ha (Korpeľ 1995).

The massif of Babia hora is built of tertiary flysch rocks, mainly sandstones, marl, claystones, slate and conglomerates. The soil types that occur in the area are leptosol, andosol and podzol, that is most frequent there due to high precipitation rates. The mean annual precipitation of the reserve is 1,600 mm and mean annual temperature 2°C. The forest stands are pure Norway spruce (*Picea abies* L./Karst.) stands with a small admixture of rowan (*Sorbus aucuparia* L.) and in the eastern part also silver fir (*Abies alba* Mill.). Average species composition calculated from the inventory data is given in Table 4.

Table 4: Tree species composition in Babia hora calculated from permanent sample plots.

Species composition	**Development stage**			
	Growth	**Maturity**	**Breakdown**	**All**
Spruce %	98.65	99.9	99.59	99.38
Other %	1.35	0.1	0.41	0.62

In the region of the Babia Hora nature reserve, 57 permanent circular sample plots were established in 2002 (Merganič et al. 2003), each with an area 0.05 ha (i.e. radius = 12.62 m). The plots are located at an elevation ranging from 1,173 m to 1,503 m above sea level, the latter representing the timber line in this region. The plots are equally divided between the three main development stages of virgin forests: stage of growth, maturity and breakdown as defined by Korpeľ (1989), i.e. each group consists of 19 plots (Figure 10).

On each sample plot, every tree with a diameter at breast height (i.e. 1.3 m) greater than 7 cm was recorded. The trees higher than 1.3 m but with d.b.h. below 7 cm were measured on the second concentric circle. Its radius was estimated directly in the field using the principle of optimum size of an inventory plot (Šmelko 1968), that is defined as the area with 15 to 25 trees on it. If the radius of the second circle exceeded the radius of the first circle, i.e. 12.62 m, it was set to this value. For every tree, the following characteristics were determined (Figure 11):

- Tree species,

- Position on the plot (the azimuth and the distance from the centre),
- Diameter at breast height and two diameters at height 0.3 m measured with a calliper or a slide calliper for the trees above and below 7 cm, respectively,
- Tree height and height to crown base measured with Vertex,
- Crown width in four directions (North, South, West and East) measured with a band,
- Branching angle and in the case of Norway spruce also the type of branching (comb, brush, plate),
- Quality of crown (5 groups), quality of stem (4 groups), stem shape and its damage.

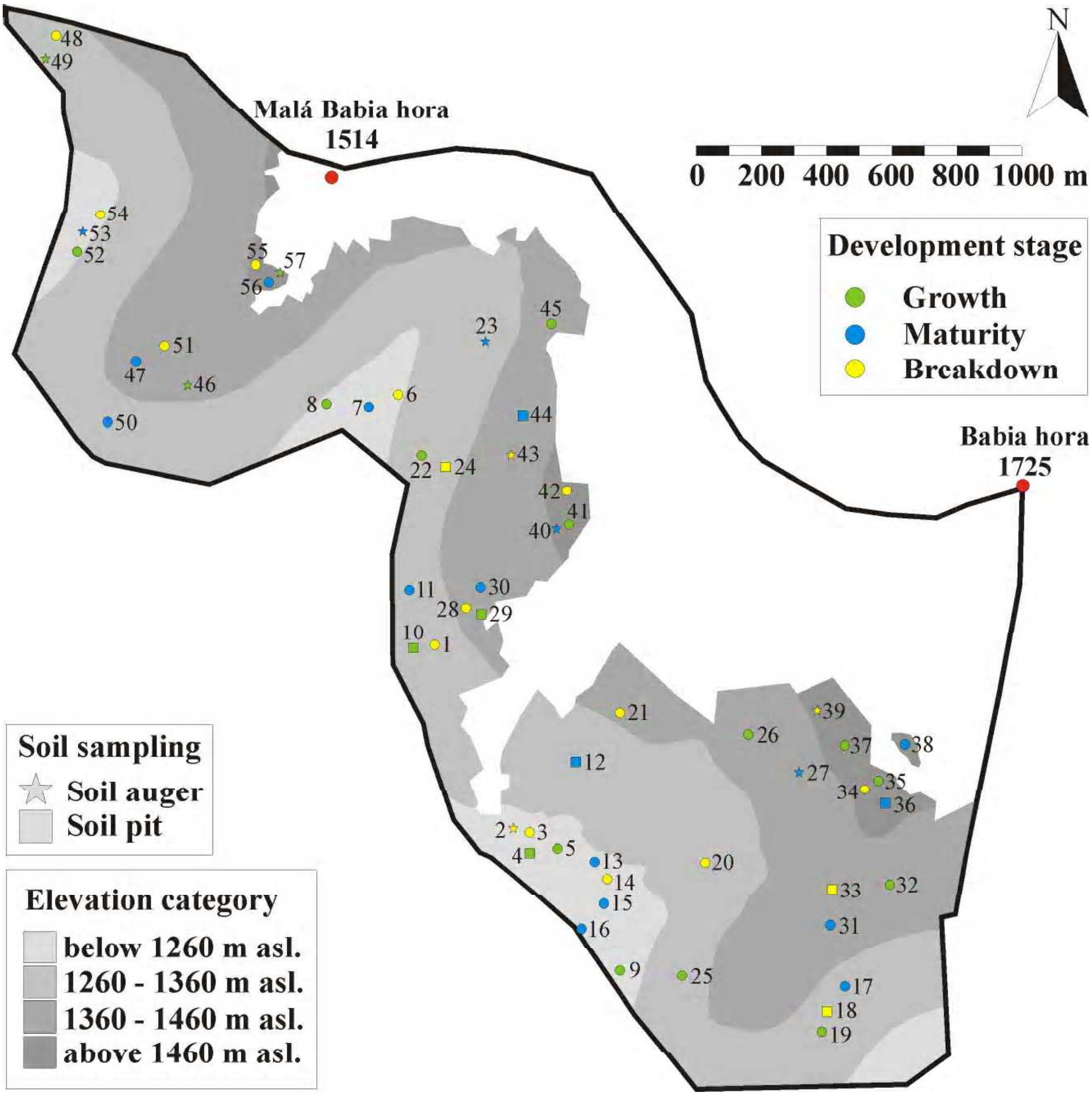

Figure 10: Location of the sample plots in Babia hora with the identification of the development stages and the plots, on which the soil samples were collected.

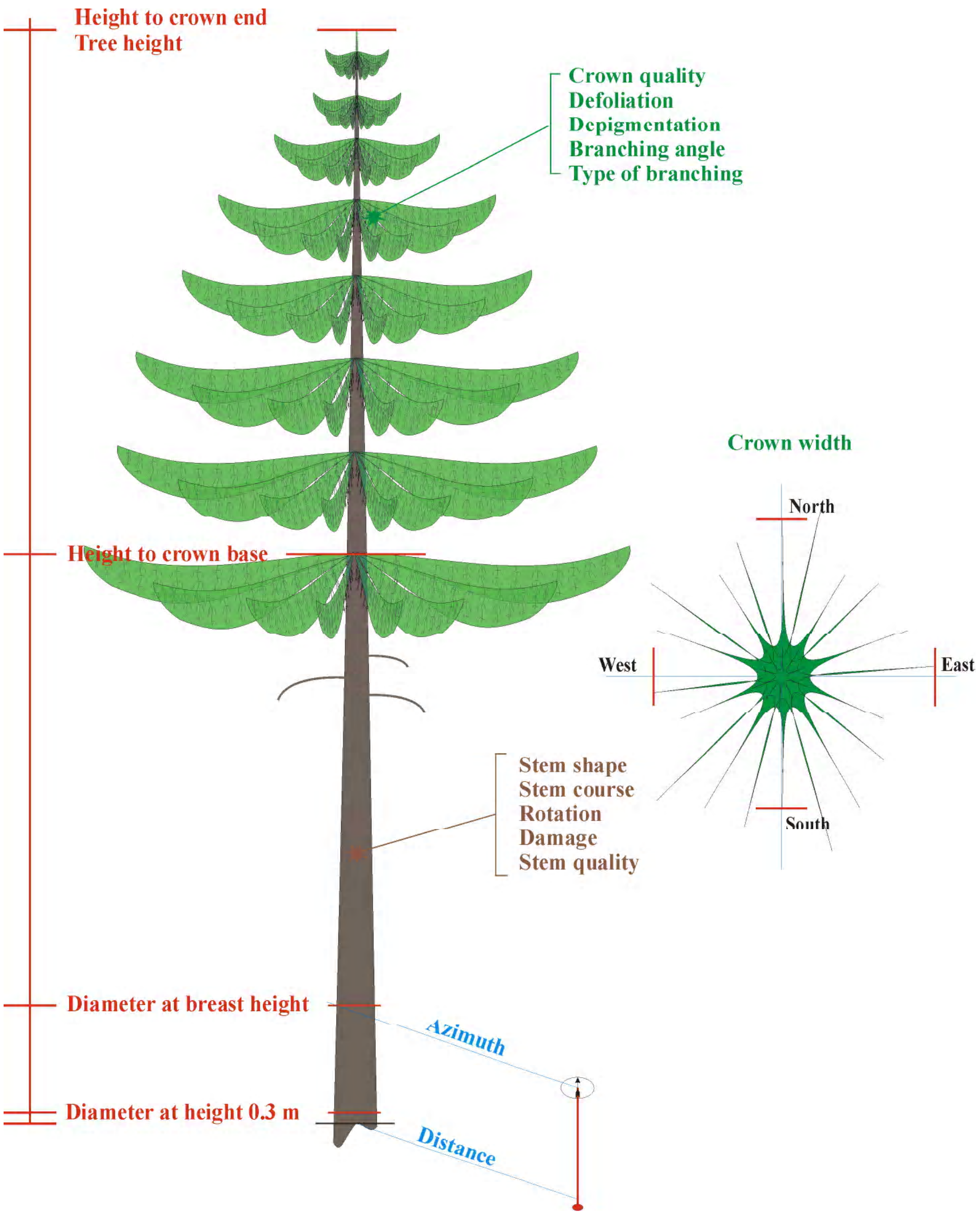

Figure 11: Measurement of the tree specific parameters (from Merganič et al. 2003).

Apart from the living trees, dead standing trees and coarse woody debris (lying stems and naturally formed stumps) with a diameter above 7 cm were recorded. For dead standing trees their tree height and diameter at breast height were assigned. In the case of dead lying wood, its total length and diameter at ½ of its length was measured, whereas for stumps only the diameter at 0.3 m height was determined. In addition, the position of dead wood on the plot was described with the azimuth and distance from the centre, in case of the stems lying on the forest floor both ends were aligned. The degree of deterioration (decay class) was assessed using the scale proposed by Holeksa (2001) as given in Table 5.

Table 5: Description of decay classes according to the scale of Holeksa (2001).

Decay class (Holeksa 2001)	**Description**
0	living trees
1	bark intact, twigs present, round shape, surface smooth, texture intact, log elevated on support points
2	bark sloughing on the bottom of the logs, large branches present, texture intact, round shape, surface smooth, logs elevated on support points
3	bark present only on the top of the logs, only stubs of branches with diameter greater than 2 cm present, round shape, crevices several mm deep present, sharp object (e.g. knife) slides up to 1 cm into log, log slightly elevated on support points
4	bark trace to absent, only stubs of branches with diameter greater than 4-5 cm present, round shape, crevices up to 0.5 cm in depth present, knife slides up to 3 cm into log, log partly in contact with ground
5	bark and branches absent, round shape, outer wood fragmented on the bottom, on side crevices with depth up to 1 cm, knife slides up to 5 cm into log, log on the ground, elevated only over small depressions
6	bark and branches absent, round shape, only core solid, outer wood fragmented on the bottom and sides of the log, log on the ground
7	bark and branches absent, elliptical shape, knife goes through the whole log, outer wood soft with crevices several cm deep, log on the ground
8	bark and branches absent, flat elliptical shape/contours of decomposed log, knife slides through the whole log, log on the ground overgrown by mosses and vascular plant species

In August 2002, forest litter and soil samples were taken from 19 plots selected out of the total 57 plots so that the full elevation range and all development stages were covered (see Figure 10). Since in Babia hora the prevailing type of humus was mor with an average depth of 10 cm, it was unnecessary to use 30 x 30 cm frames for litter sampling as it was in Rothwald. Instead, 50 mm diameter litter augers were used for litter collection. On each selected plot, four litter cores were extracted from the four corners of the phytocenological plot as shown in Figure 12. The samples were assessed as in Rothwald.

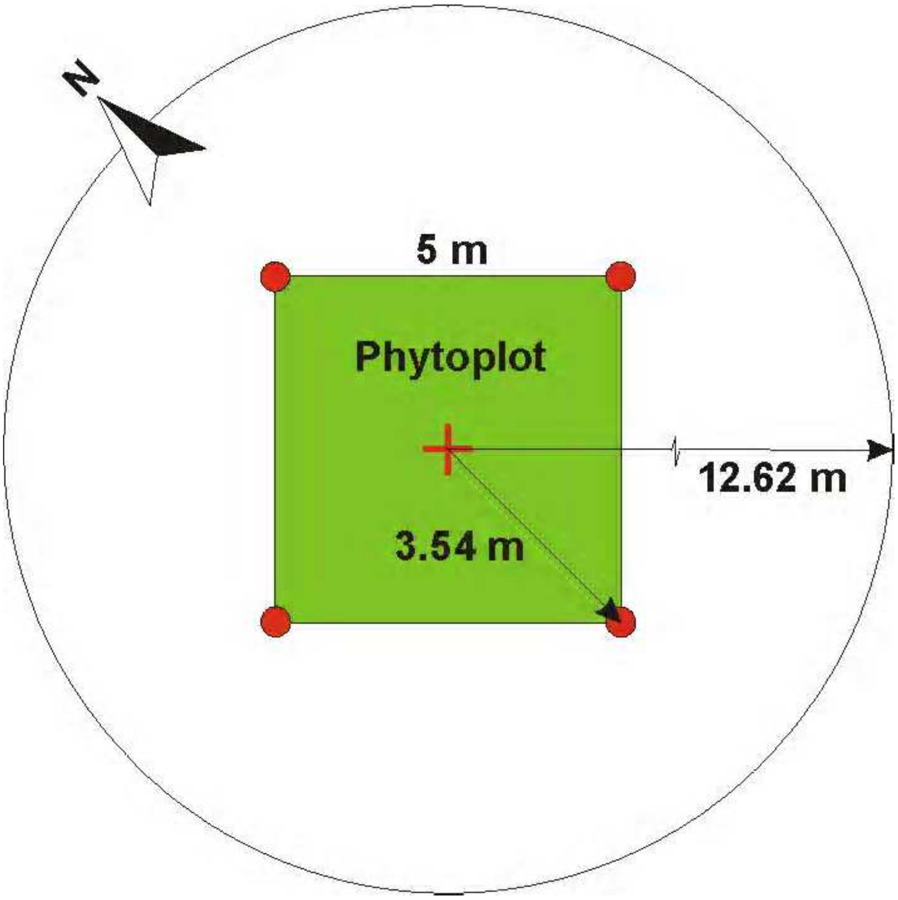

Figure 12: Applied design of soil sampling in Babia hora. Red circles indicate the points, from which the soil samples were collected.

Originally, we had planned to collect the soil samples using the same technique as in Rothwald, i.e. to extract four soil cores with the soil auger, each from the four corners of the phytoplot. However, due to the large amount of soil skeleton that highly exceeds the diameter of the soil auger, this method of soil sampling was used only on 10 inventory plots, whereas on the other 9 plots a soil pit, each at least 50 cm deep, was dug within the area of the inventory plot to ensure a representative soil sample. The soil description was performed according to the method of Rothwald.

The four litter cores extracted from one inventory plot were mixed and analysed as one sample. In case soil was collected using the soil auger, each core was divided into the genetic horizons. The samples of the particular horizon from four cores were mixed together and further analysed as one sample. The subsequent laboratory analysis of the samples followed the steps described in Rothwald.

The following Table 6 presents the average values of the main descriptive characteristics of the forest status derived from the data collected within the inventory and processed as given in Section 2.4. Site characteristics are shown in Table 9.

Table 6: Basic stand and soil characteristics of the virgin forest Babia hora, where *h* is the mean tree height, *DBH* the mean quadratic diameter at breast height, *V* the stand volume per hectare, *N* the number of trees per hectare, *SDI* the stand density index according to Reineke (1933), V_{CWD} and C_{CWD} the volume and the amount of carbon of coarse woody debris, respectively, C_{litter} and N_{litter} are carbon and nitrogen amount in litter, and C_{soil} and N_{soil} carbon and nitrogen amount in soil.

Stand characteristics	**Development stage**			
	Growth	**Maturity**	**Breakdown**	**All**
h [m]	11.42	21.16	18.39	16.99
DBH [cm]	18.2	36.52	28.41	27.71
V [m^3/ha]	239.96	465.92	233.71	313.20
N [ha^{-1}]	1,927.9	714	1,115	1,253
SDI	791.96	885.97	587.73	755.23
V_{CWD} [m^3/ha]	95	91	248	145
C_{CWD} [kgC/ha]	11,305	10,985	38,626	20,305
C_{litter}[kgC/m^2]	4.4672	5.6335	5.2343	5.1391
N_{litter}[kgN/m^2]	0.2127	0.2467	0.2220	0.2282
C_{soil} [kgC/m^2]	7.4117	5.1607	8.2279	6.8401
N_{soil} [kgN/m^2]	0.3938	0.2822	0.4588	0.3732

2.3.2 Data from managed forests

For the assessment of impact of different harvesting scenarios the data from 36 permanent inventory plots established by the Institute of Forest Growth Research, University of Natural Resources and Applied Life Sciences, Vienna (Sterba 1988), were used. The plots are situated on three different sites (Hartberg, Wilhelmsburg and Bad Zell) each comprising twelve permanent sample plots. The plots vary in their shape (Figure 13) and size (from 153 to 335 m^2) due to the establishment design, that required that each plot encompassed approximately 50 trees. For each tree its BHD and height was measured. The plots were re-measured 5 times since their establishment (Table 7).

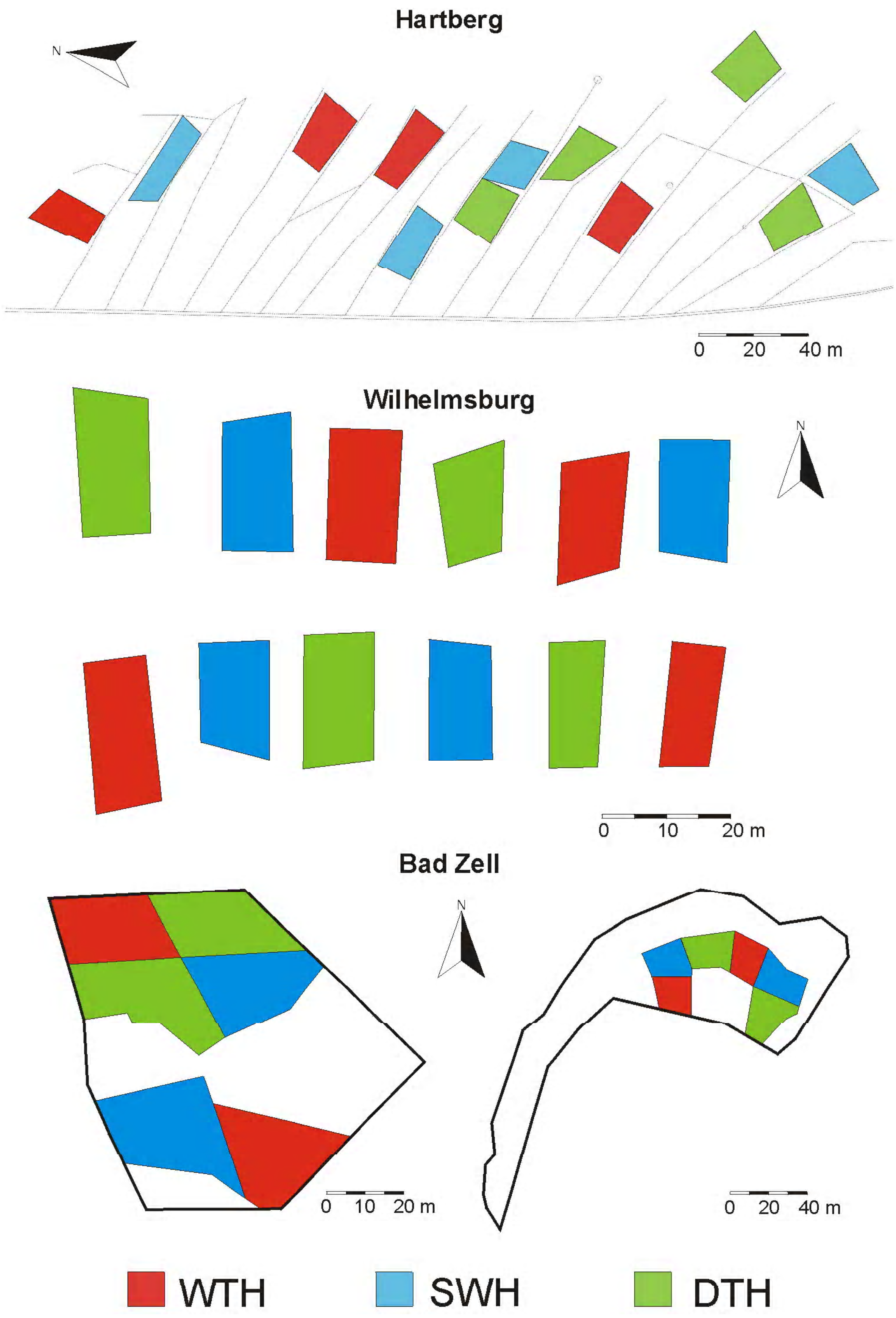

Figure 13: Location of permanent sample plots on the three management sites. The colours indicate the applied harvesting scenario on a plot, whereby WTH is whole tree harvest, SWH is stem wood harvest and DTH is delayed whole tree harvest (one year after thinning).

Table 7: Description of the temporal development and re-measurements of the forest stands per each management site.

Site	**Hartberg**	**Wilhelmsburg**	**Bad Zell Grillnberger**	**Bad Zell Kern**
	Year			
Stand establishment	1958	1964	1960	1965
1st thinning	1982	1981	1983	1983
Plot establishment, 1st measurement after thinning	1982	1982	1983	1983
1st remeasurement	1984	1984	1986	1986
2nd remeasurement	1987	1987	1989	1989
3rd remeasurement	1990	1990	1992	1992
2nd thinning	1992	1992	1992	1996
4th remeasurement	1993	1992	1996	1996
5th remeasurement	1999	1998	2002	2002

The site Hartberg is located in Styria at the elevation of 390 m above sea level. The site has a mean annual precipitation of 782 mm and a temperature of 8.2°C. The parent rock is loess and diluvial loam. The soils are mainly represented by gleyic cambisols. The natural vegetation of this location would be a mixed oak-hornbeam forest (Starlinger 2000). The current forest stands originated from the natural regeneration of Norway spruce (*Picea abies* L./Karst.) under the Scots pine (*Pinus sylvestris* L.) and silver fir (*Abies alba* Mill.) approximately in 1958. Common beech (*Fagus sylvatica* L.), pedunculate oak (*Quercus robur* L.) and other hardwood species make a small admixture in the forests. The permanent inventory plots were established in 1982. The average size of the permanent plot is 199 m^2.

Wilhelmsburg lies within the flysch zone of Lower Austria, approximately 10 km south of St. Pölten, at an elevation of 400 to 430 meters above sea level. The soils are gleyic cambisols derived from flysch (sandstone and marl). The region is characterised by an average annual precipitation of 800 mm and a mean annual temperature of 8°C. The natural forest vegetation according to Mayer (1971) was a beech dominated mixed forest. The current forest stands are spruce dominated as they originated from planting Norway spruce (*Picea abies* L./Karst.) seedlings in 1964 using 1.4 x 1.4 m spacing. Other occurring tree species, i.e. European beech (*Fagus sylvatica* L.), Scots pine (*Pinus sylvestris* L.), silver fir (*Abies alba* Mill.), European larch (*Larix decidua* Mill.), pedunculate oak (*Quercus robur* L.), sycamore (*Acer pseudoplatanus* L.), European hornbeam (*Carpinus betulus* L.) and willow (*Salix* sp.), come from natural regeneration and make only a small admixture to Norway spruce. The permanent inventory plots were established in winter 1981/1982. The average size of the plot is 197 m^2.

The site Bad Zell is located in south-east Mühlviertel, Upper Austria, about 20 km east from Linz at the elevation 530-560m above sea level. The parent rock material is in prevailing degree gneiss on which dystric cambisols have developed. The climate in this region can be characterised by a mean annual precipitation of 830 mm and a temperature of 7.2°C. The natural vegetation were mixed spruce - fir – beech forests (Mayer 1971). Currently, the forests are almost entirely pure spruce forests with less than 2% admixture of other tree species, e.g. Scots pine (*Pinus sylvestris* L.), pedunculate oak (*Quercus robur* L.), maple (*Acer* sp.), European hornbeam (*Carpinus betulus* L.), willow (Salix sp.), sweet chestnut (*Castanea sativa*). The forest stands were planted in 1960 and 1965 with 1.4 x 1.4 m spacing using 3 to 4 years' old seedlings in Bad Zell Grillenberger and Kern, respectively. The permanent inventory plots were established in 1983 and are equally divided between two nearby sites Bad Zell Grillnberger and Bad Zell Kern. The average plot size is 235 m^2.

The forest stands on all sites were subjects to two thinnings (Table 7). The first thinning was a pre-commercial one performed 19 to 23 years after the stand establishment. In Wilhelmsburg and Bad Zell every second row of the planted trees was cut, whereas in Hartberg a selective thinning from below was applied. The second commercial thinning, that took place approximately 10 years after the first one (see Table 7), was a selective thinning with the aim of releasing the dominating trees according to Johann (1982).

On all sites three different harvesting scenarios were applied after the thinning defined as follows: (1) WTH – whole tree harvest, i.e. harvest of the whole felled aboveground biomass (stem, branches and needles); (2) SWH – stem wood harvest, i.e. harvest of the commercial timber with the top diameter outside bark of at least 8 cm, whereas in Hartberg and Bad Zell no biomass was removed after the first thinning from the SWH plots; (3) DTH – delayed tree harvest, i.e. harvest of the whole felled aboveground woody biomass one year (vegetation period) after felling in order to leave the needle biomass in the stand.

Each harvesting method was applied to four plots per site distributed randomly on the site. The situation on each site is given in Figure 13.

The mean values of the main stand characteristics for all management sites are shown in Table 8. The average site characteristics for each location used in this study are given in Table 9.

Table 8: Basic stand characteristics for the three management sites, where *h* is the Lorey mean tree height, *DBH* the mean quadratic diameter at breast height, *V* the commercial stand volume per hectare, *N* the number of stems per hectare and *SDI* the stand density index according to Reineke (1933).

Stand characteristics	**Wilhelmsburg**	**Hartberg**	**Bad Zell Grillnberger**	**Bad Zell Kern**
Before 1st thinning [year]	1981	1981	1983	1983
h [m]	7.5	6.6	6.4	5.4
DBH [cm]	7.5	5.2	6.9	5.4
V [m^3/ha]	79	119	50	24
N [ha^{-1}]	5,014	14,400	5,350	4,267
SDI	726	1158	678	365
1st thinning [year]	1981	1981	1983	1983
Felled Biomass [% of V]	39.9	41.4	37.6	28.5
After 1st thinning [year]	1981	1981	1983	1983
h [m]	7.6	8.3	6.4	5.4
DBH [cm]	7.6	6.9	6.7	5.5
V [m^3/ha]	47 ± 8	70 ± 25	31 ± 13	17 ± 10
N [ha^{-1}]	2,484 ± 462	3,998 ± 533	2,278 ± 299	2,004 ± 261
SDI	360	498	276	177
Before 2nd thinning [year]	1992	1990	1992	1996
h [m]	13.9	12.4	12.4	10.4
DBH [cm]	13.8	10.2	11.9	10.9
V [m^3/ha]	236 ± 24	202 ± 42	161 ± 68	168 ± 45
N [ha^{-1}]	2,097 ± 365	3,771 ± 530	2,127 ± 293	2,563 ± 156
SDI	888	897	693	742
2nd thinning [year]	1992	1992	1992	1996
Felled Biomass [% of V]	32.1	21.3	29.4	20.1
After 2nd thinning [year]	1992	1993	1992	1996
h [m]	14.1	13.3	12.4	11.8
DBH [cm]	13.6	9.6	11.7	11.2
V [m^3/ha]	165 ± 17	194 ± 32	116 ± 45	133 ± 25
N [ha^{-1}]	1,619 ± 323	3,851 ± 1026	1,635 ± 253	2,152 ± 254
SDI	605	830	482	595

Table 9: Climate and site description of each location. Minimum and maximum temperature, vapour pressure deficit and solar radiation are daily average values calculated from all available weather records.

Site characteristics	**Rothwald**	**Babia hora**	**Hartberg**	**Wilhelmsburg**	**Bad Zell Grillnberger**	**Bad Zell Kern**
Longitude [°,’]	15°05’ - 15°06’	19°29’ - 19°31’	16°03’	15°35’	14°41’	14°40’
Latitute [°,’]	47°46’ - 47°47’	49°33’ - 49°35’	47°17’	48°04’	48°22’	48°22’
Elevation [m a s l.]	1,017 – 1,216	1,173 – 1,503	390	400 - 430	560	530
Slope [°]	0 – 30	5 - 40	0	35	20	25
Aspect	E, SE, S, NW	SE, E, SW, NW	-	N	N	S
Sand %	23 ± 8	65 ± 3	35	35	40	40
Silt %	33 ± 4	27 ± 4	40	40	40	40
Clay %	44 ± 10	8 ± 5	25	25	20	20
Soil depth [m]	0.39 ± 0.10	0.17 ± 0.06	0.39 ± 0.06	0.38 ± 0.06	0.3	0.3
Maximum temperature [°C]	12.46 ± 9.01	5.55 ± 9.44	13.41 ± 8.96	13.19 ± 9.21	12.39 ± 9.16	12.42 ± 9.17
Minimum temperature [°C]	3.00 ± 7.09	-2.74 ± 8.27	4.19 ± 7.25	4.07 ± 7.14	3.57 ± 7.13	3.61 ± 7.14
Precipitation [mm/year]	1,475 ± 233	1,808 ± 285	782 ± 110	799 ± 102	829 ± 107	827 ± 107
Number of rainy days per year	182 ± 18	173 ± 28	128 ± 13	161 ± 15	166 ± 20	165 ± 21
Vapour pressure deficit [Pa]	543 ± 408	328 ± 299	561 ± 375	560 ± 422	524 ± 398	525 ± 399
Solar radiation [$W/m^2/s$]	231 ± 120	295 ± 138	262 ± 117	187 ± 98	264 ± 129	209 ± 113
Nitrogen deposition [$gN/m^2/yr$]	1.6	1.55	0.4	1.0	1.4	1.4

2.3.3 Climate data

As we know from the description of the model BIOME-BGC (see Chapter 2.1), to perform the simulations daily climate data for the forest of our interest, namely daily minimum and maximum temperature, daily precipitation, vapour pressure deficit, solar radiation and day length, are required. However, for none of the locations used in this study long-term daily observations were available. Therefore, for Austrian sites, i.e. Rothwald, Hartberg, Wilhelmsburg and Bad Zell, the daily weather data were interpolated from surrounding climate stations using the Austrian adaptation of DAYMET (Hasenauer et al. 2003, Chapter 2.2.1). In this way, we obtained a 41 years (1960 to 2001) time series of climate records for each plot. The average values of the climate variables for each location are given in Table 9.

In Babia Hora, which is situated in Slovakia, we could not use the interpolation model DAYMET. Instead, the model MT-CLIM (Running et al. 1987, Chapter 2.2.2) was applied. The base station used for the interpolation of the weather records was the climate station Rabča located at the southern foot of the massif Babia hora (see Figure 14), at an elevation 642 m above sea level. The daily weather data of this station covering daily minimum, maximum and average temperature and daily precipitation for the period from 1961 to 2002, were provided by Slovak Hydrometeorological institute. The missing data were either generated from adjacent years or calculated from other data (e.g. if daily average and maximum temperature were available, but minimum temperature was missing, this was estimated from the linear regression $Tday = 0.618 \cdot Tmax + 0.405 \cdot Tmin$ ($R^2 = 0.95$), derived from all the observations within 42 years) or in the case of precipitation substituted for the data from the nearby precipitation stations Oravská Polhora – Hliny and Rabčice (Figure 14).

The lapse rates for precipitation, minimum and maximum temperature were estimated from Réthly (1908) and the observations of monthly precipitation in 2001 and 2002 in Rabča and Šťaviny (Vorčák 2002, personal communication). The locality "Šťaviny" is situated at an elevation of 1,320 m above sea level between the plots No. 1 and 12 (see Figure 10), and divides the monitored area of Babia hora into two parts of approximately the same size. The values of the lapse rates are –4.96°C/km, -9.68°C/km and +2.11mm/m for minimum, maximum temperature and precipitation, respectively. The average values of the climate variables are given in Table 9.

Figure 14: Geographic position of Babia hora and the nearby climate stations.

In addition to the climate data, the model also requires the information about the current nitrogen deposition to account for the effect of industrialisation during the last century. The values given in Table 9 were taken from Schneider (1998) and from the actual measurements on site during 2001 and 2002 (Merganič et al. 2003) for Austrian locations and for Babia hora, respectively.

2.4 DATA PROCESSING

Tree volume of the standing (both alive and dead) trees was calculated using one of the following methods according to their diameter at breast height. If the diameter at breast height was equal to or greater than 5 cm, tree volume was calculated using the following form factor function:

$$v = g \cdot h \cdot f = \pi/4 \cdot d^2 \cdot h \cdot f$$

where v = tree volume,

g = tree basal area,

h = tree height,

d = tree diameter at breast height,

f = form factor.

The form factor f was estimated from the formulas by Pollanschütz (1974) using either his coefficients if the tree had at least a diameter at breast height of 10.5 cm or otherwise, the coefficients derived by Schieler (1988).

Tree volume of the trees with the diameter below 5 cm was calculated using the formula of Hafellner (1985): $v = 0.5503 \cdot d^{1.86} \cdot h^{0.9256}$.

In the case of "outliers", i.e. live or dead trees with broken crowns, which frequently occurred in the virgin forests Rothwald and Babia hora, the form factor was calculated using the modelled height of the tree estimated from the diameter-height curves derived from the undamaged trees (see Figure 15 as an example). Using this procedure, we were able to prevent the volume underestimation as shown in Figure 16.

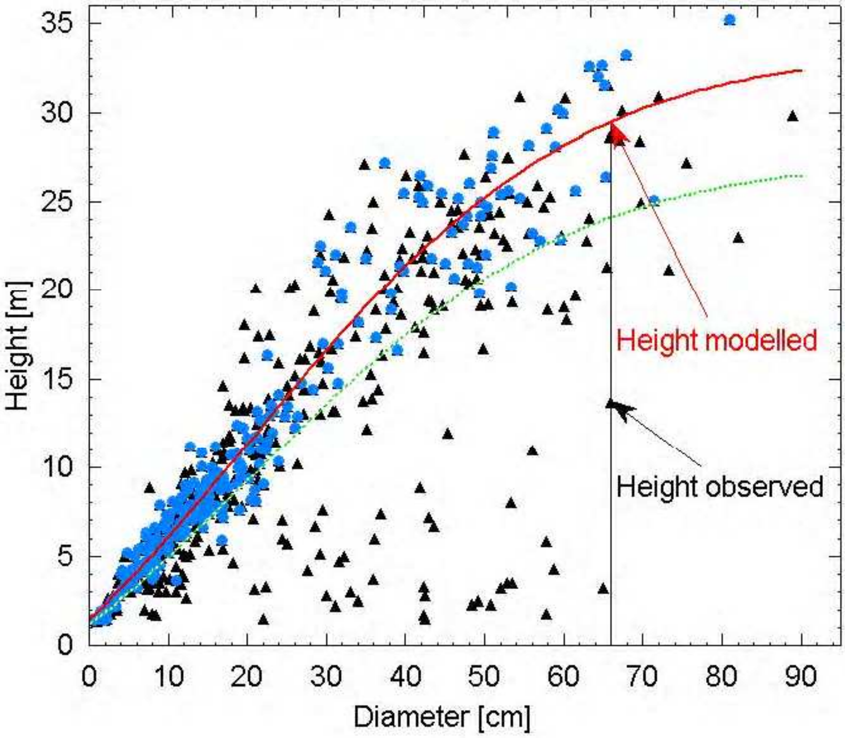

Figure 15: The example of the application of height-diameter curve (red solid line) derived from the undamaged trees (blue points) for the estimation of the modelled height of broken trees (black points). Each damaged tree with a measured height below the green solid line, defining the lower border of the confidence interval of the height-diameter curve, is assigned the modelled height used for the estimation of the form factor *f*.

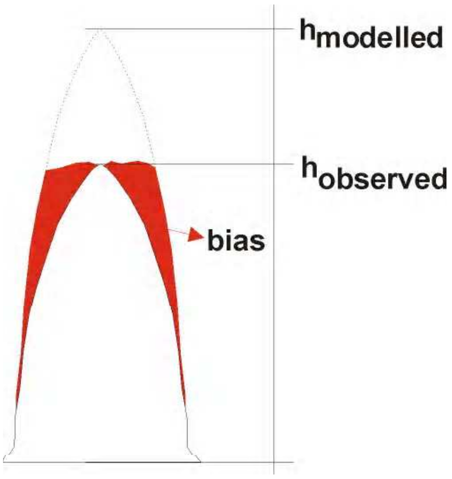

Figure 16: Graphical display of the tree volume underestimation in broken trees caused by the calculation of the form factor from the measured height.

The volume of stumps was estimated as the volume of a cylinder with the height equal to 0.3 m. The volume of lying dead wood (logs) was calculated as the volume of a second degree paraboloid (see Figure 17). In Rothwald one of the following equations was used according to the amount of available data (measured diameters) about a certain log:

1. Newton's formula: $v = h \cdot (d_B^2 + 4 * d_{1/2} + d_T^2) \cdot \pi/24$
2. Smalian's formula: $v = h \cdot (p_B + p_T)/2$
3. Huber's formula: $v = h \cdot p_{1/2}/2$.

where v = volume of the log,

h = length of the log,

d_B, p_B = basal diameter or sectional area,

$d_{1/2}$, $p_{1/2}$ = mid-section diameter or sectional area,

d_T, p_T = top diameter or sectional area.

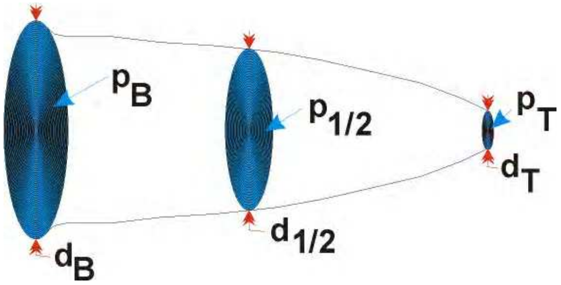

Figure 17: Parameters of the lying dead wood used for the estimation of its volume. The descriptor *p* stands for the sectional area, and *d* for diameter at the log base (*B*), mid-section (½) and top (*T*) of the log.

In Babia hora, where only the mid-section diameter was measured, Huber's formula was used.

Stand volume was obtained as a sum of volumes of all the living trees and converted to hectare values. Volume of coarse woody debris was given as a sum of volumes of dead standing trees, stumps and lying logs. In the case of management sites, the stand characteristics before the first thinning were estimated from the status of the forests immediately after the thinning, when the plots were established (Sterba 1988). The mean values of the main stand characteristics are shown in Tables 3, 6 and 8.

In the model, the variable representing stand volume is the amount of carbon in the stem wood per unit area given in kilograms of carbon per square metre [kgC/m^2]. Its conversion to the units of the observed stand volume, i.e. to cubic meters of wood per one hectare [m^3/ha], is done in the following steps.

First, the dry weight of woody mass is calculated as the amount of carbon in the model compartment "stem" C_{stem}, i.e. in the above ground woody biomass, divided by the fraction of carbon in the woody dry mass $C\%$. In general, the carbon fraction is assumed to be 50% of the woody dry mass (Stakanov et al. 1998, Coomes et al. 2002). In our work we used the following species specific values reported by Weiss et al. (2000): spruce 50.1%, fir 51.1%, beech 48.6%.

Secondly, the estimated dry weight is corrected for the average water content W in wood (44% regardless of the tree species as used in Pietsch and Hasenauer 2002) to obtain the fresh weight of the aboveground woody biomass.

In the next step, the fresh weight has to be reduced for the timber fraction of crown (*crown%*) to obtain the information about the bole timber. In the virgin forests, we presumed the fraction of crown to be constant throughout the whole development cycle: 19.1% for beech (Hochbichler et al. 1994) and 41.3% for spruce as reported by Hager (1988). The analyses of the simulation results for the managed stands showed that in the case of even-aged forests it is important to account for the changes in the timber distribution with age. Thus, for our management sites the crown fraction was calculated using the logarithmic function derived from the data published by Krapfenbauer and Buchleitner (1981):

$$crown\% = 241.618 - 102.089 \cdot \ln(age) + 11.283 \cdot \ln(age)^2$$

where $crown\%$ = timber fraction of crown in % from the aboveground woody biomass,

age = age of the forest stand.

This function can be used for the calculation of the crown fraction of Norway spruce forest stands from the age of 6 years onwards. Since all three management sites are spruce dominated, no conversion formula for other tree species was needed.

The fresh weight of the bole timber calculated in the previous step is then divided by the density of moist timber ρ_{wood} given in [kg/m^3] (spruce 800 kg/m^3, beech 950 kg/m^3, Pietsch and Hasenauer 2002) to obtain the modelled volume of bole timber per unit area, in our case cubic meters per square meter. Multiplying this value by 10,000 we get the modelled stand volume in cubic metres per hectare.

The complete conversion formula has the following form:

$$V = \frac{C_{stem}}{\frac{C\%}{100} \cdot \frac{W}{100} \cdot \rho_{wood}} \cdot \frac{100 - crown\%}{100} \cdot 10{,}000$$

where V = modelled stand volume in [m^3/ha],

C_{stem} = modelled carbon amount in the compartment “stem” in [kgC/m^2],

$C\%$ = fraction of carbon in woody dry mass in %,

W = water content in wood given in % of the fresh weight of wood,

ρ_{wood} = density of moist timber in [kg/m^3],

$crown\%$ = timber fraction of crown in % from the aboveground woody biomass.

Similarly, the units of the measured and modelled coarse woody debris differ from each other. Therefore, also in this case the conversion of the units had to be performed. In the model, coarse woody debris is regarded as one pool covering dead wood in all decay stages. However, several authors, e.g. Krankina and Harmon (1995), Harmon et al. (1999), Coomes et al. (2002) etc., reported a decrease in wood density with increasing deterioration. Due to this fact, rather than converting the modelled values, we decided to convert the observed volume of coarse woody debris into the amount of carbon fixed in CWD to account for the different decay stages.

Since no field measurements of CWD wood density were performed either in Rothwald or in Babia hora, the published values from other locations were used. For Norway spruce we used the information provided by Harmon et al. (1999), Naesset (1999) and Yatskov (2001). For common beech and silver fir no publications concerning the wood density at different decay stages of CWD were available. Hence, the information for *Fagus grandifolia* Ehrh. from MacMillan (1988), Arthur et al. (1993), Adams and Ovens (2001) and for *Abies concolor* Lindl. et Gord. from Harmon et al. (1987), respectively, were used instead.

As each study uses another scale of deterioration with different number of decay stages (3 to 8), the scales were converted to the scales of Maser et al. (1979, Table 2) used in Rothwald, and of Holeksa (2001, Table 5) applied in Babia hora, with regard to the verbal description of the decay degrees. After this harmonisation of the different scales, the values of wood density were plotted against the degree of decay, and a linear or exponential regression was applied (Table 10). These functions were used for the calculation of the final values of wood density for each decay stage and each species as given in Table 11.

Table 10: Applied models for the estimation of the basic wood density of coarse woody debris ($density_{CWD}$) using literature values for CWD decay degrees ($decDegree_{CWD}$) according to the scales of Maser et al. (1979) and Holeksa (2001) for Rothwald and Babia hora, respectively.

Location	**Rothwald**			**Babia hora**
Tree species	**Spruce**	**Fir**	**Beech**	**Spruce**
Model	linear*	exponential**	exponential**	linear*
R^2	0.866	0.983	0.756	0.884
N	32	5	9	32
a	0.4591	0.4230	0.5661	0.4283
b	-0.0702	-0.1784	-0.2194	-0.0372

*$density_{CWD} = a + b \cdot decDegree_{CWD}$

**$density_{CWD} = a \cdot exp\ (b \cdot decDegree_{CWD})$

Table 11: Basic wood density per decay class for individual tree species and location calculated from the derived models given in Table 10.

Decay class	**Basic density [g/cm^3]**			
	Rothwald			**Babia hora**
	Spruce	**Fir**	**Beech**	**Spruce**
0	0.430	0.410	0.680	0.428
1	0.389	0.354	0.455	0.391
2	0.319	0.296	0.365	0.354
3	0.249	0.248	0.293	0.317
4	0.178	0.207	0.235	0.280
5	0.108	0.173	0.189	0.242
6	-	-	-	0.205
7	-	-	-	0.168
8	-	-	-	0.131
Average	0.279	0.281	0.370	0.335

The volume of coarse woody debris was then converted to the carbon amount for each species separately using the following formula:

$$C_{CWD_i} = V_{CWD_i} \cdot \rho_{CWD_i} \cdot \frac{C\%}{100}$$

where i = degree of decay (1 to 5, or 1 to 8 according to the applied scale, see Tables 2 and 5),

C_{CWDi} = carbon amount of CWD in i^{th} decay class in [kgC/ha],

V_{CWDi} = wood volume of CWD in i^{th} decay class in [m^3/ha],

ρ_{CWDi} = wood density of CWD in i^{th} decay class taken from Table 11 in [kg/m^3],

$C\%$ = carbon content in percent of the dry mass taken from Weiss et al. (2000) for each tree species.

This formula is in fact the reverse expression of the previous formula for the conversion of stem carbon to stand volume. In contrast to the conversion of carbon in the stem, here we used the basic wood density at water content of 0% (i.e. specific gravity), and no crown fraction. Therefore, the parameters water content *W* and crown fraction *crown%* are not used in the conversion of the coarse woody debris.

As with stand volume, the total amount of carbon fixed in the coarse woody debris was calculated as the sum of all species and all decay classes.

Since in the model the pool of coarse woody debris comprises not only the above ground dead wood biomass, but also dead coarse roots, modelled CWD had to be reduced for the amount of the belowground mass to make it comparable to the measured aboveground CWD. In the model the ratio of the aboveground stemwood to the belowground coarse root mass is held constant, and pre-defined in the file of ecophysiological constants (see Appendix 2) for a particular species. Thus, in the case of spruce simulations, the modelled CWD was reduced by 23%. For beech the reduction factor was equal to 0.85, i.e. the simulated CWD was reduced by 15% representing dead coarse roots.

The values of carbon and nitrogen content in the litter and soil obtained from laboratory analyses were given in units [mg/g], whereas the corresponding modelled values are in [kg/m^2]. Therefore, also in this case the units had to be converted to allow a comparison of simulated results with the observations. From the field measurements we know the area, from which the sample was extracted: S in [m^2]. In the case of soil cores, this area is equal to the area of the soil auger hole. The weight of the soil mass m in [g] extracted from this area is known from the laboratory analyses. Dividing m/S we obtain the weight of the soil mass per 1m^2: M [g/m^2]. After multiplying the observed amount of carbon or nitrogen in 1 g of soil with this weight M and its subsequent division by 1,000,000, we get the amount of nutrient in the desired units [kg/m^2]. Hence, the conversion formula has the following form:

$$C_{Conv.} = \frac{C}{1{,}000{,}000} \cdot \frac{m}{S}$$

where $C_{conv.}$ = carbon content per 1 m^2 of litter or soil in [kg/m^2],
C = carbon content in 1 gram of litter or soil in [mg/g],
m = weight of the litter or soil mass in [g],
S = area, from which the litter or soil sample was extracted in [m^2]

It is necessary to note, that if we convert the values obtained from the mixed samples, which consist of more than one horizon, the sums of the core areas and soil mass weights have to be used.

Since the model is currently able to simulate only pure forest stands, whereas Rothwald is a mixed stand of spruce, fir and beech, the model evaluation for this location was done in two different ways. The simulations were performed using either spruce or beech parameterisation (see Section 2.5.1), whereby fir proportion was assigned to spruce and the proportion of other broadleaf species to beech. One of the following two methods was used to obtain the modelled results that were compared to the field observations:

(1) we assumed the plots to be pure according to the prevailing tree species in the living biomass (Table 12, columns 1 and 2). This means that out of a total of 18 plots, 14 plots were regarded as pure beech plots and 4 (SO, RO, IU and MWU) as pure spruce plots. This modelled output is referred to as "Rothwald pure" in the following text.

(2) all plots were simulated twice, first as pure beech stands and then as pure spruce stands. Afterwards, the modelled output from the two different species-specific simulations was combined according to the actual species composition on the plot. In the calculations, three different types of species proportions were taken into account according to the modified variable:

   a) in the case of stand volume of living biomass as well as other characteristics describing living tree layer (e.g. LAI), the species composition calculated from living trees was taken as a conversion measure (Table 12, columns 1 and 2),

   b) for the amount of coarse woody debris the species proportion in dead wood mass was used (Table 12, columns 3 and 4),

   c) litter and soil characteristics (carbon and nitrogen amount in the litter and soil) were adjusted using the average species proportion obtained from the sum of living and dead biomass, since these values are believed to represent long-term species composition of the plots (Table 12, columns 5-6).

This differentiation of species composition was considered to be important due to the large differences in species proportion between living and dead biomass (see Table 12). All types of species composition were calculated from volume values rather than basal area, which is more often used in forestry, because the model does not explicitly address basal area. Modelled output produced using this recalculation will be in the following text referred to as "Rothwald mixed".

Table 12: Species composition of individual plots in Rothwald calculated as the fraction of the particular tree species from the total volume of wood mass on the plot.

Plot	**Tree species composition** [volume of tree species / total volume]					
	Living biomass		**Dead wood**		**Average**	
	Beech + other broadleaf	Spruce + Fir	Beech + other broadleaf	Spruce + Fir	Beech + other broadleaf	Spruce + Fir
Column No	1	2	3	4	5	6
SU	0.65	0.35	0.30	0.70	0.46	0.54
SM	0.97	0.03	0.43	0.57	0.71	0.29
SO	0.35	0.65	0.39	0.61	0.36	0.64
XU	0.59	0.41	0.57	0.43	0.58	0.42
XM	0.84	0.16	0.49	0.51	0.62	0.38
XO	0.96	0.04	0.47	0.53	0.64	0.36
RU	0.58	0.42	0.27	0.73	0.45	0.55
RM	1.00	0.00	0.28	0.72	0.75	0.25
RO	0.47	0.53	0.16	0.84	0.23	0.77
IU	0.25	0.75	0.51	0.49	0.33	0.67
IO	0.66	0.34	0.52	0.48	0.58	0.42
IIU	0.70	0.30	0.14	0.86	0.47	0.53
IIO	0.78	0.22	0.16	0.84	0.42	0.58
IVU	0.66	0.34	0.27	0.73	0.44	0.56
IVO	0.60	0.40	0.30	0.70	0.45	0.55
MWU	0.15	0.85	0.30	0.70	0.20	0.80
MWM	0.99	0.01	0.26	0.74	0.48	0.52
MWO	1.00	0.00	0.31	0.69	0.49	0.51

2.5 SIMULATION RUNS

In Chapter 2.1.2 we described the general simulation steps using the species-specific adaptation of the model BIOME-BGC. In this section we present a specific description of the simulation steps for the locations used in this study.

2.5.1 Simulation of virgin forests

The simulation of the virgin forests Babia hora and Rothwald started with the spinup procedure as outlined in Section 2.1.2.1. The simulation of each plot was performed as follows. The system was first brought to steady state with the pre-industrial carbon dioxide concentration (280 ppm; IPCC WGI 1996) and nitrogen deposition level (0.0001 kgN/m^2/year; Holland et al. 1999). All the simulations were performed in both ways, i.e. with and without spinup acceleration (see Section 2.1.2.1). The "slow" or "normal" spinup without acceleration was let to run for 100,000 years to examine the length of the simulation until the ecosystem reaches a steady-state. The accelerated spinup stops automatically, if the condition about the difference in soil organic matter (SOM) is met, i.e. when the difference in SOM between two successive climate periods does not exceed the value 0.0005 kgC/m^2/year (see Section 2.1.2.1).

After the equilibrium was reached, another 237 to 624 years were simulated to account for the industrial influence starting in 1765 (IPCC WGI 1996), i.e. the simulation of the current stand was perfomed (Section 2.1.2.3). The length of this auxiliary simulation differed between the plots and was set to such a value that for the last 40 years the climate records were used for the year of their measurement, e.g. for the simulation of the year 2002 the climate data from this year were used, and in the case of dynamic mortality (Section 3.1.4) the modelled development stage of the plot coincided at the end of the simulation with its actual state given in Table 13. The development stage of the plot was either determined in the field (Babia hora, Merganič et al. 2003) or in the case of Rothwald, derived from the evaluation of the stand characteristics (tree diameter and height distributions) and the plot visualisation (see Appendix 4) using the Stand Visualisation System SVS (McGaughey 1999). Table 13 presents the list of individual plots per location that were assigned a particular development stage.

From 1765 onwards atmospheric carbon dioxide was gradually increased to current values according to the scenario provided by the IPCC (IPCC WGI 1996). Along with this, nitrogen deposition was increased at the same rate from the pre-industrial values to the sites' nowadays values (see Table 9).

Table 13: Distribution of the sample plots to development stages.

Development stage	Plots	
	Rothwald	Babia hora
Growth	IO, MWM, MWO, RO, RU, SO	4, 5, 8, 9, 10, 19, 22, 25, 26, 29, 32, 35, 37, 41, 45, 46, 49, 52, 57
Maturity	IIU, IU, IVO, RM, MWU, JU	7, 11, 12, 13, 15, 16, 17, 23, 27, 30, 31, 36, 38, 40, 44, 47, 50, 53, 56
Breakdown	IVU, JM, JO, SM, SU, IIO	1, 2, 3, 6, 14, 18, 20, 21, 24, 28, 33, 34, 39, 42, 43, 48, 51, 54, 55

For the simulations of the forest stands in Babia Hora we used a tree species-specific model parameterisation for highland spruce *Picea abies* L./Karst. (Pietsch and Hasenauer 2004, Appendix 2). In Rothwald, where mixed forests of spruce, fir and beech prevail (see Section 2.3.1.1, Table 1), we made two different simulations, one with highland *Picea abies* L./Karst. parameterisation, and the other with the tree species-specific model parameterisation for *Fagus sylvatica* L. (Pietsch and Hasenauer 2002, Appendix 2), because the model is currently able to simulate only pure forest stands. Although fir proportion was on some plots substantial (>20% from stand volume), no fir simulations could have been performed because no fir-specific parameterisation was available.

2.5.2 Simulation of managed forests

The simulation of the selected managed forest stands was performed in three steps according to the description given in Section 2.1.2, because no data defining the initial status of the ecosystems were obtained from the field measurements.

2.5.2.1 Spinup

First, the self-initialisation simulation was performed for each simulated plot using the pre-industrial carbon dioxide concentrations (280 ppm; IPCC WGI 1996) and nitrogen deposition levels (0.0001 kgN/m^2/year; Holland et al. 1999) to obtain the initial values for further simulations of the forest stands. For this purpose, we used the “slow” spinup procedure with the length set to 30,000 years. Starting with a leaf carbon pool of 0.001 kgC/m^2, the spinup procedure for a particular plot was completed after the pre-defined simulation length, when the soil carbon content, i.e. the last pool among the carbon pools to reach a steady state, was found to be in equilibrium (see Section 2.1.2.1).

For each location such a species-specific parameterisation was used within the self-initialisation simulation that represented its natural forest vegetation, i.e. in Wilhelmsburg we applied the parameterisation of common beech *Fagus sylvatica* L. (Pietsch and Hasenauer 2002, Appendix 2), in Hartberg the settings for oak *Quercus sp.* (Pietsch et al. 2003, Appendix 2) and in Bad Zell the parameterisation for lowland *Picea abies* L./Karst. (Pietsch and Hasenauer 2002, Appendix 2).

2.5.2.2 Site history

The results of the spinup procedure were in the second step corrected for possible degradation effects due to the changes in land use and forest management. This was proved to be very crucial for the accuracy of the modelled carbon and nitrogen sequestration (Pietsch and Hasenauer 2002), because intensive management may have led to a decline in nutrient status and soil fertility.

In our simulations we assess this problem by simulating 5 rotation periods with clear cutting and successive planting according to available information (see Mayer 1974, Kral 1980, Peterken 1996) for reconstructing site history. The first three rotations were simulated using the species-specific model adaptations for the prevailing natural tree species on site, i.e. common beech in Wilhelmsburg, oak in Hartberg, and lowland Norway spruce in Bad Zell. The last two rotations were simulated on all plots with lowland Norway spruce parameter settings (Appendix 2). In the case of Bad Zell, no major change in species composition took place, thus all 5 rotations were simulated with the spruce setting.

Clear cutting was simulated by (1) removing the aboveground biomass, and (2) assigning the belowground woody biomass to the coarse woody debris. The non-woody biomass of fine roots was assigned to the litter pools. Successive planting was assumed by setting the starting value for leaf carbon to 10 gC/m^2 and for stem carbon to 25 gC/m^2. Rotation lengths were set to 100, 120 and 140 years for spruce, beech and oak, respectively. Beginning with the year 1765, the values of atmospheric carbon dioxide were gradually increased from pre-industrial to industrial values according to the scenario provided by the IPCC (IPCC WGI 1996). Nitrogen deposition was increased at the same rate from the pre-industrial values to the present site values (see Table 9).

2.5.2.3 Current stand

For simulating the current forest conditions, planting was modelled at the time of the stand establishment (1958 in Hartberg, 1964 in Wilhelmsburg, 1960 in Bad Zell Grillnberger and 1965 in Bad Zell Kern) as described above. Atmospheric CO_2 concentration was raised from the value reached at the time of planting to the present values according to the IPCC (IPCC WGI 1996). Nitrogen deposition was increased at the same rate to reach the value suggested for the year 1994 (Schneider 1998, Table 9). For the period after the year 1994, both CO_2 and nitrogen were let to raise further according to the scenario provided by IPCC (IPCC WGI 1996).

Thinning was applied as the relative reduction of the aboveground woody biomass calculated from the available data about the stand volume (Table 8). Other pools, i.e. leaves, fine and coarse roots, were reduced proportionally according to the age-dependent relation between stem and a particular pool derived from the studies of Krapfenbauer and Buchleitner (1981) and Krapfenbauer (1983).

After the thinning operations, harvesting was performed as defined for each simulated plot. The three different harvesting scenarios were simulated as follows:

1. Whole tree harvest (WTH): The whole felled aboveground woody and non-woody biomass was removed and the remaining coarse and fine roots of the felled trees were added to the coarse woody debris and the litter pools, respectively.
2. Whole tree harvest after 1 year or delayed tree harvest (DTH): Total felled woody biomass was assigned to the coarse woody debris pool, whereas leaves and fine roots to the litter pools. After one year the coarse woody debris pool was corrected for the percentage of aboveground woody biomass that was added during the previous year's thinning, whereby we accounted for (a) the coarse woody debris added within this year due to mortality and (b) the coarse woody debris decline due to its decomposition to the litter pools and atmosphere. From the remaining coarse woody debris pool the percentage of the aboveground woody biomass, which was temporarily added during the previous year's thinning, was removed.
3. Stem wood harvest (SWH): Stem wood biomass (all logs with a top diameter greater than 7 cm outside bark) calculated as % of aboveground woody biomass according to tables given in Krapfenbauer and Buchleitner (1981) was removed and the branches together with the coarse roots were added to the coarse woody debris. Leaves and fine roots were assigned to the litter pools. In Hartberg and Bad Zell the first thinning resulted in no harvest and hence no biomass removed.

The simulation of the current stand was divided into five sub-simulations, so called runs (run 1 to run 5), to account for the thinning and harvesting operations performed within the forest stands as described above. An overview of the different working steps ranging from the spinup to the current stand situation is given in Table 14.

Table 14: Description of the simulation regimes for each management location. After the spinup, 5 rotation periods with different assumptions concerning the major forest type are applied to consider the management history. The simulations of the current stands are divided into 5 runs to account for the thinning regimes and the three different harvesting scenarios: WTH = whole tree harvest, DTH = delayed tree harvest and SWH = commercial stem wood harvest.

Description of simulation steps		**Wilhelmsburg**	**Hartberg**	**Bad Zell Grillnberger**	**Bad Zell Kern**
Spinup	Species	Beech	Oak	Spruce	Spruce
Rotations 1 to 3	No. Years	120	140	100	100
	Species	Beech	Oak	Spruce	Spruce
Rotation 4	No. Years	100	100	100	100
	Time period	1765-1865	1765-1868	1765-1866	1765-1867
	Species	Spruce	Spruce	Spruce	Spruce
Rotation 5	No. Years	99	93	95	100
	Time period	1865-1963	1865-1957	1865-1959	1865-1964
	Species	Spruce	Spruce	Spruce	Spruce
Current stand	No. Years	18	24	24	19
Run1	Time period	1964-1981	1958-1981	1960-1983	1965-1983
	Species	Spruce	Spruce	Spruce	Spruce
1st thinning on all plots + Harvest on WTH plots					
Current stand	No. Years	1	1	1	1
Run2	Time period	1982	1982	1984	1984
	Species	Spruce	Spruce	Spruce	Spruce
Harvest on DTH plots					
Current stand	No. Years	10	10	8	12
Run 3	Time period	1983-1992	1983-1992	1985-1992	1985-1996
	Species	Spruce	Spruce	Spruce	Spruce
2nd thinning on all plots + Harvest on WTH and SWH plots					
Current stand	No. Years	1	1	1	1
Run 4	Time period	1993	1993	1993	1997
	Species	Spruce	Spruce	Spruce	Spruce
Harvest on DTH plots					
Current stand	No. Years	5	6	9	5
Run 5	Time period	1994-1998	1994-1999	1994-2002	1998-2002
	Species	Spruce	Spruce	Spruce	Spruce

3. RESULTS

The purpose of this study is to evaluate the performance of the species-specific adaptation of the model BIOME-BGC, in particular its self-initialisation procedure and its applicability for the assessment of different harvesting regimes. These objectives can be achieved by comparing the model output with the observations from the forests. From all the available model output variables we chose the following state variables that are the best equivalents to the measurements in the field: carbon content in the stem and coarse woody debris, carbon and nitrogen amounts in both litter and soil. However, these model variables are given in different units from the field measurements and therefore, they are not directly comparable with the observations. Therefore, it was necessary to convert the values to the same units to allow a comparison between modelled and observed values according to the description given in Section 2.4.

3.1 RESULTS FROM SIMULATIONS OF VIRGIN FORESTS

The validation of the self-initialisation procedure incorporated in the model BIOME-BGC was performed by comparing the simulated output with the measurements from the two virgin forests: Rothwald in Austria, and Babia hora in Slovakia (see Figure 7).

3.1.1 Simulations with the original model set up

Using the original set up of BIOME-BGC with the annual whole plant mortality rate 0.5% and fire mortality 0.5% or 0.25% for spruce and beech, respectively, we obtained an average simulated stand volume for Rothwald pure, Rothwald mixed and Babia hora 1,726; 1,627 and 730 m^3/ha, respectively (Table 15). Whereas in Rothwald the majority of predicted stand volume exceed the highest measured stand volume on the plots (1,089 m^3/ha), in the case of Babia hora, the modelled values are at the upper range of the observed stand volume. The average values for Rothwald are twice as high as for Babia hora due to the differences between tree species and also because of different fire mortality rate for beech and spruce. Comparing the predictions with the observations for each plot, we can see that the modelled stand volume is both in Rothwald (both pure and mixed) and Babia hora overestimated (Figure 18, Tables 15 and 16).

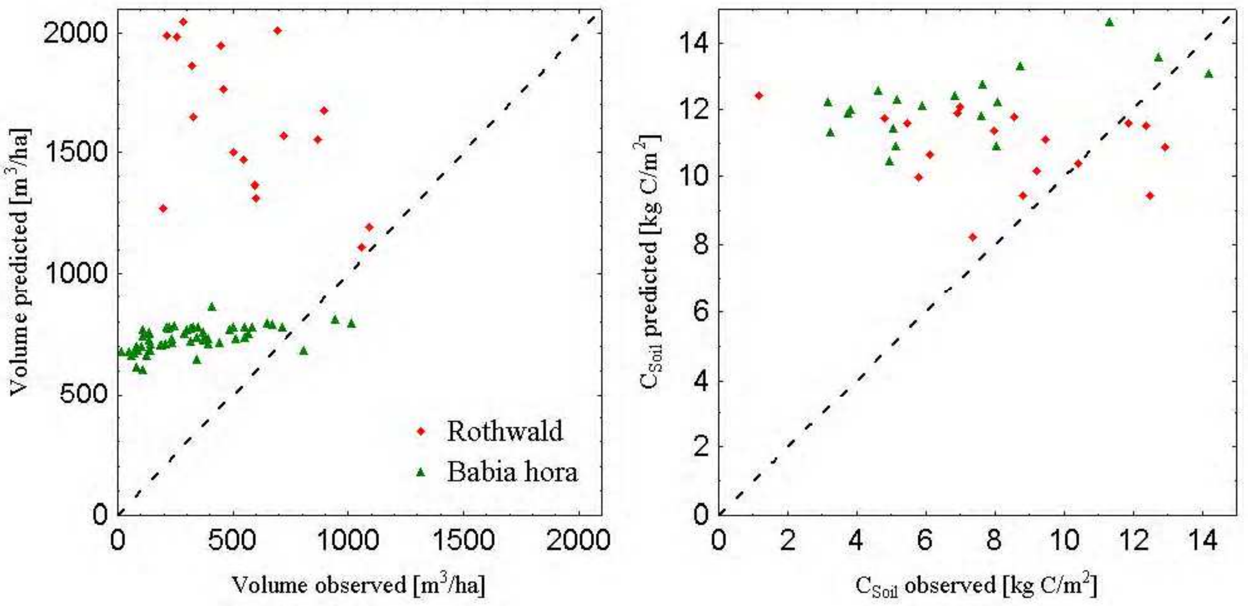

Figure 18: Observed versus predicted stand volume and carbon content in the soil obtained with the original model set up. The predictions in Rothwald are the values for the variant "Rothwald mixed". Number of observations N = 18 in Rothwald, N = 57 for stand volume in Babia hora, and N = 19 for carbon in the soil in Babia hora.

The coarse woody debris is in Rothwald underestimated and in Babia hora overestimated (Tables 15 and 16). This opposite behaviour is caused by the difference in the observed amounts of coarse woody debris in the two virgin forests: in Rothwald there is on average 4-times more coarse woody debris than in Babia hora (Tables 3 and 6). In the following analyses we take the amount of dead wood measured in Babia hora as the basis for the comparison with the simulated output, since the virgin forest Rothwald was affected several times in the 2nd half of the last century by wind-throws, which caused a much larger accumulation of dead wood on the ground in this forest .

The litter characteristics, i.e. carbon and nitrogen amount in the litter, are in both forests on average underestimated (Tables 15 and 16). At this point it is, however, necessary to point out, that the modelled values of these characteristics are hardly comparable with the measurements, because model litter encompasses dead leaf and fine root biomass and defragmented dead wood, whereas in reality litter comprises also other kinds of dead organic material, e.g. small twigs, pieces of bark, buds, flowers, etc. which can make up 20 to 40% of the dry mass of litter (Šály 1991).

In contrast to the litter parameters, carbon and nitrogen in the soil are overestimated using the model (Figure 18, Tables 15 and 16). Nevertheless, as can be seen from Figure 18 and Table 15 their absolute values are in general close to the highest observed values in both virgin forests.

The presented results suggest that using the original model set up we can obtain for the virgin forest Babia hora, i.e. for Norway spruce forest stands, similar predictions of stand volume, amount of coarse woody debris, and carbon and nitrogen content in the soil to the highest values observed in the field (Table 15). In Rothwald, this statement does hold only for soil characteristics, because modelled stand volume reaches higher values there. We assume that if the fire mortality had been doubled for beech, i.e. instead of 0.25% per year the value 0.5% had been used as for spruce, the simulated stand volume would have been decreased. However, the influence of this change was not tested since in Central Europe fire does not currently play an important role in the forest dynamics (Goldammer and Page 2000).

3.1.2 Simulations with the original regular mortality 0.5% per year

Therefore, in the next step the fire mortality was set to zero and the forest stands were simulated only with the regular mortality of 0.5% of the whole plant biomass per year. At the end of the simulation, all examined characteristics increased their values, some even by a factor 2 or more, when compared with the results of the original model set up (Table 15). This means that in Babia hora all characteristics except carbon and nitrogen in the litter, and in Rothwald also except the amount of coarse woody debris, are in comparison to observations overestimated. For example, stand volume is overestimated by about a factor 6-7 (Figure 19, Table 15). Similarly, the modelled carbon and nitrogen amount in the soil exceeded the measurements by more than 100% (Figure 19, Table 15).

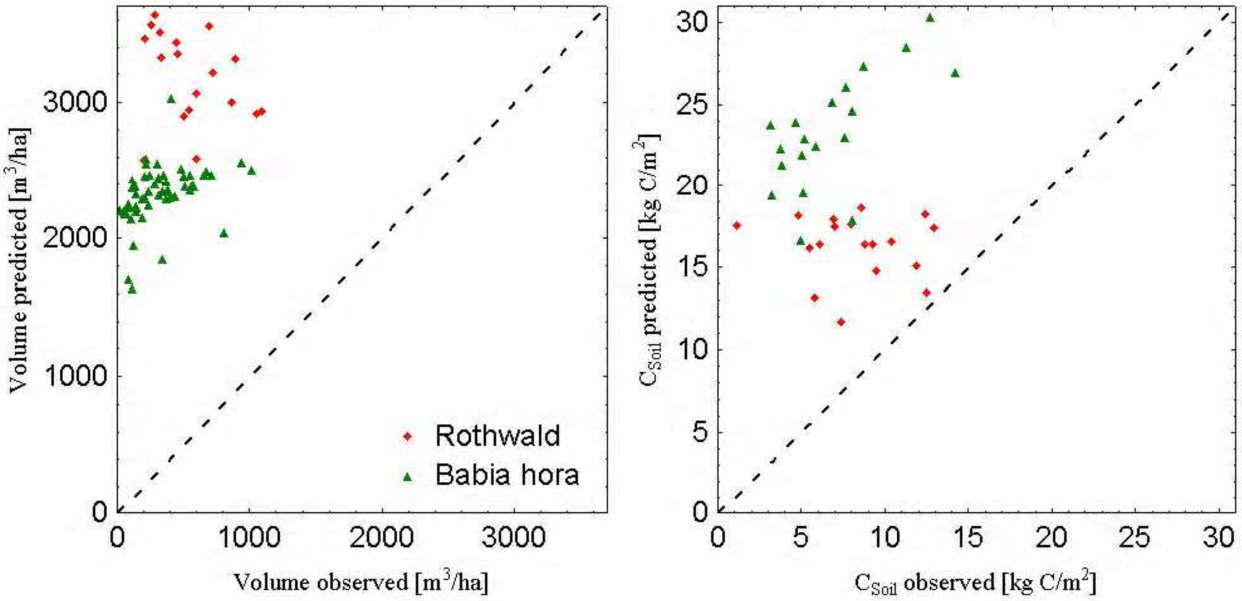

Figure 19: Observed versus predicted stand volume and carbon content in the soil obtained with the original regular mortality 0.5% per year and fire mortality switched off. The predictions in Rothwald are the values for the variant "Rothwald mixed". Number of observations N = 18 in Rothwald, N = 57 for stand volume in Babia hora, and N = 19 for carbon in the soil in Babia hora.

The results presented in Figure 19 and Table 15 show that when the fire mortality is switched off, the steady state obtained at the end of the spinup simulation does not represent the actual equilibrium that can be observed in the undisturbed ecosystems of Central Europe. The values of the aboveground biomass as well as the soil nutrient status do not correspond with the measurements from the two locations and highly exceed also other published values from Central European virgin forests (e.g. Korpeľ 1995).

3.1.3 Simulations with the regular mortality 2% per year

One possibility of obtaining a more realistic output from the model under the assumption that no fire mortality occurs in the ecosystem would be to increase the regular mortality rate. Thus, we changed the original 0.5% annual mortality rate to 2% according to Little (1995), who presents this value as a mortality in natural mature ecosystems.

The results from the simulations with a 2% annual mortality show that the modelled values of all examined variables were reduced compared to the previous simulations with 0.5% mortality rate per year (Table 15, Figures 19 and 20). The average modelled stand volume dropped from 3,252; 3,183 and 2,322 m^3/ha to 798, 783 and 541 m^3/ha for Rothwald pure, Rothwald mixed and Babia hora, respectively (Table 15). The other variables were affected by a higher mortality in the

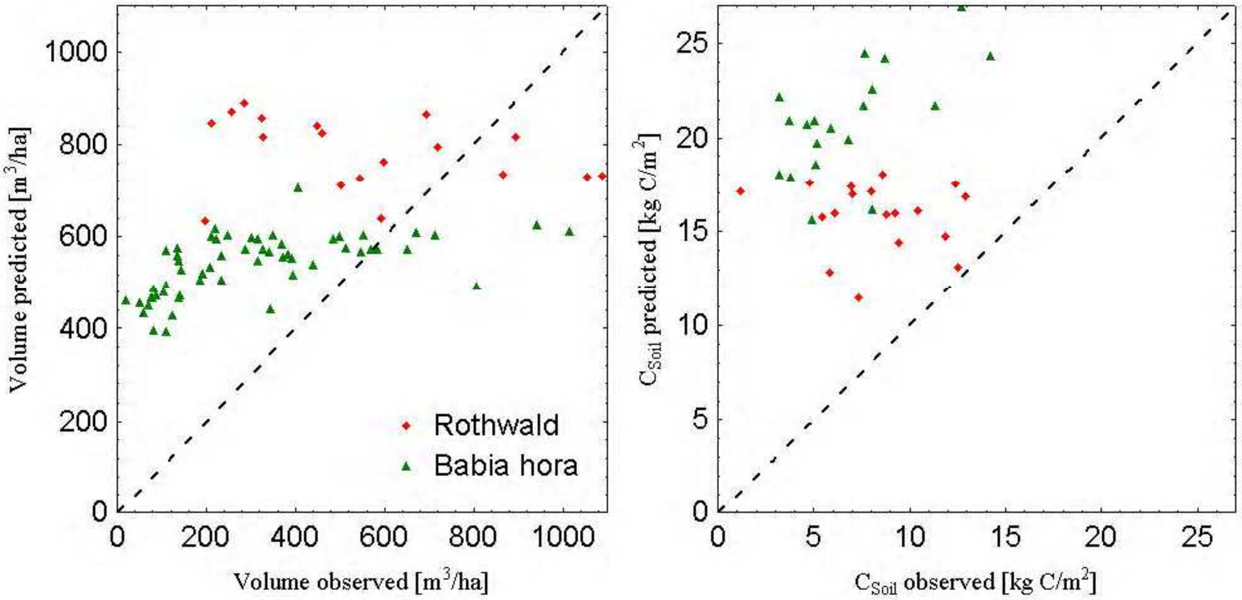

Figure 20: Observed versus predicted stand volume and carbon content in the soil obtained with the regular mortality 2% per year and fire mortality switched off. The predictions in Rothwald are the values for the variant "Rothwald mixed". Number of observations N = 18 in Rothwald, N = 57 for stand volume in Babia hora, and N = 19 for carbon in the soil in Babia hora.

same manner as the stand volume. Firstly, the opposite reaction was expected, since a higher mortality rate produces more coarse woody debris, which is a potential source of nutrients for litter and soil. However, the lower values of coarse woody debris, carbon and nitrogen amount in litter and soil are the result of the lower aboveground biomass, from which 2% makes approximately the same amount as 0.5% from the original stand volume (e.g. for Babia hora 10.82 versus 11.61 m^3/ha). Although the higher mortality rate caused the reduction in all studied pools of the ecosystem (stem, CWD, litter and soil), the decrease of all variables except the stand volume was relatively small. In fact, the soil characteristics, e.g. carbon content in the soil, and in Babia hora also CWD are still overestimated by the model (Figure 20, Table 15).

Comparing the results obtained with 2% annual mortality rate with those produced by the original model set up, i.e. 0.5% regular mortality and fire module switched on, we can see that including fire improves the predictions of litter and soil compartments (Tables 15, 16). The reason for this difference is the fact that fire does not only increase the mortality rate itself, but also causes carbon and nitrogen loss from the ecosystem due to burning. If the fire module is switched off and only regular mortality is simulated, no such losses of nutrients occur, and nutrients are accumulated in the ecosystem. Therefore, the modelled litter and soil pools are higher for the variant with regular mortality 2% per year than for the original model set up (see Table 15). Since the modelled carbon and nitrogen amount in soil obtained with the increased mortality rate 2% per year is still overestimated by about a factor 2 to 5, whereas the predicted average stand volume differs from the measured values by less than 80% (Table 15), we can conclude that a further increase of mortality rate will not lead to the desired results.

Table 15: Summary statistics of the observations and the output of slow (normal) spinup for each simulation variant, location and all examined variables. C_{CWD}, C_{Litter}, C_{Soil} are carbon contents in coarse woody debris, litter and soil, respectively, and N_{Litter} and N_{Soil} are nitrogen contents in the litter and soil, respectively. *Stdev* is the standard deviation and *CV* is the coefficient of variation.

Variant		Reality		Original mortality 0.5% + fire			Original mortality 0.5%			Mortality 2%			Dynamic mortality		
Location		Rothwald	Babia hora	Rothwald		Babia hora	Rothwald		Babia hora	Rothwald		Babia hora	Rothwald		Babia hora
Species		Mixed	Spruce	Pure	Mixed	Spruce	Pure	Mixed	Spruce	Pure	Mixed	Spruce	Pure	Mixed	Spruce
Number of plots		18	57 (19)*	18	18	57 (19)*	18	18	57 (19)*	18	18	57 (19)*	18	18	57 (19)*
Variable: Volume [m^3/ha]	Mean	559.20	313.20	1726.22	1626.67	729.85	3252.33	3183.50	2321.72	798.21	782.61	540.49	635.42	633.30	294.27
	Stdev	280.03	230.01	445.87	303.50	49.56	392.05	326.95	215.06	91.83	77.82	64.86	310.37	301.55	142.04
	Min	197.09	18.65	880.90	1108.00	603.79	2334.00	2583.00	1636.26	577.50	634.00	393.57	284.10	297.50	118.07
	Max	1089.00	1014.06	2055.00	2048.00	859.23	3641.00	3636.00	3029.94	890.30	889.30	705.21	1080.00	1076.00	646.75
	CV [%]	50.08	73.44	25.83	18.66	6.79	12.05	10.27	9.26	11.50	9.94	12.00	48.85	47.62	48.27
C_{CWD} [kg C/ha]	Mean	86139.33	20305.32	40195.56	28028.33	27912.87	54911.67	43455.00	56396.05	53362.78	41956.67	50278.58	31485.00	26498.89	19531.68
	Stdev	19825.55	22573.71	12389.67	4095.15	1380.63	12650.25	6235.97	5048.24	12456.48	5929.74	4737.18	14794.63	12897.30	10209.65
	Min	56769.27	0.00	16650.00	19920.00	23832.15	26420.00	29470.00	39415.79	25610.00	28590.00	36912.89	10380.00	11550.00	8962.85
	Max	132471.00	100095.16	50620.00	34100.00	33429.36	67420.00	52050.00	70944.04	65610.00	50160.00	62972.24	56400.00	47070.00	39229.67
	CV [%]	23.02	111.17	30.82	14.61	4.95	23.04	14.35	8.95	23.34	14.13	9.42	46.99	48.67	52.27
C_{Litter} [kg C/m^2]	Mean	0.9523	5.1391	0.5489	0.4622	0.4042	0.6260	0.5309	0.6606	0.5986	0.5071	0.5661	0.7044	0.6986	0.3441
	Stdev	0.4449	1.9270	0.1349	0.0615	0.0389	0.1570	0.0788	0.0839	0.1504	0.0744	0.0691	0.4980	0.5402	0.1853
	Min	0.3877	1.8622	0.2552	0.3037	0.3391	0.2915	0.3442	0.5271	0.2801	0.3296	0.4424	0.1662	0.1918	0.1705
	Max	1.9014	8.9786	0.6927	0.5466	0.4727	0.8016	0.6297	0.8321	0.7668	0.6025	0.6787	1.5770	1.5500	0.7615
	CV [%]	46.7184	37.4972	24.5732	13.3102	9.6227	25.0815	14.8482	12.7077	25.1331	14.6670	12.2132	70.6902	77.3257	53.8401
N_{Litter} [kg N/m^2]	Mean	0.0319	0.2282	0.0052	0.0042	0.0033	0.0057	0.0046	0.0051	0.0055	0.0045	0.0045	0.0039	0.0038	0.0023
	Stdev	0.0142	0.0741	0.0015	0.0006	0.0003	0.0017	0.0008	0.0007	0.0016	0.0007	0.0006	0.0012	0.0006	0.0004
	Min	0.0138	0.0975	0.0020	0.0026	0.0027	0.0022	0.0028	0.0040	0.0022	0.0028	0.0035	0.0016	0.0021	0.0016
	Max	0.0626	0.3637	0.0067	0.0051	0.0039	0.0075	0.0057	0.0067	0.0072	0.0055	0.0055	0.0057	0.0046	0.0030
	CV [%]	44.6712	32.4594	29.1114	14.9165	10.3898	30.2666	16.4942	13.8943	29.8226	16.1874	12.9009	31.4507	15.6531	18.2162
C_{Soil} [kg C/m^2]	Mean	8.2633	6.8401	12.5719	10.8896	12.2008	17.1306	16.2744	23.3589	16.7217	15.8056	20.8927	8.9070	8.6092	6.9183
	Stdev	3.0901	3.2529	2.6635	1.0973	1.0059	2.2653	1.9292	3.5687	2.2537	1.8320	2.9174	1.1663	1.0489	1.2441
	Min	1.1631	3.1849	7.3370	8.2150	10.4547	11.2300	11.7300	16.6408	10.9300	11.4300	15.6408	6.3120	6.4630	5.0685
	Max	12.9178	14.2040	15.1600	12.3900	14.6273	19.7300	18.5800	30.2927	19.3000	18.0000	26.9460	10.7000	9.8470	9.4645
	CV [%]	37.3955	47.5557	21.1865	10.0762	8.2448	13.2239	11.8543	15.2778	13.4776	11.5909	13.9639	13.0938	12.1831	17.9821
N_{Soil} [kg N/m^2]	Mean	0.4843	0.3732	1.2545	1.0866	1.2174	1.7092	1.6239	2.3308	1.6686	1.5771	2.0847	0.8886	0.8589	0.6902
	Stdev	0.1867	0.1879	0.2659	0.1095	0.1003	0.2258	0.1925	0.3561	0.2249	0.1829	0.2911	0.1164	0.1047	0.1242
	Min	0.0567	0.1549	0.7321	0.8197	1.0431	1.1210	1.1710	1.6603	1.0900	1.1400	1.5606	0.6298	0.6449	0.5056
	Max	0.8012	0.8157	1.5130	1.2360	1.4594	1.9680	1.8540	3.0229	1.9260	1.7960	2.6889	1.0680	0.9826	0.9444
	CV [%]	38.5393	50.3550	21.1925	10.0799	8.2426	13.2136	11.8524	15.2768	13.4796	11.5994	13.9639	13.0995	12.1839	17.9871

Table 16: Results of model validation for each simulation variant with slow (normal) spinup, location and all examined variables. *Mean Dif.* is the mean difference between predicted and observed values, *Stdev Dif.* its standard deviation and *Mean Dif./MeanReal* and *Mean Dif./MeanModel* are relative mean differences to observed and modelled values, respectively.

		Variant	Original mortality 0.5% + fire			Original mortality 0.5%			Mortality 2%			Dynamic mortality		
		Location	Rothwald		Babia hora	Rothwald		Babia hora	Rothwald		Babia hora	Rothwald		Babia hora
		Species	Pure	Mixed	Spruce	Pure	Mixed	Spruce	Pure	Mixed	Spruce	Pure	Mixed	Spruce
		Number of plots	18	18	57 (19)*	18	18	57 (19)*	18	18	57 (19)*	18	18	57 (19)*
Variable														
Volume	[m^3/ha]	Mean Dif.	1167.02	1067.47	416.65	2693.13	2624.30	2008.52	239.01	223.41	227.29	76.22	74.10	-18.93
		Stdev Dif.	605.11	514.04	206.90	530.36	493.20	245.00	311.43	311.24	199.73	171.56	167.71	156.98
	[%]	Mean Dif./MeanReal	208.69	190.89	133.03	481.60	469.29	641.29	42.74	39.95	72.57	13.63	13.25	-6.04
		Mean Dif./MeanModel	67.61	65.62	57.09	82.81	82.43	86.51	29.94	28.55	42.05	11.99	11.70	-6.43
		t	8.18	8.81	15.20	21.54	22.57	61.89	3.26	3.05	8.59	1.88	1.87	-0.91
C_{CWD}	[kgC/ha]	Mean Dif.	-45943.83	-58111.06	7607.55	-31227.72	-42684.39	36090.73	-32776.61	-44182.72	29973.26	-54654.39	-59640.50	-773.64
		Stdev Dif.	23891.43	20723.79	22492.30	24592.60	20269.39	22904.12	24463.89	20202.07	21239.38	21688.93	19141.63	16862.53
	[%]	Mean Dif./MeanReal	-53.34	-67.46	37.47	-36.25	-49.55	177.74	-38.05	-51.29	147.61	-63.45	-69.24	-3.81
		Mean Dif./MeanModel	-114.30	-207.33	27.25	-56.87	-98.23	64.00	-61.42	-105.31	59.61	-173.59	-225.07	-3.96
		t	-8.16	-11.90	2.55	-5.39	-8.93	11.90	-5.68	-9.28	10.65	-10.69	-13.22	-0.35
C_{litter}	[kgC/m^2]	Mean Dif.	-0.4034	-0.4901	-6.4819	-0.3263	-0.4214	-6.2255	-0.3537	-0.4452	-6.3200	-0.2479	-0.2537	-6.5420
		Stdev Dif.	0.4574	0.4419	1.4438	0.4630	0.4446	1.4372	0.4611	0.4438	1.4466	0.6951	0.7328	1.4701
	[%]	Mean Dif./MeanReal	-42.36	-51.46	-126.13	-34.27	-44.25	-121.14	-37.14	-46.75	-122.98	-26.03	-26.64	-127.30
		Mean Dif./MeanModel	-73.49	-106.03	-1603.69	-52.14	-79.36	-942.43	-59.09	-87.79	-1116.50	-35.19	-36.32	-1901.23
		t	-3.74	-4.71	-19.57	-2.99	-4.02	-18.88	-3.25	-4.26	-19.04	-1.51	-1.47	-19.40
N_{litter}	[kgN/m^2]	Mean Dif.	-0.0266	-0.0277	-0.2910	-0.0261	-0.0272	-0.2892	-0.0263	-0.0274	-0.2898	-0.0279	-0.0281	-0.2920
		Stdev Dif.	0.0142	0.0141	0.0536	0.0142	0.0141	0.0535	0.0142	0.0141	0.0536	0.0141	0.0143	0.0537
	[%]	Mean Dif./MeanReal	-83.64	-86.82	-127.54	-82.05	-85.53	-126.74	-82.70	-85.99	-127.01	-87.73	-88.22	-127.99
		Mean Dif./MeanModel	-511.25	-658.67	-8850.83	-457.21	-590.91	-5647.76	-477.93	-613.77	-6438.94	-714.81	-748.95	-12847.13
		t	-7.98	-8.31	-23.69	-7.83	-8.18	-23.56	-7.89	-8.22	-23.58	-8.40	-8.32	-23.72
C_{soil}	[kgC/m^2]	Mean Dif.	4.3086	2.6263	4.0272	8.8673	8.0112	15.1854	8.4584	7.5423	12.7191	0.6437	0.3460	-1.2553
		Stdev Dif.	3.3997	2.7754	2.2157	2.5907	2.6970	4.4389	2.6082	2.6848	3.7802	2.6118	2.8123	2.1162
	[%]	Mean Dif./MeanReal	52.14	31.78	58.88	107.31	96.95	222.00	102.36	91.27	185.95	7.79	4.19	-18.35
		Mean Dif./MeanModel	34.27	24.12	33.01	51.76	49.23	65.01	50.58	47.72	60.88	7.23	4.02	-18.14
		t	5.38	4.01	7.92	14.52	12.60	14.91	13.76	11.92	14.67	1.05	0.52	-2.59
N_{soil}	[kgN/m^2]	Mean Dif.	0.7701	0.6022	0.7764	1.2249	1.1396	1.8899	1.1843	1.0927	1.6438	0.4043	0.3746	0.2493
		Stdev Dif.	0.2901	0.1617	0.1649	0.2047	0.1969	0.3986	0.2063	0.1914	0.3311	0.1557	0.1750	0.1582
	[%]	Mean Dif./MeanReal	159.01	124.34	208.06	252.90	235.29	506.42	244.52	225.62	440.46	83.48	77.35	66.79
		Mean Dif./MeanModel	61.39	55.43	63.78	71.66	70.17	81.08	70.97	69.29	78.85	45.50	43.61	36.11
		t	11.26	15.80	20.53	25.39	24.55	20.67	24.35	24.23	21.64	11.01	9.08	6.87

3.1.4 The new dynamic mortality model

As already stated, the data used in this study comes from the Central European virgin forests, where the so called "small" succession cycle (Chapter 1.1) usually takes place with competition and ageing (senescence) as the main forces for driving ecosystem dynamics rather than large-scale disturbances. Several publications, e.g. Harcombe (1987), Peterken (1996), Monserud and Sterba (1999), Lorimer et al. (2001) etc., indicate that mortality in natural forest ecosystems has a U-shape with high mortality rates in small and large diameter classes. Based on this information and the theory of the temporal dynamics of stand volume in natural forests (See Chapter 1.1, Figure 2) we presume that the mortality rate is in virgin forests not constant over time, but fluctuates similarly to the stand volume, although in the opposite manner. According to this hypothesis, a new dynamic mortality model was developed and implemented in the model BIOME-BGC. In the proposed mortality model, the annual mortality rate follows an elliptic trajectory (Figure 21), which best mimics the observed U-curve from the juvenile stages of the forest stand up to its senescence.

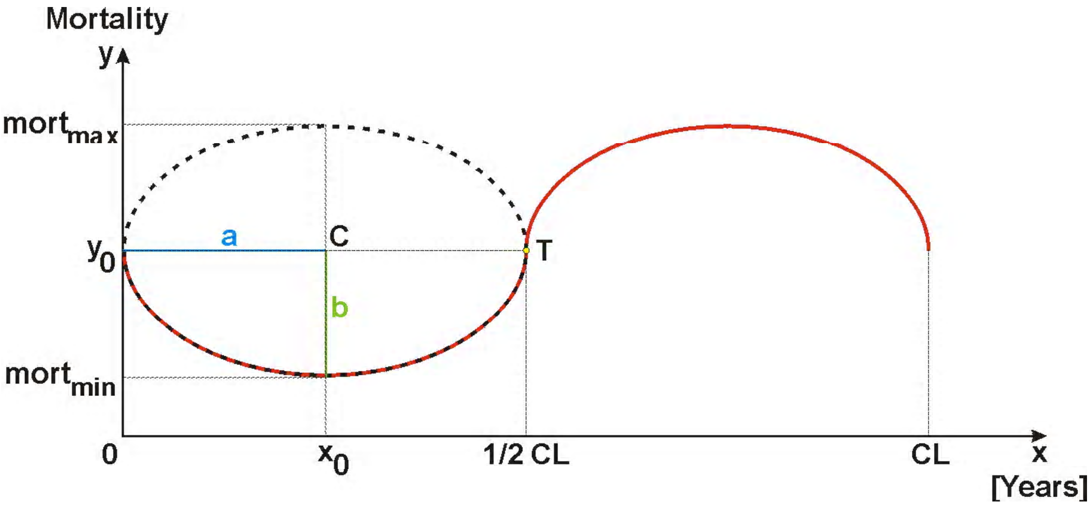

Figure 21: The new dynamic mortality model based on the elliptic trajectory. *C* is the centre of the ellipse with the coordinates (x_o, y_o), *T* is the transition point from concave to convex form, *CL* is the cycle length, $mort_{min}$ and $mort_{max}$ are minimum and maximum annual mortality rates, respectively.

The mathematic formula of the ellipse with the centre *C* in (x_o, y_o) is as follows:

$$\frac{(x-x_0)^2}{a^2}+\frac{(y-y_0)^2}{b^2}=1$$

where x = the year of the cycle, i.e. it can obtain values from the interval $\langle 0, CL\rangle$, with CL equal the length of the cycle,

y = the actual mortality rate *mort*,

a = semi-major axis, in our case a is equal ¼ of the length of the succession cycle,

b = semi-minor axis, here defined as $\frac{(mort_{max} - mort_{min})}{2}$ (see Figure 21).

Solving the given function for y, i.e. the actual mortality rate, we obtain the following formula:

$$y = y_0 \pm \frac{b}{a} \cdot \sqrt{x^2 - 2ax}$$

As shown in Figure 21, the ellipse consists of two branches: the lower concave branch (below the ellipse centre) and the upper convex (above the ellipse centre) one. The mortality rate of the concave branch, i.e. within the interval $\left[0, \frac{CL}{2}\right)$, can be derived by the subtraction of $\frac{b}{a} \cdot \sqrt{x^2 - 2ax}$ from y_o, whereas the mortality within the convex branch by its addition to y_o.

Substituting a, b and y_o in the previous equation for ¼ CL, $\frac{(mort_{max} - mort_{min})}{2}$ and $\frac{(mort_{max} + mort_{min})}{2}$, respectively, and its consequent simplification we get the final formula for the calculation of the actual mortality rate *mort* in the year x:

$$mort = \frac{(mort_{max} + mort_{min})}{2} \pm \frac{(mort_{max} \quad mort_{min})}{2} \cdot \frac{4}{CL} \cdot \sqrt{x^2 - x \cdot \frac{CL}{2}}$$

where *mort* = annual whole plant mortality rate in the year x,

CL = pre-defined length of the cycle,

x = the year of the cycle, i.e. it can obtain values from the interval $\langle 0, CL \rangle$,

$mort_{max}$ = pre-defined maximum annual whole plant mortality rate within one cycle,

$mort_{min}$ = pre-defined minimum annual whole plant mortality rate within one cycle.

The mortality model begins with the concave branch (Figure 21) supposing that the mortality rate is moderate at the beginning of the forest stand development (juvenile stage). As the stand grows (i.e. its average stand age increases), mortality decreases until the minimum mortality rate is reached (maturity). Afterwards, aging effects are assumed, due to which an increase in mortality occurs (see Figure 21). At the transition point T (at ½ of the cycle), the curve changes its shape from concave to convex. After this point, mortality increases until its maximum, and then begins to decline again. After one full cycle the starting point is reached, from which the process is repeated.

The mortality trajectory is defined by the cycle length *CL*, and the minimum and maximum rates of mortality ($mort_{min}$ and $mort_{max}$, Figure 21). For the simulations of our virgin forests, the length of the cycle *CL* was taken from Korpeľ (1995). In the case of Babia hora virgin forest, Korpeľ's length of cycle was also compared with the age of the oldest trees estimated from the bored cores (Merganič et al. 2003). Hence, for both beech and spruce we used the length of the cycle equal to 300 years.

The minimum and maximum mortality rates ($mort_{min}$, $mort_{max}$) were derived from the publications by Harcombe et al. (1990), Harmon and Hua (1991), Greene et al. (1992), Vacek et al. (1996), White et al. (2000), and Sist and Nguyen-Thé (2002).

However, here it is necessary to note that in scientific literature there is a lack of information about the mortality dynamics over time with regard to biomass loss due to mortality. Most papers dealing with mortality assess only the number of trees that died during a certain period, but no information is given about the equivalent wood mass. In Central Europe, studies about the mortality dynamics are in general very rare. Actually, from the publications used for the estimation of the boundary mortality values only Vacek et al. (1996) evaluates Central European forest stands, namely forests of common beech (*Fagus sylvatica L.*) in Krkonoše, Czech Republic.

Due to the lack of information, the minimum and maximum mortality rates estimated from the above-cited literature (0.5% and 4.6% of the whole plant biomass, respectively) were assessed directly in the model simulations and if necessary changed to obtain the best coincidence between the simulated results and the available observations. As a result of this procedure, the upper and lower limits were set to 0.6% and 4.0% mortality of the whole plant per year for spruce in Rothwald, 0.68% and 4.0% for spruce in Babia hora, and 0.76% and 4.1% for beech in Rothwald.

3.1.5 Simulations with dynamic regular mortality

The new dynamic mortality model accounts implicitly for the temporal dynamics of forest ecosystems due to internal factors such as ageing and competition. Therefore, it should allow us to mimic the "small" succession cycle properly.

Prior to the simulations with this new dynamic mortality model, the time when the modelled forest ecosystem reaches a particular development stage (growth – maturity – breakdown, see Section 1.1) had to be specified. The initial idea to define these stages only according to the modelled mortality rate had to be refused, because the analysis of the temporal development revealed that the changes in mortality influence other model state variables, e.g. carbon amount in the stem, in a different manner as expected (see Section 3.1.7.4). We were particularly interested in the development of stand volume, because the theories about its fluctuation over time are known from several studies related to the dynamics of natural forest ecosystems (e.g. Korpeľ 1995,

Figure 2, Chapter 1.1). Accordingly, we expected that the dynamics of stand volume would copy the development of mortality in an inverted way, i.e. when the mortality is at a minimum, the stand volume will be maximum etc. However, as shown in Figure 22, this hypothesis does not hold for the model, since the trajectory of the stand volume development has a different shape as the mortality rate curve.

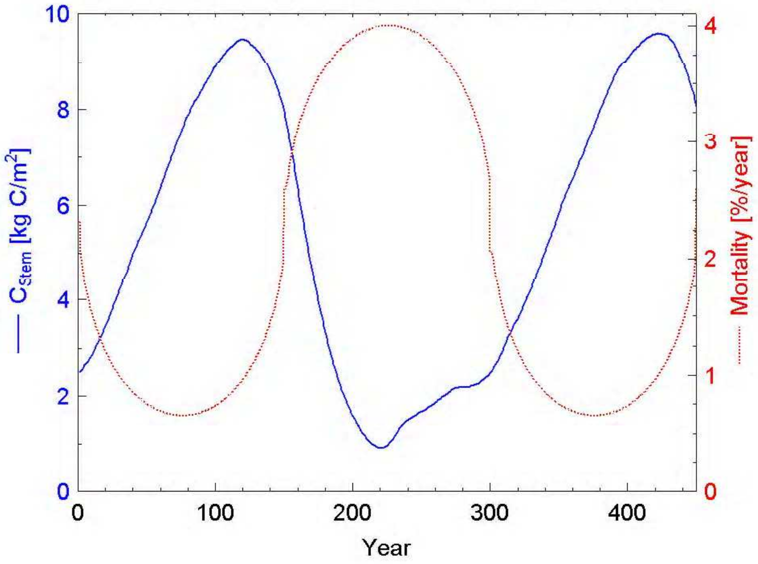

Figure 22: The temporal development of carbon amount in the stem (C_{stem}) and annual mortality rate in the model.

Due to this fact, the development stages in the model were determined considering the temporal changes of mortality, stand volume and coarse woody debris together (see Figure 23). For example, the maturity stage was set to such a period of cycle, where the mortality rate and the

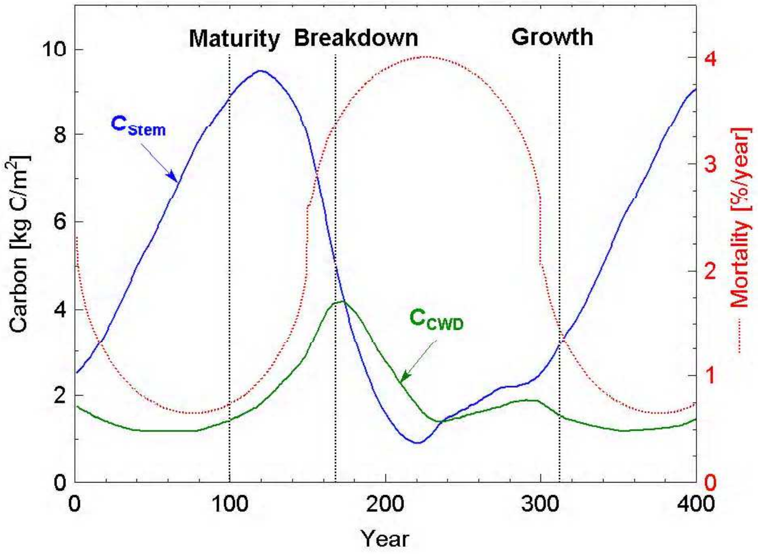

Figure 23: Estimation of the three development stages (growth-maturity-breakdown) in the model, whereby C_{stem} is the amount of carbon in the stem and C_{CWD} is the amount of carbon in the coarse woody debris.

amount of coarse woody debris were low, whereas the stand volume was close to its maximum. The estimated time points for the three main development stages for spruce and beech with a 300 year cycle are given in Table 17.

Table 17: Determination of the development stages for Norway spruce and common beech in model simulations.

Tree species	Cycle length [years]	Development stage [year]		
		Growth	Maturity	Breakdown
		Year from the beginning of one cycle		
Spruce	300	12	100	168
Beech	300	12	100	168

The comparison of the simulation results produced using the new dynamic mortality model with the field observations for stand volume and carbon amount in the soil is presented in Figure 24. From this figure as well as from the values given in Tables 15 and 16 we can see that after the incorporation of dynamic mortality the predictions of stand volume and carbon in the soil are on average unbiased. For example, an average predicted stand volume was 635, 633 and 295 m^3/ha for Rothwald pure, mixed and Babia hora, respectively, whereas from the observations we obtained an average value of stand volume 559 m^3/ha in Rothwald and 313 m^3/ha in Babia hora. Similarly, the modelled soil carbon, and in Babia hora also the amount of coarse woody debris do not differ significantly from the measured values (Table 16).

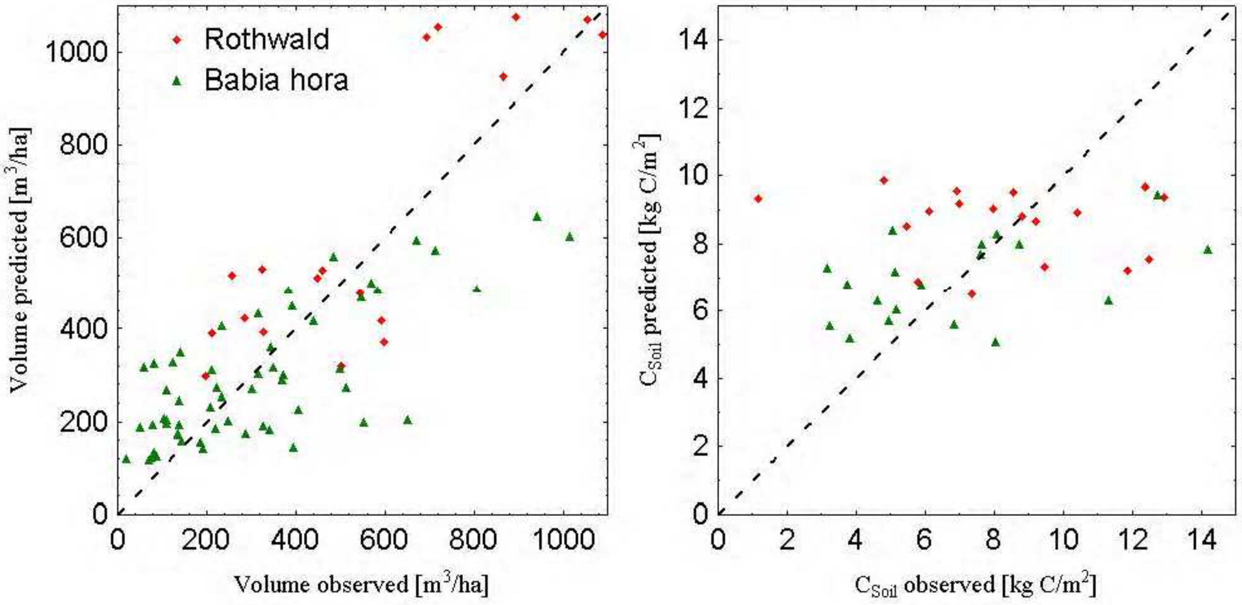

Figure 24: Observed versus predicted stand volume and carbon content in the soil obtained with the dynamic mortality. The predictions in Rothwald are the values for the variant "Rothwald mixed".

3.1.6 Comparison of the simulation variants

The results shown in Figure 25, as well as those given in Tables 15 and 16 suggest that the implementation of the dynamic mortality into the model resulted in significant improvements of the model output. The results of all the evaluated state variables, except nitrogen in the litter and in Babia hora also carbon in the litter, obtained with the new dynamic mortality model are significantly better than those produced with the original model set up or with the other two simulation variants with constant regular mortality rate. In contrast to the first three simulations, using the dynamic mortality the modelled stand volume and soil carbon do not differ significantly from the measured values in either of the virgin forests (Table 16). These results are also confirmed in Figure 25, from which we can see that the predictions of stand volume as well as carbon content in the soil using the dynamic mortality correspond best with the observations from all the analysed simulation variants. In Babia hora, we also obtained unbiased estimates of the amount of coarse woody debris, which was in previous simulation variants overestimated by factors 1.4 to 2.8 depending on the variant. Although soil nitrogen is still overestimated, its prediction was significantly improved after the implementation of the dynamic mortality, as its overestimation was reduced from approximately 300% to 180% (Table 15).

Moreover, the dynamic mortality also increased the modelled variation between the plots, particularly in stand volume, coarse woody debris and litter characteristics (Table 15). In case of the original set up or constant annual mortality rate, the variation of these variables was much smaller than in reality. For example, the coefficient of variation of modelled stand volume was 7 - 20% using the original model set up, which is ⅒ to ½ of the observed variability of stand volume (50 and 70% for Rothwald and Babia hora, respectively). After the implementation of dynamic mortality the coefficient of variation of stand volume was increased to 48% on both locations. Although this simulated variation is still lower than the actual observed variability, particularly in Babia hora (Table 15), it approximates the real variation.

The analysis of the development of the model state variables over time revealed that under the assumption of constant annual mortality a very small temporal variability of the model characteristics can be observed once the modelled ecosystem achieved an equilibrium (Figure 26). In fact, the existing inter-annual variation of the model state variables reflects only the climate variation. On the contrary, the dynamic mortality causes temporal fluctuations of other ecosystem pools, which mimics the development of the virgin forest on a small scale more realistically. According to Korpeľ (1995) a really stable equilibrium with a minimum variation of ecosystem state variables can be found only on a larger area of approximately 30 to 60 ha, where all development stages occur.

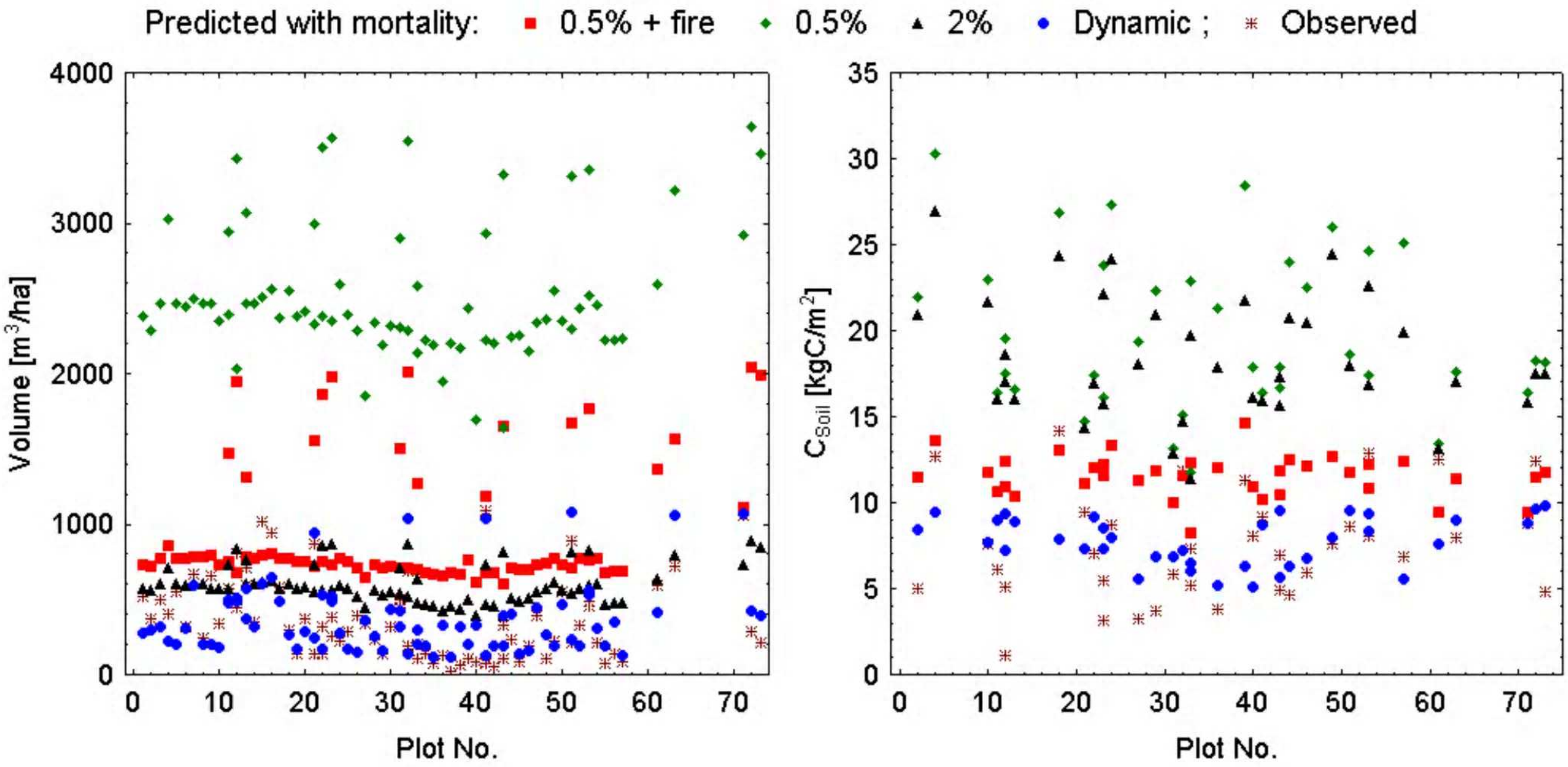

Figure 25: Comparison of the model predictions of stand volume and carbon content in the soil produced by different simulation variants with measured values.

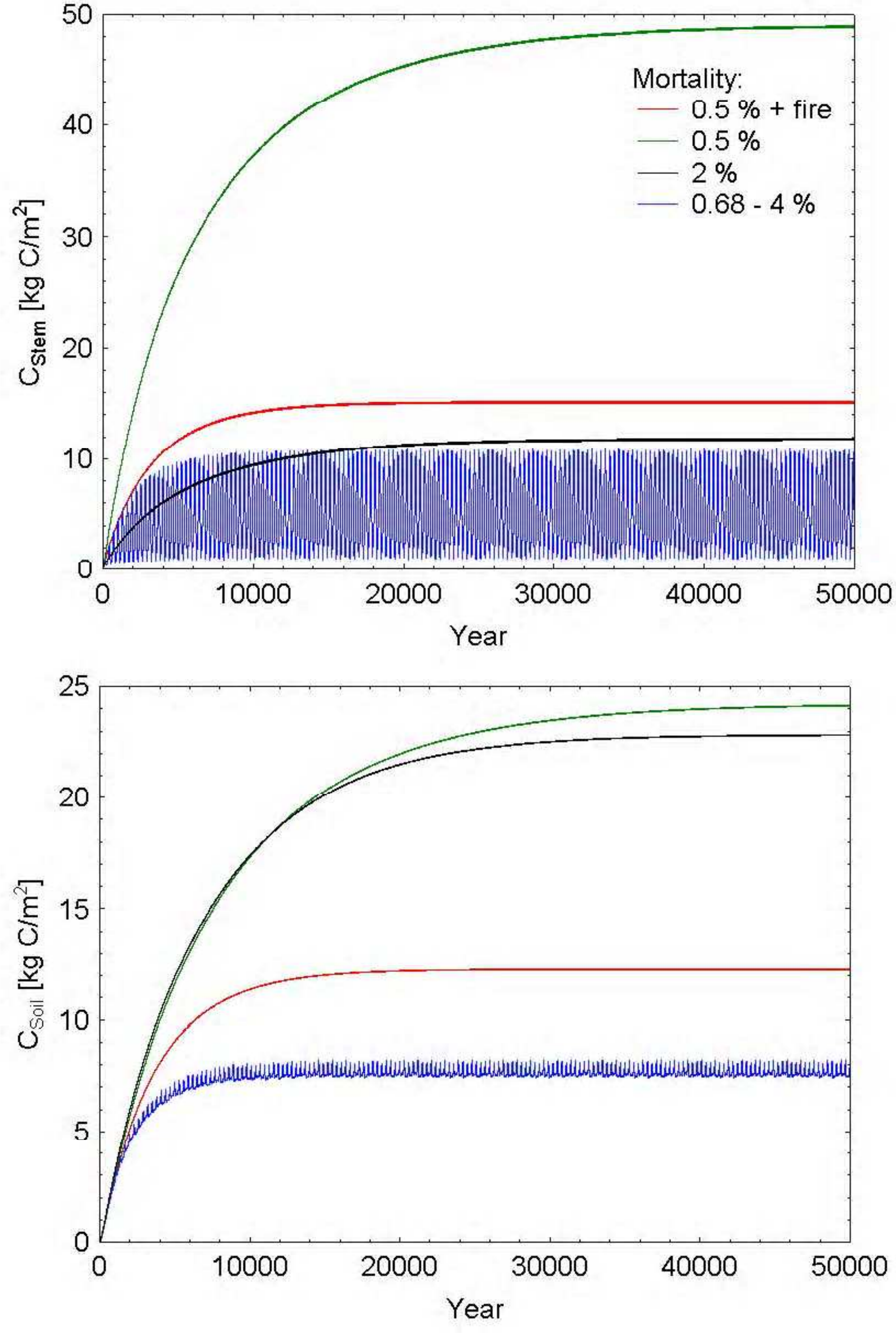

Figure 26: Comparison of all the tested spinup simulation variants defined by the annual mortality rate, whereby C_{stem} and C_{soil} are the amounts of carbon in the stem and soil, respectively. The curves represent an output of the slow spinup with the Norway spruce parameterisation for plot No. 1 in Babia hora. The blue curves show the result of the model after the incorporation of the new dynamic mortality rate with a cycle length equal to 300 years.

3.1.7 Validation of the model behaviour after the implementation of the new mortality model

In the previous section the improvements in model predictions using the new dynamic mortality model versus the original model set up were presented and discussed. The following chapters are aimed at a closer examination of the model performance after incorporating the dynamic mortality into the BIOME-BGC model.

3.1.7.1 Simulations of development stages

First, we were interested in the model performance within the individual development stages, i.e. stage of growth, maturity and breakdown. We hypothesised that after the implementation of the dynamic mortality model into the model structure, the model BIOME-BGC should be able to reproduce the three defined development stages correctly, since the simulated dynamic mortality mimics the small development cycle of the climax forests (see Section 3.1.4).

Tables 18 and 19 present the summary statistics for each development stage and each examined variable together with the statistical test of the differences between the modelled and observed values in Babia hora and Rothwald, respectively. The values indicate that the simulated stand volume coincides with the observations at the different development stages, when only the stage of growth in Babia hora was found to be significantly underestimated at the 95% significance level (Table 19). Coarse woody debris is underestimated for all stages in Rothwald. In Babia hora the mean observed and modelled C_{CWD} values do not differ significantly in any of the three stages. The predictions of carbon in the soil are better in Rothwald, where no significant difference between the observed and modelled mean was detected for any of the stages. In contrast, in Babia hora only the stage of growth showed no statistically significant deviation of simulated soil carbon from the observations. Litter characteristics and nitrogen in the soil were for both locations and all development stages similarly biased as the overall mean values.

The presented results suggest that with the dynamic mortality it is possible to simulate all development stages of the small succession cycle within natural forests as defined e.g. by Korpel' (1995). Hence, we can be confident that the model is able to account for such temporal dynamics in the forest ecosystem.

Table 18: Comparison of the simulated output using the dynamic mortality model for the individual development stages with the observations in Rothwald. Relative mean difference is the ratio of the mean difference to the observed or predicted value of the variable according to the line, in which it is shown.

Development stage	Variable		Number of observations	Mean	Standard deviation	Median	Minimum	Maximum	Coeficient of variation [%]	Mean difference	Standard deviation of difference	Relative mean difference [%]	Student's t value	Significance *95% **99%
Stage of growth	Volume [m^3/ha]	*Observed*	6	***353.82***	***162.17***	***306.63***	***197.09***	***597.81***	***45.83***	11.66	172.97	***3.30***	0.17	
		Predicted		365.48	47.91	380.55	297.50	422.60	13.11			3.19		
	C_{CWD} [kg C/ha]	*Observed*	6	***83556.50***	***19885.91***	***91549.50***	***57388.00***	***104349.00***	***23.80***	-66883.17	20024.90	***-80.05***	-8.18	**
		Predicted		16673.33	3658.02	18000.00	11550.00	20560.00	21.94			-401.14		
	C_{Litter} [kg C/m^2]	*Observed*	6	***1.0146***	***0.5226***	***0.8030***	***0.5643***	***1.9014***	***51.5111***	-0.7235	0.5339	***-71.3028***	-3.3189	*
		Predicted		0.2912	0.0653	0.3151	0.1918	0.3469	22.4308			-248.4663		
	N_{Litter} [kg N/m^2]	*Observed*	6	***0.0332***	***0.0174***	***0.0287***	***0.0171***	***0.0626***	***52.3923***	-0.0299	0.0175	***-90.0784***	-4.1844	**
		Predicted		0.0033	0.0008	0.0035	0.0021	0.0040	23.4367			-907.9047		
	C_{Soil} [kg C/m^2]	*Observed*	6	***7.9377***	***4.0082***	***8.1104***	***1.1631***	***12.9178***	***50.4962***	0.6208	3.5171	***7.8215***	0.4324	
		Predicted		8.5585	1.5041	9.2555	6.4630	9.8470	17.5742			7.2541		
	N_{Soil} [kg N/m^2]	*Observed*	6	***0.5001***	***0.2460***	***0.5420***	***0.0567***	***0.8012***	***49.1976***	0.3540	0.1932	***70.7832***	4.4869	**
		Predicted		0.8540	0.1501	0.9236	0.6449	0.9826	17.5760			41.4462		
Maturity stage	Volume [m^3/ha]	*Observed*	6	***886.43***	***164.41***	***879.94***	***693.17***	***1089.00***	***18.55***	149.76	164.09	***16.89***	2.24	
		Predicted		1036.18	46.75	1046.00	947.10	1076.00	4.51			14.45		
	C_{CWD} [kg C/ha]	*Observed*	6	***78168.33***	***14365.33***	***82238.00***	***56769.00***	***93589.00***	***18.38***	-58995.00	13102.14	***-75.47***	-11.03	**
		Predicted		19173.33	2306.24	19955.00	14690.00	21240.00	12.03			-307.69		
	C_{Litter} [kg C/m^2]	*Observed*	6	***0.9420***	***0.4315***	***0.8928***	***0.3877***	***1.5881***	***45.8047***	-0.5693	0.4371	***-60.4338***	-3.1899	*
		Predicted		0.3727	0.0263	0.3706	0.3423	0.4088	7.0511			-152.7407		
	N_{Litter} [kg N/m^2]	*Observed*	6	***0.0337***	***0.0151***	***0.0337***	***0.0138***	***0.0557***	***44.6956***	-0.0298	0.0151	***-88.3377***	-4.8472	**
		Predicted		0.0039	0.0003	0.0040	0.0035	0.0043	6.8259			-757.4635		
	C_{Soil} [kg C/m^2]	*Observed*	6	***9.2906***	***2.6238***	***8.6862***	***6.1266***	***12.4962***	***28.2418***	-0.8536	2.1573	***-9.1879***	-0.9692	
		Predicted		8.4370	0.9422	8.7565	7.2380	9.5240	11.1676			-10.1175		
	N_{Soil} [kg N/m^2]	*Observed*	6	***0.5066***	***0.1276***	***0.4763***	***0.3918***	***0.7271***	***25.1864***	0.3352	0.1665	***66.1644***	4.9304	**
		Predicted		0.8418	0.0940	0.8736	0.7222	0.9503	11.1714			39.8186		
Stage of breakdown	Volume [m^3/ha]	*Observed*	6	***437.35***	***127.94***	***453.67***	***256.62***	***592.86***	***29.25***	60.88	164.41	***13.92***	0.91	
		Predicted		498.23	44.21	516.05	417.40	533.50	8.87			12.22		
	C_{CWD} [kg C/ha]	*Observed*	6	***96693.33***	***22729.87***	***93121.00***	***71476.00***	***132471.00***	***23.51***	-53043.33	23609.95	***-54.86***	-5.50	**
		Predicted		43650.00	3690.30	44295.00	36690.00	47070.00	8.45			-121.52		
	C_{Litter} [kg C/m^2]	*Observed*	6	***0.9003***	***0.4534***	***0.8194***	***0.4700***	***1.7811***	***50.3673***	0.5316	0.4749	***59.0482***	2.7418	*
		Predicted		1.4318	0.1238	1.4675	1.1970	1.5500	8.6471			37.1260		
	N_{Litter} [kg N/m^2]	*Observed*	6	***0.0286***	***0.0118***	***0.0261***	***0.0158***	***0.0506***	***41.1977***	-0.0246	0.0119	***-85.9252***	-5.0448	**
		Predicted		0.0040	0.0004	0.0040	0.0035	0.0046	8.7475			-610.4882		
	C_{Soil} [kg C/m^2]	*Observed*	6	***7.5615***	***2.7441***	***6.8947***	***4.7878***	***11.8804***	***36.2909***	1.2706	2.6504	***16.8040***	1.1743	
		Predicted		8.8322	0.7015	9.0800	7.5610	9.3920	7.9423			14.3865		
	N_{Soil} [kg N/m^2]	*Observed*	6	***0.4463***	***0.1976***	***0.4327***	***0.2063***	***0.7059***	***44.2633***	0.4347	0.1797	***97.3889***	5.9249	**
		Predicted		0.8810	0.0700	0.9058	0.7543	0.9369	7.9408			49.3386		

Table 19: Comparison of the simulated output using the dynamic mortality model for the individual development stages with the observations in Babia hora. Relative mean difference is the ratio of the mean difference to the observed or predicted value of the variable according to the line, in which it is shown.

Development stage	Variable		Number of observations	Mean	Standard deviation	Median	Minimum	Maximum	Coeficient of variation [%]	Mean difference	Standard deviation of difference	Relative mean difference [%]	Student's t value	Significance *95% **99%
Stage of growth	Volume	*Observed*	19	***239.96***	***171.38***	***191.87***	***18.65***	***651.73***	***71.42***	-74.85	148.93	***-31.19***	-2.19	*
	[m^3/ha]	Predicted		165.11	32.44	173.24	118.07	225.65	19.65			-45.34		
	C_{CWD}	*Observed*	19	***11305.40***	***10672.78***	***9784.51***	***0.00***	***44086.81***	***94.40***	1895.79	9878.33	***16.77***	0.84	
	[kg C/ha]	Predicted		13201.19	2104.03	13635.96	10122.56	17455.47	15.94			14.36		
	C_{Litter}	*Observed*	6	***4.4672***	***1.3562***	***5.1206***	***2.6914***	***5.6209***	***30.3592***	-6.3132	2.2993	***-141.3227***	-6.7257	**
	[kg C/m^2]	Predicted		0.2296	0.0422	0.2262	0.1705	0.2944	18.3996			-2749.4118		
	N_{Litter}	*Observed*	6	***0.2127***	***0.0757***	***0.2333***	***0.1175***	***0.2856***	***35.5978***	-0.2768	0.0890	***-130.1677***	-7.6186	**
	[kg N/m^2]	Predicted		0.0021	0.0004	0.0021	0.0016	0.0027	17.9396			-12972.1509		
	C_{Soil}	*Observed*	6	***7.4117***	***2.9814***	***7.2243***	***3.7427***	***12.7302***	***40.2260***	0.3005	2.6052	***4.0545***	0.2825	
	[kg C/m^2]	Predicted		7.3923	1.3171	7.2593	5.5956	9.4645	17.8174			4.0652		
	N_{Soil}	*Observed*	6	***0.3938***	***0.1157***	***0.3856***	***0.2283***	***0.5524***	***29.3830***	0.3455	0.1618	***87.7520***	5.2316	**
	[kg N/m^2]	Predicted		0.7376	0.1314	0.7244	0.5583	0.9444	17.8202			46.8451		
Maturity stage	Volume	*Observed*	19	***465.92***	***280.66***	***440.37***	***60.21***	***1014.06***	***60.24***	-2.82	193.82	***-0.60***	-0.06	
	[m^3/ha]	Predicted		463.11	101.18	469.26	316.15	646.75	21.85			-0.61		
	C_{CWD}	*Observed*	19	***10984.52***	***8299.42***	***10402.25***	***1046.61***	***27888.76***	***75.56***	1323.48	7247.69	***12.05***	0.80	
	[kg C/ha]	Predicted		12308.00	2276.93	12597.63	8962.85	16262.08	18.50			10.75		
	C_{Litter}	*Observed*	7	***5.6335***	***2.0042***	***6.2596***	***3.0737***	***7.6951***	***35.5761***	-6.8428	0.9310	***-121.4659***	-19.4470	**
	[kg C/m^2]	Predicted		0.2347	0.0434	0.2332	0.1850	0.2999	18.4915			-2915.0071		
	N_{Litter}	*Observed*	7	***0.2467***	***0.0694***	***0.2715***	***0.1425***	***0.3235***	***28.1115***	-0.3008	0.0264	***-121.9363***	-30.1126	**
	[kg N/m^2]	Predicted		0.0024	0.0004	0.0024	0.0019	0.0030	17.6194			-12544.1335		
	C_{Soil}	*Observed*	7	***5.1607***	***2.0962***	***4.6368***	***3.1849***	***8.0647***	***40.6179***	-2.1206	1.4676	***-41.0909***	-3.8229	**
	[kg C/m^2]	Predicted		6.4071	1.2240	6.2745	5.0685	8.2960	19.1040			-33.0974		
	N_{Soil}	*Observed*	7	***0.2822***	***0.1155***	***0.2364***	***0.1549***	***0.4234***	***40.9473***	0.1597	0.1634	***56.6142***	2.5866	*
	[kg N/m^2]	Predicted		0.6392	0.1221	0.6260	0.5056	0.8277	19.1079			24.9897		
Stage of breakdown	Volume	*Observed*	19	***233.71***	***139.64***	***210.62***	***51.35***	***514.21***	***59.75***	20.89	108.03	***8.94***	0.84	
	[m^3/ha]	Predicted		254.60	46.05	267.64	188.66	316.55	18.09			8.20		
	C_{CWD}	*Observed*	19	***38626.04***	***29513.56***	***29754.80***	***1349.51***	***100095.16***	***76.41***	-5540.20	26426.72	***-14.34***	-0.91	
	[kg C/ha]	Predicted		33085.85	4835.07	34711.56	25851.57	39229.67	14.61			-16.74		
	C_{Litter}	*Observed*	6	***5.2343***	***2.4113***	***5.0397***	***1.8622***	***8.9786***	***46.0669***	-6.4198	1.1163	***-122.6493***	-14.0865	**
	[kg C/m^2]	Predicted		0.5861	0.1294	0.5731	0.4604	0.7615	22.0753			-1095.2755		
	N_{Litter}	*Observed*	6	***0.2220***	***0.0862***	***0.2143***	***0.0975***	***0.3637***	***38.8169***	-0.2970	0.0345	***-133.7513***	-21.0984	**
	[kg N/m^2]	Predicted		0.0023	0.0005	0.0022	0.0018	0.0029	20.2794			-13103.4677		
	C_{Soil}	*Observed*	6	***8.2279***	***3.8939***	***6.9364***	***4.9415***	***14.2040***	***47.3260***	-1.8017	1.5618	***-21.8970***	-2.8257	*
	[kg C/m^2]	Predicted		7.0407	1.1771	7.0619	5.6857	8.4201	16.7189			-25.5893		
	N_{Soil}	*Observed*	6	***0.4588***	***0.2641***	***0.3640***	***0.2058***	***0.8157***	***57.5630***	0.2574	0.0973	***56.1043***	6.4808	**
	[kg N/m^2]	Predicted		0.7023	0.1175	0.7045	0.5672	0.8400	16.7225			36.6502		

3.1.7.2 Regression analysis between the observations and model predictions

Next, we evaluated the calculated linear regressions between the predicted and observed values for each virgin forest separately. In the case of Rothwald, we used the predicted values for mixtures, since the two model variants (pure vs. mixed stands) do not differ much from each other (see Table 15). The examined relations were statistically tested for the correlation with the F-test for the coefficient of determination R^2. Secondly, the deviation of the calculated linear regression from the ideal case, i.e. y=x, was tested. Within this analysis we used the t-test or 95% confidence interval to determine if the absolute coefficient of the calculated regression differs from 0 and the regression coefficient from 1. The results of the statistical analysis are shown in Tables 20 and 21.

As Figures 27 to 33 and Tables 20 and 21 indicate, all relations except the litter characteristics in Rothwald are positively correlated, though not all of the correlations are statistically significant.

Stand volume exhibited the best coincidence between the modelled and observed values for both virgin forests (Figure 27, Table 20). The correlation is higher in Rothwald than in Babia hora (R^2=0.67 versus 0.55). Moreover, unlike Rothwald, the calculated linear regression between the predicted and observed stand volume in Babia hora was found to differ significantly from the ideal regression y=x (Table 21, Figure 27).

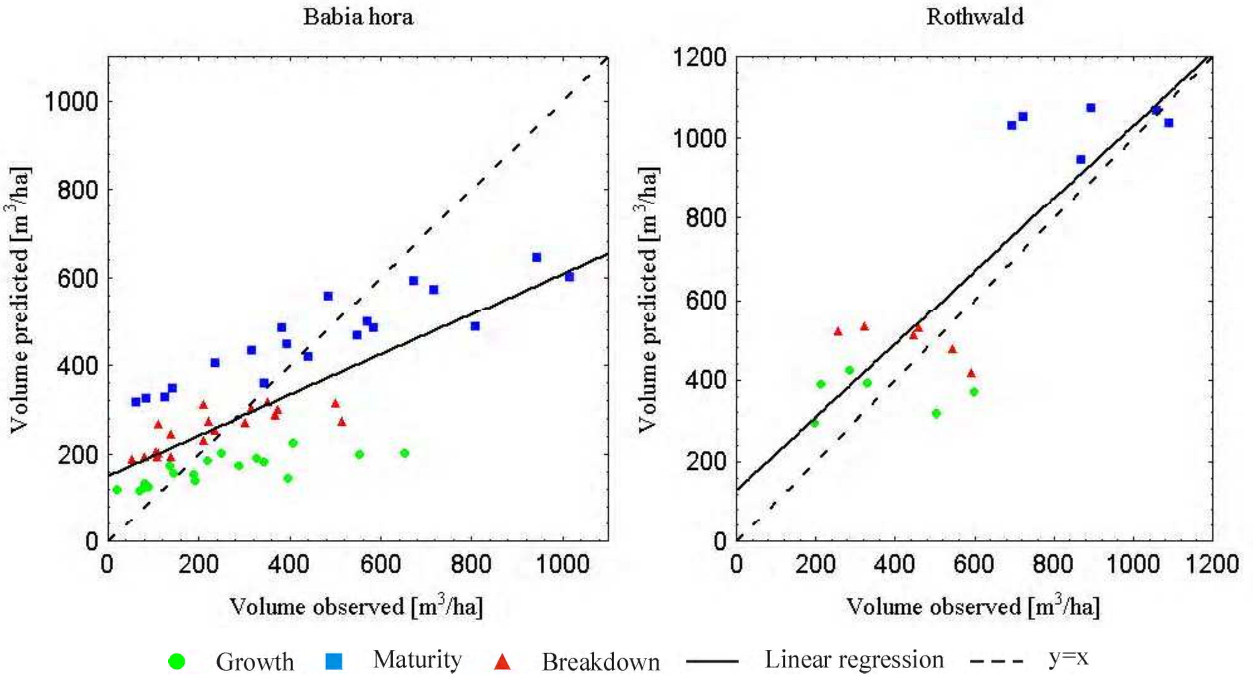

Figure 27: Predicted versus observed stand volume for Babia hora and Rothwald with the identification of individual development stages and calculated linear regression.

The results presented in Figure 27 also confirm the findings from the previous section 3.1.7.1 that on average no systematic bias can be observed in the individual development stages.

Table 20: Correlation analysis between the observations and the model predictions obtained using the dynamic mortality model. *SS* is the sum of squares, *df* is the number of degrees of freedom, *MS* is the mean square and *p* the level of significance.

Location	**Variable**	**R**	**R^2**	**Adjusted R^2**	**SS Model**	**df Model**	**MS Model**	**SS Residual**	**df Residual**	**MS Residual**	**F**	**p**	**Significance *95% **99%**
Rothwald	Volume [m^3/ha]	0.84	0.70	0.68	1,080,937	1	1,080,937	464,947	16	29,059	37.20	0.00	**
	C_{CWD} [kg C/ha]	0.38	0.14	0.09	402,722,398	1	402,722,398	2,425,063,779	16	151,566,486	2.66	0.12	
	C_{Litter} [kg C/m^2]	0.10	0.01	-0.05	0.05	1	0.05	4.91	16	0.31	0.16	0.70	
	N_{Litter} [kg N/m^2]	0.16	0.02	-0.04	0.00	1	0.00	0.00	16	0.00	0.40	0.53	
	C_{Soil} [kg C/m^2]	0.42	0.18	0.13	3.34	1	3.34	15.36	16	0.96	3.48	0.08	
	N_{Soil} [kg N/m^2]	0.39	0.15	0.10	0.03	1	0.03	0.16	16	0.01	2.85	0.11	
Babia hora	Volume [m^3/ha]	0.74	0.55	0.54	620,890	1	620,890	508,989	55	9,254.36	67.09	0.00	**
	C_{CWD} [kg C/ha]	0.71	0.51	0.50	2,982,223,418	1	2,982,223,418	2,855,051,655	55	51,910,030	57.45	0.00	**
	C_{Litter} [kg C/m^2]	0.08	0.01	-0.05	0.0039	1	0.0039	0.6139	17	0.0361	0.11	0.75	
	N_{Litter} [kg N/m^2]	0.19	0.03	-0.02	0.00	1	0.00	0.00	17	0.00	0.62	0.44	
	C_{Soil} [kg C/m^2]	0.47	0.22	0.18	6.16	1	6.16	21.70	17	1.28	4.82	0.04	*
	N_{Soil} [kg N/m^2]	0.34	0.12	0.07	0.03	1	0.03	0.24	17	0.01	2.29	0.15	

Table 21: Statistical test of the absolute (*a*) and regression (*b*) coefficients of the linear regressions between the observations and model predictions obtained with the dynamic mortality model for each examined variable and each location. The significance indicates, if the absolute coefficient is significantly different from 0 and the regression coefficient from 1.

Location	Variable		Parameter	Standard Error	t	p	Confidence interval -95.00%	Confidence interval +95.00%	Significance *95% **99%
Rothwald	Volume [m^3/ha]	***a***	129.76	91.82	1.41	0.18	-64.89	324.41	
		b	0.90	0.15	-0.67	0.51	0.59	1.21	
	C_{CWD} [kg C/ha]	***a***	5,351	13,293	0.40	0.69	-22,830	33,533	
		b	0.25	0.15	-5.01	0.00	-0.07	0.56	**
	C_{Litter} [kg C/m^2]	***a***	0.81	0.32	2.57	0.02	0.14	1.48	*
		b	-0.12	0.30	-3.71	0.00	-0.76	0.52	**
	N_{Litter} [kg N/m^2]	***a***	0.00	0.00	11.18	0.00	0.00	0.00	**
		b	-0.01	0.01	-98.76	0.00	-0.03	0.02	**
	C_{Soil} [kg C/m^2]	***a***	7.42	0.68	10.98	0.00	5.99	8.86	**
		b	0.14	0.08	-11.14	0.00	-0.02	0.31	**
	N_{Soil} [kg N/m^2]	***a***	0.75	0.07	11.28	0.00	0.61	0.89	**
		b	0.22	0.13	-6.06	0.00	-0.06	0.49	**
Babia hora	Volume [m^3/ha]	***a***	150.89	21.65	6.97	0.00	107.50	194.28	**
		b	0.46	0.06	-9.70	0.00	0.35	0.57	**
	C_{CWD} [kg C/ha]	***a***	12,967	1,288	10.06	0.00	10,384	15,550	**
		b	0.32	0.04	-15.87	0.00	0.24	0.41	**
	C_{Litter} [kg C/m^2]	***a***	0.30	0.1272	2.40	0.03	0.04	0.57	*
		b	0.01	0.0232	-42.69	0.00	-0.04	0.06	**
	N_{Litter} [kg N/m^2]	***a***	0.00	0.0003	6.38	0.00	0.00	0.00	**
		b	0.00	0.0013	-749.91	0.00	0.00	0.00	**
	C_{Soil} [kg C/m^2]	***a***	5.65	0.6319	8.95	0.00	4.32	6.99	**
		b	0.18	0.0842	-9.67	0.00	0.01	0.36	**
	N_{Soil} [kg N/m^2]	***a***	0.60	0.0640	9.42	0.00	0.47	0.74	**
		b	0.23	0.1548	-4.95	0.00	-0.09	0.56	**

The correlation of the observed versus predicted amount of coarse woody debris was found to be significant only for Babia hora. As the evaluation of the average values of coarse woody debris in Rothwald already showed, in this virgin forest the amount of dead wood (i.e. C_{CWD}) is systematically underestimated by the model (Tables 15 and 16). This is likely to be due to the frequent wind-throws in this region during the 2nd half of the last century.

In Babia hora, a similar diverging trend from the ideal 1:1 relationship as for the stand volume was evident for the coarse woody debris (Figure 28), as both the absolute and the regression coefficients are significantly different from 0 and 1, respectively (Table 21). However, even in this case the correlation between the observed and predicted coarse woody debris in Babia hora is highly significant (at the 99% significance level) and no systematic deviations in individual development stages can be observed (Figure 28, Table 19).

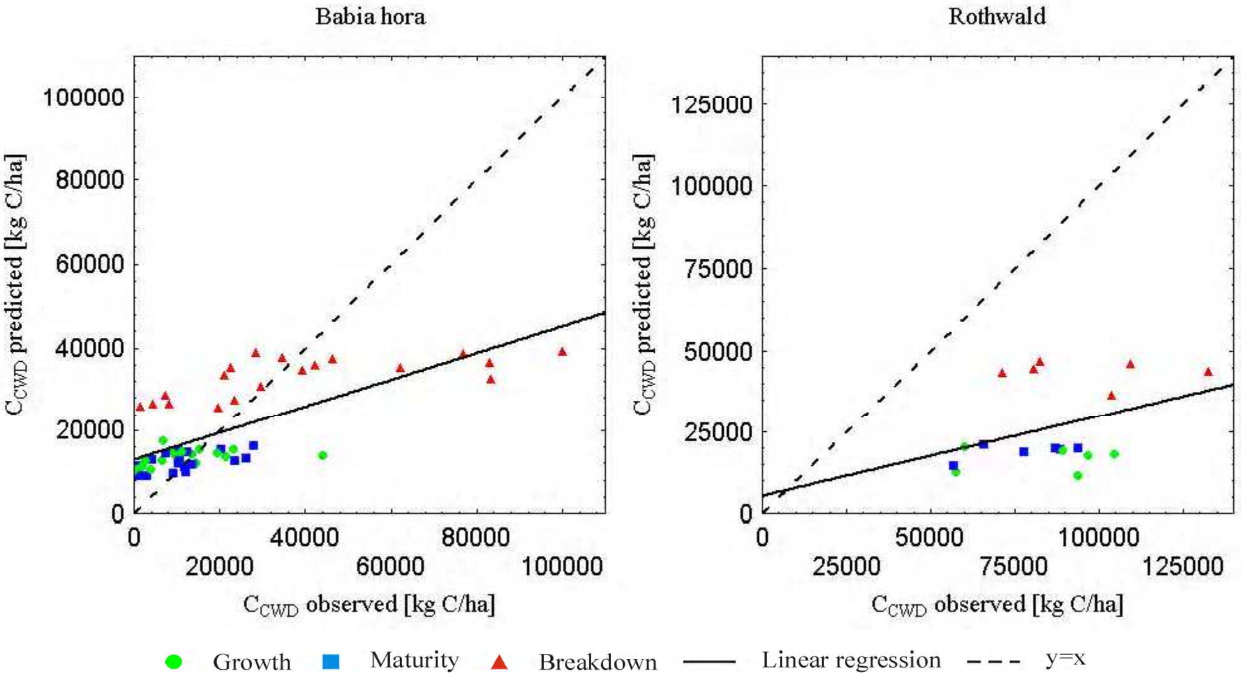

Figure 28: Predicted versus observed amount of coarse woody debris for Babia hora and Rothwald with the identification of development stages and calculated linear regression.

The correlations between the observed and predicted litter characteristics are very low ($R^2 < 0.03$) and insignificant in both virgin forests (Table 20). In addition, in Rothwald the regression coefficients for these variables are negative (Table 21). Figures 29 and 30 document that both carbon and nitrogen in the litter are in general underestimated. Only the breakdown plots in Rothwald exhibited in reality lower carbon content in the litter than it was simulated by the model (Figure 29). The nitrogen in the litter in both virgin forests is significantly underestimated by a factor between 10 to 100 against the observed values (Figure 30). The results shown in Figures 29 and 30 also indicate that the underestimation of the examined litter characteristics is much larger in Babia hora than in Rothwald.

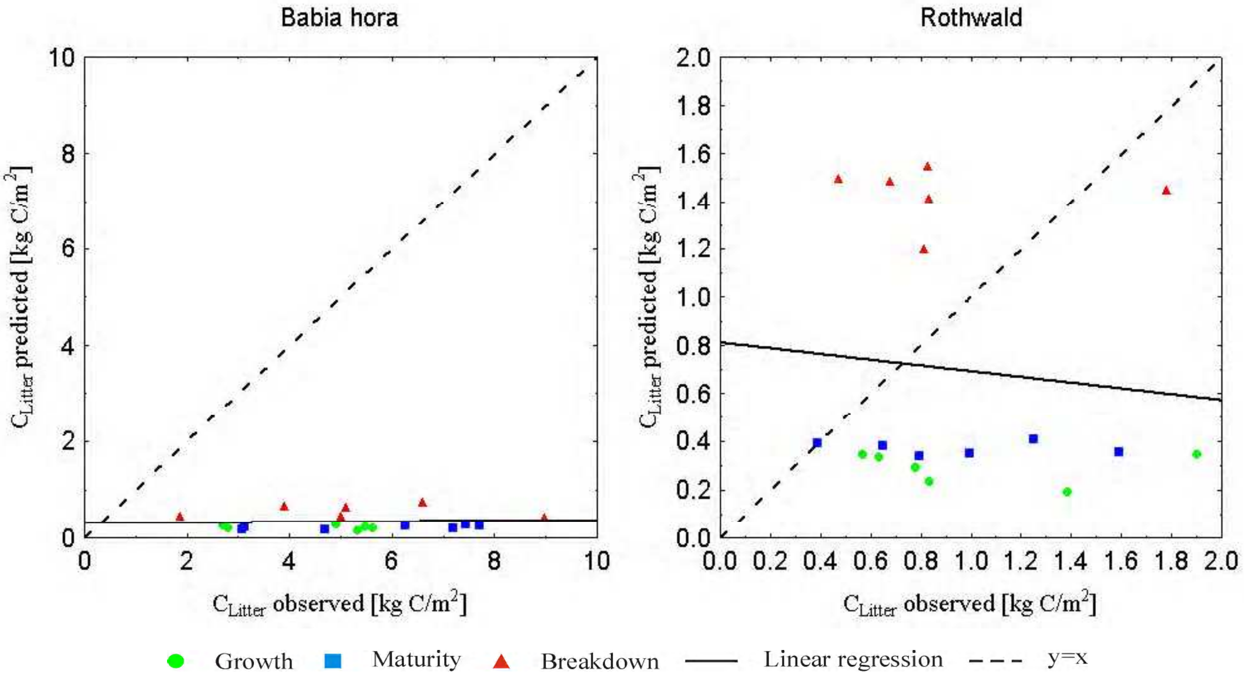

Figure 29: Predicted versus observed amount of carbon in the litter for Babia hora and Rothwald with the identification of development stages and calculated linear regression.

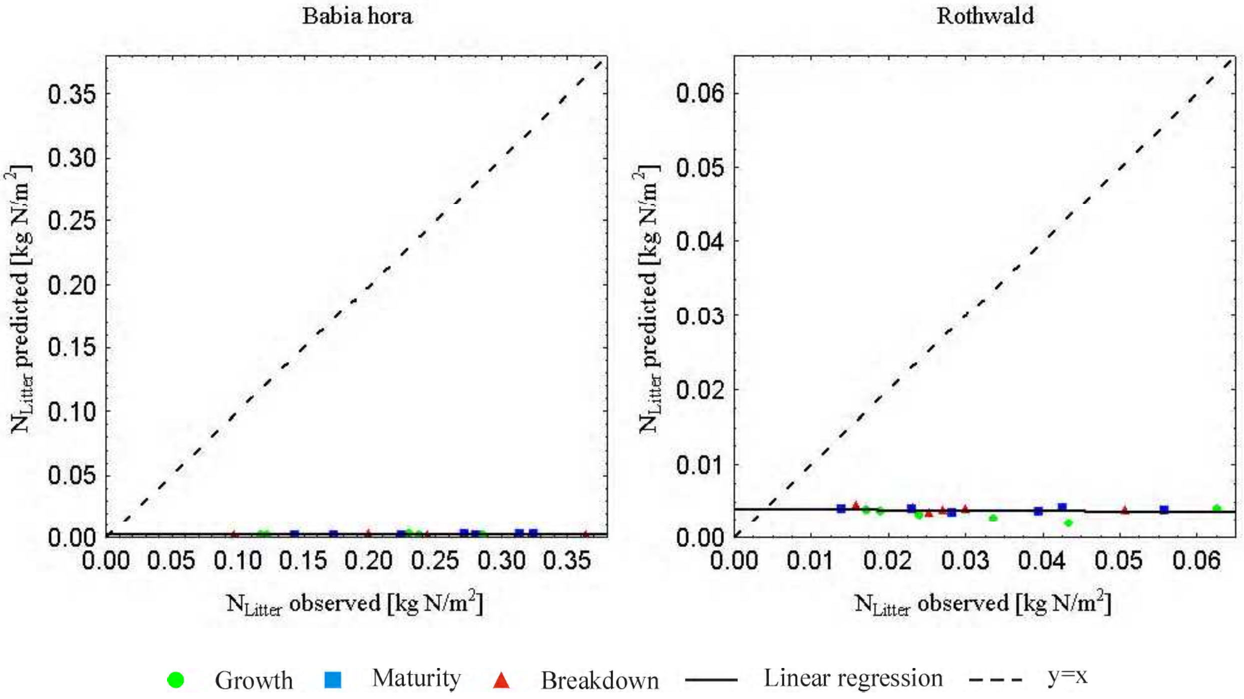

Figure 30: Predicted versus observed amount of nitrogen in the litter for Babia hora and Rothwald with the identification of development stages and calculated linear regression.

From all the examined litter and soil variables carbon content in the soil is best estimated by the model (Figure 31). Nevertheless, the analysis of correlation between the predictions and observations showed that the relation between them is in both forests rather weak (R^2=0.22 or 0.18

for Babia hora and Rothwald, respectively), although for Babia hora the correlation was significant at the 95% significance level (Table 20). In both forests, the absolute and regression coefficients differ significantly from 0 and 1, respectively (Table 21). Similarly to stand volume, no systematic trend to overestimate or underestimate carbon amount in the soil in individual development stages was detectable (Figure 31).

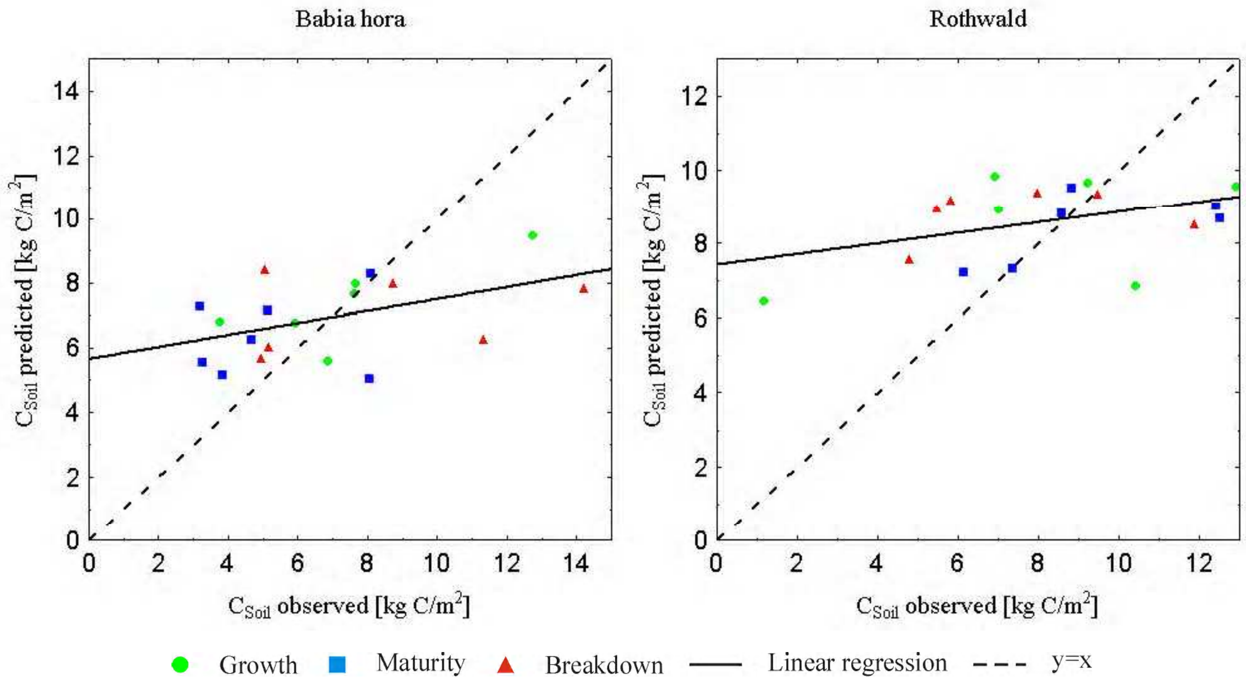

Figure 31: Predicted versus observed amount of carbon in the soil for Babia hora and Rothwald with the identification of development stages and calculated linear regression.

In Babia hora, all the soil samples taken from one permanent plot were mixed prior to the laboratory analysis. Since in Rothwald some samples were analysed separately and averaged only afterwards, we could also estimate the confidence interval of the observed values of carbon and nitrogen in the litter and soil. This allowed us to take into account the sampling error and test if the modelled values are within the estimated confidence interval, i.e. from *(mean - $t_{\alpha/2,f}$ · standard error)* to *(mean + $t_{\alpha/2,f}$ · standard error)*. The results for carbon and nitrogen in the soil as well as in the litter are given in Figure 32. From this Figure it is obvious that for soil carbon 15 out of the 18 plots fall within the 95% probability range of the observed values. From the three cases, for which the model predictions lie outside the 95% probability range of the observed mean, only one difference (plot RO) is really distinct.

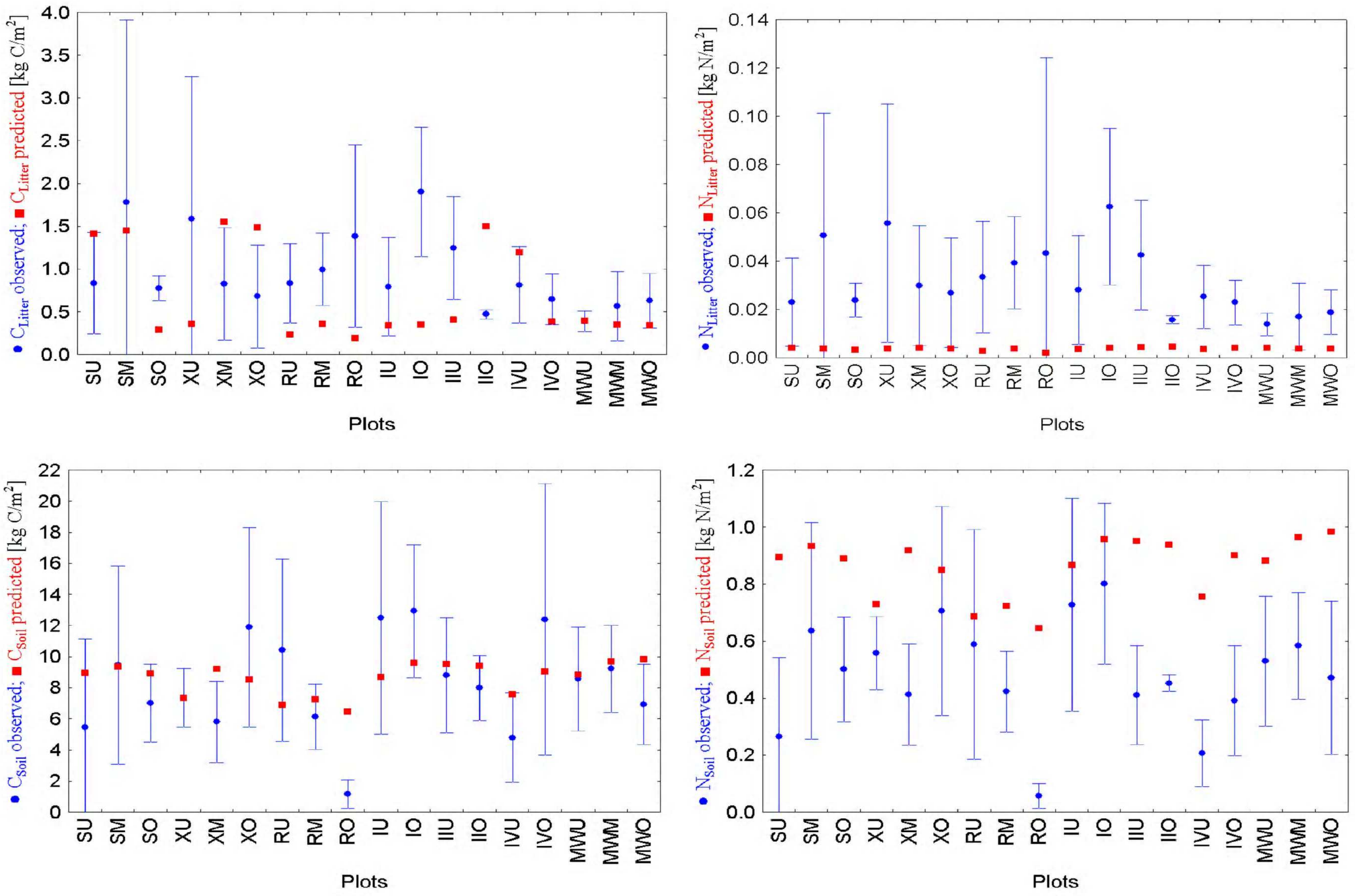

Figure 32: Range plots of the observed (blue points) and predicted (red points) values of litter and soil characteristics in Rothwald. For the observed values the 95% probability intervals of the estimated mean are given (blue intervals).

As already shown in the overall evaluation of the model performance, nitrogen in the soil is overestimated in both virgin forests. This statement is valid not only for the overall means, but also for the individual plots except one plot in Rothwald (under the condition that in Rothwald only the mean observed values are used without the error range, see Figure 33). Although the correlations are in both forests positive, neither is significant (Table 20). This can be explained by the variation already mentioned for soil carbon. The analysis that accounts for the measurement error revealed that on 5 plots the modelled values fall within the 95% confidence interval of the actual value of soil nitrogen (Figure 32).

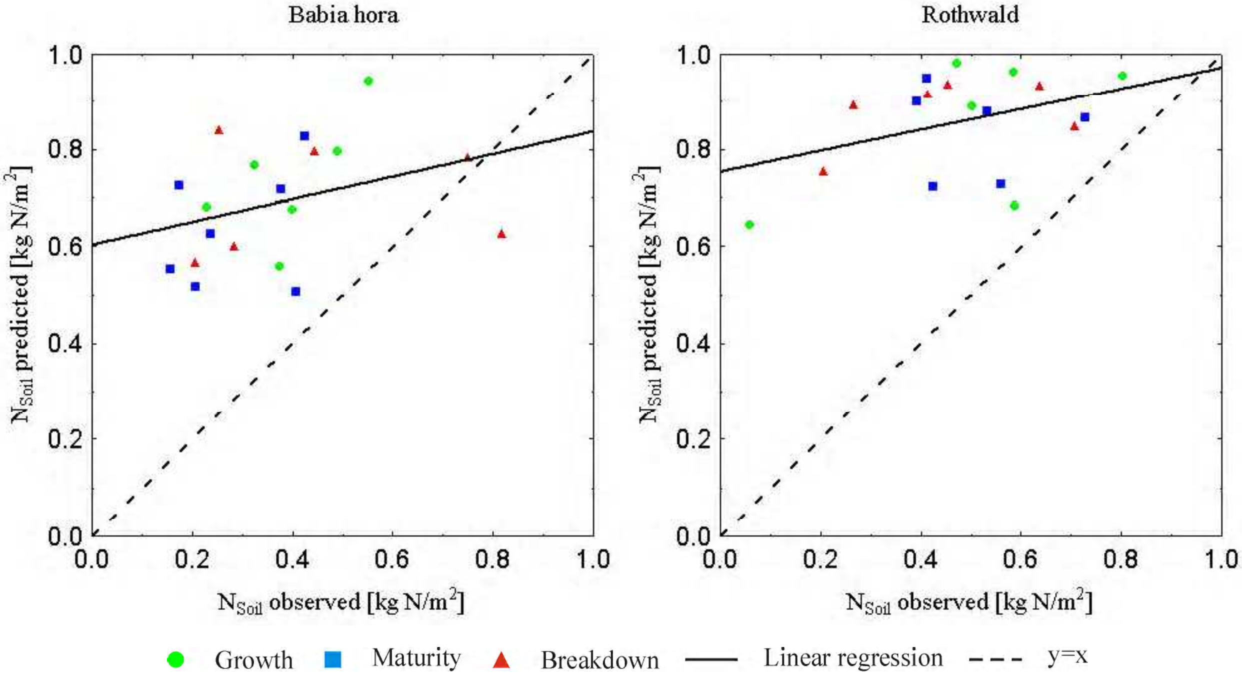

Figure 33: Predicted versus observed amount of nitrogen in the soil for Babia hora and Rothwald with the identification of development stages and calculated linear regression.

3.1.7.3 Residual analysis with regard to selected site and stand parameters

Since the correlation analysis and the scatter plots of the observed versus predicted values revealed some significant deviations from 1:1 line (Tables 20 and 21, Figures 27 to 33), in the next part we examined the possible causes of these trends. The analysis was performed on the relative differences of a particular variable (i.e. difference between modelled and observed value divided by the modelled value), and consisted of two parts. First, the possible influence of site characteristics, i.e. elevation, aspect and slope, was analysed. In the second part we examined the relationships of the model behaviour to stand characteristics, which are not explicitly addressed in the model structure, namely the stand density index, stocking, and mean quadratic diameter.

Elevation

First, we looked if there exists a significant relationship between the elevation and the relative differences of the examined characteristics. The statistical analysis revealed that elevation is a significant factor in Babia hora, but not in Rothwald, where only nitrogen in the litter was significantly correlated to elevation (see Table 22). From Figure 34 we can see that in Babia hora

Table 22: Correlation analysis of the relative modelled differences of the examined variables with elevation for Rothwald and Babia hora.

Location	Variable	R	R^2	Adjusted R^2	SS Model	df Model	MS Model	SS Residual	df Residual	MS Residual	F	P	Significance *95% **99%
Rothwald	Volume [m^3/ha]	0.02	0.00	-0.06	0.00	1	0.00	1.92	16	0.12	0.01	0.92	
	C_{CWD} [kg C/ha]	0.28	0.08	0.02	3.57	1	3.57	41.89	16	2.62	1.36	0.26	
	C_{Litter} [kg C/m^2]	0.47	0.22	0.17	13.35	1	13.35	48.13	16	3.01	4.44	0.06	
	N_{Litter} [kg N/m^2]	0.61	0.37	0.33	141.19	1	141.19	236.46	16	14.78	9.55	0.01	**
	C_{Soil} [kg C/m^2]	0.18	0.03	-0.03	0.07	1	0.07	2.05	16	0.13	0.52	0.48	
	N_{Soil} [kg N/m^2]	0.07	0.00	-0.06	0.00	1	0.00	0.80	16	0.05	0.07	0.79	
Babia hora	Volume [m^3/ha]	0.62	0.38	0.37	8.27	1	8.27	13.53	55	0.25	33.61	0.00	**
	C_{CWD} [kg C/ha]	0.48	0.23	0.22	6.49	1	6.49	21.79	55	0.40	16.39	0.00	**
	C_{Litter} [kg C/m^2]	0.46	0.21	0.17	531.91	1	531.91	1,959	17	115.25	4.62	0.05	*
	N_{Litter} [kg N/m^2]	0.79	0.62	0.60	15,520	1	15,520	9,510	17	559.46	27.74	0.00	**
	C_{Soil} [kg C/m^2]	0.61	0.37	0.34	0.60	1	0.60	0.99	17	0.06	10.17	0.01	**
	N_{Soil} [kg N/m^2]	0.47	0.22	0.18	0.12	1	0.12	0.43	17	0.03	4.83	0.04	*

both stand volume as well as the coarse woody debris are underestimated at the lower elevations. With increasing elevation the underestimation decreases and at about 1,330 to 1,360 m above sea level (1,365 m for stand volume and 1,332 m for C_{CWD} calculated from linear regressions) the model produces unbiased estimates of these parameters (Figure 34). Above this elevation, the model tends to overestimate both stand volume and amount of coarse woody debris in Babia hora. On the other hand, the deviations of litter and soil parameters show a negative relationship with elevation, since the regression coefficients are always lower than 0 (Table 23). The relative differences of carbon in the litter and soil as well as nitrogen in the litter increase with increasing elevation, whereas those for nitrogen in the soil decrease (Figure 34).

Table 23: Statistical test of the absolute (*a*) and regression (*b*) coefficients of the linear regressions between the relative modelled differences of the examined state variables and elevation with the 95% confidence interval. The significance says at which significance level the coefficients are different from 0.

Location	Variable		Parameter	Standard Error	t	p	Confidence interval		Significance *95% **99%
							-95%	+95%	
Rothwald	Volume [m^3/ha]	***a***	-0.05	1.44	-0.04	0.97	-3.10	3.00	
		b	0.00	0.00	0.10	0.92	0.00	0.00	
	C_{CWD} [kg C/ha]	***a***	4.99	6.72	0.74	0.47	-9.26	19.24	
		b	-0.01	0.01	-1.17	0.26	-0.02	0.01	
	C_{Litter} [kg C/m^2]	***a***	13.85	7.20	1.92	0.07	-1.43	29.12	
		b	-0.01	0.01	-2.11	0.05	-0.03	0.00	
	N_{Litter} [kg N/m^2]	***a***	41.37	15.97	2.59	0.02	7.52	75.22	*
		b	-0.05	0.01	-3.09	0.01	-0.08	-0.01	**
	C_{Soil} [kg C/m^2]	***a***	-1.02	1.49	-0.69	0.50	-4.18	2.13	
		b	0.00	0.00	0.72	0.48	0.00	0.00	
	N_{Soil} [kg N/m^2]	***a***	0.19	0.93	0.20	0.84	-1.79	2.16	
		b	0.00	0.00	0.27	0.79	0.00	0.00	
Babia hora	Volume [m^3/ha]	***a***	-5.85	1.00	-5.84	0.00	-7.86	-3.84	**
		b	0.00	0.00	5.80	0.00	0.00	0.01	**
	C_{CWD} [kg C/ha]	***a***	-5.06	1.27	-3.98	0.00	-7.61	-2.51	**
		b	0.00	0.00	4.05	0.00	0.00	0.01	**
	C_{Litter} [kg C/m^2]	***a***	69.77	43.64	1.60	0.13	-22.30	161.84	
		b	-0.07	0.032	-2.15	0.05	-0.14	0.00	*
	N_{Litter} [kg N/m^2]	***a***	372.27	96.15	3.87	0.00	169.41	575.12	**
		b	-0.37	0.0702	-5.27	0.00	-0.52	-0.22	**
	C_{Soil} [kg C/m^2]	***a***	2.91	0.9832	2.96	0.01	0.84	4.99	**
		b	0.00	0.0007	-3.19	0.01	0.00	0.00	**
	N_{Soil} [kg N/m^2]	***a***	1.75	0.6433	2.73	0.01	0.40	3.11	*
		b	0.00	0.0005	-2.20	0.04	0.00	0.00	*

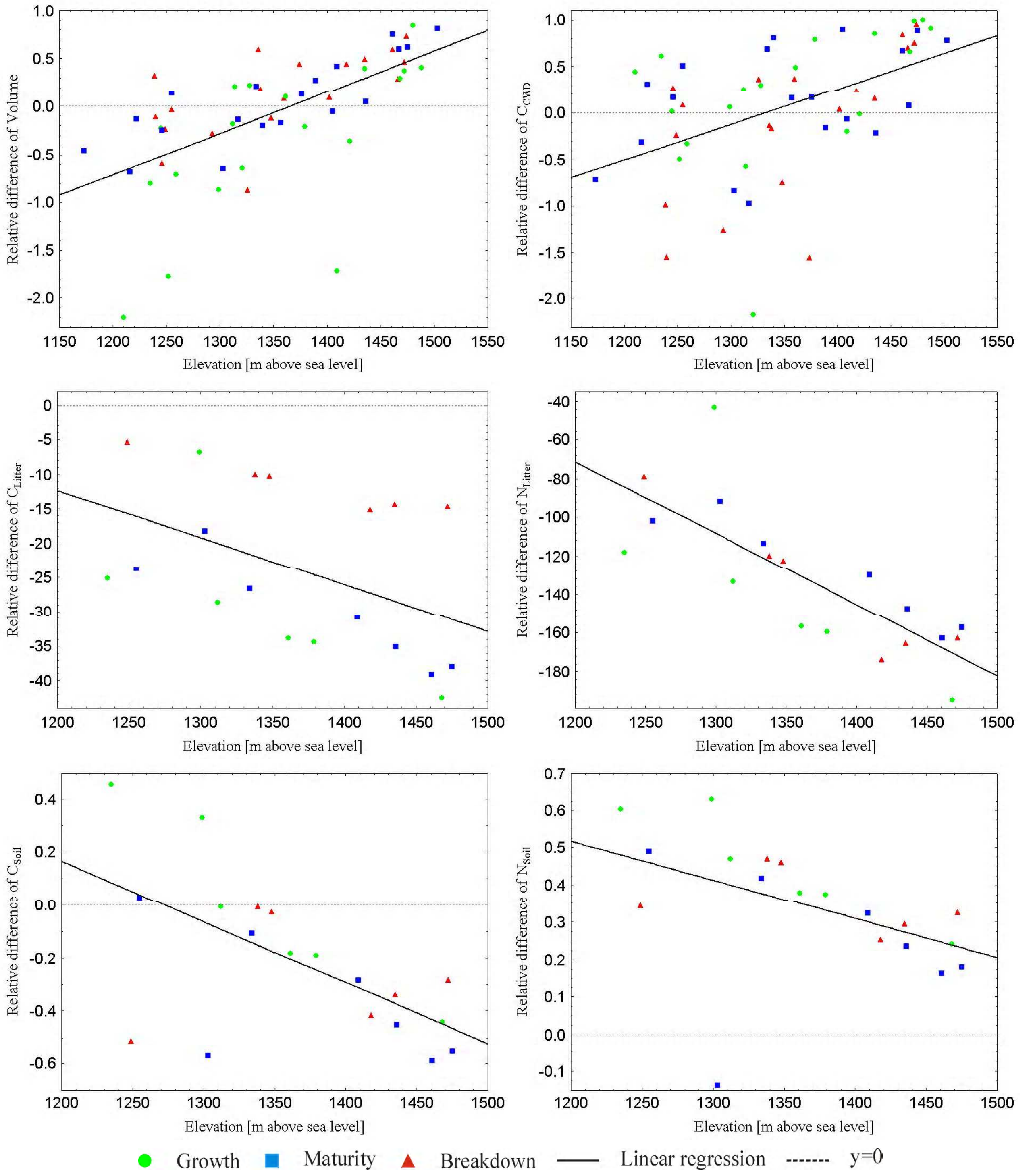

Figure 34: Relative modelled differences versus elevation for all examined variables in Babia hora with the calculated linear regressions.

Soil depth

Next, we analysed the impact of the soil depth on the relative modelled differences. The correlation analysis showed that in Rothwald the relative differences of none of the examined litter and soil characteristics are significantly correlated with soil depth. In Babia hora, the differences of carbon and nitrogen in the soil were found to be statistically significantly related to soil depth (Table 24, Figure 35).

Table 24: Correlation analysis of the relative differences of the examined variables with soil depth for Rothwald and Babia hora.

Location	Variable	R	R^2	Adjusted R^2	SS Model	df Model	MS Model	SS Residual	df Residual	MS Residual	F	p	Significance *95% **99%
Rothwald	C_{Litter} [kg C/m^2]	0.23	0.05	-0.01	3.23	1	3.23	58.24	16	3.64	0.89	0.36	
	N_{Litter} [kg N/m^2]	0.29	0.09	0.03	32.36	1	32.36	345.29	16	21.58	1.50	0.24	
	C_{Soil} [kg C/m^2]	0.32	0.10	0.05	0.21	1	0.21	1.91	16	0.12	1.80	0.20	
	N_{Soil} [kg N/m^2]	0.45	0.20	0.15	0.16	1	0.16	0.65	16	0.04	3.96	0.06	
Babia hora	C_{Litter} [kg C/m^2]	0.24	0.06	0.00	146.18	1	146.18	2344.97	17	137.94	1.06	0.32	
	N_{Litter} [kg N/m^2]	0.15	0.02	-0.04	557.14	1	557.14	24473.79	17	1439.63	0.39	0.54	
	C_{Soil} [kg C/m^2]	0.67	0.44	0.41	0.71	1	0.71	0.88	17	0.05	13.55	0.00	**
	N_{Soil} [kg N/m^2]	0.59	0.35	0.31	0.19	1	0.19	0.36	17	0.02	9.16	0.01	**

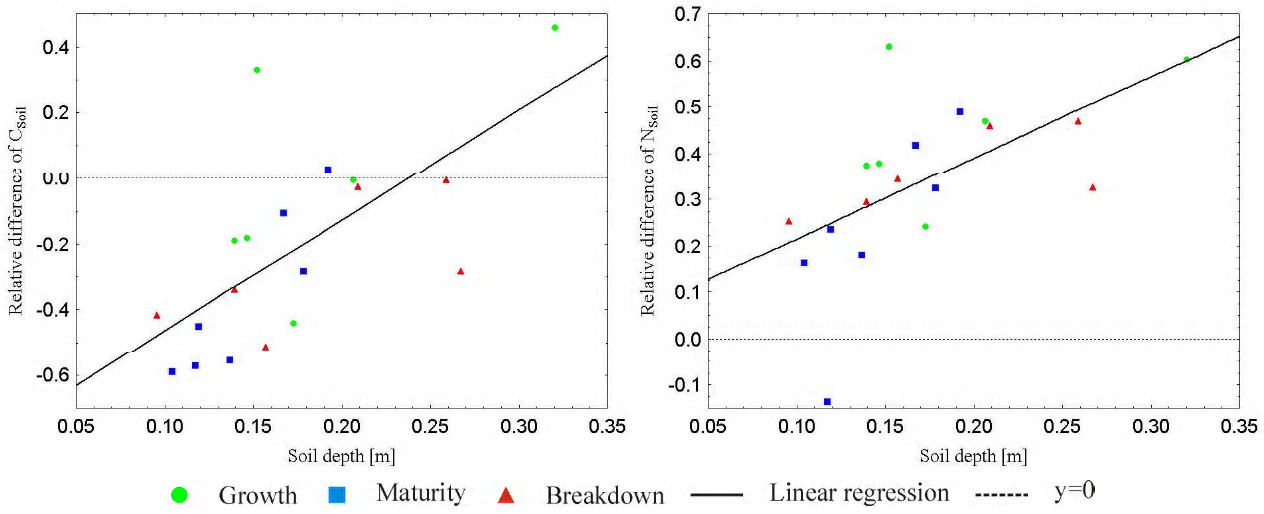

Figure 35: Relative modelled differences of carbon and nitrogen amount in the soil versus soil depth in Babia hora.

As presented in Table 22, a significant relationship between the differences of these soil characteristics and elevation was also detected. In addition, the regression analysis of the soil depth and elevation showed that in Babia hora soil depth decreases with increasing elevation (R^2=0.127). Therefore, we hypothesised that the significant correlation of the relative differences of the soil characteristics to soil depth can be caused by the detected correlation between elevation and soil depth.

However, the multiple regression analysis with elevation and soil depth revealed that both site parameters influence the model bias significantly, whereby the partial correlation coefficient was higher for soil depth (partial correlations were –0.54 and 0.61 for elevation and soil depth, respectively). Therefore, our assumption that behind one of the two analysed factors (elevation and soil depth) the second factor is hidden could not be confirmed.

Slope and aspect

The analysis of the relative differences with regard to the other two site parameters, i.e. slope and aspect, revealed only one significant relationship (Tables 25, 26). From all of the tested relationships, only nitrogen in the litter at Rothwald was found to be significantly correlated with slope (Table 26).

However, this correlation as well as the correlation of the same variable with elevation (Table 22) becomes insignificant, if the multiple regression is calculated for this variable with elevation and slope taken as independent variables. This result can be explained by the significant relationship between elevation and slope in Rothwald (R^2=0.824).

Table 25: Correlation analysis of the relative differences of the examined variables with aspect.

Location	Variable	R	R^2	Adjusted R^2	SS Model	df Model	MS Model	SS Residual	df Residual	MS Residual	F	p	Significance *95% 99%
Rothwald	Volume [m^3/ha]	0.01	0.00	-0.06	0.00	1	0.00	1.92	16	0.12	0.00	0.97	
	C_{CWD} [kg C/ha]	0.11	0.01	-0.05	0.58	1	0.58	44.89	16	2.81	0.21	0.66	
	C_{Litter} [kg C/m^2]	0.14	0.02	-0.04	1.23	1	1.23	60.25	16	3.77	0.33	0.58	
	N_{Litter} [kg N/m^2]	0.09	0.01	-0.05	3.18	1	3.18	374.47	16	23.40	0.14	0.72	
	C_{Soil} [kg C/m^2]	0.10	0.01	-0.05	0.02	1	0.02	2.10	16	0.13	0.17	0.69	
	N_{Soil} [kg N/m^2]	0.42	0.17	0.12	0.14	1	0.14	0.67	16	0.04	3.39	0.08	
Babia hora	Volume [m^3/ha]	0.06	0.00	-0.01	0.08	1	0.08	21.72	55	0.39	0.20	0.65	
	C_{CWD} [kg C/ha]	0.05	0.00	-0.02	0.06	1	0.06	28.22	55	0.51	0.12	0.73	
	C_{Litter} [kg C/m^2]	0.04	0.00	-0.06	3.90	1	3.90	2487.25	17	146.31	0.03	0.87	
	N_{Litter} [kg N/m^2]	0.01	0.00	-0.06	0.76	1	0.76	25030.2	17	1472.4	0.00	0.98	
	C_{Soil} [kg C/m^2]	0.03	0.00	-0.06	0.00	1	0.00	1.59	17	0.09	0.02	0.89	
	N_{Soil} [kg N/m^2]	0.01	0.00	-0.06	0.00	1	0.00	0.55	17	0.03	0.00	0.96	

Table 26: Correlation analysis of the relative differences of the examined variables with slope.

Location	Variable	R	R^2	Adjusted R^2	SS Model	df Model	MS Model	SS Residual	df Residual	MS Residual	F	P	Significance *95% **99%
Rothwald	Volume [m^3/ha]	0.10	0.01	-0.05	0.02	1	0.02	1.90	16	0.12	0.17	0.69	
	C_{CWD} [kg C/ha]	0.15	0.02	-0.04	1.06	1	1.06	44.41	16	2.78	0.38	0.55	
	C_{Litter} [kg C/m^2]	0.32	0.10	0.05	6.40	1	6.40	55.08	16	3.44	1.86	0.19	
	N_{Litter} [kg N/m^2]	0.50	0.25	0.20	93.08	1	93.08	284.57	16	17.79	5.23	0.04	*
	C_{Soil} [kg C/m^2]	0.13	0.02	-0.04	0.04	1	0.04	2.08	16	0.13	0.27	0.61	
	N_{Soil} [kg N/m^2]	0.04	0.00	-0.06	0.00	1	0.00	0.81	16	0.05	0.03	0.88	
Babia hora	Volume [m^3/ha]	0.24	0.06	0.04	1.31	1	1.31	20.49	55	0.37	3.51	0.07	
	C_{CWD} [kg C/ha]	0.23	0.05	0.04	1.52	1	1.52	26.75	55	0.49	3.13	0.08	
	C_{Litter} [kg C/m^2]	0.06	0.00	-0.06	8.65	1	8.65	2482.50	17	146.03	0.06	0.81	
	N_{Litter} [kg N/m^2]	0.16	0.03	-0.03	634.09	1	634.09	24396.8	17	1435.11	0.44	0.52	
	C_{Soil} [kg C/m^2]	0.00	0.00	-0.06	0.00	1	0.00	1.59	17	0.09	0.00	1.00	
	N_{Soil} [kg N/m^2]	0.15	0.02	-0.04	0.01	1	0.01	0.54	17	0.03	0.37	0.55	

Stand density index (SDI)

Stand density is not explicitly addressed within the BIOME-BGC model structure. Therefore, possible trends in the differences between the modelled and observed values in relation to stand density index SDI according to Reineke (1933) were tested. Although after the incorporation of dynamic mortality we did not expect to find any significant relationship, since the development stages and thus different stand densities should already be implicitly included in the model, the differences in stand volume exhibited a decreasing trend with the increasing SDI (Figure 36). This means that the model overestimates the volume of loose stands, whereas the volume of the overstocked stands is underestimated. This linear trend is particularly obvious in Babia hora, where the relationship was found to be highly significant (at the 99% significance level). Although the Rothwald data of stand volume appear to have a similar trend (Figure 36), the correlation is much lower (R^2=0.14) and insignificant (Table 27). From the other tested variables, only nitrogen in the litter in Babia hora showed to be significantly correlated with SDI (Table 27). Also in this case we tried to calculate multiple regressions, because in Babia hora SDI is significantly correlated with elevation (R^2=0.30). The results revealed that stand volume depends on both factors, whereas nitrogen in the litter is correlated only with elevation.

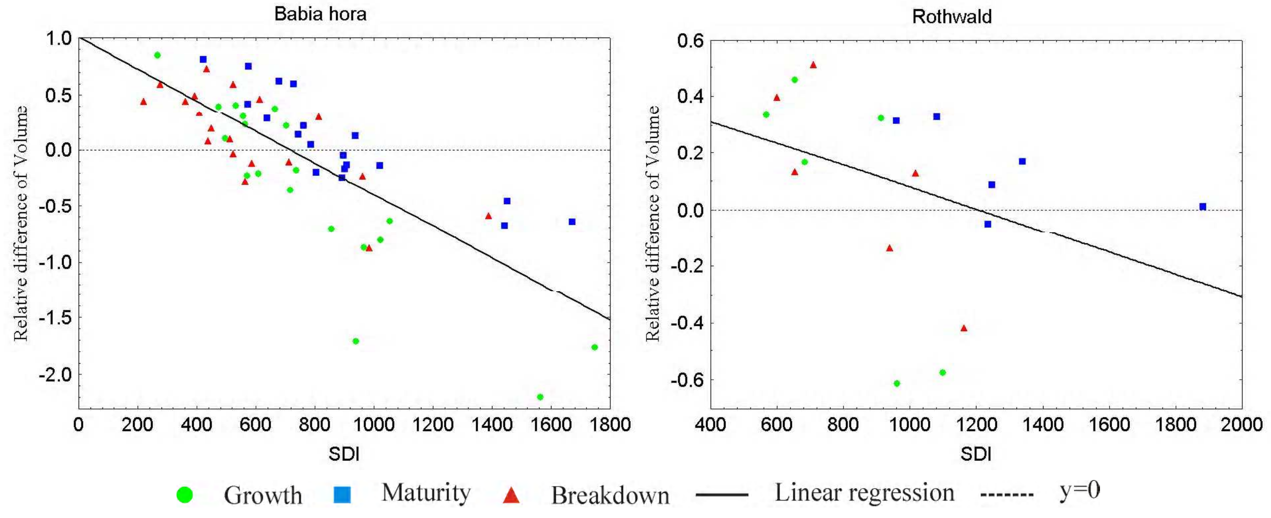

Figure 36: Relative modelled differences of stand volume versus SDI (Reineke 1933).

Table 27: Correlation analysis of the relative modelled differences of the selected state variables versus SDI (Reineke 1933).

Location	Variable	R	R^2	Adjusted R^2	SS Model	df Model	MS Model	SS Residual	df Residual	MS Residual	F	P	Significance *95%, **99%
Rothwald	Volume [m^3/ha]	0.38	0.14	0.09	0.27	1	0.27	1.64	16	0.10	2.67	0.12	
	C_{CWD} [kg C/ha]	0.06	0.00	-0.06	0.14	1	0.14	45.33	16	2.83	0.05	0.83	
	C_{Litter} [kg C/m^2]	0.13	0.02	-0.05	1.01	1	1.01	60.47	16	3.78	0.27	0.61	
	N_{Litter} [kg N/m^2]	0.20	0.04	-0.02	14.67	1	14.67	362.98	16	22.69	0.65	0.43	
	C_{Soil} [kg C/m^2]	0.24	0.06	0.00	0.12	1	0.12	2.00	16	0.12	0.98	0.34	
	N_{Soil} [kg N/m^2]	0.21	0.04	-0.02	0.03	1	0.03	0.77	16	0.05	0.71	0.41	
Babia hora	Volume [m^3/ha]	0.77	0.60	0.59	13.09	1	13.09	8.71	55	0.16	82.71	0.00	**
	C_{CWD} [kg C/ha]	0.21	0.04	0.03	1.26	1	1.26	27.01	55	0.49	2.57	0.11	
	C_{Litter} [kg C/m^2]	0.16	0.03	-0.03	65.09	1	65.09	2426.06	17	142.71	0.46	0.51	
	N_{Litter} [kg N/m^2]	0.63	0.40	0.36	10017.12	1	10017.1	15013.8	17	883.17	11.34	0.00	**
	C_{Soil} [kg C/m^2]	0.04	0.00	-0.06	0.00	1	0.00	1.59	17	0.09	0.03	0.86	
	N_{Soil} [kg N/m^2]	0.28	0.08	0.03	0.04	1	0.04	0.50	17	0.03	1.49	0.24	

Stocking

Another measure of forest stand density is the stocking of the forest stand, which was unlike the SDI estimated in the field. This variable is categorical and for one vertical layer of the forest stand it can obtain values between 1 and 10, where 1 represents the loosest stands and 10 the stands (layers) that are fully stocked (Šmelko 2000). If the forest stand consists of more than one layer its overall stocking level is obtained as the sum of the stockings of all the layers. Thus, the stocking of such a forest stand can exceed a value of 10. This parameter was determined in Babia hora only, but not in Rothwald. Therefore, in the virgin forest Rothwald the analysis of its influence could not be accomplished.

The analysis for Babia hora revealed significant correlations between stocking and the relative differences of stand volume and carbon content in the soil (Table 28). A closer evaluation of Figure 37, however, revealed that the significant correlation between soil carbon and stocking is caused by one isolated value in the upper right corner of the graph (Figure 37). Removing this value from the data set results in the insignificant correlation. Unlike SDI, the nitrogen in the litter is not significantly correlated to stocking. Therefore, the analysis of the two stand density measures, i.e. SDI and stocking, suggests that in Babia hora stand volume is the only variable significantly affected by stand density.

Table 28: Correlation analysis of the relative modelled differences versus stocking for the location Babia hora.

Location	Variable	R	R^2	Adjusted R^2	SS Model	df Model	MS Model	SS Residual	df Residual	MS Residual	F	p	Significance *95% **99%
Babia hora	Volume [m^3/ha]	0.78	0.60	0.59	13.13	1	13.13	8.68	55	0.16	83.21	0.00	**
	C_{CWD} [kg C/ha]	0.11	0.01	-0.01	0.36	1	0.36	27.91	55	0.51	0.72	0.40	
	C_{Litter} [kg C/m^2]	0.16	0.03	-0.03	64.12	1	64.12	2427.03	17	142.77	0.45	0.51	
	N_{Litter} [kg N/m^2]	0.31	0.10	0.04	2409.05	1	2409.05	22621.88	17	1330.70	1.81	0.20	
	C_{Soil} [kg C/m^2]	0.49	0.24	0.19	0.37	1	0.37	1.22	17	0.07	5.24	0.04	*
	N_{Soil} [kg N/m^2]	0.31	0.10	0.04	0.05	1	0.05	0.49	17	0.03	1.80	0.20	

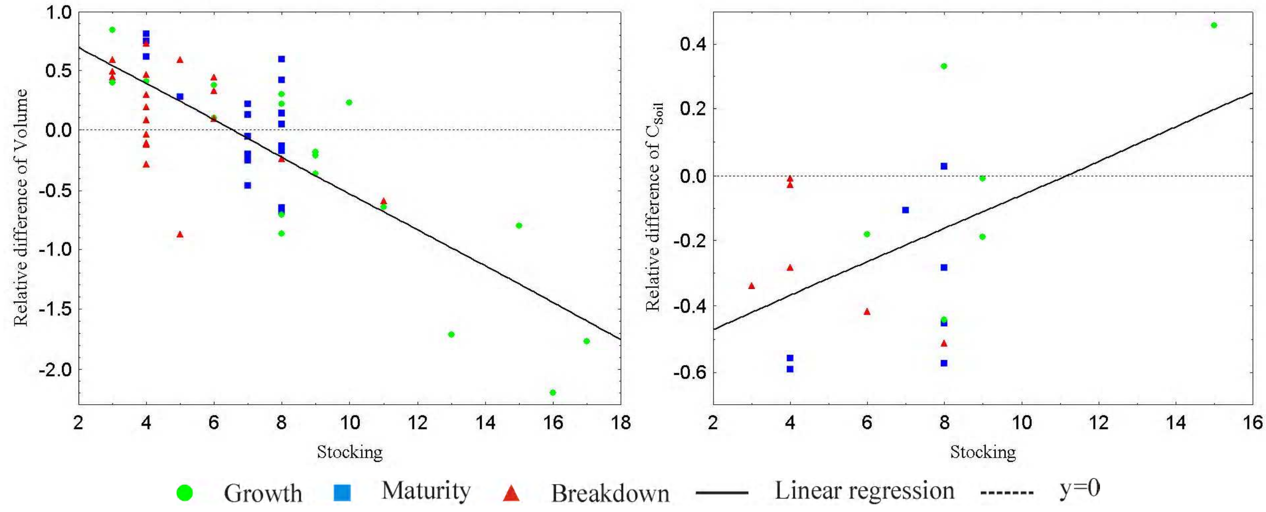

Figure 37: Relative modelled differences versus stocking for statistically significant relationships in Babia hora.

Mean quadratic diameter (Dg)

The mean quadratic diameter (*Dg*) can be regarded as an indicator of the forest stand maturity or its development stage. Young forest stands commonly exhibit a lower *Dg* compared to mature forest stands or stands at the breakdown stage. The highest value of *Dg* is characteristic of stands at the optimal stage.

We hypothesised that if the dynamic mortality addresses the temporal changes of the forest stand status correctly, no trends should be detectable across the range of *Dg*. The results presented in Table 29 confirm our expectations, because no examined variables are significantly correlated to the mean quadratic diameter.

Table 29: Correlation analysis of the relative modelled differences versus quadratic mean diameter.

Location	Variable	R	R^2	Adjusted R^2	SS Model	df Model	MS Model	SS Residual	df Residual	MS Residual	F	p	Significance *95%, **99%
Rothwald	Volume [m^3/ha]	0.11	0.01	-0.05	0.02	1	0.02	1.89	16	0.12	0.20	0.66	
	C_{CWD} [kg C/ha]	0.35	0.12	0.06	5.43	1	5.43	40.03	16	2.50	2.17	0.16	
	C_{Litter} [kg C/m^2]	0.22	0.05	-0.01	3.00	1	3.00	58.48	16	3.65	0.82	0.38	
	N_{Litter} [kg N/m^2]	0.25	0.06	0.01	24.13	1	24.13	353.52	16	22.10	1.09	0.31	
	C_{Soil} [kg C/m^2]	0.29	0.09	0.03	0.18	1	0.18	1.94	16	0.12	1.52	0.24	
	N_{Soil} [kg N/m^2]	0.13	0.02	-0.04	0.01	1	0.01	0.79	16	0.05	0.28	0.60	
Babia hora	Volume [m^3/ha]	0.13	0.02	0.00	0.38	1	0.38	21.42	55	0.39	0.96	0.33	
	C_{CWD} [kg C/ha]	0.02	0.00	-0.02	0.01	1	0.01	28.27	55	0.51	0.01	0.90	
	C_{Litter} [kg C/m^2]	0.08	0.01	-0.05	17.93	1	17.93	2473.22	17	145.48	0.12	0.73	
	N_{Litter} [kg N/m^2]	0.14	0.02	-0.04	485.20	1	485.20	24545.73	17	1443.87	0.34	0.57	
	C_{Soil} [kg C/m^2]	0.02	0.00	-0.06	0.00	1	0.00	1.59	17	0.09	0.01	0.93	
	N_{Soil} [kg N/m^2]	0.11	0.01	-0.05	0.01	1	0.01	0.54	17	0.03	0.19	0.67	

3.1.7.4 Temporal changes of several model parameters caused by dynamic mortality

In the previous sections, we analysed the model performance after the incorporation of the dynamic mortality model by comparing simulated output with the field observations. However, these analyses provide us with information only if the steady state achieved in the model is comparable with the expected equilibrium in nature. Thus, with these results we can only examine how well the model steady state can reproduce the natural sustainable potential of the particular site under given climate conditions. For the assessment, if the model is able to simulate the flux of water, energy, carbon and nitrogen through the ecosystem properly, repeated and more detailed field measurements would be needed. Since from our virgin forests no such data were available, we examined the temporal behaviour of several model parameters considering the mortality changes and relations to other variables. The performance of the examined parameters was studied after the steady state was achieved in the model (i.e. after approximately 20,000 years). The pattern of their response was very similar on all plots, and thus, we present here only the results for plot No. 1 from Babia hora (Figures 38 to 45).

The first examined variable was carbon in the stem representing stand volume. As already presented in Section 3.1.5, stem carbon and mortality rate follow a different type of trajectory, although they develop almost inversely (Figure 38), that is with decreasing mortality carbon in the stem gradually increases. It reaches its maximum value later than mortality reaches its minimum (C_{stem} maximum is at age 130, whereas the mortality minimum is at age 75). After this peak, stem carbon steadily decreases until it attains its minimum approximately at the same time as the mortality is the highest. During the next 80 years during a period of a quite high, though, decreasing mortality the increment of stem carbon is relatively small. After this period, carbon in the stem begins to grow faster again.

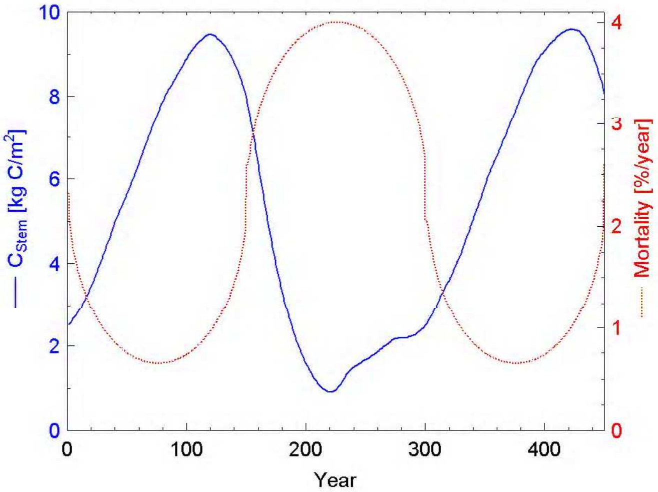

Figure 38: Temporal performance of the simulated carbon content in the stem (C_{stem}) in relation to annual mortality rate for plot No. 1 in Babia hora.

Examining the coarse woody debris across the development cycle (Figure 39), we can see that during the first half of the cycle this pool behaves similarly to the mortality rate. In the second half of the cycle, the coarse woody debris develops differently. It reaches its maximum in the middle between the peaks of stem carbon and mortality rate (approximately at age 170), after which it drops relatively quickly (in about 60 years) to its starting value. Surprisingly, the minimum coarse woody debris is simulated at maximum mortality rate. However, at this point the stem carbon is also very low (Figure 38), which indicates that a high relative mortality rate results in a low absolute input of biomass into the coarse woody debris pool. Afterwards, the amount of coarse woody debris increases again until it reaches the second, lower peak several years before the end of one development cycle (at age 300 years).

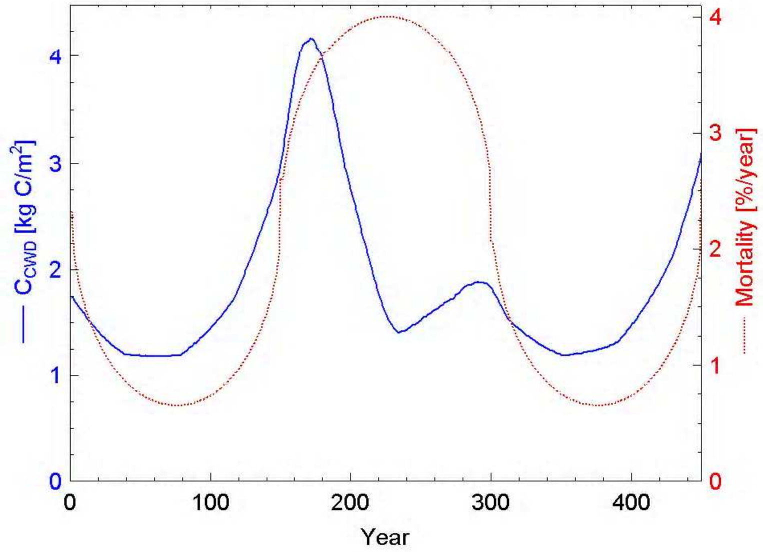

Figure 39: Temporal performance of the simulated carbon amount in the coarse woody debris in relation to annual mortality rate for plot No. 1 in Babia hora.

Carbon in the litter has a similar development pattern to the coarse woody debris (compare Figures 39 and 40). However, unlike CWD, carbon in the litter has only one significant maximum at the same time as CWD reaches its first distinct maximum. The similarity of these two curves can be explained by a close interconnection between the two parameters in the model. The defragmented material of coarse woody debris is in the next step assigned to the litter pool (Section 2.1). Hence, the peak of carbon amount in the litter reflects the flow of the defragmented dead wood to the litter.

Apart from the overall pattern across one development cycle, distinct inter-annual variation of litter carbon is evident (Figure 40). This inter-annual pattern is repeated approximately every 40 years, which corresponds with the length of the available climate data (here 41 years from 1961 to 2002), that are used repeatedly throughout the simulations.

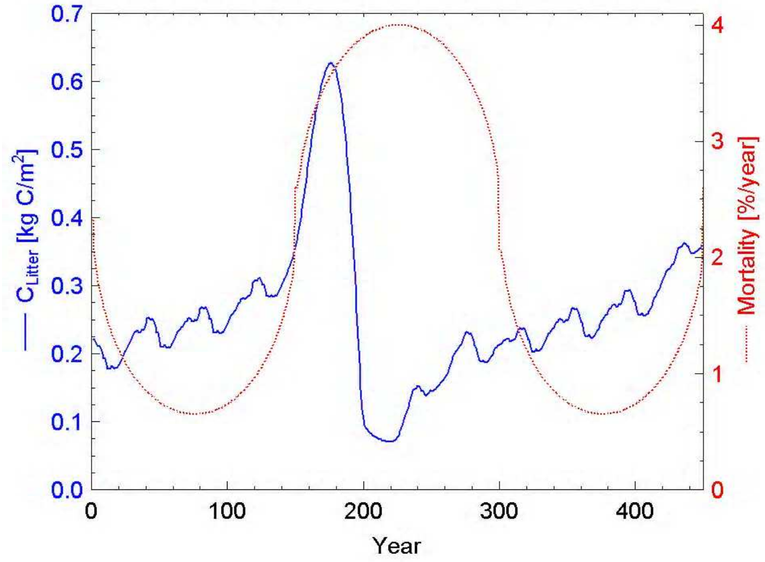

Figure 40: Temporal performance of the simulated carbon content in the litter in relation to annual mortality rate for plot No. 1 in Babia hora.

Nitrogen in the litter follows a different trajectory when compared with carbon in the litter. As Figure 41 shows, this parameter has no distinct maximum over the whole development cycle, but a very distinct minimum, which is reached at the same time as the lowest carbon amount in the litter. Since the coarse woody debris is a pool with a wide C:N ratio, its accumulation has a much lower effect on the nitrogen amount in the litter than on the litter carbon. This parameter is, similarly as carbon in the litter, very sensitive to inter-annual variation in climate. Therefore, also in the temporal development of litter nitrogen we can detect the cycles of the used climate data.

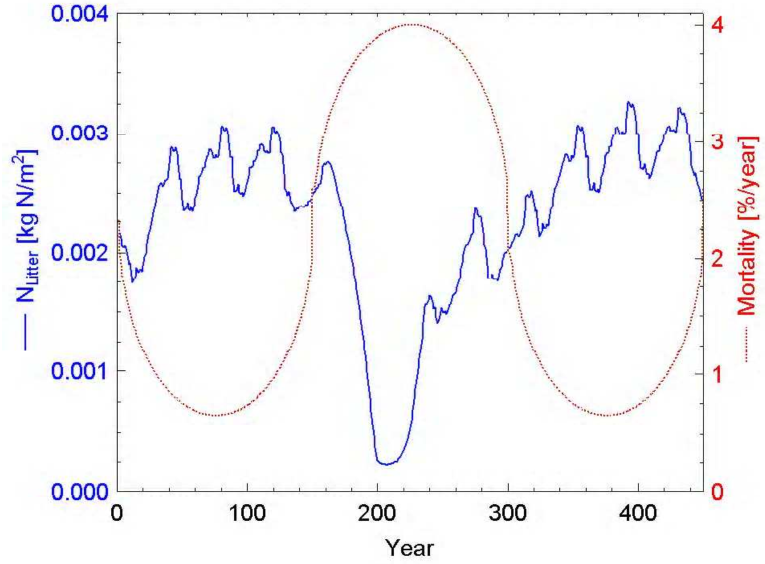

Figure 41: Temporal performance of the simulated nitrogen content in the litter in relation to annual mortality rate for plot No. 1 in Babia hora.

Except for the peak of carbon stores in the litter, both litter parameters closely follow the changes in mortality and stem carbon, i.e. when mortality is low and the amount of carbon in the stem is high, litter pools are large and vice versa.

Carbon and nitrogen in the soil follow the same trajectory because they are closely coupled in the model (Figure 42). As expected, the examined soil characteristics develop in the opposite direction to the litter characteristics, i.e. they reach their highest values when the stocks in litter are at their lowest values (Figures 40, 41 and 42). After the peak they fall quickly to their former values. Similarly to the litter characteristics, both carbon and nitrogen in the soil react sensitively to climate, because in their development repeated cycles of inter-annual variation are evident.

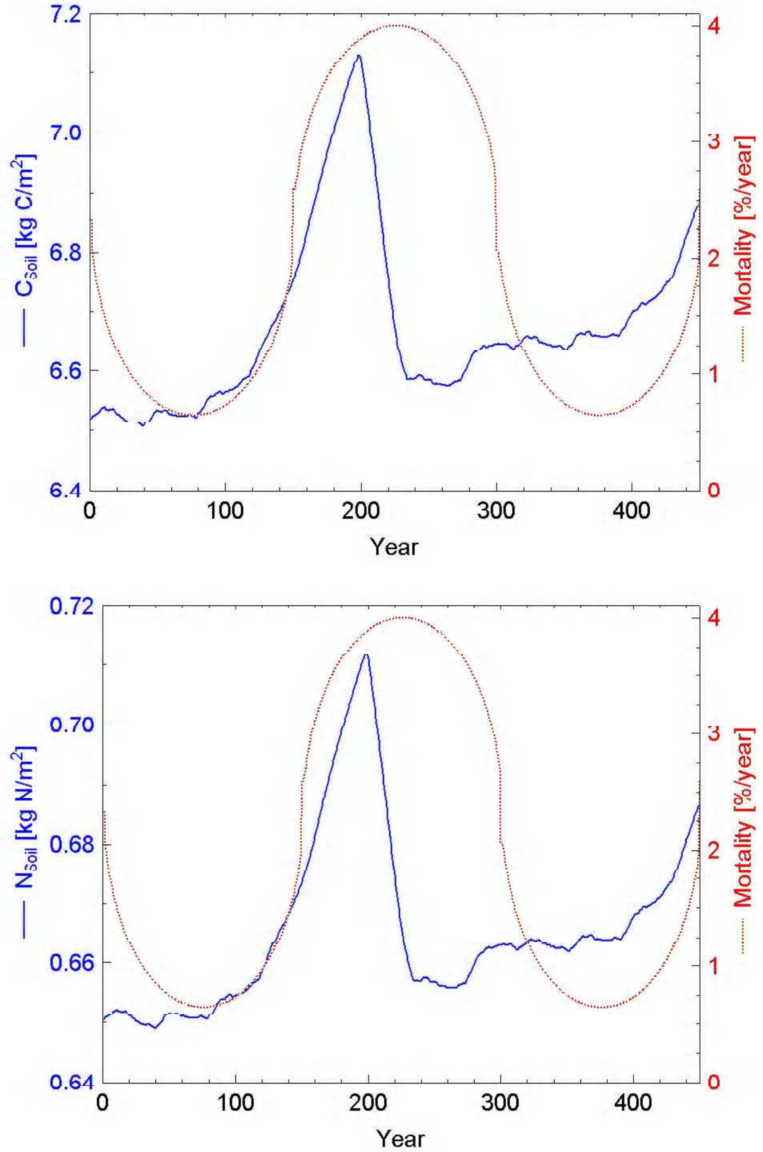

Figure 42: Temporal performance of the simulated carbon and nitrogen amounts in the soil in relation to annual mortality rate for plot No. 1 in Babia hora.

Leaf area index (LAI) is a variable characterising the crown canopy status of the forest ecosystem. Thus, it is closely connected to stem carbon and to mortality. If mortality is low, stem carbon is high, and the leaf area is large (see Figures 38 and Figure 43). The higher mortality rate reduces both the stem carbon and the leaf area. Likewise the litter characteristics, also the leaf area reacts sensitively to the changing climatic conditions from year to year, which can be confirmed by the inter-annual variation of LAI as shown in Figure 43.

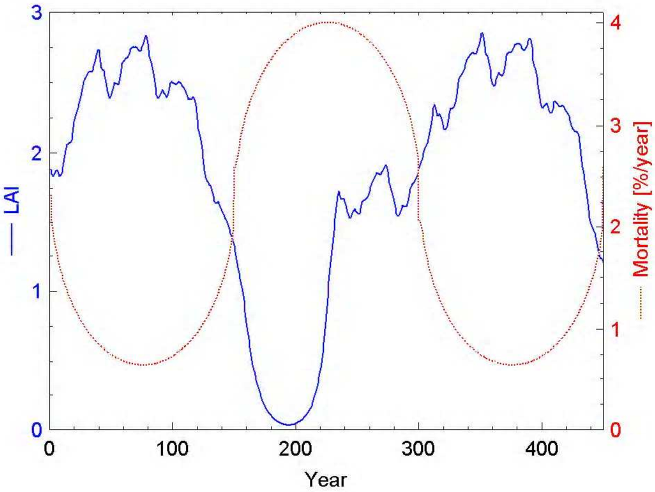

Figure 43: Temporal performance of the simulated leaf area index (LAI) in relation to annual mortality rate for plot No. 1 in Babia hora.

The next two examined variables are radiation absorption and evapotranspiration. Radiation absorption is here defined as the ratio of the absorbed photosynthetically active radiation (APAR) to the total available amount of photosynthetically active radiation (PAR). Evapotranspiration includes evaporation from the plant canopy and its transpiration. Both parameters react to the status of the leaf area. If the leaf area is large, i.e. LAI has high values, more radiation can be absorbed and more water will be lost through evapotranspiration (see Figure 44).

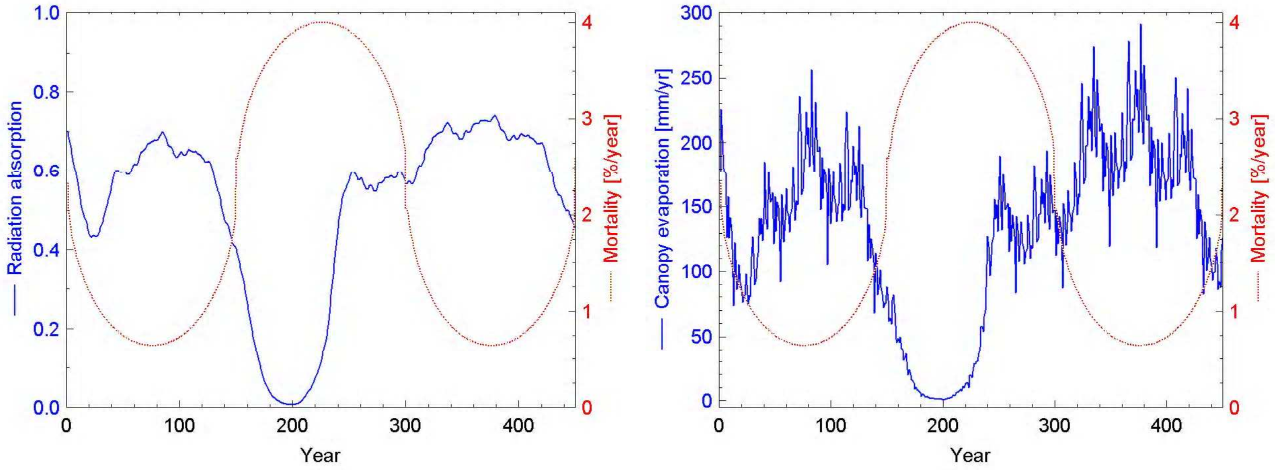

Figure 44: Temporal performance of the simulated radiation absorption and evapotranspiration in relation to annual mortality rate for plot No. 1 in Babia hora. Radiation absorption is defined as the ratio of the absorbed photosynthetically active radiation (APAR) to the total available amount of photosynthetically active radiation (PAR).

Soil evaporation behaves in the opposite way to evapotranspiration, which characterises the water loss from the plants. When the mortality rate is high and the aboveground biomass is low, evapotranspiration will also be low and the soil evaporation will increase (Figure 45).

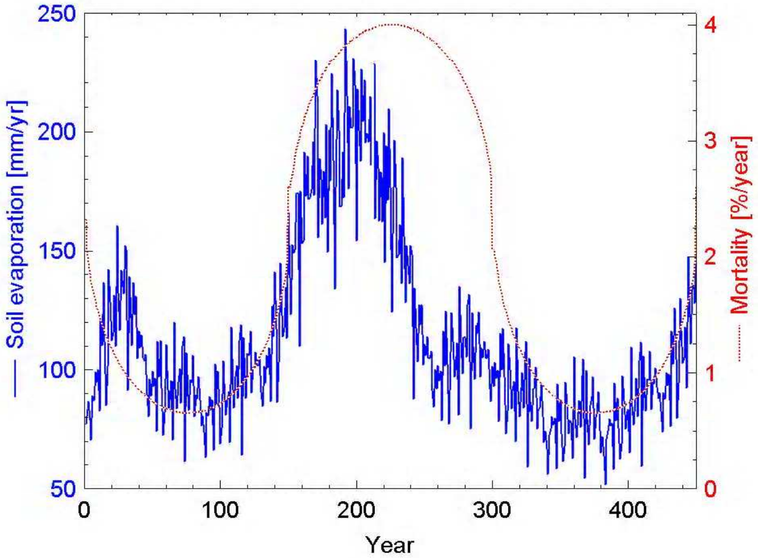

Figure 45: Temporal performance of the simulated soil evaporation in relation to annual mortality rate for plot No. 1 in Babia hora.

The examination of the behaviour of individual parameters with respect to the changing annual mortality rate over time revealed that all variables react logically to the mortality changes and changes in other variables that are closely connected to them. Although we cannot evaluate the absolute values of these variables, this analysis showed that the processes appear to be simulated by the model correctly.

3.1.8 Comparison of beech and spruce simulations in Rothwald

As addressed in Section 2.5.1, for Rothwald as a mixed forest stand two simulations with different species-specific parameterisation, i.e. Norway spruce and common beech, were performed. These simultaneous simulations allowed us to compare the output produced by the two different tree species settings for the same site and climatic conditions. Table 30 presents the average values of all the tested model state variables for all the simulation variants. Note that the results of the first simulation variant, which uses the original model set up, cannot be directly compared because of different fire mortality rates for each tree species (for spruce 0.5% per year, whereas for beech only 0.25% per year). The comparison of the last variant using the dynamic mortality is also restricted due to the different minimum and maximum annual mortality rates (for beech 0.76 to 4.1%, and for spruce 0.60 to 4.0%).

From the values given in Table 30 we can see that for the given site and climate conditions beech seems to be a more efficient tree species than spruce, because the predictions of the total accumulated stand volume are higher when using the beech parameterisation. In addition, beech forests tend to accumulate more nutrients, since all the simulated nutrient pools, i.e. the amount of coarse woody debris, as well as carbon and nitrogen amounts in litter and soil, are larger from the simulations using beech settings versus the spruce parameterisation.

Table 30: The output of the slow (normal) spinup for beech and spruce in Rothwald and each simulation variant, where C_{CWD}, C_{Litter}, C_{Soil} are carbon contents in coarse woody debris, litter and soil, respectively, and N_{Litter} and N_{Soil} are nitrogen contents in the litter and soil, respectively. S*tdev* is the standard deviation and *CV* is the coefficient of variation.

Simulation variant			**Mortality 0.5% + fire**		**Mortality 0.5%**		**Mortality 2%**		**Dynamic mortality**	
Tree species			**Beech**	**Spruce**	**Beech**	**Spruce**	**Beech**	**Spruce**	**Beech**	**Spruce**
Number of plots			18	18	18	18	18	18	18	18
Variable	**Volume [m^3/ha]**	Mean	1936.65	949.25	3365.71	2731.20	822.70	680.73	629.58	617.69
		Stdev	116.54	28.23	269.90	245.68	66.17	63.35	294.46	289.93
		Min	1611.67	880.90	2616.71	2270.39	640.11	561.01	312.82	267.05
		Max	2055.34	980.88	3640.56	2980.53	890.26	741.97	1075.66	1079.53
		CV [%]	6.02	2.97	8.02	9.00	8.04	9.31	46.77	46.94
	C_{CWD} [kg C/ha]	Mean	45998	18670	59905	34718	58313	33283	33545	22627
		Stdev	3813	761	6358	5379	6209	4903	12727	12610
		Min	37545	16655	45343	24795	44174	24238	17854	9765
		Max	50623	19697	67421	41173	65609	39173	56398	43109
		CV [%]	8.29	4.08	10.61	15.49	10.65	14.73	37.94	55.73
	C_{Litter} [kg C/m^2]	Mean	0.6037	0.3246	0.6885	0.3781	0.6585	0.3604	0.7317	0.6676
		Stdev	0.0663	0.0409	0.0819	0.0579	0.0788	0.0524	0.4744	0.6024
		Min	0.4693	0.2481	0.5238	0.2739	0.4983	0.2660	0.2795	0.1618
		Max	0.6927	0.4038	0.8016	0.4479	0.7668	0.4239	1.5768	1.5870
		CV [%]	10.98	12.60	11.89	15.31	11.97	14.54	64.84	90.23
	N_{Litter} [kg N/m^2]	Mean	0.0059	0.0026	0.0065	0.0028	0.0062	0.0028	0.0044	0.0033
		Stdev	0.0006	0.0003	0.0007	0.0004	0.0007	0.0004	0.0010	0.0013
		Min	0.0046	0.0020	0.0050	0.0021	0.0047	0.0021	0.0024	0.0016
		Max	0.0067	0.0033	0.0075	0.0033	0.0072	0.0033	0.0057	0.0054
		CV [%]	10.37	13.06	11.43	14.56	11.52	13.81	22.66	39.06
	C_{Soil} [kg C/m^2]	Mean	13.7321	8.2019	17.5603	14.8471	17.1807	14.2989	8.9721	8.1396
		Stdev	1.1428	0.3212	1.8709	2.3379	1.8426	2.1675	1.1026	1.2882
		Min	11.2101	7.3371	13.2481	10.5366	12.9533	10.2915	6.8829	5.5836
		Max	15.1600	8.6934	19.7261	17.6112	19.3049	16.8642	10.7004	9.5695
		CV [%]	8.32	3.92	10.65	15.75	10.73	15.16	12.29	15.83
	N_{Soil} [kg N/m^2]	Mean	1.3702	0.8184	1.7522	1.4816	1.7143	1.4269	0.8951	0.8121
		Stdev	0.1140	0.0321	0.1867	0.2333	0.1839	0.2163	0.1100	0.1285
		Min	1.1185	0.7321	1.3219	1.0514	1.2925	1.0269	0.6865	0.5571
		Max	1.5127	0.8675	1.9683	1.7574	1.9263	1.6829	1.0678	0.9550
		CV [%]	8.32	3.92	10.65	15.75	10.73	15.16	12.29	15.83

3.1.9 Spinup length

Apart from the main aim to validate the self – initialisation procedure implemented in BIOME-BGC, we were also interested if the slow (normal) and the accelerated spinup produce the same output and to workout the average length of both types of spinup. The accelerated spinup refers to the self-initialisation procedure, in which the mineral nitrogen is not the limiting factor for the plant growth. Therefore, with this spinup the ecosystem achieves its steady state much faster than when using the slow spinup, that accounts for the competition for the mineral nitrogen between microorganisms and plants. For more details see Section 2.1.2.1.

The length of the spinup with and without acceleration varied between the simulations and depended on the simulation variant (mortality rate and fire module switched on or off), tree species and site (Table 31). In general, the accelerated spinup in Babia hora lasted longer than in Rothwald. In Rothwald, the Norway spruce accelerated self-initialisation was shorter for all simulation variants than the spinup using the common beech ecophysiology.

For the original model set up, i.e. regular mortality 0.5% per year and fire mortality 0.5% or 0.25% per year for spruce and beech, respectively, the accelerated spinup lasted on average 3,409 ± 1,831 years, whereas the spinup without acceleration and with the original version of the mortality model took approximately 30,000 years. These values are a little higher than the values reported by Thornton et al. (2002), who stated that a slow spinup lasts approximately 20,000 years and the accelerated procedure reduces the spinup time by about a factor of 10, i.e. to 2,000 years. However, our results document the length of the spinup for two locations only and therefore, they cannot be regarded as a general average value of the spinup length.

Table 31: The length of spinup according to the simulation variant and location. Note that the length of the slow (normal) spinup is derived from the assessment of one plot.

	Spinup							
	with acceleration				without acceleration			
Mortality	0.5% + fire	0.5%	2%	Dynamic	0.5% + fire	0.5%	2%	Dynamic
Number of years after which the steady state is achieved								
Rothwald Beech	1664 ± 810	2002 ± 426	2028 ± 520	-	40,000	50,000	30,000	15,000
Rothwald Spruce	1547 ± 727	1846 ± 310	1911 ± 441	2158 ± 336	25,000	40,000	15,000	20,000
Babia hora	4549 ± 1316	3043 ± 1034	2279 ± 723	4924 ± 992	25,000	70,000	52,000	20,000
Together	3409 ± 1831	2609 ± 1003	2159 ± 654	4260 ±1478	30,000	53,333	32,333	18,333

When the fire mortality was set to 0 and regular mortality was left constant either at the original rate 0.5% or at the increased annual rate of 2%, the accelerated spinup was on average shortened by 1,000 years in comparison to the simulations with the original model set up, whereas the "slow" spinup lasted between 40,000 to 70,000 years depending on the locality and tree species (see Table 31).

The implementation of the new dynamic mortality model (Section 3.1.4) reduced the length of the normal initialisation, i.e. without acceleration, to 15,000 – 20,000 years. The duration of the accelerated spinup using the dynamic mortality was the longest from all the tested variants (Table 31). In Rothwald, the length of the accelerated spinup using the dynamic mortality for beech could not be determined (see next Section 3.1.10).

3.1.10 Comparison of the output obtained from accelerated and slow spinup

The comparison of the output from the two variants of spinup, i.e. with and without the acceleration mechanism as described in Section 2.1.2.1, revealed that both of them produce very similar results (compare Tables 15 and 32, Figure 46). The accelerated spinup gives in general slightly higher values of the state variables when compared with the slow spinup (Figure 46). The overestimation of carbon in the soil and stand volume (i.e. carbon in the stem) by the accelerated spinup varies between 2-15% and 2-12% depending on the simulation variant.

However, the output of the two spinups is similar only when using the constant regular mortality. After the implementation of the dynamic mortality, the slow and accelerated spinup produced significantly different results (Tables 15 and 32, Figure 47). Moreover, the accelerated spinup showed a much smaller variation of the state variables over time due to the succession cycle. As Table 32 indicates, for Rothwald no output could have been produced by the accelerated spinup for beech after the incorporation of the dynamic mortality, because in case the beech species-specific parameterisation was used, the results from this simulation variant were equal to zero.

Based on this comparison of the slow and the accelerated spinup and on the fact, that the suggested dynamic mortality model was developed for the slow self-initialisation variant, it would be recommended to use the non-accelerated version of the spinup after the implementation of the dynamic mortality.

Table 32: Summary statistics of the observations and the output of the accelerated spinup for each simulation variant, location and all examined variables. C_{CWD}, C_{Litter}, C_{Soil} are carbon contents in coarse woody debris, litter and soil, respectively, and N_{Litter} and N_{Soil} are nitrogen contents in the litter and soil, respectively. *Stdev* is the standard deviation and *CV* is the coefficient of variation.

	Variant	Reality		Original mortality 0.5% + fire			Original mortality 0.5%			Mortality 2%			Dynamic mortality		
	Location	Rothwald	Babia hora	Rothwald		Babia hora	Rothwald		Babia hora	Rothwald		Babia hora	Rothwald		Babia hora 0.68-4.0% 300yrs
	Species	Mixed	Spruce	Pure	Mixed	Spruce	Pure	Mixed	Spruce	Pure	Mixed	Spruce	Pure	Mixed	Spruce
	Number of plots	18	57 (19)*	18	18	57 (19)*	18	18	57 (19)*	18	18	57 (19)*	18	18	57 (19)*
Variable: Volume [m^3/ha]	Mean	559.20	313.20	1866.80	1759.44	815.79	3380.56	3296.44	2490.36	825.97	807.27	551.78	-	-	550.29
	Stdev	280.03	230.01	474.52	333.29	45.37	452.60	368.68	200.74	106.39	89.32	64.28	-	-	223.47
	Min	197.09	18.65	929.40	1222.00	670.58	2344.00	2621.00	1812.21	578.60	639.20	412.63	-	-	261.80
	Max	1089.00	1014.06	2231.00	2223.00	960.72	3856.00	3841.00	3028.15	939.50	936.10	703.63	-	-	1018.46
	CV [%]	50.08	73.44	25.42	18.94	5.56	13.39	11.18	8.06	12.88	11.07	11.65	-	-	40.61
C_{CWD} [kg C/ha]	Mean	86139.33	20305.32	44213.89	30926.67	31861.96	57887.22	44892.22	61611.92	55906.67	43176.11	51617.18	-	-	39545.86
	Stdev	19825.55	22573.71	13615.36	4679.56	1862.15	14399.04	6780.69	4965.17	13978.73	6421.13	4797.67	-	-	19688.26
	Min	56769.27	0.00	17700.00	21200.00	26581.63	26550.00	29800.00	44002.77	25670.00	28760.00	39392.29	-	-	17442.19
	Max	132471.00	100095.16	56280.00	38160.00	38058.12	72550.00	54290.00	71439.59	70280.00	52080.00	63341.09	-	-	73758.11
	CV [%]	23.02	111.17	30.79	15.13	5.84	24.87	15.10	8.06	25.00	14.87	9.29	-	-	49.79
C_{Litter} [kg C/m^2]	Mean	0.9523	5.1391	0.5646	0.4730	0.4339	0.6339	0.5353	0.6750	0.6057	0.5111	0.5566	-	-	0.5677
	Stdev	0.4449	1.9270	0.1468	0.0690	0.0400	0.1620	0.0809	0.0628	0.1549	0.0764	0.0583	-	-	0.3691
	Min	0.3877	1.8622	0.2587	0.3085	0.3570	0.2913	0.3448	0.5346	0.2801	0.3302	0.4493	-	-	0.2448
	Max	1.9014	8.9786	0.7222	0.5657	0.5050	0.8136	0.6374	0.7618	0.7784	0.6086	0.6691	-	-	1.2731
	CV [%]	46.7184	37.4972	25.9999	14.5943	9.2187	25.5483	15.1069	9.2981	25.5789	14.9409	10.4677	-	-	65.0149
N_{Litter} [kg N/m^2]	Mean	0.0319	0.2282	0.0054	0.0043	0.0035	0.0058	0.0047	0.0051	0.0056	0.0045	0.0044	-	-	0.0037
	Stdev	0.0142	0.0741	0.0017	0.0007	0.0003	0.0018	0.0008	0.0005	0.0017	0.0007	0.0004	-	-	0.0009
	Min	0.0138	0.0975	0.0020	0.0026	0.0029	0.0022	0.0028	0.0041	0.0022	0.0028	0.0035	-	-	0.0025
	Max	0.0626	0.3637	0.0070	0.0053	0.0041	0.0076	0.0058	0.0059	0.0073	0.0056	0.0052	-	-	0.0055
	CV [%]	44.6712	32.4594	30.9058	16.4445	9.2647	30.7273	16.7969	9.2338	30.2745	16.5415	10.2833	-	-	23.9795
C_{Soil} [kg C/m^2]	Mean	8.2633	6.8401	13.9184	12.0950	14.0570	18.0300	16.8822	25.8101	17.5000	16.3278	21.2844	-	-	15.5537
	Stdev	3.0901	3.2529	2.9202	1.3746	1.2222	2.7261	2.1382	3.2100	2.6713	2.0137	2.7197	-	-	2.2586
	Min	1.1631	3.1849	7.8120	8.7600	11.8553	11.2900	11.8700	18.8517	10.9500	11.5000	16.9372	-	-	11.6795
	Max	12.9178	14.2040	16.8600	13.8300	16.9408	21.2500	19.2100	30.4359	20.7100	18.5500	27.0814	-	-	20.0172
	CV [%]	37.3955	47.5557	20.9810	11.3654	8.6944	15.1198	12.6655	12.4371	15.2644	12.3327	12.7779	-	-	14.5211
N_{Soil} [kg N/m^2]	Mean	0.4843	0.3732	1.3890	1.2067	1.4027	1.7991	1.6847	2.5755	1.7462	1.6292	2.1239	-	-	1.5520
	Stdev	0.1867	0.1879	0.2915	0.1372	0.1219	0.2720	0.2135	0.3203	0.2664	0.2010	0.2714	-	-	0.2254
	Min	0.0567	0.1549	0.7796	0.8741	1.1830	1.1270	1.1840	1.8812	1.0930	1.1470	1.6901	-	-	1.1656
	Max	0.8012	0.8157	1.6830	1.3800	1.6904	2.1210	1.9170	3.0372	2.0660	1.8510	2.7024	-	-	1.9976
	CV [%]	38.5393	50.3550	20.9841	11.3726	8.6935	15.1180	12.6749	12.4368	15.2582	12.3402	12.7780	-	-	14.5207

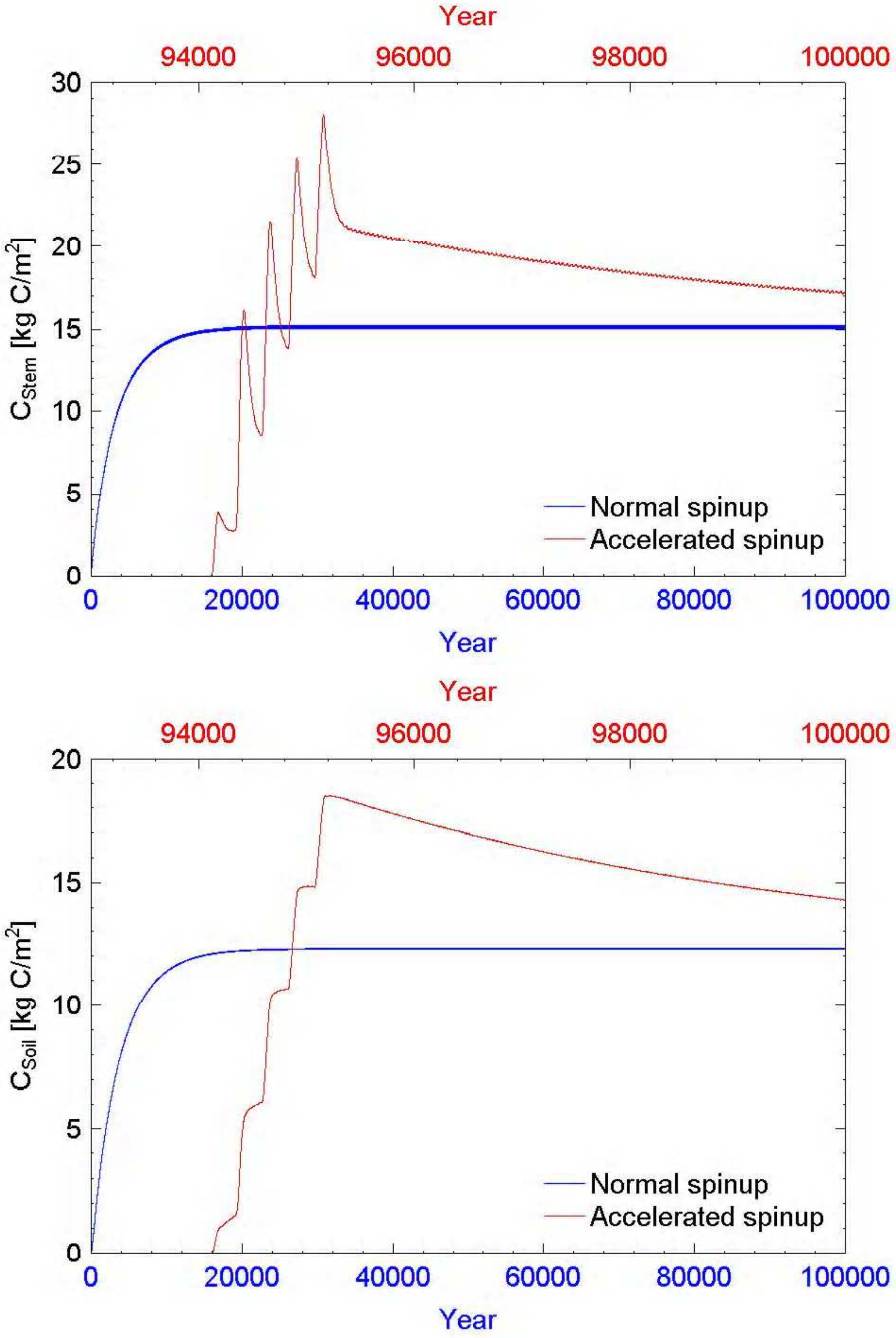

Figure 46: Comparison of the simulations of carbon amount in the stem (C_{stem}) and the soil (C_{soil}) during the normal and accelerated spinup using the original model set up, i.e. regular mortality 0.5% and fire mortality 0.5% per year, for plot No. 1 in Babia hora.

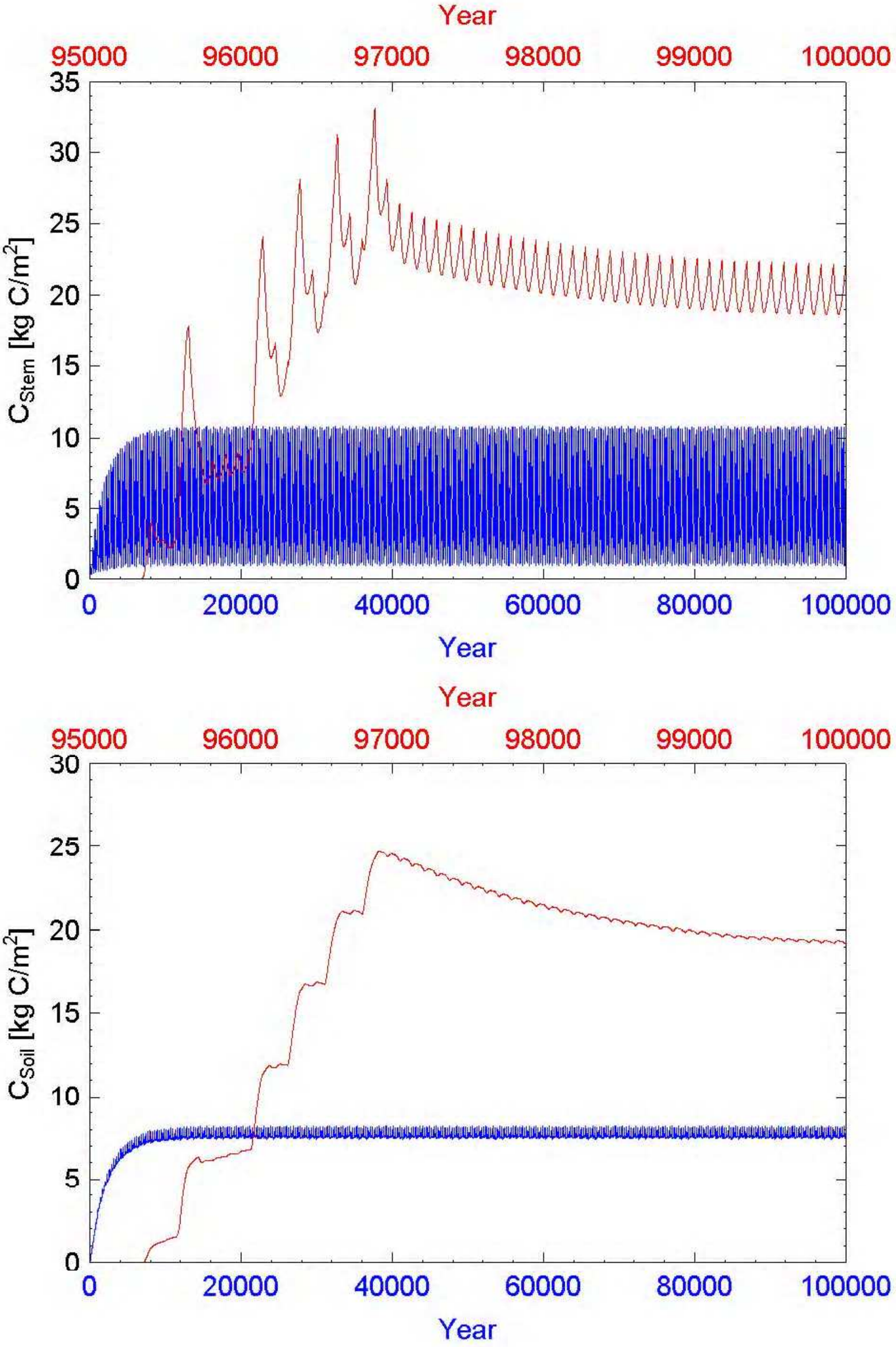

Figure 47: Comparison of the simulations of carbon amount in the stem (C_{stem}) and the soil (C_{soil}) during the normal (blue line) and accelerated (red line) spinup using the dynamic mortality model for plot No. 1 in Babia hora.

3.2 RESULTS FROM SIMULATIONS OF MANAGED FORESTS

In the second part of this study we tested if the species-specific version of the model BIOME-BGC is able to assess the growth response of the forest stands to different harvesting scenarios, which were applied after thinning operations. For this task we used the available field observations from the three different management sites: Hartberg, Wilhelmsburg and Bad Zell, as described in Section 2.3.2. Unlike for virgin forests, for these plots we only have information about stand volume, and no litter or soil data. On the other hand, the advantage of the observations on these plots is the availability of the repeated measurements, since for each of the 36 plots we have six successive observations of stand volume and hence, information about the five increment periods.

The actual influence of the three examined harvesting scenarios (WTH = whole tree harvest, DTH = delayed tree harvest and SWH = commercial stem wood harvest, Section 2.3.2) on the forest growth was evaluated by Sterba (1988), Arzl (1991), Brunner (2002), Gugganig (2002) and Hauser (2003). Their analysis of the impact of the harvesting scenarios on the actual volume or basal area growth suggested that the best growth responses can be expected if the whole felled aboveground biomass is left in the stand or if only the stem wood is extracted. Already three years after the first thinning, the plots where whole tree harvesting was applied had the lowest mean volume and basal area increment of the remaining stand. The three-year mean annual basal area and volume increment per hectare was on the WTH plots reduced by 15.5% and 13.3%, respectively, when compared with the variant SWH. If the felled trees were left on the cutting site for one year prior to removal, i.e. DTH variant, the differences in mean annual volume and basal area increments were reduced by 6.8% and 9.2% in comparison to SWH. For two of the three locations the detected differences by harvesting scenario were statistically significant (Sterba 1988).

The main goal of this chapter is to examine if the model reactions to different harvesting scenarios correspond with the responses observed in the field and thus, to document that biogeochemical models can be used as efficient diagnostic tools in the management studies to assess the complex issue of ecosystem sustainability encompassing a balance between plant, air and soil.

The first step within the analysis was a comparison of the predicted stand volume with the observed values to ensure that no bias or systematic shift in the relationship between the modelled and observed results exists. As already mentioned, the model gives us information about the carbon amount in the compartment stem. This parameter was converted to stand volume units, i.e. to cubic meters per ha [m^3/ha], according to the description given in Chapter 2.4. The comparison of the predictions versus observations is given in Figure 48.

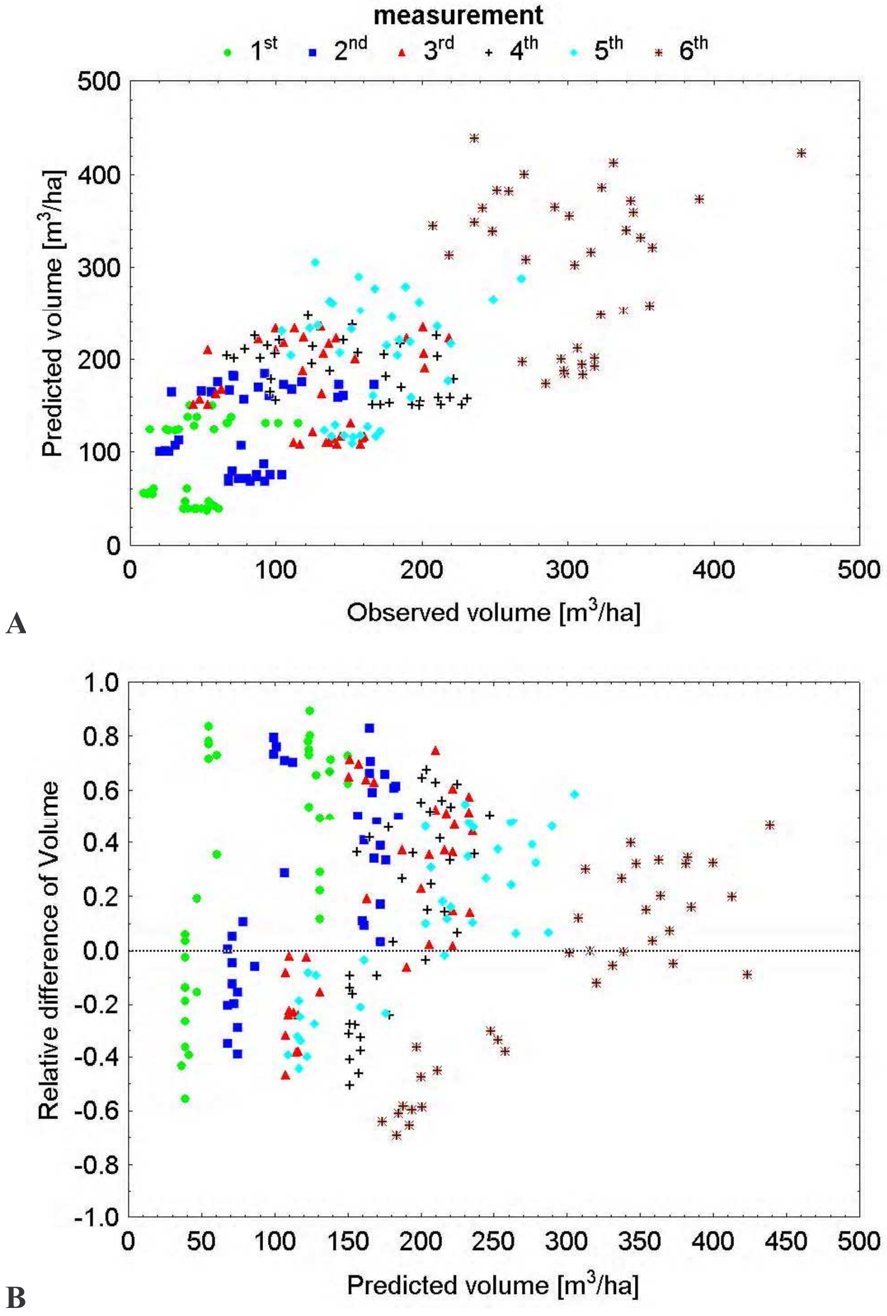

Figure 48: Predicted versus observed stand volume per hectare including all 36 examined plots and 6 re-measurements per plot (A) and the analysis of the relative model residuals calculated as the difference between the predicted and observed stand volume divided by the predicted stand volume (B).

The correlation between the predicted and observed stand volume was found to be highly significant (R^2=0.51, n=216, t=17.1** > $t_{\alpha=0.01}$=2.58). Residual analysis revealed no systematic trends between predicted and observed stem volume. Furthermore, the prediction interval, a measure for the expected range of future model applications (see Reynolds 1984) across all 36 plots and observations (n= 216) ranged between -51.9 and 66.3 m^3/ha or –37.3% to 47.7% of the mean value, which was 139 m^3/ha. This is within the expected range reported by Pietsch and Hasenauer (2002) who suggest a prediction interval for the model simulations of lowland Norway spruce forest ecosystems between -288.6 to 259.0 m^3/ha, (average stand volume equal to 520 m^3/ha) or -55.5% to 49.8%.

Next, we were interested in assessing the correlations between predicted and observed stand volume as well as volume increment for each location (Hartberg, Wilhelmsburg, Bad Zell) and harvesting scenario. Table 33 gives the correlation between the predicted versus observed stand volume and periodic volume increment rates per hectare. All correlations were significant suggesting that we can be confident that our modelling environment seems to adequately address the complex ecophysiological processes as they depend on site-specific conditions.

Table 33: Summary statistics of the correlation analysis between the predicted and observed volume and volume increment per location and harvesting scenario (WTH whole tree harvest; DTH delayed tree harvest; STH stem wood harvest). At each location every variant consists of 4 plots with 6 volume observations and 5 volume increment periods, which means that the total number of observations for each scenario at a particular location is 24 for stand volume and 20 for stand volume increment. All relationships were significant at α=0.05.

Location	**Harvesting scenario**	**Stand volume**				**Stand volume increment**			
		R^2	Intercept	Regression Coefficient	Std. Error of Estimates	R^2	Intercept	Regression Coefficient	Std. Error of Estimates
Hartberg	WTH	0.74*	94.93	0.86	41.87	0.27*	11.97	0.53	1.72
	DTH	0.79*	100.95	0.89	32.10	0.32*	8.52	0.57	2.65
	SWH	0.72*	115.34	0.85	29.67	0.41*	5.27	0.64	1.88
	All	0.71*	104.13	0.84	37.43	0.17*	8.94	0.41	3.01
Wilhelmsburg	WTH	0.97*	10.48	0.99	9.15	0.65*	9.47	0.81	0.72
	DTH	0.90*	26.59	0.95	18.27	0.26*	9.37	0.51	1.88
	SWH	0.93*	29.35	0.97	13.02	0.16*	11.03	0.40	1.28
	All	0.93*	22.69	0.96	14.63	0.24*	10.20	0.49	1.46
Bad Zell	WTH	0.74*	108.99	0.86	55.11	0.32*	17.66	0.57	1.56
	DTH	0.82*	93.69	0.90	40.08	0.49*	14.06	0.70	1.86
	SWH	0.82*	107.72	0.90	37.86	0.27*	14.59	0.52	1.83
	All	0.78*	104.45	0.88	44.72	0.37*	15.17	0.61	1.98

Therefore, in the following part of the analysis we evaluated the model ecosystem responses on the harvesting scenarios. For this purpose, we calculated relative stand volume increments to the modelled stand volume to exclude possible differences in their absolute values, which could hide the actual growth reactions. First attempts to assess the influence of harvesting across all three locations together failed because the forest stands in Wilhelmsburg, Hartberg and Bad Zell differ from each other in their status (stand age and site conditions), and the time of thinning. Thus, for the evaluation we combined only the simulation results of the 4 plots at each location with the same harvesting scenario after thinning, in the case of Bad Zell only 2 plots in Grillnberger and 2 plots in Kern.

As can be seen from Figure 49 and Table 34, the modelled growth responses contradict the observations, particularly immediately after the intervention, because the WTH plots, where all felled aboveground biomass was removed from the forests, have the largest stand volume increments in the model, whereas the increment on the SWH plots is the smallest. Although over time the model behaviour begins to correspond with the field observations, the opposite model response as in reality was for us surprising, because considering the observed reactions of the different harvesting scenario (see Sterba 1988) we expected that on the SWH plots the relative volume increments would be higher compared to the WTH plots, where the whole above ground biomass and thus high amount of nutrients was removed. These results suggest that the model may have some difficulties to simulate immediate ecosystem reactions to such abrupt changes correctly.

Table 34: Comparison of the development of simulated relative stand volume increments calculated as the ratio of the absolute simulated stand volume increment to the initial simulated stand volume after the interventions for each location and each harvesting scenario, whereby WTH is whole tree harvest; DTH delayed tree harvest; SWH commercial stem wood harvest.

Site	**Period [years]**	**Relative stand volume increment [%]**			**Site**	**Period [years]**	**Relative stand volume increment [%]**		
		Harvesting scenario					Harvesting scenario		
		WTH	DTH	SWH			WTH	DTH	SWH
Hartberg	82-85	11.00	8.16	7.69	**Wilhelmsburg**	81-84	31.08	25.11	28.00
	85-88	9.91	9.51	6.74		84-87	18.67	19.56	18.64
	88-90	8.03	8.77	5.81		87-90	12.70	13.86	13.04
	90-93	6.30	6.79	5.51		90-92	9.02	9.72	9.33
	93-99	7.10	7.81	7.69		92-97	11.30	9.78	10.27
Bad Zell Grillnberger	83-86	14.54	11.99	11.38	**Bad Zell Kern**	83-86	30.74	27.42	27.81
	86-89	11.37	11.66	9.51		86-89	17.41	18.49	17.65
	89-92	8.23	8.71	7.44		89-92	10.95	11.45	11.34
	92-96	10.00	9.50	8.12		92-96	9.16	9.48	9.31
	96-02	7.96	9.75	8.55		96-02	8.70	9.07	8.96

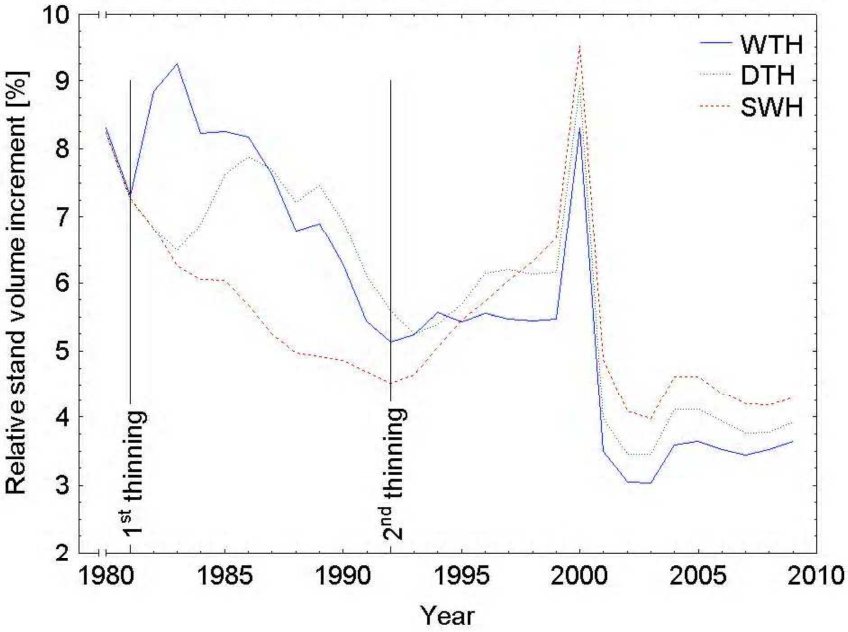

Figure 49: Development of the relative modelled stand volume increments calculated as the ratio of the absolute simulated stand volume increment to the initial simulated stand volume after the interventions for Hartberg and each harvesting scenario, whereby WTH is whole tree harvest; DTH delayed tree harvest; SWH commercial stem wood harvest.

Due to these findings, in the next section we try to analyse the causes of the model performance on the base of other parameters describing the ecosystem processes. From over 500 different output variables, that can be obtained from the model, we selected at least one from each cycle simulated by the model, i.e. from carbon, nitrogen, water and energy cycles.

Photosynthesis is the key physiological process determining plant growth (Sievänen et al. 1988). The atmospheric CO_2 fixed during this process is utilised for the autotrophic respiration of the plants and for the new production of plant tissues, i.e. for net primary production NPP (Jiang et al. 1999). Their sum represents the gross primary production of the ecosystem, GPP. The ratio of NPP/GPP defines the growth efficiency of the ecosystem, which is our first examined variable. Similarly to relative volume increments, growth efficiency describes the forest stand response to current growth conditions. However, this parameter reflects the overall forest reaction in terms of utilising the photosynthetic assimilation potential for net carbon uptake, while volume increment describes only the changes in the stem pool of the forest stand. The simulation results for this variable according to the different harvesting scenarios are for all studied locations presented in Figure 50.

From this figure we can see similar reactions of growth efficiency to those detected for increment immediately after the first thinning. The WTH and DTH plots exhibited in Hartberg and Bad Zell higher modelled growth efficiency in comparison to the SWH variant, characteristic by leaving all felled biomass on site after 1st intervention. In Wilhelmsburg, the order of the reactions is due to different harvesting on the SWH plots (from these plots the commercial timber was harvested also after 1st thinning) different.

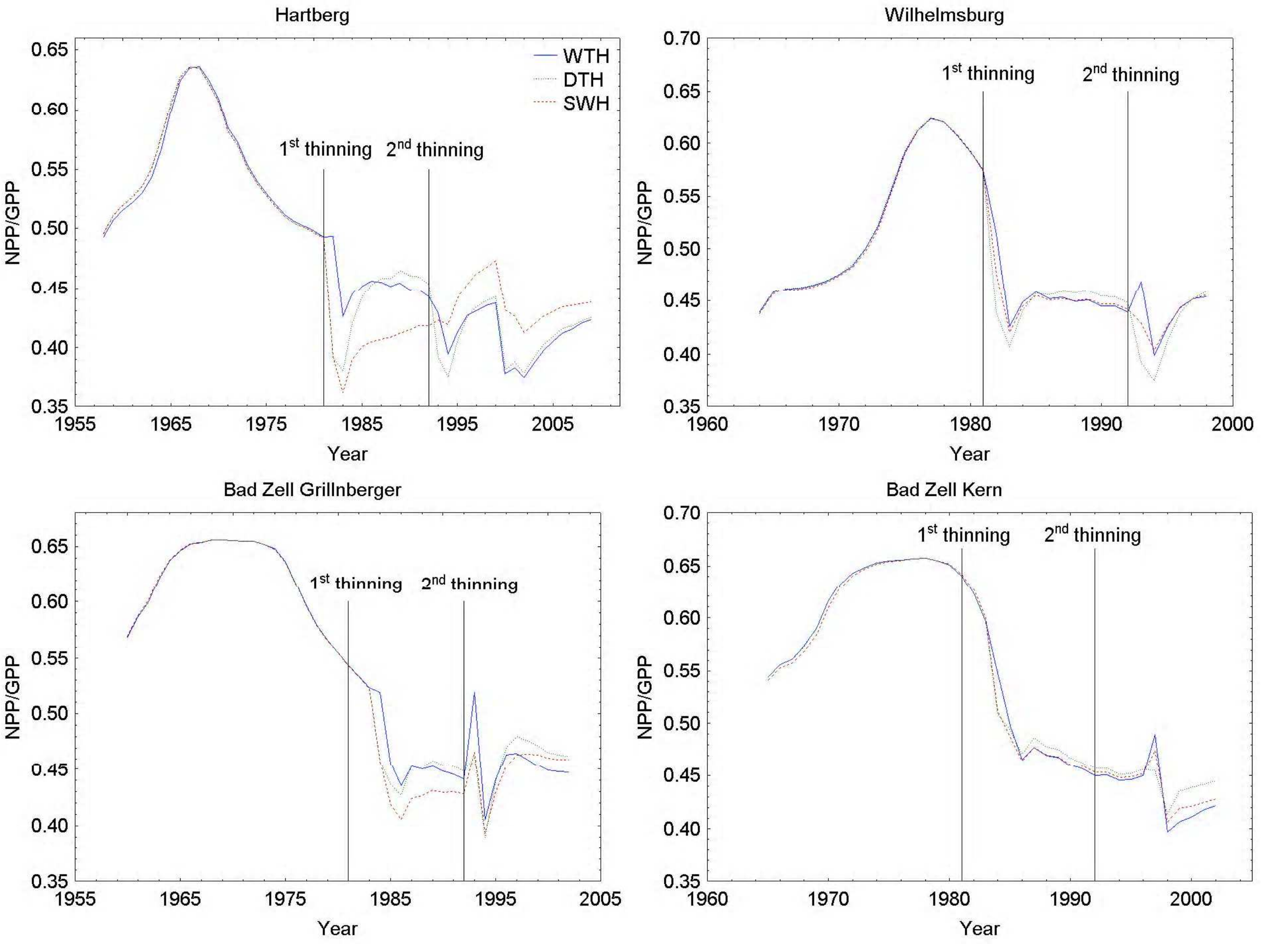

Figure 50: Development of the modelled growth efficiency from the stand establishment until present for each location and all harvesting scenarios, whereby WTH is whole tree harvest; DTH delayed tree harvest; SWH commercial stem wood harvest.

Photosynthesis is in the model simulated using the modified version of Farquhar biochemical model (Farquhar et al. 1980), in which photosynthetic assimilation is regulated by daily meteorological conditions, namely air temperature, air pressure, solar irradiance, and canopy leaf area. Since the plots within a particular location are situated next to each other (Chapter 2.3.2, Figure 13), no significant differences in climate can be detected between them. Therefore, the differences between the harvesting scenarios can only be caused by different leaf area of the stands. Examining the performance of the leaf area index (LAI) in Figure 51 revealed that the SWH plots have the lowest LAI and the WTH plots have the highest LAI after the intervention.

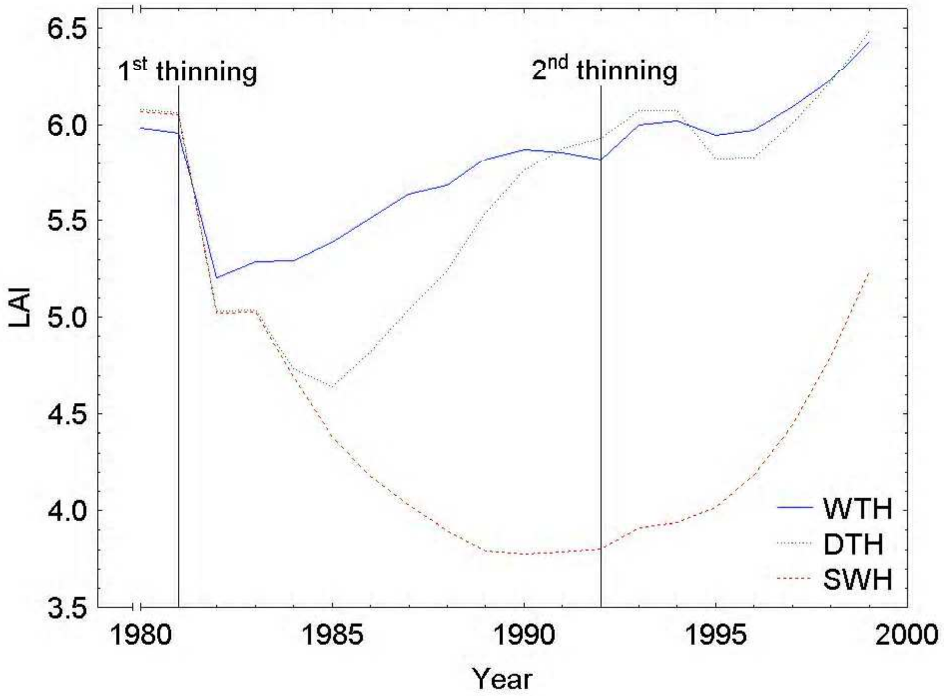

Figure 51: Development of the modelled leaf area index (LAI) for each harvesting scenario (WTH whole tree harvest; DTH delayed tree harvest; SWH commercial stem wood harvest) from 1980 until present for the location Hartberg.

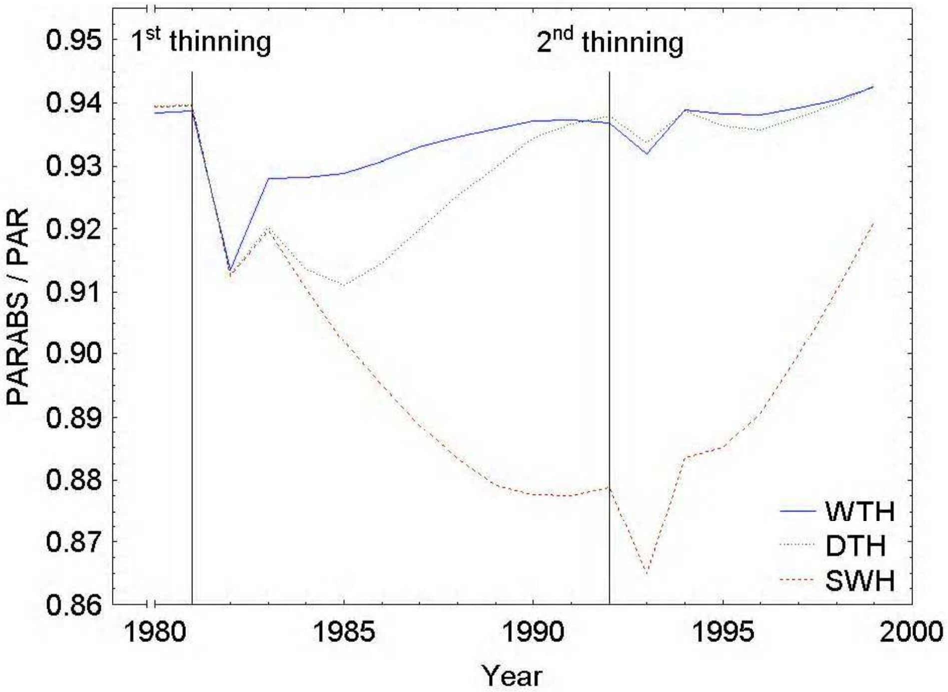

Figure 52: Development of the modelled canopy absorption, expressed as the ratio of photosynthetically active radiation absorbed by plants (PARABS) to the total amount of incoming photosynthetically active radiation (PAR), for each harvesting scenario (WTH whole tree harvest; DTH delayed tree harvest; SWH commercial stem wood harvest) from 1980 until present for the location Hartberg.

Another factor determining photosynthetic assimilation is the absorption of the photosynthetically active radiation by plants. The amount of the radiation that is absorbed by the forest canopy is influenced by the actual leaf area of the forest stand and thus, it is directly affected by the changes in the aboveground biomass of the forest ecosystem due to thinning operations. In this study we analyse the ratio of the photosynthetically active radiation absorbed by plants (PARABS) to the total amount of photosynthetically active radiation coming to the ecosystem (PAR). According to the results shown in Figure 52, the highest proportion of the photosynthetically active radiation is absorbed by the WTH plots with the highest simulated LAI, whereas the SWH plots absorb the lowest amount of radiation. Similarly to LAI, the differences in radiation absorption between the harvesting scenarios occur with one year delay after the intervention because the thinning intensity was on all plots similar.

Management operations influence directly not only the aboveground biomass, but also the characteristics of the litter and soil. Therefore, in the next step we examined the simulated carbon and nitrogen contents in the litter and soil. The simulation results of these pools are for the location Hartberg given in Figure 53. The SWH plots exhibited an improved nutritional status of carbon and nitrogen both in the litter and soil when compared with the other two harvesting scenarios, which extracted more felled biomass from the forest stand after the intervention. Note that the values in Figure 53 are unit less, since they are standardised to pre-thinning values (in 1980) to make the different harvesting scenarios comparable. The absolute modelled values of the carbon and nitrogen amount in the litter and soil are for each studied location given in Tables 35 and 36.

The SWH plots in Hartberg and Bad Zell, where no harvest was performed, exhibited an improved nutritional status of carbon and nitrogen in the litter for about 16 years. On the plots with delayed tree harvesting (DTH) the improved trend in the litter due to leaving the leaf mass on the spot lasted only half of the time versus the plots with whole tree harvesting (WTH), i.e. for about 8 years after the first thinning. In Wilhelmsburg the order of the reactions is different due to the different handling of the SWH plots after the first thinning. Unlike at the other two locations, in Wilhelmsburg on the SWH plots the commercial stem wood was harvested. Therefore, during the first couple of years after the thinning operation, these plots are characteristic by a lower amount of carbon and nitrogen in the litter versus the DTH plots (Figure 54).

The effect of thinning on carbon and nitrogen amount in the soil was not as distinct as in the litter. For example, while in case of the SWH plots in Hartberg (where no harvest was performed after 1st thinning) the litter carbon and nitrogen doubled their original mass after the treatment; their amount in the soil was enlarged by less than 1%. However, the positive effect of leaving the felled

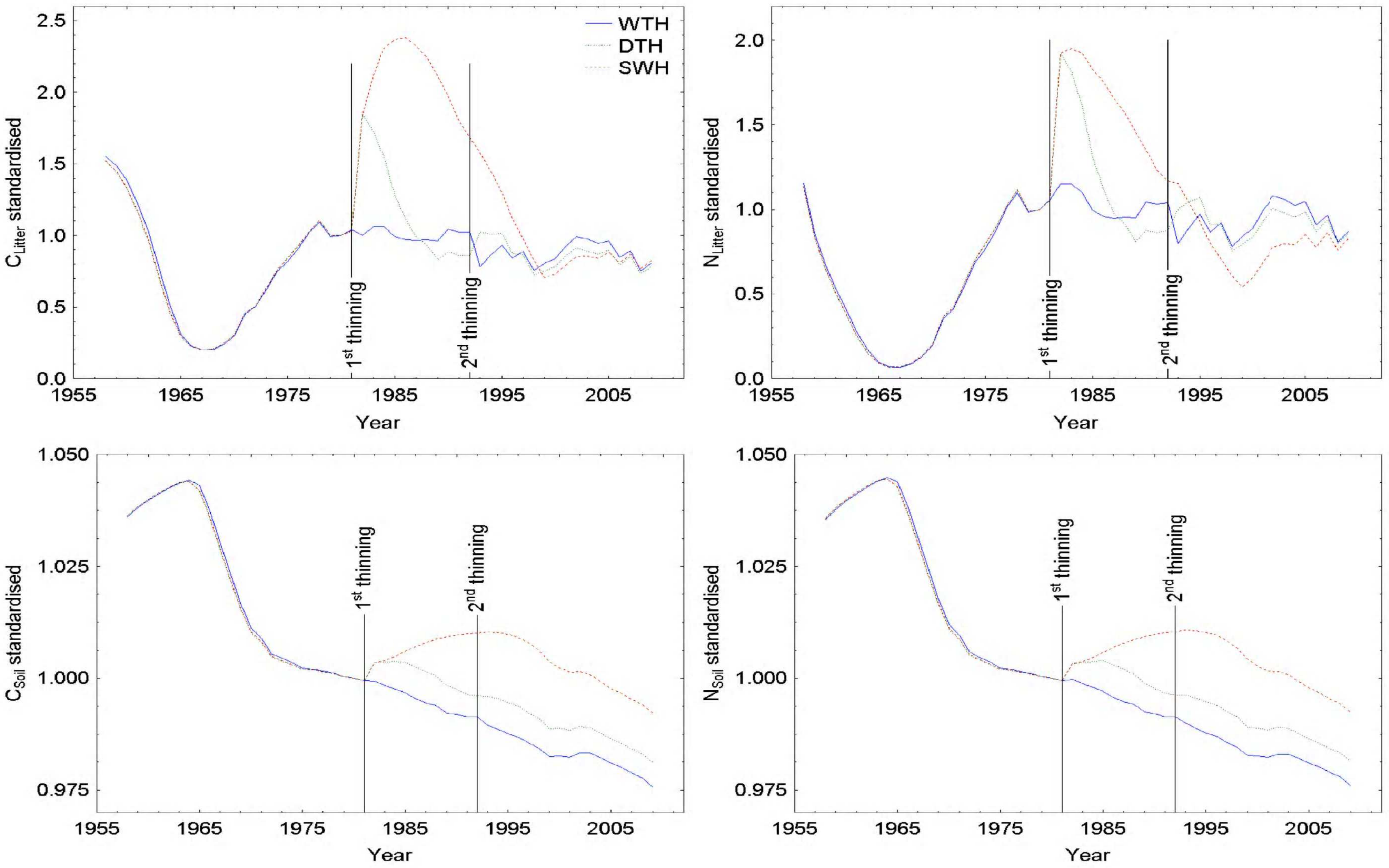

Figure 53: Development of the modelled carbon and nitrogen contents in the litter and in the soil for each harvesting scenario (WTH whole tree harvest; DTH delayed tree harvest; SWH commercial stem wood harvest) from the stand establishment until present in Hartberg. All values are standardised as the ratio of actual annual value versus the simulation value prior to the first thinning in 1980.

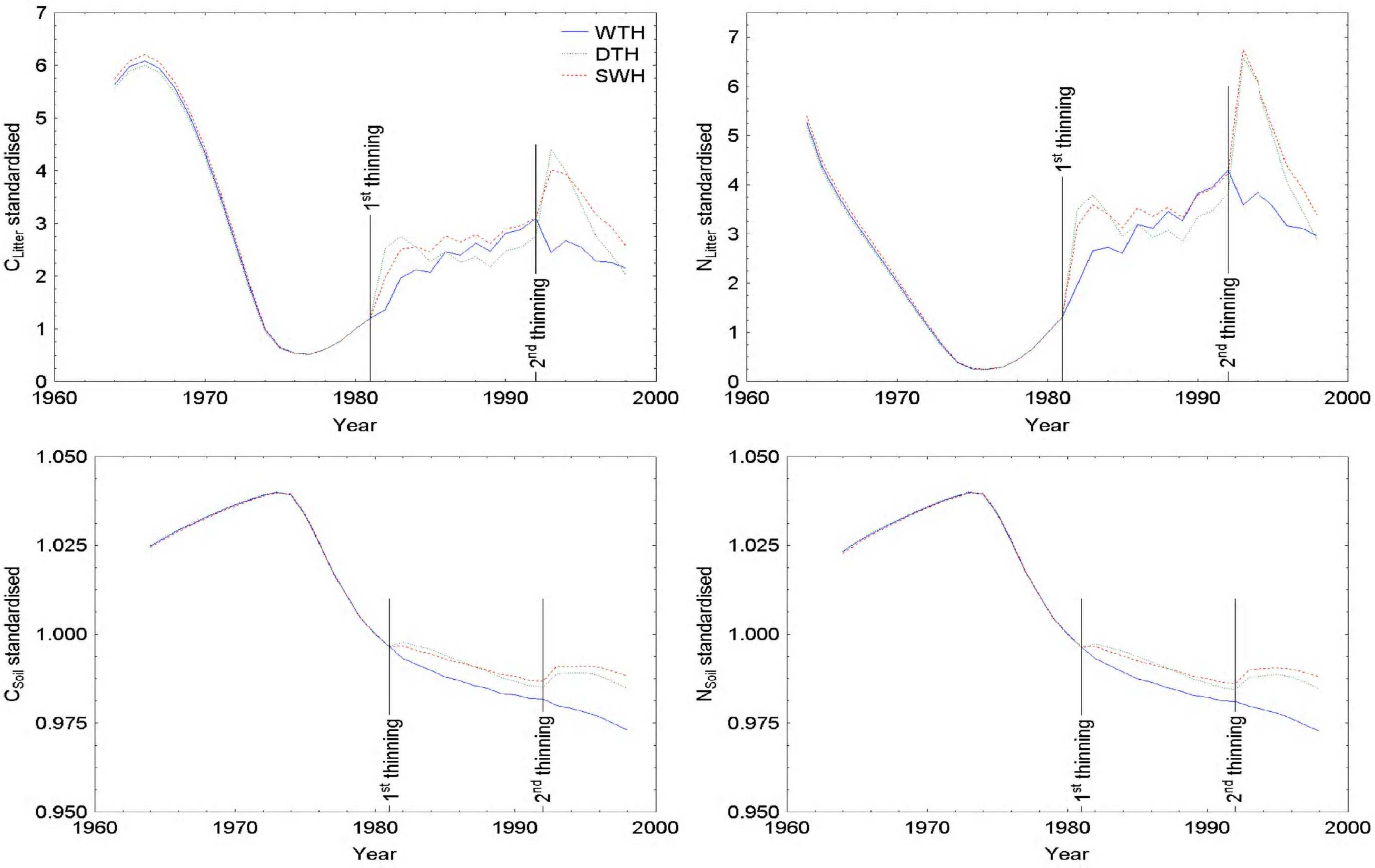

Figure 54: Development of carbon and nitrogen contents in the litter and the soil from stand establishment to present for each harvesting variant (WTH - whole tree harvest, DTH - delayed tree harvest, and SWH - commercial stem wood harvest) in Wilhelmsburg. All values are standardised to pre-thinning values in 1980.

biomass on site versus its whole or partial harvesting is also here obvious. Similarly to litter characteristics, the order of the examined harvesting scenarios is in Wilhelmsburg immediately after the first thinning different with the DTH plots having the highest amount of carbon and nitrogen in the soil due to the already mentioned differences in harvesting. Nevertheless, this ranking changes over time and already 8 years after 1st intervention their order corresponds with the other two locations (Figure 54).

The second thinning exhibited similar although smaller changes of the examined litter and soil pools as the first thinning, particularly on Hartberg and Bad Zell SWH plots, where there was a change in post-thinning operation from no harvest to stem wood harvest.

Heterotrophic respiration is a measure of the decomposition activity within a stand (Zimmermann and Frey 2002). In the model, this parameter represents the amount of carbon that is respired by microorganisms. This parameter changes over time due to climate variations, amount of litter input and its quality. It is stimulated by inputs of dead biomass. Therefore, this parameter should be the highest on the SWH plots characterised by the largest amount of felled biomass left on site. The model results are for this parameter and the location Hartberg presented in Figure 55, from which we can see that the simulated response is consistent with our expectations. The WTH plots are in Hartberg and Bad Zell the plots, where the heterotrophic respiration is the lowest, whereas on the SWH plots the decomposition activity measured by heterotrophic respiration is the highest. Similarly to other examined parameters, e.g. litter characteristics, in Wilhelmsburg the DTH plots are the plots with the highest values of heterotrophic respiration immediately after 1st

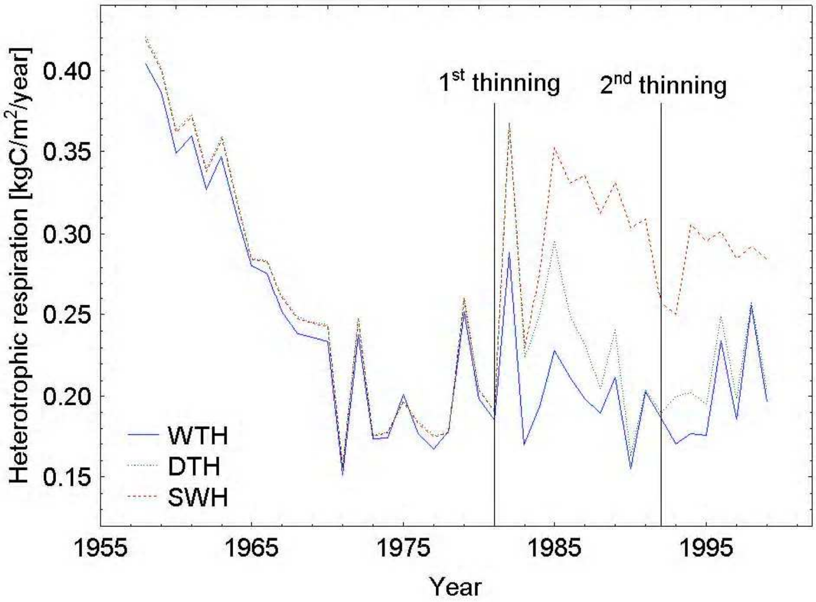

Figure 55: Development of heterotrophic respiration from stand establishment to present for each harvesting variant (WTH - whole tree harvest, DTH - delayed tree harvest, and SWH - commercial stem wood harvest) in Hartberg.

intervention, because from the SWH plots commercial timber was extracted, whereas on the same plots in Hartberg and Bad Zell all biomass was left in the forest (Table 35).

Stand production is closely related to the water balance determined by input, loss and storage of water in the ecosystem (Eamus 2001). Here we estimated water balance by the input of water into ecosystem through precipitation reduced by the losses due to interception, evapotranspiration and water outflow. In the model, precipitation is intercepted only by canopy (see Section 2.1). Canopy interception is determined by the leaf area. Since the pre-thinning state of the forest canopy was similar on all plots, no immediate differences of interception, and thus, also of other examined water cycle parameters, between the harvesting scenarios should be observable immediately after the thinning, since the thinning regime and intensity was on all plots situated within one location same. We expected that the differences in water balance would occur only after the differences in growth between the plots with different harvesting scenarios become obvious.

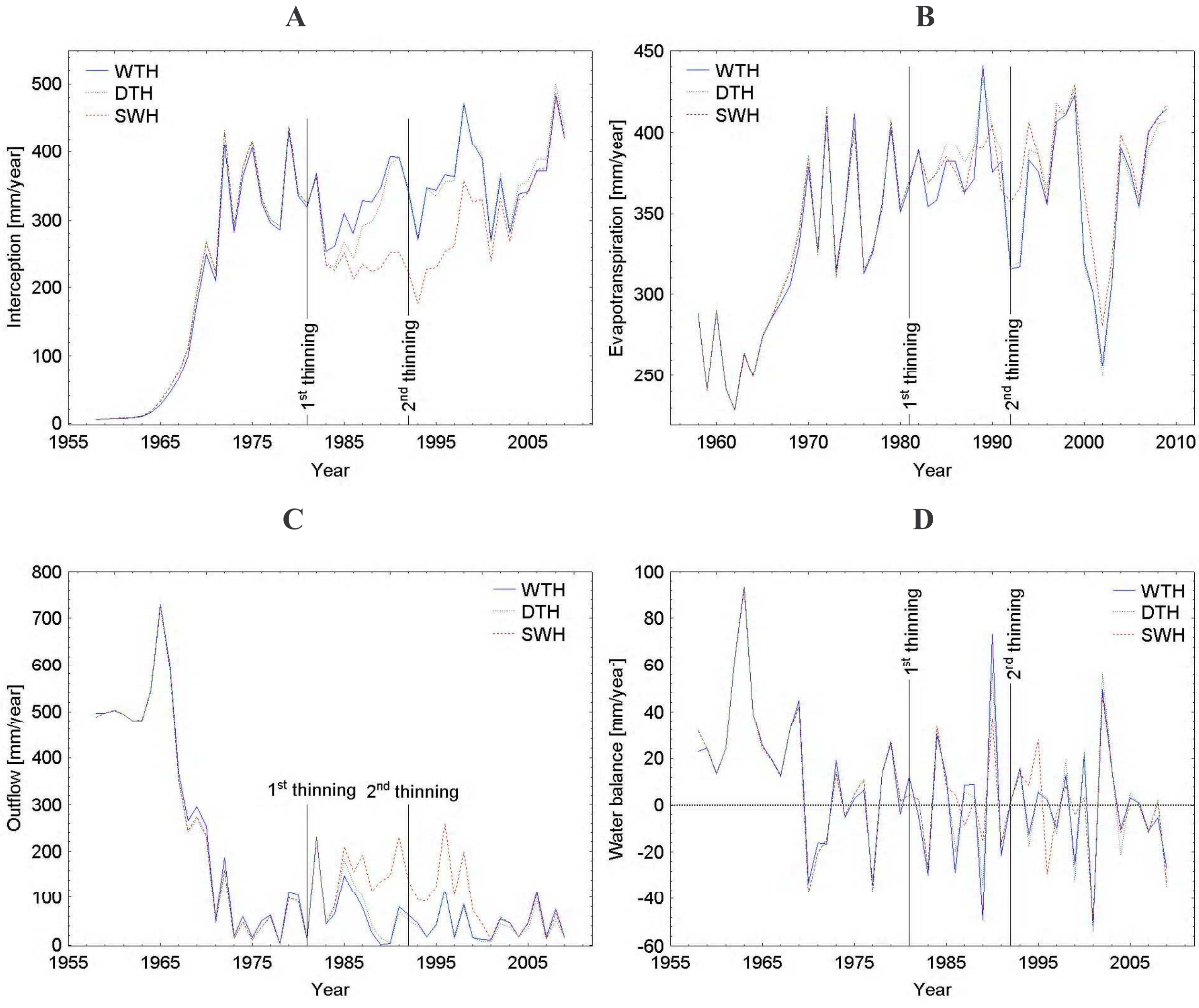

Figure 56: Development of water cycle constituents from stand establishment to present for each harvesting variant (WTH - whole tree harvest, DTH - delayed tree harvest, and SWH - commercial stem wood harvest) in Hartberg. (A) Canopy interception; (B) Evapotranspiration; (C) Soil water outflow; (D) Water balance.

The model results shown in Figure 56 confirm our expectations, since in the development of all the water variables we can see that the applied harvesting scenarios do not differ from each other immediately after the 1st intervention. However, as time proceeds the deviations begin to occur. The SWH plots, where the total felled biomass was left in the stand after the 1st thinning in Hartberg, have approximately 3 or 4 years after the thinning the lowest canopy interception and the highest soil water outflow. The parameter evapotranspiration does not react in a certain direction on the applied harvesting variant, because in this context evaporation includes both canopy and soil evaporation (Figure 56B).

In the model, the growth of the forest stand depends on the availability of mineral nitrogen for plant growth. The plants characteristic by the same photosynthetic assimilation rate can allocate more assimilated carbon if they take up more mineral nitrogen. Thus, we next analysed the model pool of mineral nitrogen considering its utilisation by plants and microorganisms and its loss from the ecosystem due to leaching and/or trace gas volatilisation, i.e. the processes that are simulated by the model. Figure 57 presents the amounts of mineral nitrogen by harvesting scenario for the location Hartberg. The values characterise the status of mineral nitrogen at the end of each year, because this pool strongly depends on seasonal trends and changes within days (Wehrmann et al. 1982). The results shown in this figure present that the SWH plots have the highest amount of mineral nitrogen versus the two other harvesting scenarios.

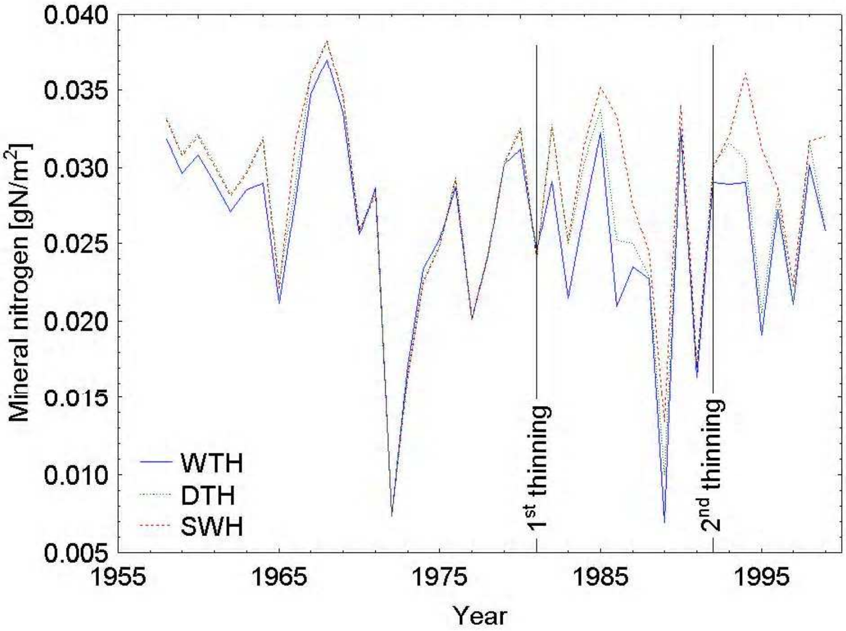

Figure 57: Development of the modelled mineral nitrogen pool for each harvesting scenario (WTH whole tree harvest; DTH delayed tree harvest; SWH commercial stem wood harvest) from the stand establishment until present in Hartberg.

The simulated losses of mineral nitrogen from the forest ecosystem caused by leaching and trace gas volatilisation were found to be higher on the SWH plots than on the WTH or DTH plots (Figure 58).

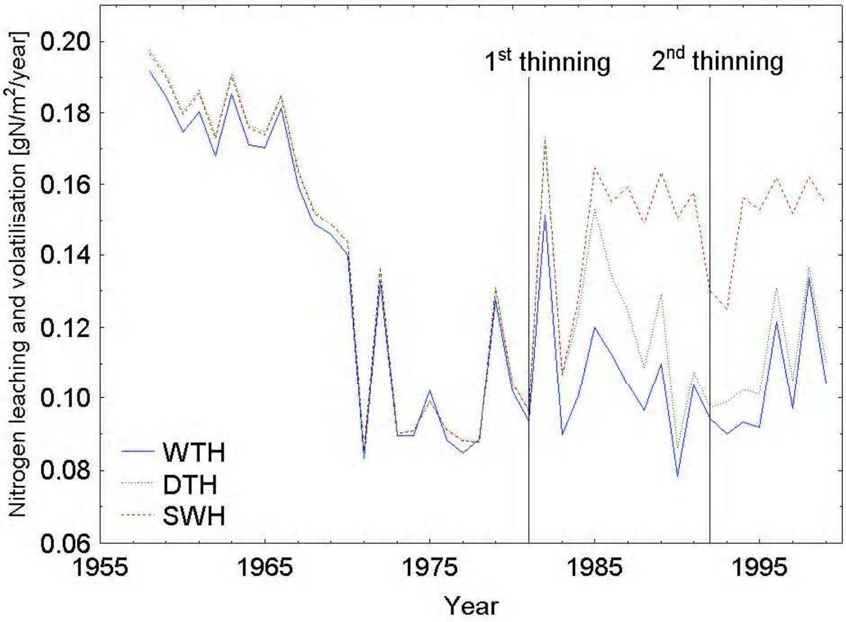

Figure 58: Development of the modelled nitrogen loss due to leaching and volatilisation for each harvesting scenario (WTH whole tree harvest; DTH delayed tree harvest; SWH commercial stem wood harvest) from the stand establishment until present in Hartberg.

In contrast to the amount of mineral nitrogen in the ecosystem, we detected that immediately after the intervention the plants on the SWH plots take up less mineral nitrogen than on the DTH or the WTH plots (Figure 59), whereas the WTH plots are characteristic by the highest plant uptake of

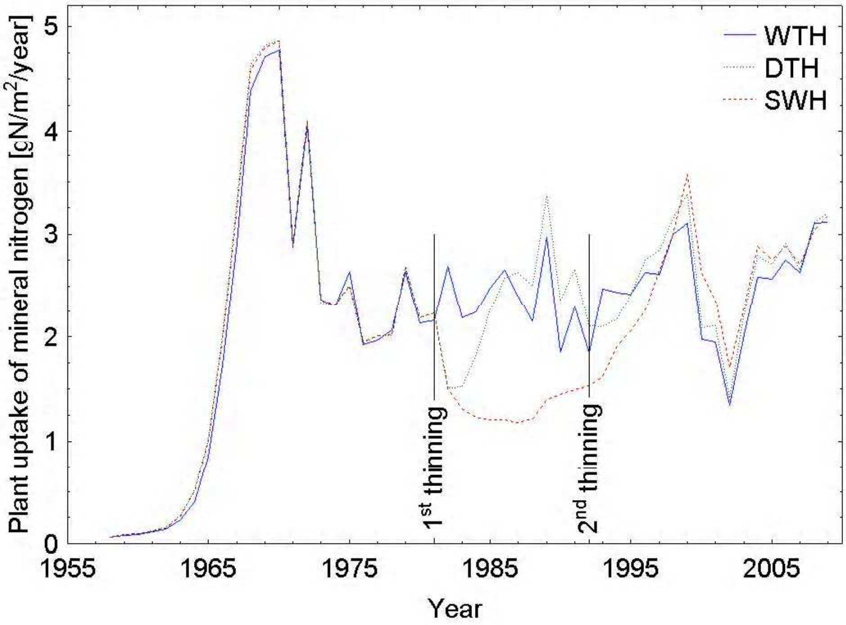

Figure 59: Development of the modelled plant mineral nitrogen uptake for each harvesting scenario (WTH whole tree harvest; DTH delayed tree harvest; SWH commercial stem wood harvest) from the stand establishment until present in Hartberg.

mineral nitrogen. The situation changes over time, when 3 years after the harvesting the DTH plots are the most efficient in nitrogen uptake by plants. The SWH plots slightly overtake the other two harvesting scenarios 14 years after the first thinning. Afterwards, the differences between the scenarios diminish and at the end of the simulation period all three scenarios are identical.

Microbial demand for mineral nitrogen is driven by the amount of material available for decomposition (Recous et al. 1992). Considering this fact, the model response of the microbial population on different harvesting scenarios (see Figure 60) seems to be logical, because the highest nitrogen immobilisation by microorganisms occurs on the SWH plots, on which the highest amount of felled biomass remained after the thinning, whereas on the WTH plots no long-term changes of microbial uptake are detectable because their decomposition pools were left unchanged (Figure 53).

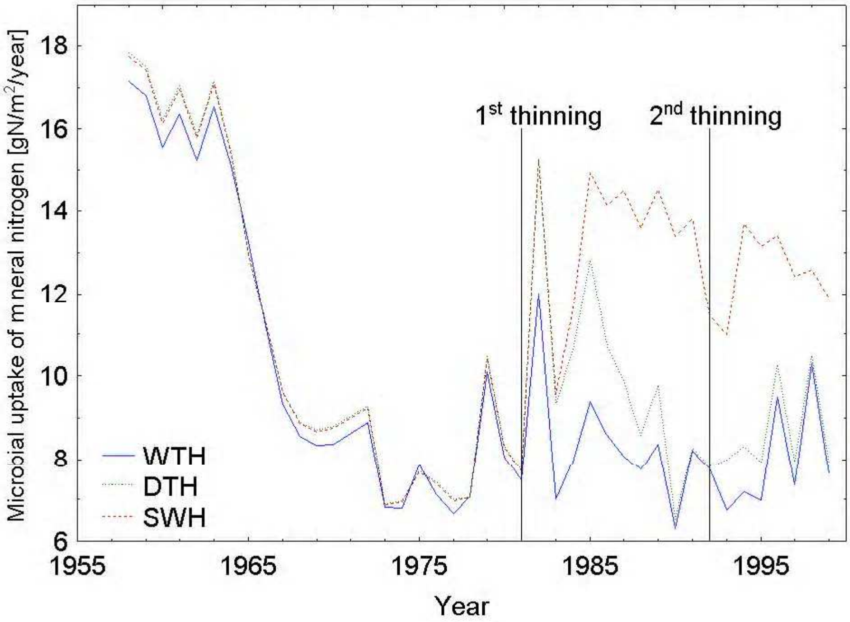

Figure 60: Development of the modelled microbial immobilisation of mineral nitrogen for each harvesting scenario (WTH whole tree harvest; DTH delayed tree harvest; SWH commercial stem wood harvest) from the stand establishment until present in Hartberg.

It is well documented that plants and microorganisms compete for mineral nitrogen in ecosystems (Näsholm et al. 1998, Puri and Ashman 1999). The model also accounts for this competition in the distribution of the mineral nitrogen between them with regard to its available amount in the simulated ecosystem. In case there is enough mineral nitrogen available to meet all the requirements, each dependant obtains what is asked. If, however, the total demand exceeds the mineral nitrogen supply, the particular group gets only the proportion of the available nitrogen according to its supply/demand ratio (see Section 2.1).

Regarding this partition of mineral nitrogen, we also analysed its distribution in the ecosystem. Since this variable strongly depends on seasonal trends and changes within days

(Wehrmann et al. 1982), instead of annual values we calculated annual means of the daily values for each sink (plants, microorganisms, excess, loss due to leaching and trace gas volatilisation), and then expressed them as relative ratios of its daily average content in a particular year. These values represent the proportion of the mineral nitrogen assigned to a particular pool, which means that their sum is always equal to 1. The results of this analysis are presented in Figure 61.

As can be seen from this graph, mineral nitrogen is almost during the whole development of the forest stand in a shortage, because its excess occurred only for about a period of 9 years at the beginning of the forest growth. Due to this fact, the proportion of the mineral nitrogen lost from the ecosystem via leaching and volatilisation is negligible and in the figure not observable. Microorganisms consume during the whole simulation more than 50% of the available mineral nitrogen, and the rest is used by plants. As it was already shown in Figure 59, after the intervention the plants on the SWH plots receive less mineral nitrogen in comparison to the WTH and DTH plots (Figure 61).

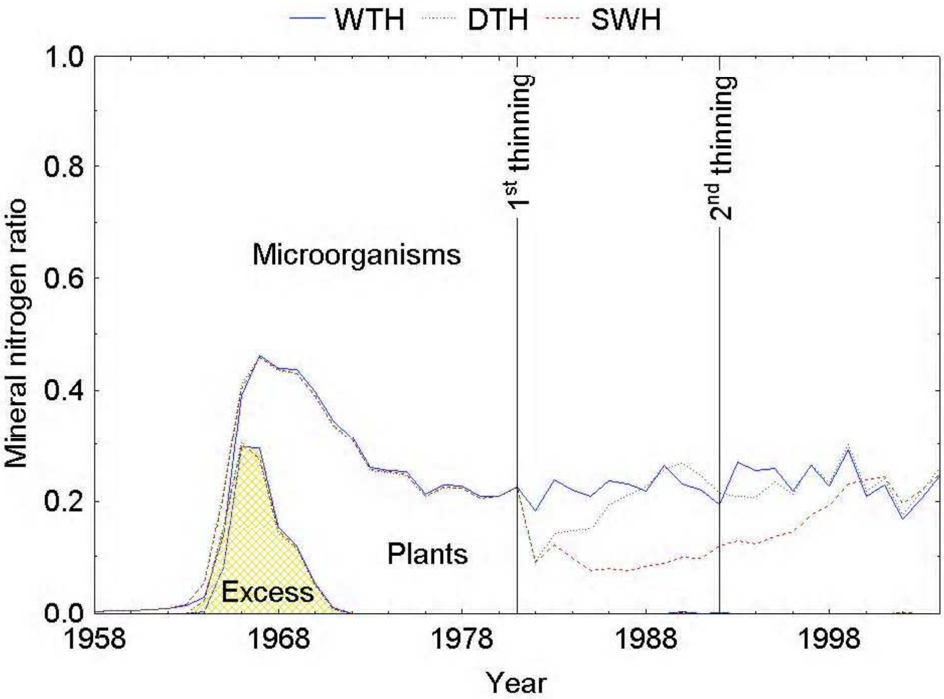

Figure 61: Development of the modelled distribution of mineral nitrogen between microorganisms and plants for each harvesting scenario (WTH whole tree harvest; DTH delayed tree harvest; SWH commercial stem wood harvest) from the stand establishment until present in Hartberg.

Table 35: The summary of the model output for Wilhelmsburg and Hartberg, each harvesting scenario and all analysed variables, whereby C_{litter}, N_{litter}, C_{soil} and N_{soil} are the amounts of carbon and nitrogen in litter and soil, respectively, N_{loss} the loss of mineral nitrogen via leaching and volatilisation, N_{micr} and N_{plant} the microbial and plant uptake of mineral nitrogen, respectively.

Variable	**Harvesting scenario**	**Wilhelmsburg**					**Hartberg**				
		Before 1st thin	1yr after	Before 2nd thin	1yr after	End	Before 1st thin	1yr after	Before 2nd thin	1yr after	End
Year		1980	1983	1992	1994	1998	1980	1983	1992	1994	1999
Growth efficiency	WTH	0.54	0.43	0.39	0.40	0.46	0.44	0.43	0.39	0.39	0.45
	DTH	0.53	0.41	0.40	0.37	0.48	0.44	0.38	0.40	0.38	0.46
	SWH	0.54	0.42	0.40	0.40	0.47	0.44	0.36	0.42	0.42	0.49
LAI	WTH	3.90	4.84	5.24	4.67	5.19	5.99	5.29	5.83	6.02	6.43
	DTH	3.83	4.54	4.99	3.86	4.28	6.07	5.03	3.81	3.94	5.24
	SWH	3.94	4.48	5.25	4.19	4.62	6.08	5.04	5.94	6.07	6.49
Heterotrophic respiration [gC/m^2]	WTH	148	117	141	137	177	198	170	187	176	196
	DTH	149	140	141	172	184	205	224	189	203	204
	SWH	146	126	143	165	193	204	230	257	306	285
C_{litter} [gC/m^2]	WTH	77	151	238	205	165	320	340	327	276	257
	DTH	78	215	215	312	158	334	574	287	336	251
	SWH	75	188	234	295	194	332	703	557	478	235
N_{litter} [gN/m^2]	WTH	0.46	1.22	1.97	1.77	1.36	2.49	2.87	2.59	2.22	2.09
	DTH	0.47	1.77	1.79	2.84	1.34	2.60	4.70	2.27	2.71	2.06
	SWH	0.45	1.60	1.88	2.72	1.51	2.59	5.03	3.00	2.67	1.40
C_{soil} [gC/m^2]	WTH	4566	4527	4483	4471	4443	6632	6621	6576	6556	6516
	DTH	4602	4587	4534	4552	4532	6948	6973	6920	6916	6870
	SWH	4490	4469	4431	4449	4437	6912	6939	6981	6981	6936
N_{soil} [gN/m^2]	WTH	456	452	447	446	443	662	661	656	654	650
	DTH	460	458	452	454	452	693	696	691	690	686
	SWH	448	446	442	444	443	690	692	697	697	692
N_{loss} [gN/m^2/year]	WTH	0.09	0.06	0.07	0.07	0.09	0.10	0.09	0.09	0.09	0.10
	DTH	0.09	0.07	0.07	0.09	0.10	0.10	0.11	0.10	0.10	0.11
	SWH	0.09	0.07	0.07	0.08	0.10	0.10	0.11	0.13	0.16	0.15
N_{micr} [gN/m^2/year]	WTH	5.34	4.55	5.74	5.58	7.00	8.06	7.01	7.74	7.17	7.63
	DTH	5.36	5.67	5.67	7.14	7.46	8.33	9.34	7.81	8.33	7.92
	SWH	5.25	5.06	5.81	6.92	8.00	8.30	9.57	11.44	13.69	11.91
N_{plant} [gN/m^2/year]	WTH	3.11	2.14	1.64	1.91	2.53	2.14	2.19	1.85	2.44	3.11
	DTH	3.12	1.78	1.77	1.46	2.68	2.19	1.52	2.11	2.18	3.39
	SWH	3.09	1.93	1.66	1.61	2.27	2.18	1.31	1.53	1.92	3.57
Canopy interception [mm/year]	WTH	199	220	296	259	318	336	253	342	348	412
	DTH	195	207	281	214	261	341	234	223	228	327
	SWH	202	206	297	231	281	341	235	346	347	414
Evapotranspiration [mm/year]	WTH	305	324	319	327	349	351	355	316	382	423
	DTH	303	326	320	332	333	354	369	357	407	429
	SWH	306	332	319	334	338	354	368	317	389	427
Outflow [mm/year]	WTH	268	95	93	122	143	105	44	63	18	16
	DTH	272	97	104	158	215	92	46	138	92	73
	SWH	265	100	94	143	193	92	45	53	18	16
Water balance [mm/year]	WTH	19.86	-30.3	-4.84	-0.79	12.58	-3.66	-29.6	1.28	-12.9	-25.3
	DTH	19.95	-26.6	-4.97	0.43	12.60	1.78	-27.2	1.26	-17.8	-31.7
	SWH	19.74	-23.3	-4.56	1.06	11.98	1.70	-26.3	1.78	8.71	-4.17

Table 36: The summary of the model output for Bad Zell Grillnberger and Kern, each harvesting scenario and all analysed variables, whereby C_{litter}, N_{litter}, C_{soil} and N_{soil} are the amounts of carbon and nitrogen in litter and soil, respectively, N_{loss} the loss of mineral nitrogen via leaching and volatilisation, N_{micr} and N_{plant} the microbial and plant uptake of mineral nitrogen, respectively.

Variable	**Harvesting scenario**	**Bad Zell Grillnberger**					**Bad Zell Kern**				
		Before 1st thin	1 yr after	Before 2nd thin	1yr after	End	Before 1st thin	1yr after	Before 2nd thin	1yr after	End
Year		1980	1985	1992	1994	2002	1980	1985	1996	1998	2002
Growth efficiency	WTH	0.48	0.46	0.41	0.41	0.44	0.65	0.50	0.49	0.40	0.44
	DTH	0.48	0.44	0.42	0.39	0.45	0.65	0.49	0.49	0.41	0.46
	SWH	0.48	0.42	0.42	0.39	0.46	0.65	0.49	0.49	0.41	0.44
LAI	WTH	6.62	6.93	6.76	6.43	7.62	2.18	6.31	6.75	7.50	7.27
	DTH	6.64	6.47	5.46	4.98	6.56	1.95	5.75	6.33	6.65	6.61
	SWH	6.59	6.43	6.57	5.52	7.60	2.18	5.91	6.82	6.21	6.71
Heterotrophic respiration [gC/m^2]	WTH	208	214	234	195	252	219	217	252	196	245
	DTH	208	259	231	238	249	219	246	251	253	249
	SWH	209	269	276	254	289	214	253	259	224	261
C_{litter} [gC/m^2]	WTH	216	281	317	241	238	58	141	207	173	197
	DTH	215	383	297	390	204	58	174	197	272	179
	SWH	218	480	522	516	273	56	190	228	243	228
N_{litter} [gN/m^2]	WTH	1.61	2.43	2.60	2.01	2.01	0.20	1.06	1.69	1.46	1.67
	DTH	1.61	3.39	2.44	3.43	1.73	0.20	1.41	1.62	2.47	1.52
	SWH	1.63	3.72	3.35	3.58	1.88	0.18	1.38	1.73	2.01	1.78
C_{soil} [gC/m^2]	WTH	9859	9812	9779	9747	9660	8892	8705	8631	8591	8569
	DTH	9811	9794	9753	9766	9660	8891	8733	8645	8649	8616
	SWH	9930	9917	9924	9932	9867	8656	8493	8426	8412	8395
N_{soil} [gN/m^2]	WTH	984	980	976	973	964	888	869	862	858	855
	DTH	979	977	973	975	964	888	872	863	863	860
	SWH	991	990	990	991	985	865	848	841	840	838
N_{loss} [gN/m^2/year]	WTH	0.11	0.12	0.12	0.11	0.13	0.16	0.13	0.14	0.11	0.13
	DTH	0.11	0.13	0.12	0.12	0.14	0.16	0.14	0.14	0.13	0.14
	SWH	0.11	0.13	0.14	0.13	0.16	0.15	0.14	0.14	0.12	0.14
N_{micr} [gN/m^2/year]	WTH	8.07	8.53	9.62	7.96	10.00	7.00	8.23	9.94	7.86	9.79
	DTH	8.07	10.54	9.53	10.01	9.77	7.00	9.77	9.85	10.50	10.08
	SWH	8.12	10.95	11.81	11.01	11.99	6.79	10.11	10.43	9.26	10.70
N_{plant} [gN/m^2/year]	WTH	3.00	3.08	2.30	2.68	3.19	3.74	4.00	3.53	2.82	3.02
	DTH	2.98	2.61	2.44	2.09	3.50	3.74	3.72	3.62	2.61	3.27
	SWH	3.00	2.28	1.82	1.88	3.15	3.39	3.46	3.29	2.64	2.78
Canopy interception [mm/year]	WTH	355	446	440	385	530	94	389	456	530	504
	DTH	356	417	356	301	453	84	360	427	470	458
	SWH	354	417	428	334	527	94	369	460	439	462
Evapotranspiration [mm/year]	WTH	304	363	301	307	311	243	375	341	323	297
	DTH	304	384	343	346	335	234	371	344	349	306
	SWH	302	383	306	330	310	243	377	340	366	309
Outflow [mm/year]	WTH	104	75	119	82	113	415	150	168	44	148
	DTH	104	86	160	119	164	435	190	192	77	185
	SWH	106	91	127	105	118	415	172	165	91	178
Water balance [mm/year]	WTH	32.77	36.36	-25.94	7.42	0.14	41.54	3.36	-4.01	19.97	0.31
	DTH	34.24	30.77	-25.91	12.06	-0.45	41.63	-0.11	-4.13	19.78	0.47
	SWH	32.42	33.51	-24.99	13.72	0.90	40.89	-2.29	-3.57	19.86	0.47

4. DISCUSSION

4.1 DISCUSSION OF RESULTS FROM SIMULATIONS OF VIRGIN FORESTS

The validation of the spinup procedure performed in the first part of this study revealed that for the correct simulation of the undisturbed forest ecosystems in Central Europe the temporal changes in the development of the forest stand, that achieved its long-term steady state, should be taken into account. We incorporated this temporal dynamics into the model BIOME-BGC through a new dynamic mortality sub-model. The results summarised in Figure 25 and Tables 15 and 16 document the improvements achieved after the implementation of the dynamic mortality into the model structure. With this new version of the model we do not only obtain improved predictions of the forest ecosystem status, but it also allows us to simulate its temporal development changes due to senescence and competition and thus, to account for the different development stages of virgin forests (Tables 18 and 19). The simulation of this temporal dynamics was not possible with the original version of the model BIOME-BGC, because the mortality rate was held constant during the whole simulation process.

Unlike the simulations with the original model set up (regular mortality 0.5% per year + fire mortality) or with the constant mortality rates 0.5% and 2% per year, the simulations with the dynamic mortality produced on average unbiased estimates of stand volume and carbon content in soil in both virgin forests (Tables 15 and 16). However, although the average predictions of stand volume and soil carbon are not statistically significantly different from the observations, the regression analysis detected that all linear regressions between the predicted and observed values except the one for stand volume in Rothwald deviate significantly from the ideal relationship y=x (Table 21).

In Babia hora the calculated regression of stand volume differs from 1:1 line (Figure 27) most probably due to the type of the climate interpolation used for this location, because climate is the main driving force of the model behaviour. As it was said in Section 2.3.3, climate was interpolated using two different models DAYMET and MT-CLIM. DAYMET, used in Rothwald, can be regarded as a more accurate model, because it uses information from several surrounding climate stations, while MT-CLIM, applied in Babia hora, estimates the climate of the particular point of interest from one nearby station. This means that although both models presume the linear relation of a particular climate parameter (e.g. temperature) to elevation, in case of DAYMET this regression is calculated daily from multiple measurements, whereas in MT-CLIM a fixed gradient is used for all plots and all days. If the altitude range is large, but the temperature and precipitation gradients are derived from single site measurements, as it is in the case of Babia hora (see Section 2.3.3), we can expect that the model predictions will be best at the elevation of site climate measurement. The results of the residual analysis shown in Figure 34 and Table 23 confirm the given hypothesis, since the model produces the best output for the elevation close to that one, where the field measurements of precipitation were made (i.e. 1,320 m above sea level), based on which the precipitation lapse rate was derived.

Moreover, DAYMET also accounts for the horizontal distance between a particular climate station and a point of interest, which is used for the estimation of station's weight in interpolation. On the contrary, MT-CLIM extrapolates the climate variables only in a vertical direction. This makes this model inappropriate for climate extrapolations on sites that are horizontally distant from the base station. In our case, the horizontal distance between the climate station Rabča and the Babia hora sample plots was in average 7 - 7.5 km.

Low correlations between the observed and predicted amount of carbon in soil (Table 20), as well as the significance of the linear regressions calculated between them (Table 21, Figure 31) can be explained by the difference in the variation of the modelled and observed values. Simulated soil carbon appears to vary 2-3 times less than its field measurements (Table 15, Figure 31). We presume this is caused by two factors: (1) the model simplifies the ecosystem situation, since in the model soil is considered to be homogeneous, and the temporal changes occur over the whole modelled area with the same intensity, (2) in reality soil characteristics vary greatly in space. Taking into account the variation of carbon amount within each plot we found that in Rothwald out of 18 plots 15 predictions of carbon amount in the soil are within the 95% probability range of the observations (Figure 32). From the three cases, for which the model predictions lie outside the 95% probability range of the observed mean, only one difference (plot RO) is really distinct. The nutrient amounts measured on this plot are in fact not representative, because the soil samples were taken only from the upper soil horizon up to 7 cm depth. Moreover, the probability range was calculated only from the two values obtained from the two mixed samples. Therefore, we can presume that the actual values of carbon amount in soil would exceed the values obtained from the measurements on this plot. This analysis documents the importance of the information about the fluctuation of the examined litter and soil characteristics in the field for the validation of the model performance

The amount of coarse woody debris was correctly predicted only in Babia hora. In Rothwald its amount is systematically underestimated (Tables 15 and 16, Figure 28), which is, according to our assumption, caused by frequent wind-throws in this region during the 2nd half of the last century (in the years 1966, 1976 and 1990; Neumann 1978, Schrempf 1985, Splechtna 2003 pers.

communication). The repeated occurrence of wind-throws within a relatively short time resulted in an large accumulation of dead wood on the plots also when compared with other central European virgin forests of similar species composition (e.g. Korpeľ 1997, Saniga 1999, Jaworski and Paluch 2001, Vrška et al. 2001a, 2001b, 2001c). In our simulations we did not account for the wind-throws, therefore this underestimation of coarse woody debris in Rothwald was expected.

In addition, since in Rothwald only the amount of lying dead wood on the whole permanent sample plot (100 x 100 m or 100 x 20 m) was recorded with no exact position (i.e. with X, Y coordinates) of individual pieces, the "observed" amount of lying dead wood on the analysed 20 x 20 m plots does not necessarily have to correspond with the real situation on the plot. This means that the quasi observed amount of coarse woody debris per simulated plot is charged with the error from the measurement technique of an unknown magnitude.

Both litter characteristics, i.e. carbon and nitrogen amount in litter, are on average underestimated by the model (Tables 15 and 16). We presume that this underestimation results from the different understanding of litter in the model and field measurements. While in the model litter encompasses dead leaf and fine root biomass and defragmented dead wood, in reality litter comprises also other kinds of dead organic material, e.g. small twigs, pieces of bark, buds, flowers, etc., which can make up 20 to 40% of the dry mass of litter (Šály 1991).

Moreover, the results shown in Figures 29 and 30 indicate that the underestimation is much larger in Babia hora than in Rothwald. This is caused by the fact that the two virgin forests differ significantly in the absolute measured values of carbon and nitrogen content in the litter (e.g. average values of carbon in the litter are 0.952 versus 5.139 kgC/m^2 for Rothwald and Babia hora, respectively), whereas the model produces more similar values for both locations (Table 15). The large difference in the observed carbon in the litter between the two locations results probably from the different species composition. Spruce forests are known to accumulate more organic material on the forest floor than beech or mixed spruce-beech forests (Glatzel et al. 2000, Neubauer 2000, 2002, Berger 2001, Berger et al. 2002), which corresponds with the measured values of carbon and nitrogen in the litter in the two virgin forests used in this analysis.

However, if we compare the absolute modelled values of carbon in the litter obtained in Babia hora and Rothwald, we see that a higher amount of litter carbon is accumulated in Rothwald, where beech prevails (Table 15). This contradicts the observations in the field as well as the findings of the mentioned authors. The assumption that the model performance is caused by the differences in site and climate conditions between the two forests does not hold, because higher carbon content in the litter was also simulated for the Rothwald virgin forest with beech settings than when using the spruce parameterisation (Section 3.1.8, Table 30). Therefore, it is probable that other factors, e.g. phenology or decomposition processes, should be re-evaluated. Since no data with the necessary information had been collected within our experiment, it was impossible for us to define the real cause and change the model parameters or the model inner structure.

The underestimation of nitrogen in the litter is possibly coupled with the overestimation of nitrogen in soil (Figure 32). If this is true, then the simulated movement of nitrogen from litter to soil is faster than in reality. Similarly to the carbon content in the litter, litter nitrogen is much more underestimated in Babia hora than in Rothwald (in Babia hora by approximately a factor 100, whereas in Rothwald by a factor 10). Here also, this difference is caused by the great difference in the observed values between the two virgin forests rather than the differences in model predictions (see Table 15). The high nitrogen values in the litter of Babia hora can also be due to a higher nitrogen deposition in this region before 1989, since this mountain is surrounded from the north and west by the former large industrial regions of Eastern Europe (Katowice, Ostrava etc.). Since no exact values of industrial deposition are known for the time period prior to 1989, this fact could not have been taken into consideration in the simulations.

Nevertheless, as for carbon in the litter an opposite relationship can be observed in the model output of litter nitrogen as in nature. While nitrogen in the litter is in reality higher in Babia hora than in Rothwald, i.e. spruce forest, the model produces a higher amount of nitrogen in Rothwald with a higher proportion of beech, which contradicts not only with our data, but also with the comparisons of spruce and beech or mixed spruce-beech forests made in the field by other authors on comparable sites (Glatzel et al. 2000, Neubauer 2000, 2002, Berger 2001, Berger et al. 2002).

A more detailed examination of this result was performed in Section 3.1.8, where we compared the simulations of Rothwald plots using the spruce and beech ecophysiological settings. From the simulation results presented in Table 30 we can see that under the same climate and soil conditions, beech forests tend to accumulate more carbon and nitrogen than spruce forests both in the aboveground plant biomass as well as in the litter and soil pools. This result is quite surprising since beech forests are generally known to produce less woody biomass than spruce (Šebík and Polák 1990). Also the cycle of the nutrients is believed to be faster in beech forests than in spruce stands, which are characterised as the forests with slower decomposition processes and thus a higher accumulation of carbon and nitrogen in litter and soil (Glatzel et al. 2000, Neubauer 2000, 2002, Berger 2001, Berger et al. 2002). However, these statements are derived from the comparison of the ecosystems situated in different conditions or outside the natural distribution of one species, usually spruce, where this species was introduced in the past. Although the results of the model do not correspond with our expectations and the information obtained from literature, the evaluation of the model behaviour with respect to the two tree species was not possible due to the lack of data.

The implementation of the dynamic mortality into the model resulted in the dynamic performance of other ecosystem variables as shown in Section 3.1.7.4. Although the simulated response of stand volume to a changing mortality rate is plausible (Figure 22), its temporal development does not coincide with the published curves in e.g. Korpeľ (1995). From the modelled results we can see that for approximately 100 years the simulated forest stand exhibits a very low stand volume with a very small annual increment (Figure 22). On the other hand, coarse woody debris has very fast dynamics with one very distinct peak over the development cycle. After reaching this peak, the simulated carbon amount in coarse woody debris is reduced by more than 50% in about 70 years. This suggests its faster decomposition in the model than in reality, because e.g. Holeksa (2001) reported that in Babia hora the decomposition of dead wood lasts approximately 150 years.

However, since our data do not comprise the repeated measurements, it was not possible to validate the simulated dynamics against the observations. We can presume that a simplified description of some processes in the model can cause deviations in the model output compared to reality. For example, it is possible that mortality develops in another way as currently implemented in the model. Though several publications reported the U-form of mortality in virgin forests (Harcombe 1987, Peterken 1996, Monserud and Sterba 1999, Lorimer et al. 2001), it is not clear if the temporal change of mortality follows the trajectory of multiple Us or rather the sine waves or a completely different trajectory. In the development of our mortality model, we assumed that the mortality dynamics corresponds more or less with the waves of stand volume presented in the publications about virgin forests (e.g. Korpeľ 1995).

Another possibility can be that the actual dynamics of natural forests differs from the current theoretical concepts. In fact, the longest time series from undisturbed forest ecosystems in Central Europe cover 30 to 50 years (Saniga 1999, Saniga and Schütz 2001a, 2001b), which is too short to evaluate these concepts. The long-term measurements can help us to understand both the natural dynamics as well as the model responses and consequently to enhance our knowledge about nature and to explain the model behaviour.

In addition, it should not be omitted that the proposed dynamic model of mortality is entirely an explicit formulation of the assumed mortality dynamics in the ecosystem driven by the constants: length of development cycle, minimum and maximum mortality rate; rather than by the ecophysiological status of the modelled ecosystem. Since the model, into which this mortality simulation is implemented, belongs to biogeochemical models, it would be more suitable to simulate mortality rate in dependence to the physiological processes. However, the inner driving processes leading to tree death are not well known (Hawkes 2000). Therefore, a proper process-based approach is rather rare in gap or mechanistic models (Mäkelä 2003), which usually use simple empirical assumptions of the mortality. Those mechanistic mortality algorithms that were developed and implemented in the process models, e.g. Mäkelä and Hari (1986), do not seem to work well (Hawkes 2000, Mäkelä 2003).

As already mentioned, with the current dynamic mortality the model BIOME-BGC is able to simulate only the so called small development cycle driven mainly by competition and senescence. However, a "large" development cycle caused by large-scale disturbances, e.g. fire, wind-throw, insect outbreak etc., also occurs in nature. Unlike fire, the two latter catastrophic events are quite frequent in Central Europe, mainly in the several last decades. Therefore, it would be desirable to implement the simulations of such catastrophic events into the model.

In spite of all the stated uncertainties, constraints and questions for future research, the presented results showed that using the new dynamic mortality model we can obtain reasonable initial values of simulated forest ecosystems, which correspond with the equilibrium that can be observed in undisturbed forest ecosystems of Central Europe. This is a significant improvement of the model, because, as our analysis showed, the spinup procedure using the original constant regular mortality produced an output, that did not coincide with the observations from virgin forests. Hence, after the incorporation of the dynamic mortality into the model BIOME-BGC, this model can provide the user with the important information about the natural potential of a particular locality under certain climate conditions.

4.2 DISCUSSION OF RESULTS FROM SIMULATIONS OF MANAGED FORESTS

The results of the second part of the study, in which we tested the applicability of the mechanistic model for the assessment of the influence of biomass removal from the forest stands showed that the model is sensitive to the applied harvesting scenario. The different harvesting scenarios affected the growth of the remaining stand as they influence the availability of nutrients, water and energy for plant uptake. However, the immediate growth response of the forest ecosystem contradicted with the observed reactions, according to which the sites with the highest amount of biomass left in the forests, i.e. the SWH plots, have the highest basal area and volume increments (see Sterba 1988). On the contrary, our results revealed that immediately after the first thinning the WTH plots exhibited a better growth in comparison to the SWH plots, since their relative stand volume increments as well as growth efficiency are higher than for the SWH variant (Figure 49 and 50, Tables 34, 35 and 36). This trend lasted for about 8 to 10 years, after which a shift in the model reactions could be observed (Figure 49 and 50).

Therefore, we next analysed several model output variables, that describe the simulated water, energy, carbon and nitrogen cycles, to reveal the cause of these unexpected model reactions. We found that the changes of carbon and nitrogen content in the litter and soil, the amount of mineral nitrogen in the ecosystem, its loss from the ecosystem due to leaching and volatilisation, microbial immobilisation of mineral nitrogen and heterotrophic respiration are consistent with our expectations based on the logical evaluation and literature review.

The analysis of the litter and soil characteristics revealed that the temporal effect of harvesting lasts much longer on the soil parameters than on the litter pools (Figures 53 and 54). While in litter the great differences, that occur between the scenarios immediately after the 1st thinning, quickly diminish with time and approximately 10 years after the first thinning are not detectable any longer, the soil parameters of the particular harvesting scenarios differ during the whole examined period, i.e. approximately 20 years after the 1st intervention, which is a pattern well corresponding with the findings from field observations (Krapfenbauer 1983, Olsson et al. 1996).

Moreover, Figures 53 and 54 suggest that the time necessary for reaching a new stable level of these pools depends not only on the amount of the added biomass to the litter pools, but also on its character. After the sole addition of leaf mass, carbon and nitrogen in the litter reach the pre-intervention values twice as fast as if also the slower decomposable wood biomass was left in the forest (Figure 53). This performance corresponds with the field observations, which confirmed the long-term beneficial fertilising effect of the coarse woody debris for the stand development (Aber et al. 1978, Laiho and Prescott 1999, Rouvinen et al. 2002).

Microbial activity, expressed as the amount of the mineral nitrogen immobilised by microorganisms and the amount of carbon expired by them (i.e. heterotrophic respiration), was found to be the highest on the SWH plots characteristic by the largest amount of biomass left in the forest after thinning (Figures 55 and 60). These reactions were expected since it is known that the activity of microorganisms and consequently their demand for mineral nitrogen rises with the increasing amount of decomposable material (Recous et al. 1992, Zimmermann and Frey 2002).

Similarly, the model patterns of nitrogen loss by leaching and volatilisation are consistent with the findings by Ågren and Bosatta (1988), Aber (1992), McNulty et al. (1996), Olsson et al. (1996) and Aber et al. (1998) showing that nitrogen losses due to these processes increase with the amount of mineral nitrogen stored in the ecosystem (compare Figures 57 and 58).

In the rest of the variables, the analysis revealed unexpected responses of the simulated forest ecosystem to the different harvesting scenarios when compared with the field observations reported by Sterba (1988) and Arzl (1991). From their analysis of the growth reactions of the plots they concluded that the detected differences in volume growth correspond with the differences in the nutritional status of the remaining trees immediately after thinning and three years later, which was determined by investigating the element concentration of the top whorl of the remaining trees. The lowest increments were evident on the WTH plots with the lowest nutrient content in the top whorl. These differences are assumed to be the result of the differing input of nutrients to the forest floor resulting from the varying amounts of slash and leaves left in the forest by one of the three harvesting scenarios (Sterba 1988).

Therefore, we expected that the SWH plots with the largest amount of biomass left on site would have a higher leaf area and would be the most efficient in the uptake of mineral nitrogen. However, our results showed the opposite pattern. After the intervention, the SWH plots are characteristic by the smallest and the WTH plots by the highest leaf area index LAI (Figure 51). Considering the model structure, these results explain the lower simulated growth of the SWH plots, since the photosynthetic assimilation depends on the canopy leaf area. The smaller available leaf area results in the lower absorption of the photosynthetically active radiation (Figure 52) and thus, in the lower simulated plant growth. The lower leaf area of the SWH plots also explains the lower canopy interception and the higher soil water outflow from these plots when compared with the other two harvesting scenarios (Figures 56A and 56C). These results suggest that the utilisation of radiation, water cycle and the net carbon fixation are simulated in the model correctly, since their reactions to lower LAI are logical.

Hence, the question is, why on the SWH plots the leaf area is the lowest, when these plots have the highest amount of nutrients coming from the biomass left in the forest stand after the intervention. In the model, the growth of the leaf area is driven by the availability of the mineral nitrogen for plant growth. Our hypothesis that after the intervention the plants on SWH plots take up less mineral nitrogen than on the WTH or the DTH plots was confirmed by the analysis of plant nitrogen uptake (Figure 59).

Nevertheless, this finding was surprising, because the SWH plots are characteristic by more nutrients stored in the litter and soil compartments, i.e. in the potential sources of the mineral nitrogen (Figure 53), as well by the higher absolute amount of the mineral nitrogen itself (Figure 57) than the two other scenarios. Therefore, the simulated plant uptake on the SWH plots could be negatively affected only by other competing mechanisms utilising mineral nitrogen, namely nitrogen loss via leaching and trace gas volatilisation, and microbial immobilisation.

Although the losses caused by leaching and volatilisation were found to be higher on the SWH plots than on the WTH or the DTH plots (Figure 58), these processes could not cause the reduction of plant mineral nitrogen uptake, because they are in the model activated only if there is an excess of mineral nitrogen in the ecosystem after the plant and microbial demands are satisfied. Thus, microbial immobilisation of mineral nitrogen is most probably the reason why the plants on the SWH plots with the largest nutrient pools receive less mineral nitrogen than those on the DTH or WTH plots. In spite of this assumption, higher microbial uptake of the mineral nitrogen on the plots with more biomass left on site, i.e. on the SWH plots, does not have to mean that microorganisms negatively effect the plant nourishment. In fact, such a response could be expected, since in general microbial demand for nitrogen depends on the amount of material available for decomposition (Recous et al. 1992).

Due to this, we analysed the relative proportions of the mineral nitrogen utilised by each consumer as shown in Figure 61. This graph confirms the assumption that the lower mineral nitrogen plant uptake on SWH plots versus WTH and DTH really results from the simulated competition of plants with microbial population for the mineral nitrogen (see Section 2.1 for details). The competition algorithm can work well in stable ecosystems, but problems arise when any abrupt interference of the ecosystem, such as thinning or wind throw, is simulated, because the population density of the microorganisms is in the model defined by the amount of available decomposition material. This means that the model microbial population reacts to the improved living conditions immediately, which causes a prompt shift in the mineral nitrogen utilisation between microorganisms and plants with microorganisms taking an advantage from the changed situation in ecosystem.

Although microorganisms are known to be more competitive for the mineral nitrogen than plants (Puri and Ashman 1999, Zechmeister-Boltenstern 2001, Stark and Hart 2003), their immediate response in the model to the changes due to thinning and post-thinning operations seems to be improbable (Figure 60), because microbial colonisation processes may last several weeks to some months. For example, Hasewaga and Takeda (1996) observed nitrogen immobilisation in pine needle litter only 3 months after its placement in the forest.

Based on the current knowledge that tree growth is affected by nitrogen supply (Merilä 2002), we presume that the discrepancy of the model growth reactions documented by relative stand volume increments (Figure 49 and Table 34) results from the presented differences in plant nitrogen uptake between the three harvesting scenarios. However, since for our plots no measurements of soil processes and soil microbial activity exist, it is not possible to examine the obtained model reactions and explain their possible deviations from reality. If our hypothesis that the plants actually take more mineral nitrogen than they receive in the model is correct, there may be a number of other explanations, why this happens. For example, according to Hasewaga and Takeda (1996), the first changes of nitrogen mass in the litter are caused by leaching from the litter, the process currently not included in the model. Additionally, the existence of mycorrhizal symbiosis between plant roots and fungi allowing higher nutrient uptake of trees (Tamm 1991, Paul and Clark 1996) is also not addressed in the model structure. This relation can play an important role in the ecosystem, since fungal associations make organic nitrogen available for plants (Kirschbaum and Paul 2002). Moreover, Chapin et al. (1993) and Näsholm et al. (1998) reported for boreal forests and tundra that even non - mycorrhizal plants are able to utilise organic sources of nitrogen. Other authors, e.g. Lipson et al. (1999), suggest the existence of seasonal differences in the nitrogen demand between plants and microorganisms, with plants taking up nitrogen in the vegetative growth periods while microorganisms are more important during the rest of the year. Since the works dealing with the nitrogen uptake are often controversial, further research is needed to identify the complex interactions between plants and microbial population, their dynamics and seasonal variations.

The presented results suggest that the model requires some changes in order to be able to adequately assess the growth processes of the forest stands affected by different management scenarios. Although the long-term model behaviour corresponds with the field observations, short-term reactions of the model on the disturbance can be misleading. The model is apparently able to simulate ecosystems in stable conditions, but for a correct reproduction of short-term responses on external influences, such as thinning followed by harvest, the model description of the processes seems to be oversimplified. Therefore, further research to enhance the model behaviour in such conditions is needed.

5. SUMMARY AND CONCLUSION

The main goal of the presented work was to evaluate if a biogeochemical modelling environment is an appropriate tool to assess the sustainability of forest ecosystems and forest management. In the study we used a species-specific adaptation of the biogeochemical model BIOME-BGC (Pietsch and Hasenauer 2004). The analysis was based on the underlying assumption that the model adequately simulates the growth processes in a forest.

The work is divided into two major parts. In the first part we evaluated the self-initialisation procedure, the so called spinup run, which was developed in order to estimate the necessary initial information about the forest stand for its further simulation with the model BIOME-BGC (Thornton et al. 2002). This procedure brings the modelled ecosystem into dynamic equilibrium. In Central Europe, the virgin forests represent a steady state that is achievable in nature. Therefore, the validation of the procedure was performed against the data collected in the two virgin forests: Rothwald, Austria, and Babia hora, Slovakia.

The level at which the modelled steady state is reached depends on several parameters. Our analyses revealed that apart from the climate and site conditions, mortality rate is an important influencing factor. As the results showed, the original self-initialisation of the model produced unrealistic values of the examined variables for the conditions in Central Europe, unless the fire mortality was switched on. Stand volume, carbon and nitrogen amounts in the soil, and in the case of Babia hora also the amount of coarse woody debris, were highly overestimated. Since fire is not considered to be an important factor for driving the forest dynamics in Central Europe (Goldammer and Page 2000), it was required from the model to produce reasonable output of the self-initialisation for these conditions also when fire mortality is set to zero.

First, we tried to achieve improved results by increasing the regular whole plant mortality (i.e. the mortality caused by competition and senescence) rate from the original value 0.5% per year to 2% per annum, which resembles an upper border of the mortality in natural mature ecosystems as suggested by Little (1995). Although this increase of the annual whole plant mortality improved the results of the simulated stand volume considerably, it did not have a desired effect on the carbon and nitrogen contents in the soil. We presumed that the overestimation of soil parameters is caused by not accounting for the succession dynamics of natural forests, i.e. the shift of the individual development stages: stage of growth – maturity – breakdown according to Korpeľ (1995). This was confirmed after we incorporated the new dynamic mortality model. In contrast to the original regular mortality model, which was based on the assumption of constant mortality rate per annum, the mortality in the new model fluctuates between the pre-defined maximum and minimum mortality rates on the elliptic trajectory. The length of one development cycle is also pre-defined and depends on the tree species.

Using this new dynamic mortality we obtained improved modelled values not only for stand volume, but also for the soil characteristics. From the results we can conclude that with this dynamic mortality the model is suitable for the simulation of virgin forests following the small development cycle. After the implementation of the dynamic mortality, the spinup procedure produces the steady state that corresponds with the equilibrium observable in Central European virgin forests. This is a significant improvement in the model behaviour, which can now provide us with information about the natural potential of a particular site under certain climate conditions. Such information can enhance our understanding of ecosystem sustainability. It also enables us to analyse the current status of an examined managed ecosystem with regard to its natural potential.

As can be seen, this study uncovered new possibilities for the utilisation of biogeochemical models. However, it also revealed several questions for future research. For example, it would be desired to analyse the physiological processes causing tree death, which could lead to the development of a physiologically-based mortality model. Long-term measurements from virgin forests would enhance our knowledge about the temporal performance of stand volume, mortality or other parameters in natural ecosystems. Such information could help us to understand both the natural dynamics as well as the model responses, and consequently to explain the model behaviour and if necessary suggest its improvements.

In spite of the stated uncertainties, the presented results showed that with the new dynamic mortality model we obtain initial values observable in reality that can be used for further simulations of the forest management stands.

In the second part of this work, we verified the applicability of the mechanistic modelling theory for evaluating the long-term impacts of management decisions on ecosystem. For this task we used the data from three management sites situated around Austria: Hartberg, Bad Zell and Wilhelmsburg, on which the influence of three different harvesting scenarios on the remaining forest stand applied after the thinning operations was tested. The examined harvesting scenarios included: WTH = whole tree harvest, where all felled aboveground biomass had been removed from the forest, i.e. stem, crown and leaves, DTH = delayed tree harvest meaning that the whole aboveground woody biomass was extracted from the forest 1 year after the thinning in order to leave the leaves on site, and SWH = commercial stem wood harvest, where only commercial timber with a top diameter equal to or greater than 7 cm outside bark had been harvested.

The results surprisingly revealed that the immediate simulated growth response did not correspond with the observed reactions in the field. Unlike Sterba (1988) and others, who reported the highest volume and basal area increments on the SWH plots and the smallest increments on the WTH plots, the output from the model suggested that immediately after the intervention the WTH plots will grow best, whereas the forest growth on the SWH plots will be the slowest. The analysis of other parameters effecting forest growth revealed that the cause of the model opposite reaction as in reality is the plant uptake of mineral nitrogen. This is in the model on the SWH plots, characteristic by the largest amount of felled biomass left in the forest, reduced compared to the DTH or WTH plots, because the larger proportion of mineral nitrogen is immobilised by microorganisms that limit the availability of mineral nitrogen for plants. We hypothesise that this imbalance in plant and microbial uptake in the model is caused by the simulation of the immediate reaction of microorganisms to improved living conditions. This response of the microbial population seems to be improbable, since several studies reported that microbial colonisation processes may last several weeks to some months (Hasewaga and Takeda 1996). According to the literature review, other explanations of the model behaviour are possible. The model does not account for such processes in the ecosystem as leaching from litter and coarse woody debris, mycorrhizal symbiosis between plant roots and fungi, or the seasonal shift in the nitrogen uptake between plants and microorganisms. Since for our plots only the measurements of the forest stand volume are available with no observations of soil processes, it was not possible to examine the obtained model responses with regard to the actual state of the ecosystem and explain their possible discrepancies in comparison to reality. In addition, after a time lag of about 8 years the simulation results correspond with the observed feedback related to the treatment regime, i.e. the growth response is the lowest on the plots with the whole tree harvest followed by delayed tree harvest and stem wood harvest, suggesting that the modelled population of decomposers has been stabilised.

The presented results demonstrate new application possibilities of the biogeochemical models in forestry. From the analyses we can conclude that the BGC model used in this study is able to simulate ecosystems in stable conditions. After the implementation of the new dynamic mortality sub-model, the spinup procedure produces the steady state that corresponds with the equilibrium observable in Central European virgin forests. Therefore, these results can be in future works regarded as the natural potential of a particular site under certain climate conditions. Although the long-term modelled responses of the forest ecosystem on applied forest management mirror field observations, for correct reproduction of the short-term responses to external influences, such as thinning followed by harvest, further research is needed. Considering these restrictions, we can conclude that BGC models can be regarded as suitable tools for the assessment of forest ecosystem sustainability and as diagnostic instruments for evaluating long-term impacts of management decisions on ecosystems.

6. ZUSAMMENFASSUNG

Hauptziel der vorliegenden Arbeit war es zu evaluieren, ob die biogeochemische (BGC) Modelierungsumgebung ein geeignetes Instrument für die Bestimmung der Nachhaltigkeit des Forstökosystems und des Forstmanagements ist. Für die Arbeit benutzten wir die baumartenspezifische Anpassung des biogeochemischen Modells BIOME-BGC (Pietsch und Hasenauer 2004). Ausgangspunkt der Analyse war die Annahme, dass das Modell die grundsätzlichen Wachstumsprozesse in Waldökosystemen richtig nachbildet.

Die Arbeit besteht aus zwei Teilen. Im ersten Teil evaluierten wir die Selbstinitialisierungsprozedur (Spinup run), die für die Generierung der Anfangsbedingungen für die weiteren Simulationen mittels des Modells BIOME-BGC entwickelt wurde (Thornton et al. 2002). Diese Prozedur bringt das modellierte Ökosystem in den dynamischen Gleichgewichtszustand. In Mitteleuropa repräsentieren die Urwälder den Gleichgewichtszustand, der in der Natur erreicht werden kann. Deshalb haben wir diese Prozedur mit in zwei Urwäldern (Rothwald, Österreich, und Babia hora, Slowakei) erhobenen Daten validiert.

Die Ergebnisse der Selbstinitialisierungsprozedur hängen von mehreren Einflussvariablen ab. Abgesehen von den Klima- und Standortsbedingungen ist der erreichte Gleichgewichtszustand auch von der Mortalitätsrate abhängig. Die Modellberechnungen haben gezeigt, dass das Modell für mehrere Variablen unrealistische Werte produziert, wenn die Feuermortalität bei der Simulation auf Null gesetzt wird. Bestandesvolumina, Kohlenstoff- und Stickstoffgehalt im Boden - und in Babia hora zusätzlich die Totholzmenge - wurden alle stark überschätzt. Weil in Mitteleuropa Feuer nicht als wichtiger Faktor für die Dynamik des Waldökosystems angesehen wird (Goldammer and Page 2000), war es notwendig, das Modell so anzupassen, dass die Ergebnisse der Selbstinitialisierungsprozedur mit der Realität vergleichbar sind, auch wenn Feuermortalität im Modell nicht berücksichtigt wird.

Zuerst haben wir versucht, bessere Ergebnisse mit erhöhter regulärer Mortalität, d.h. der Mortalität durch Konkurrenz und Alterung, zu erreichen. Dafür haben wir die ursprüngliche Mortalitätsrate von 0.5% pro Jahr durch 2% ersetzt, was Little (1995) für die obere Mortalitätsgrenze in erwachsenen Naturwäldern hält. Obwohl nach dieser Mortalitätserhöhung die Schätzungen von Bestandesvolumina signifikant besser waren, wurden die modellierten Kohlenstoff- und Stickstoffgehalte im Boden immer noch überschätzt. Unsere Vermutung war, dass die Überschätzung der Bodenparameter deshalb entstanden ist, weil das Modell nicht fähig ist, die Sukzessionsdynamik in Naturwäldern, d.h. den Wechsel der Sukzessionsstadien, zu simulieren. Aus diesem Grund haben wir ein neues dynamisches Mortalitätsmodell entwickelt. Gegenüber dem ursprünglichen Modell, in dem die Mortalität als Konstante angenommen wurde, fluktuiert die

Mortalität in dem neuen Modell zwischen den vordefinierten Minimum- und Maximumwerten entlang der elliptischen Trajektorie. Die Länge eines Sukzessionszyklus' ist auch vordefiniert und hängt von der Baumart ab.

Simulationen mit der dynamischen Mortalität lieferten verbesserte Schätzungen sowohl der Bestandesvolumina als auch der Bodenparameter. Anhand dieser Ergebnisse können wir behaupten, dass das Modell mit der dynamischen Mortalität für die Simulationen der Naturwäldern, deren Entwicklung mit dem kleinen Sukzessionszyklus (Korpeľ 1995) beschrieben werden kann, geeignet ist. Nach der Einführung der dynamischen Mortalität in das Modell entspricht der simulierte Gleichgewichtszustand, der durch die Selbstinitialisierungsprozedur erreicht wird, jenem Zustand, der auf einem Waldstandort in Mitteleuropa ohne menschlichen Einfluß möglich ist. Mithilfe dieser Verbesserung war es nun also möglich, vom Modell die Informationen über das natürliche Potenzial des Standortes unter bestimmten Klimabedingungen zu bekommen. Solche Informationen können unser Verständnis über die Nachhaltigkeit des Ökosystems erweitern. Außerdem wird es dadurch möglich, den derzeitigen Zustand des vom Menschen gestörten Waldökosystems zu analysieren.

Diese Studie zeigt somit neue Möglichkeiten für die Benutzung von BGC-Modellen in der Waldökosystemforschung auf. Zugleich haben die Ergebnisse aber auch Fragen für die zukünftige Forschung aufgedeckt. Zum Beispiel wäre es wünschenswert, die physiologischen Prozesse, die zum Tod des Baumes führen, zu erklären. Anhand von solchen Erkenntnissen wäre es möglich, ein physiologisch bedingtes Mortalitätsmodell zu entwickeln. Um die Gültigkeit der Entwicklung des simulierten Waldökosystems beurteilen zu können, bedarf es des Vergleiches mit Langzeitbeobachtungen aus den Urwäldern. Solche Daten würden uns ermöglichen, nicht nur die natürliche Entwicklungsdynamik besser zu verstehen, sondern auch die Modellreaktionen zu erklären und damit Verbesserungsvorschläge für die Modellstruktur ergeben.

Im zweiten Teil der Arbeit haben wir die Benutzung des biogeochemisch-mechanistischen Modells für die Evaluierung des langfristigen Einflusses von Forstmanagement auf das Waldökosystem überprüft. Für diese Aufgabe haben wir die Daten von drei bewirtschafteten Waldstandorten in Österreich benutzt (Hartberg, Bad Zell und Wilhelmsburg), an denen die Auswirkungen von Biomassenentzug auf den Zuwachs von Beständen untersucht wurden. Im Zuge der Durchforstung wurden folgende drei Behandlungsvarianten zur Anwendung gebracht: WTH = Entnahme der ganzen Bäume inklusive Äste und Nadeln unmittelbar nach dem Fällen, DTH = Entnahme der ganzen Bäume ein Jahr nach der Schlägerung, so-dass die Nadeln im Bestand verblieben, und SWH = Entnahme des Schaftholzes.

Die simulierten Ergebnisse haben überraschenderweise gezeigt, dass die modellierten Wachstumsreaktionen den beobachteten Reaktionen nicht entsprechen. Sterba (1988) und andere haben herausgefunden, dass die SWH-Flächen die höchsten Grundflächen- und Volumszuwächse aufweisen und die Zuwächse auf den WTH-Flächen am kleinsten sind. Nach den Modellberechnungen sollten die WTH-Flächen unmittelbar nach dem Eingriff am besten und die SWH-Flächen am langsamsten wachsen. Die Analyse von anderen Parametern, die das Waldwachstum beeinflussen, hat gezeigt, dass die zur Realität entgegengesetzte Modellreaktion mit der Simulation der Aufnahme von Mineralstickstoff von Pflanzen zusammenhängt. Auf den SWH-Flächen bekommen die Pflanzen im Modell wesentlich weniger Mineralstickstoff als die Pflanzen auf DTH- oder WTH-Flächen, weil der größere Teil von Stickstoff durch die Aktivität von Mikroorganismen immobilisiert wird. Wir vermuten, dass dieses Ungleichgewicht zwischen pflanzlicher und mikrobieller Aufnahme von Mineralstickstoff sich aus der simulierten Sofortreaktion von Mikroorganismen auf die verbesserten Lebensbedingungen ergibt. Solche sofortige Antwort der mikrobiellen Population scheint sehr unwahrscheinlich, da mehrere Studien gezeigt haben, dass die Besiedlungsprozesse von Mikroorganismen mehrere Wochen bis Monate dauern können (Hasewaga and Takeda 1996). Die Fachliteraturuntersuchung bietet noch andere mögliche Erklärungen des Modellverhaltens. Einige Prozesse sind im Modell nicht berücksichtigt, z. B. die Auswaschung von Mineralstoffen aus Streu oder Totholz, Mykhorhiza, oder saisonale Änderung in der Aufnahme des Mineralstickstoffes von Pflanzen und Mikroorganismen. Da für unsere Flächen nur die Messungen von Bestandesvolumina zur Verfügung standen, war es unmöglich die Ursachen der modellierten Wachstumsreaktion festzustellen. Außerdem, langfristig gesehen entsprachen die simulierten Ergebnisse den Beobachtungen, denn ungefähr 8 Jahre nach dem Eingriff wuchsen auch im Modell die SWH-Flächen am besten und die WTH- und DTH-Flächen wiesen gegenüber der SWH-Variante eine Zuwachsminderung auf.

Die präsentierten Ergebnisse demonstrieren neue Anwendungsmöglichkeiten biogeochemischer Modelle in der Forstwirtschaft. Die Analysen zeigen, dass das in dieser Arbeit benutzte Modell geeignet ist, stabile Ökosysteme zu simulieren. Nach der Implementierung unseres neuen dynamischen Mortalitätsmodells liefert das BGC-Modell mit der Selbstinitialisierungsprozedur einen so Gleichgewichtszustand, dass er dem Zustand in mitteleuropäischen Urwäldern entspricht. Somit können die modellierten Ergebnisse in zukünftigen Arbeiten als das natürliche Potenzial des untersuchten Standortes betrachtet werden. Obwohl die modellierten langfristigen Reaktionen des Waldökosystems auf den menschlichen Eingriff mit den Beobachtungen übereinstimmen, ist für die korrekte Wiedergabe der sofortigen Reaktionen weitere Forschungsarbeit notwendig. Unter Berücksichtigung der oben genannten Einschränkungen können wir feststellen, dass die BGC-Modelle ein geeignetes Instrument für die Bewertung der Nachhaltigkeit von Waldökosystemen und die Bewertung des Einflusses der Waldbewirtschaftung auf den Waldbestand darstellen.

7. ZHRNUTIE

Hlavným cieľom predkladanej práce bolo preveriť vhodnosť použitia biogeochemického modelu na hodnotenie trvalej udržateľnosti lesných ekosystémov a lesného hospodárenia. V práci sme použili druhovo-špecifickú adaptáciu modelu BIOME-BGC pre stredoeurópske dreviny (Pietsch and Hasenauer 2004). Analýza bola založená na predpoklade, že model je schopný adekvátne simulovať základné rastové procesy lesa.

Práca je rozdelená do dvoch hlavných častí. V prvej časti sme hodnotili tzv. samoinicializačnú spinup procedúru, ktorá bola vyvinutá za účelom získania potrebných počiatočných hodnôt o lesnom poraste nevyhnutných pre ďalšie simulácie porastu modelom BIOME-BGC (Thornton et al. 2002). Pomocou tejto procedúry sa modelovaný ekosystém dovedie do dynamického rovnovážneho stavu. V prirodzených podmienkach strednej Európy predstavujú takýto rovnovážny stav pralesy. Preto sme na validáciu modelovaného rovnovážneho stavu použili údaje z dvoch stredoeurópskych pralesov: Rothwaldu v Rakúsku a Babej hory na Slovensku.

Dosiahnutý modelový rovnovážny stav závisí od viacerých faktorov. Z analýz sme zistili, že okrem klimatických a stanovištných podmienok je dôležitým faktorom mortalita. Model simuluje jednak tzv. regulárnu mortalitu spôsobenú konkurenciou a starnutím, a mortalitu v dôsledku požiarov. Výsledky ukázali, že v prípade, ak je mortalita spôsobená ohňom z modelovania vylúčená, model produkuje nerealistické rovnovážne stavy. Porastová zásoba, množstvo uhlíka a dusíka v pôde a pri Babej hore aj množstvo moderového dreva boli v takýchto prípadoch modelom vysoko nadhodnotené. Keďže oheň sa v podmienkach strednej Európy nepovažuje za dôležitý faktor ovplyvňujúci dynamiku vývoja lesných porastov (Goldammer and Page 2000), bolo potrebné upraviť štruktúru modelu tak, aby výsledky jeho spinup simulácií korešpondovali so stavom v skutočnosti.

V prvom kroku sme sa pokúsili získať adekvátne výsledky zvýšením regulárnej mortality porastu z pôvodných 0.5% celkovej rastlinnej biomasy za rok na 2% ročne, t.j. na hodnotu, ktorú Little (1995) považuje za hornú hranicu mortality v zrelých prirodzených lesných ekosystémoch. Aj keď toto zvýšenie mortality nám signifikantne zlepšilo výsledky porastovej zásoby, na obsah uhlíka a dusíka v pôde nemalo výrazný vplyv. Predpokladali sme, že nadhodnocovanie pôdnych parametrov modelom je spôsobené tým, že pri simulácii sa neberie do úvahy vývoj porastu cez jednotlivé vývojové štádiá, ako ich definoval napr. Korpeľ (1995). Preto sme pôvodný mortalitný model, ktorý bol založený na predpoklade konštantnej mortality, nahradili novým modelom simulujúcim dynamickú mortalitu. Dynamická mortalita sa vyvíja po eliptickej trajektórii a fluktuuje medzi preddefinovanou minimálnou a maximálnou hodnotou. Dĺžka jedného vývojového cyklu je tiež preddefinovaná a závisí od druhu dreviny.

Použitím dynamickej mortality sme získali zlepšené odhady porastovej zásoby ako aj pôdnych charakteristík v oboch pralesoch. Na základe dosiahnutých výsledkov môžeme tvrdiť, že pomocou dynamickej mortality je model schopný simulovať pralesy vyvíjajúce sa cez tzv. malý vývojový cyklus (Korpeľ 1995). Navyše, po implementácii dynamickej mortality dosiahneme spinup procedúrou rovnovážny stav, ktorý korešponduje s rovnovážnym stavom pozorovateľným v pralesoch strednej Európy. Tým sme signifikantne zlepšili správanie sa modelu, keďže teraz je možné z modelu získať informácie o prirodzenom potenciáli sledovanej lokality za určitých predom stanovených klimatických podmienok. Takéto informácie môžu nielen zlepšiť naše chápanie trvalej udržateľnosti, ale umožňujú aj analýzu súčasného stavu obhospodarovaného ekosystému s ohľadom na jeho prirodzený potenciál.

Tieto výsledky dokumentujú nové možnosti využitia biogeochemických modelov. Avšak naše analýzy odhalili aj otázky pre budúci výskum. Bolo by žiadúce analyzovať fyziologické procesy spôsobujúce resp. vedúce k smrti stromu. Ich objasnenie by umožnilo vytvoriť mortalitný model založený na fyziologických pochodoch, ktorý by bol pre aplikáciu v mechanistických modeloch vhodnejší. Ďalšou otázkou vyžadujúcou pozornosť je zhodnotenie vývoja modelovaného porastu v čase. Na jej zodpovedanie sú potrebné opakované merania pralesov, ktoré nám umožňujú jednak lepšie porozumieť prirodzenej dynamike lesov, ako aj pochopiť a vysvetliť reakcie modelu, a následne navrhnúť potrebné zlepšenia.

V druhej časti práce sme overovali aplikovateľnosť mechanistického modelovania pre hodnotenie dlhodobých vplyvov hospodárskych opatrení na lesný ekosystém. Pre riešenie tejto úlohy sme použili údaje z troch rakúskych lokalít: Hartberg, Bad Zell a Wilhelmsburg. V rámci daných lokalít sa testoval vplyv troch rozdielnych ťažbových scenárov aplikovaných po prebierke. Testované ťažbové scenáre sú definované nasledovne: WTH = ťažba a približovanie „zelených“ stromov, t.j. stromová metóda, kedy sa z porastu odstráni celá spílená nadzemná biomasa vrátane kmeňa, koruny a lístia; DTH = ťažba celého stromu s oneskoreným približovaním, t.j. 1 rok po prebierke, aby ostala listová biomasa v poraste; a SWH = ťažba a približovanie komerčnej drevnej suroviny, t.j. kmeňová metóda, kedy sa z porastu odstránila drevná hmota s minimálnou hornou hrúbkou 7 cm.

Výsledky analýzy prekvapivo ukázali, že okamžitá simulovaná rastová reakcia porastu bola opačná ako reakcie pozorované v porastoch. Na rozdiel od Sterbu (1988) a ďalších, ktorí zistili najvyššie prírastky na objeme a kruhovej základni na SWH plochách a naopak najnižšie na WTH plochách, výstup z modelu dokumentoval, že okamžite po zásahu WTH plochy rastú najlepšie, kým

SWH plochy sa vyznačujú najpomalším rastom. Z analýzy ostatných parametrov, ktoré vplývajú na rast lesa, vyplýva, že opačná reakcia modelu ako v skutočnosti je spôsobená príjmom minerálneho dusíka rastlinami. Ten je na SWH plochách, ktoré sú charakterizované najväčším množstvom biomasy ponechanej po prebierke v poraste, nižší v porovnaní s DTH a WTH plochami, pretože väčšia časť minerálneho dusíka je v modeli imobilizovaná mikroorganizmami. Vyšší príjem dusíka mikroorganizmami následne limituje dostupnosť minerálneho dusíka pre rastliny. Predpokladáme, že tento nerovnovážny stav medzi rastlinami a mikroorganizmami v modeli je spôsobený okamžitou reakciou mikroorganizmov na zlepšené životné podmienky. Simulovaná okamžitá odpoveď mikrobiálnej populácie sa zdá byť nepravdepodobná, keďže viacero štúdií dokumentuje, že kolonizačné procesy mikroorganizmov trvajú v lese niekoľko týždňov až mesiacov (Hasewaga and Takeda 1996). Na základe prehľadu literatúry prichádzajú do úvahy aj ďalšie vysvetlenia opačnej reakcie modelu. Napríklad, model nesimuluje také procesy, ako je odtok živín z opadanky alebo moderového dreva, neberie do úvahy mykoríznu symbiózu medzi rastlinnými koreňmi a hubami, alebo sezónne striedanie sa rastlín a mikroorganizmov v príjme dusíka. Keďže pre naše plochy sme mali k dispozícii len merania porastovej zásoby, nebolo možné preveriť, čo bolo hlavnou príčinou inej okamžitej reakcie modelu ako v teréne. Avšak po určitom časovom odstupe 8 rokov sa výsledky simulácií zhodujú s terénnymi pozorovaniami, t.j. najnižší rast vykazujú WTH plochy, ktoré sú nasledované DTH plochami a najlepšie rastú SWH plochy. Tieto reakcie nasvedčujú o tom, že modelová populácia dekompozítorov sa stabilizovala.

Prezentované výsledky demonštrujú nové možnosti využitia mechanistického modelovania v lesníctve. Z analýzy vyplýva, že biogeochemický model použitý v tejto práci je schopný simulovať stabilné ekosystémy. Po implementácii dynamickej mortality do modelu dosiahneme samoinicializačnou spinup procedúrou rovnovážny stav, ktorý zodpovedá stavu pozorovanému v pralesoch strednej Európy. Hoci z dlhodobého hľadiska korešpondujú reakcie modelu na aplikované hospodárske opatrenia s pozorovaniami v teréne, pre správnu reprodukciu krátkodobých reakcií na vonkajšie vplyvy, ako je prebierka alebo ťažba, je potrebný ďalší výskum. S ohľadom na tieto obmedzenia môžeme tvrdiť, že biogeochemické modely sa môžu považovať za vhodné nástroje na hodnotenie trvalej udržateľnosti lesných ekosystémov ako aj na preverenie vplyvov hospodárskych opatrení na ekosystém ako celok.

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8. APPENDIX

APPENDIX 1: SITE SPECIFIC CHARACTERISTICS

Effective soil depth corrected for rock fraction	[m]
Sand percentage by volume in rock-free soil	[%]
Silt percentage by volume in rock-free soil	[%]
Clay percentage by volume in rock-free soil	[%]
Site elevation	[m]
Site latitude (- for Southern Hemisphere)	[°]
Site shortwave albedo	DIM
Wet and dry atmospheric deposition of nitrogen	[kgN/m^2/yr]
Symbiotic and asymbiotic fixation of nitrogen	[kgN/m^2/yr]
Industrial deposition of nitrogen	[kgN/m^2/yr]

APPENDIX 2: ECOPHYSIOLOGICAL CHARACTERISTICS

Characteristic	***Picea abies* lowland**	***Picea abies* highland**	***Fagus sylvatica***	***Quercus spp.***	**Units**
Day of year when the new growth starts	0	0	0	122	[yday]
Day of year when the litterfall finishes	0	0	0	310	[yday]
Transfer growth period as fraction of growing season	0.3	0.3	0.2	0.25	[prop]
Litterfall as fraction of growing season	0.3	0.3	0.2	0.3	[prop]
Annual leaf and fine root turnover fraction	0.1935	0.1935	1	1	[1/year]
Annual live wood turnover fraction	0.7	0.7	0.7	0.7	[1/year]
Annual whole-plant mortality fraction	0.005	0.005	0.005	0.006	[1/year]
Annual fire mortality fraction	0	0	0	0	[1/year]
New fine root C allocation : new leaf C allocation	0.262	0.762	0.545	1	[ratio]
New stem C allocation : new leaf C allocation	3.03	2.09	3.8	1.29	[ratio]
New live wood C allocation : new total wood C allocation	0.076	0.059	0.154	0.12	[ratio]
New coarse root C allocation: new stem C allocation	0.12	0.23	0.115	0.25	[ratio]
Current growth allocation : storage growth allocation	0.5	0.5	0.5	0.5	[ratio]
C:N of leaves	58.8	42.5	26.9	26.9	[kgC/kgN]
C:N of leaf litter, after re-translocation	116	85	44.0	63.3	[kgC/kgN]
C:N of fine roots	58.1	42.5	47.6	73.5	[kgC/kgN]
C:N of live wood	65	55	54.0	63.5	[kgC/kgN]
C:N of dead wood	535	435	550	450	[kgC/kgN]
Leaf litter labile proportion	0.44	0.44	0.124	0.2	[prop]
Leaf litter cellulose proportion	0.35	0.35	0.561	0.56	[prop]
Leaf litter lignin proportion	0.21	0.21	0.315	0.24	[prop]
Fine root labile proportion	0.427	0.427	0.34	0.34	[prop]
Fine root cellulose proportion	0.381	0.381	0.44	0.44	[prop]
Fine root lignin proportion	0.192	0.192	0.22	0.22	[prop]
Dead wood cellulose proportion	0.72	0.7	0.77	0.704	[prop]
Dead wood lignin proportion	0.28	0.3	0.23	0.296	[prop]
Canopy water interception coefficient	0.036	0.031	0.034	0.038	[1/LAI/d]
Canopy light extinction coefficient	0.67	0.51	0.6	0.54	[DIM]
All-sided to projected leaf area ratio	2.3	2.3	2	2	[DIM]
Canopy average specific leaf area (projected area basis)	10.2	9.4	48	35	[m^2/kgC]
Ratio of shaded SLA : sunlit SLA	2	1.8	2	2	[DIM]
Fraction of leaf N in Rubisco	0.06	0.035	0.162	0.088	[DIM]
Maximum stomatal conductance (projected area basis)	0.002	0.002	0.006	0.004	[m/s]
Cuticular conductance (projected area basis)	0.00006	0.00006	0.00006	0.00002	[m/s]
Boundary layer conductance (projected area basis)	0.09	0.09	0.01	0.005	[m/s]
Leaf water potential: start of conductance reduction	-0.5	-0.5	-0.34	-0.7	[MPa]
Leaf water potential: complete conductance reduction	-1.5	-1.5	-1.7	-3.5	[MPa]
Vapour pressure deficit: start of conductance reduction	500	500	600	200	[Pa]
Vapour pressure deficit: complete conductance reduction	2500	2500	3000	2550	[Pa]
Night temperature: start of conductance reduction	-2	-2	0	0	[℃]
Night temperature: complete of conductance reduction	-10	-10	-8	-8	[℃]

APPENDIX 3: VALUES NECESSARY FOR MODEL INITIALISATION

Water state variables

Water stored in snowpack	$[kg/m^2]$
Initial soil water as a proportion of saturation	DIM

Carbon state variables

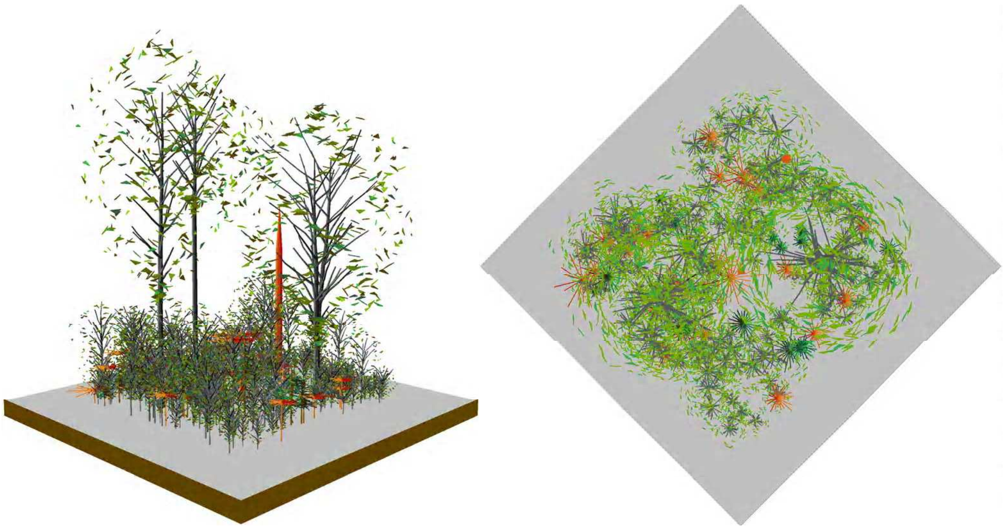
First-year maximum leaf carbon	$[kgC/m^2]$
First-year maximum stem carbon	$[kgC/m^2]$
Carbon in coarse woody debris	$[kgC/m^2]$
Litter carbon, labile pool	$[kgC/m^2]$
Litter carbon, unshielded cellulose pool	$[kgC/m^2]$
Litter carbon, shielded cellulose pool	$[kgC/m^2]$
Litter carbon, lignin pool	$[kgC/m^2]$
Soil carbon, fast microbial recycling pool	$[kgC/m^2]$
Soil carbon, medium microbial recycling pool	$[kgC/m^2]$
Soil carbon, slow microbial recycling pool	$[kgC/m^2]$
Soil carbon, recalcitrant SOM (slowest)	$[kgC/m^2]$

Nitrogen state variables

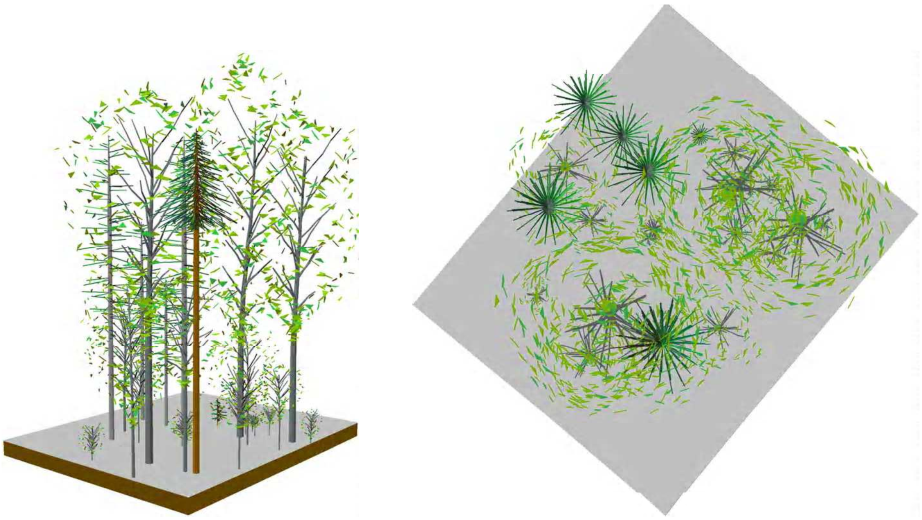
Litter nitrogen, labile pool	$[kgN/m^2]$
Soil nitrogen, mineral pool	$[kgN/m^2]$

APPENDIX 4: VISUALISATION OF SELECTED PLOTS IN ROTHWALD WITH THE STAND VISUALISATION SYSTEM SVS (McGaughey 1999)

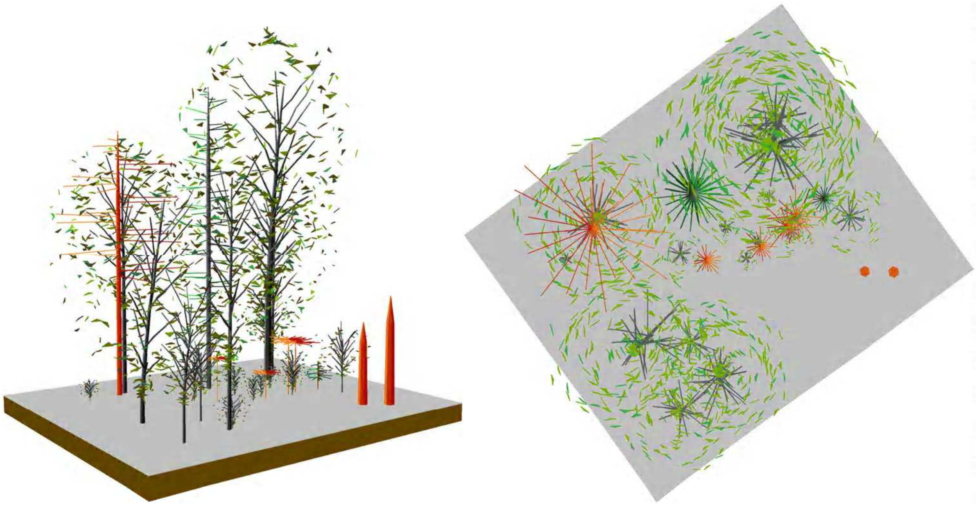
PLOT No. 72 assigned to stage of growth



PLOT No. 63 assigned to stage of maturity

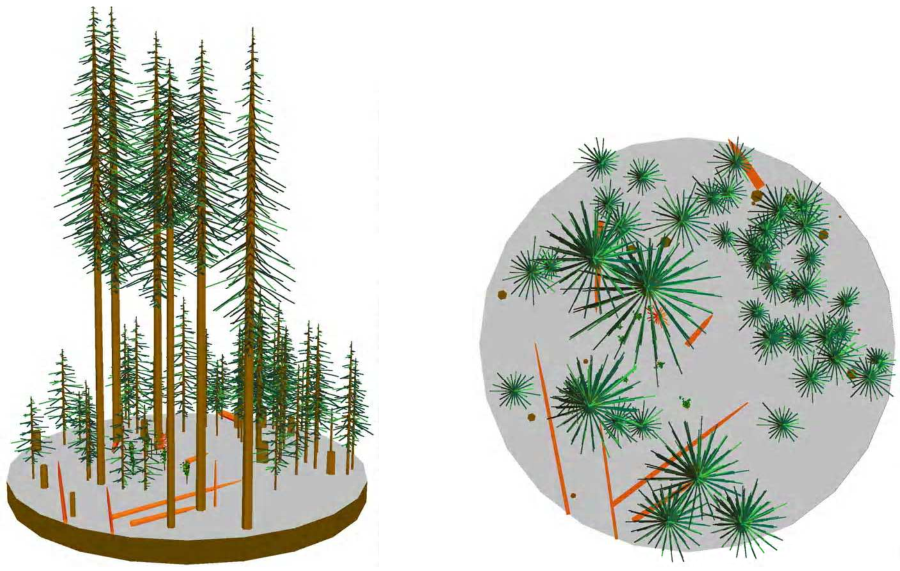


PLOT No. 22 assigned to stage of breakdown

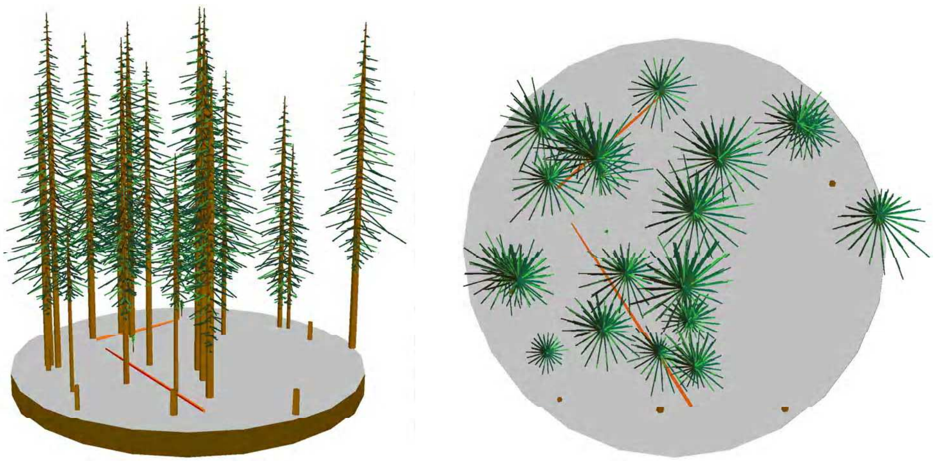


APPENDIX 5: VISUALISATION OF SELECTED PLOTS IN BABIA HORA WITH THE STAND VISUALISATION SYSTEM SVS (McGaughey 1999)

PLOT No. 4 assigned to stage of growth



PLOT No. 31 assigned to stage of maturity



PLOT No. 48 assigned to stage of breakdown