

Evaluating the accuracy and generality of a hybrid patch model

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Summary Forest patch models have been used extensively to simulate vegetation development under current and changing environmental conditions. However, their physiological foundation is subject to criticism and recent validation experiments against long-term growth and yield data have shown major deficiencies in reproducing observed growth patterns of mixed-species forests. Here we describe the modified forest patch model PICUS Version 1.3, a model variant that couples the structurally detailed three-dimensional patch model PICUS Version 1.2 and the physiologically based stand-level production module of the 3-PG (Physiological Principles in Predicting Growth) model. The approach attempts to combine the ability of PICUS v1.2 to simulate forest dynamics on time scales relevant to forest succession with a simplified but successful production model based on the concept of radiation-use efficiency. We evaluated the hybrid model in a series of simulation experiments. Results indicated a realistic response to a climate sensitivity experiment: the response to environmental gradients was well captured both in terms of productivity on time scales of a rotation length and of forest succession over several hundreds of years. Testing against independent long-term growth and yield data revealed good correspondence between observed and predicted values of volume production and stand structure. Further model development should include a dynamic soil component to consider effects of nutrient cycling.

Keywords: 3-PG, model coupling, PICUS, productivity, species composition, validation.

Introduction

Increasing awareness of the influences of climate change on forest growth and ecosystem development has led to increased demand for process-based models applicable in forest management (e.g., Peng 2000, Mäkelä et al. 2000, Matala et al. 2003). Statistical growth and yield models, which are the traditional predictive tools in forest resource planning, fail in situations where environmental conditions are expected to change at time scales of a few decades (Battaglia and Sands 1998). Although there is considerable progress in the development of detailed process-based models, their applicability in opera-

tional decision making is still limited. Reasons for this limitation are the complex structure of process-based models; their need for many detailed model parameters, which may not be readily available; their large computational demand due to superficially complex process descriptions; their inability to consider silvicultural management activities realistically; and their failure to provide output variables, such as volume of merchantable timber or dimensions of individual trees, with sufficient accuracy to be useful to resource managers (e.g., Running and Coughlan 1988, McMurtrie et al. 1990, Kellomäki and Väisänen 1997, Kirschbaum 2000). Moreover, few process models can simulate uneven-aged, multi-layer mixed-species stands. Experience from traditional growth and yield research has shown that to include forest management realistically, process-based models must operate at the individual tree level. Furthermore, broadscale applicability in forest resource planning requires that models be initialized with readily available forest inventory data. A rare example that satisfies these needs is the 4C model (Bugmann et al. 1997, Lasch et al. 2005). Examples of models suitable for mono-species stands include FinnFor (Kellomäki and Väisänen 1997) and GOTILWA (Gracia et al. 1999). Patch (or gap) models are another type of ecological model that have been applied in numerous climate change impact assessments (e.g., Kienast and Kuhn 1989, Solomon and Bartlein 1992, Lasch et al. 1999, Lindner et al. 2000, Lexer et al. 2001). Models of this class are appealing because of their applicability to multi-species forests and the ease with which they are parameterized. Also, the data required to initialize and drive them is not difficult to acquire. However, patch models have been heavily criticized for their weak physiological foundation (e.g., Loehle and LeBlanc 1996, Schenk 1996) and questionable scaling assumptions (Bugmann 2001). Yaussy (2000) questioned the general applicability of all gap models because of their weak performance in predicting short- to mid-term growth pattern of mixed-species stands.

To bridge the gap between the potential but as yet undelivered advantages of detailed process-based models and the demand for decision-making tools for sustainable forest management, several authors propose hybridizing model concepts (e.g., Peng 2000, Robinson and Ek 2003). Such an approach is meant to reconcile the conflicting aims of accuracy and pa-

parameter parsimony on the one hand, and generality and biological realism on the other hand (cf. Battaglia and Sands 1998, Liu and Ashton 1995, Mäkelä et al. 2000). The success of such an approach has yet to be tested in comprehensive model evaluation studies.

In this paper, we attempt to combine the strengths of two existing, well-studied forest models, PICUS v1.2 and 3-PG, with the aim of thereby circumventing their individual limitations. The three-dimensional patch model PICUS v1.2 (Lexner and Hönninger 2001) builds on the classical gap model approach but includes several advanced submodels such as a detailed model of the light regime within the canopy, a seed production and dispersal model, a submodel to account for bark-beetle-induced mortality in conifer forests (Lexner and Hönninger 1998) and a fuzzy-logic-based approach to link site nutrient status to tree growth (Lexner et al. 2000). PICUS v1.2 has been successfully tested in simulating natural vegetation composition in the eastern Alps in Austria under current climate conditions (Lexner 2001), and has been employed in a large-scale climate change impact assessment for Austrian forests (Lexner et al. 2002). Although PICUS is capable of mimicking competitive relationships among tree species, its physiological foundation in simulating forest productivity is more descriptive than explanatory.

The 3-PG model (Physiological Principles in Predicting Growth; Landsberg and Waring 1997) is a physiology-based, stand-level model of net primary production for monospecific stands with a simple tree population structure. The 3-PG model has been tested in several studies (e.g., Coops et al. 1998, Landsberg et al. 2000, 2003, White et al. 2000) and has been successfully applied to a wide range of forest ecosystems (e.g., Waring 2000, White et al. 2000, Sands and Landsberg 2002, Almeida et al. 2004, Dye et al. 2004, Stape et al. 2004).

The objectives of this paper are twofold: (1) the concept of merging PICUS v1.2 and 3-PG is introduced, and core model formulations are presented; and (2) the new model is tested in a series of simulation experiments designed to evaluate the generality and accuracy of the hybrid model.

Methods and materials

Hybridizing PICUS v1.2 and 3-PG

The patch model PICUS v1.2 To hybridize the models, we started from the original patch model PICUS v1.2. A detailed description of the model is given by Lexner and Hönninger (2001) and Lexner (2001), so only a brief overview of the model logic is presented here. PICUS simulates growth, reproduction and death of individual trees on an array of $10 \times 10\text{-m}^2$ patches. The vertical dimension of a simulated forest is represented explicitly by crown cells of 5 m in depth up to a maximum height of 60 m. The $10 \times 10 \times 5\text{-m}^3$ structural base elements contain all of the information on the distribution of tree biomass in space. Tree biomass is evenly distributed within the cells. The physico-chemical environment of trees is represented by radiation; a thermal heat sum above a threshold of 5.5°C (growing degree days; GDD); minimum winter temperatures represented by the

coldest month of the year; a proxy for drought (SMI) that is derived from a refined water balance model (cf. Lexner and Hönninger 2001); site nutrient status characterized by soil pH and the C:N ratio of the uppermost 30 cm of mineral soil; and the soil water-holding capacity. PICUS includes a light model that accounts for direct and diffuse radiation, both above and within the canopy. In modeling the effects of site factors on tree growth, PICUS differs from other conventional patch models with respect to several features. First, tree growth is not constrained at super-optimal temperatures. Second, the formulation of tree responses to GDD and SMI is based on empirical growth data of the Austrian Forest Inventory (AFI) (Lexner 2001). Third, minimum winter temperature is evaluated twice: (1) as an indicator of frost occurrence damaging regeneration of susceptible species, and (2) in relation to chilling requirements for species requiring dormancy (Sykes et al. 1996). Fourth, PICUS employs a fuzzy logic control unit, which makes use of qualitative expert knowledge on the interrelationship of tree growth and site nutrient status to model the effect of site nutrient status on tree growth (Lexner et al. 2000). The effect of each environmental factor is expressed as a dimensionless multiplier. Finally, in calculating the combined effect of the site factors considered, compensation as well as intensification of limiting factors are taken into account. The model version 1.2 requires monthly temperature and precipitation provided either as time series input or stochastically generated by a weather generator within PICUS.

Tree mortality is modeled as in other patch models (cf. Keane et al. 2001). Trees either die from an intrinsic risk of death, which is independent of tree growth and size, or from an increased stress-related mortality based on the assumption that slow-growing trees with an unfavorable carbon budget are at higher risk of being killed by insects and pathogens. PICUS v1.2 also includes a submodel that accounts for tree mortality in Norway spruce (*Picea abies* (L.) Karst.) caused by infestations of bark beetles, a major disturbance factor in coniferous forests at low elevations (Lexner and Hönninger 1998).

New trees are generated stochastically by a recruitment submodel and enter the stand with a size of approximately 1.0 cm in DBH. In contrast to other patch models, PICUS explicitly considers seed production and seed dispersal within the simulated forest. Seed production is modeled as a function of species, tree size and absorbed light. Seed dispersal is represented as a cone-shaped distribution centered around each mature tree. Total seed availability for each species per patch is then calculated from the integrals of all the distribution cones overlapping within a particular patch. Germination of seed is a function of chemo-physical site properties and bioclimatic variables.

The 3-PG model The forest productivity model 3-PG has two major components, one calculating stand biomass production on a monthly time step, and one allocating produced biomass to tree components (for details, see Landsberg and Waring 1997, Sands and Landsberg 2002 and Landsberg et al. 2003). The structure of the simulated tree population is kept fairly simple to utilize available data on allometric relation-

ships of individual trees. Tree population size is controlled through the universal relationship between individual tree size (i.e., mean stem mass) and population density (i.e., stems ha^{-1}). To estimate net primary productivity (NPP), 3-PG calculates intercepted radiation, which is converted to gross primary productivity (GPP) by multiplying by an estimate of quantum-use efficiency (QE). The QE is obtained by reducing a maximum value for effects of the environment (temperature, soil water supply, VPD), site fertility and stand age (Landsberg et al. 2003). The NPP is calculated as a constant ratio of GPP. The ratio of absorbed to useable radiation determines the percentage of NPP that is allocated to root growth.

The hybrid model version PICUS v1.3 In describing the new hybrid model variant PICUS v1.3, we distinguish among bottom-up components, which are taken from PICUS v1.2, and top-down components, from the 3-PG production model. We build on previous experiences with the PICUS v1.2 model and assume that the model captures inter- and intraspecific competition well. The strength of the 3-PG approach is the estimation of stand-level NPP based on radiation-use efficiency. Thus, by linking species- and tree-based indices of competitiveness as generated by the original patch model approach to reliable estimates of stand-level NPP, we expect to increase physiological reliability and accuracy of growth predictions.

In the hybrid model version, bottom-up estimates of tree growth are based on potential height development instead of potential diameter growth (cf. Bugmann 2001). The original model version PICUS v1.2 included the potential diameter growth equation as described by Moore (1989). This expression is replaced by an empirical equation for species-specific potential height development that is parameterized from dominant height data of the AFI as described by Lexer (2001). Because dominant height is a stand-level indicator of growth performance and individual trees will grow taller, the resulting tree height estimates were increased as proposed by Kahn (1994). As an example, Equations 1a and 1b represent the equations for Norway spruce (*Picea abies* (L.) karst.) and beech (*Fagus sylvatica* L.), respectively:

$$H_{\text{pot(PA)}} = (e^{4.0632 - 39.2845/(\text{age} + x)})1.138 \quad (1a)$$

$$H_{\text{pot(FS)}} = (e^{3.85 - 25.5/(\text{age} + x)})1.132 \quad (1b)$$

where $H_{\text{pot(PA)}}$ and $H_{\text{pot(FS)}}$ = potential height of *P. abies* and potential height of *F. sylvatica*, respectively; age = tree age; and x = number of years it takes a tree to reach breast height (130 cm).

To estimate potential diameter increment, we used the diameter–height relationships of open-grown trees reported by Hasenauer (1997) and Hasenauer et al. (1994):

$$\ln(\text{DBH}) = a + b\ln(H) \quad (2)$$

where DBH = diameter at breast height (cm); H = tree height (m); and a and b = empirical coefficients.

The height of a Norway spruce tree i at any given time step t

(i.e., year) is used to calculate potential DBH(t, i). Inverting Equation 1 for tree age and inserting the height estimate $H(t + 1)$ in Equation 2 yields the potential DBH($t + 1, i$). The difference between DBH(t) and DBH($t + 1$) is the potential diameter increment $\Delta\text{DBH}_{\text{pot}}$ of tree i . Accordingly, $\Delta\text{DBH}_{\text{pot}}(t)$ is derived. To calculate the actual diameter increment as influenced by the environment a tree experiences, the original approach described by Lexer and Hönninger (2001) is used to combine the effects of heat sum > 5.5 °C, soil water content, site nutrient supply and the light regime (see previous description of PICUS v1.2). To allow for the realistic simulation of complex stand structures, an approach from Lindner et al. (1997) was employed to model actual height growth (Equation 3) where f_{site} is the combined effect of temperature, soil water content and nutrient supply as used for the estimation of actual diameter growth. Parameter f_{light} characterizes the empirical finding that many tree species show maximum height growth at high stand densities. Relative species-specific stand density in PICUS v1.3 is represented by the available light a tree experiences and its subsequent light response value (Equation 4):

$$\frac{\Delta H_i}{\Delta H_{\text{pot}(i)}} = f_{\text{light}} f_{\text{site}} \quad (3)$$

$$\begin{aligned} f_{\text{light}(i,j)} = & -0.0041 + 13.376\text{LR}_{(i,j)} \\ & - 64.604\text{LR}_{(i,j)}^2 + 149.01\text{LR}_{(i,j)}^3 - 185.78\text{LR}_{(i,j)}^4 \\ & + 120.24\text{LR}_{(i,j)}^5 - 31.62\text{LR}_{(i,j)}^6 \end{aligned} \quad (4)$$

Equation 4 is parameterized such that a tree i of species j growing without competition (i.e., light response (LR) $\equiv 1.0$) will attain the height of an open-grown tree, which is less than that of a dominant or codominant tree growing in a stand. At values for f_{light} representative for dominant trees growing in a closed stand under non-limiting environmental conditions (i.e., f_{site}), Equation 3 envelops the dominant height curve ensemble of the Austrian yield tables (Marschall 1975).

After estimates of diameter and height increment for each tree have been calculated by the bottom-up component, above-ground tree biomass components (total biomass, stem, branches, leaves) are calculated from DBH based on allometric relationships taken from the literature (e.g., Krapfenbauer and Buchleitner 1981, Hochbichler et al. 1994, Ter-Mikaelian and Korzhukin 1997, Sterba and Eckmüller 1998, Daxner et al. 1999, E. Hochbichler, Institute of Silviculture/BOKU, Vienna, Austria, personal communication) (Equation 5). Merchantable timber volume is calculated from DBH and H according to Pollanschütz (1974) (Equation 6). For those cases where no species-specific information could be found in the literature we used the parameters of ecologically similar species:

$$\text{Biom}_{\text{total}(i,g)} = a\text{DBH}^b \quad (5)$$

$$V_{(i,j)} = \frac{\pi}{4(1000)} \left(\frac{b1(DBH^2)H + b2(DBH^2)}{(H)LN^2(DBH) + b3(DBH^2)} + \frac{b4(DBH)H + b5H + b6(DBH) + b7}{(H)LN^2(DBH) + b3(DBH^2)} \right) \quad (6)$$

where $Biom_{total(i,g)}$ = total biomass of tree i of species g (kg_{DM}); a and b = species-specific empirical coefficients; $V_{(i,j)}$ = stem volume over bark of tree i of species j (m^3); H = tree height (dm); and $b1$ – $b7$ = species-specific empirical coefficients.

The top-down estimate of NPP is based on absorbed radiation. In the current version of the model, mean daily global radiation per month is input to the model and converted to photosynthetically active radiation (PAR) by multiplying by 0.5. Direct and diffuse radiation intercepted and attenuated by leaves of three species groups is aggregated to monthly values over the vegetation period as defined for the three species groups (evergreen conifers: temperature $> 0^\circ C$; winter-deciduous broadleaves: temperature $> 5^\circ C$; winter-deciduous conifers (i.e., *Larix decidua* Mill.): temperature $> 3^\circ C$). Monthly values of absorbed PAR for the species groups are converted to “usable” PAR:

$$\Phi_{p.a.u.(g,m)} = \Phi_{p.a.(g,m)} \min(SMR_{av(j,m)}; MTD_{VPD(m)}) \quad (7)$$

where $\Phi_{p.a.u.(g,m)}$ = usable PAR of species group g in month m ; $SMR_{av(j,m)}$ = monthly mean soil water response of all species j of species group g ; $MTD_{F(m)}$ = monthly frost response; $MTD_{T(g,m)}$ = monthly temperature response of species group g ; and $MTD_{VPD(m)}$ = monthly response to vapor pressure deficit.

The soil water response (SMR) is identical to that of the bottom-up component. The SMR_{av} is calculated as the mean SMR of all present species within species group g , weighted with their biomass shares. The multiplier for vapor pressure deficit, MTD_{VPD} , is defined according to:

$$MTD_{VPD(m)} = \exp(-Z_1(VPD^{Z_2})) \quad (8)$$

where Z_1, Z_2 = coefficients (default: $Z_1 = 0.3, Z_2 = 2.3$); and VPD = monthly mean for mean daily vapor pressure deficit (kPa).

The temperature response of the top-down component is based on simplified physiology (e.g., Larcher 1995) and assumes, on a daily time step, a parabolic response of photosynthesis to temperature. Temperature values are interpolated from monthly means to a quasi-daily basis, and the effect of temperature is calculated with Equations 9 and 10:

$$f(T)_{d,g} = 4(T_d - Z_3)(Z_4 - T_d) / (Z_3 - Z_4)^2 \quad (9)$$

$$MTD_{T(g,m)} = \frac{\sum_{d=1}^{30} f(T)_{d,g}}{30} \quad (10)$$

where T = temperature; Z_3 = minimum temperature value for photosynthesis (0 for conifers, 2 for broadleaves); Z_4 = maximum temperature value for photosynthesis (35 for conifers, 40 for broadleaves); T_d = interpolated daily temperature; and $f(T)_{d,g}$ = temperature response for species group g on day d ; if $T_d < 0$ or $T_d > 35$ then $f(T)_g = 0$. This approach is similar to the formulation used in the FORSKA model (Prentice et al. 1993).

Currently, the effect of frost within the vegetation period is identical for all species groups and is based on the number of frost days within a month (i.e., temperature $< 0^\circ C$):

$$MTD_{F(m)} = 1 - \frac{n(\text{frost})_m}{30} \quad (11)$$

where $n(\text{frost})_m$ = number of frost days per month m .

In the original model formulation, Landsberg and Waring (1997) included an expression for the effect of aging that was based on the assumption that plant hydraulic conductivity decreases with increasing age, and introduced a parameter for maximum age. This might work well with even-aged plantation-like stands. Because PICUS should also be applicable to uneven-aged stands, maximum age is replaced by an expression for attainable mean tree height in a stand:

$$f(\text{age}) = \frac{1}{1 + \left(\frac{h_g}{40}\right)^3} \quad (12)$$

where $f(\text{age})$ = age-related effect on quantum-use efficiency; and h_g = mean tree height (m).

Sands and Landsberg (2002) introduced a fertility multiplier to scale quantum-use efficiency according to site fertility. In PICUS v1.3, the species-specific nutrient response values from the patch model component of all species within a species group are averaged, and weighted with their biomass shares. Both the nutrient multiplier and the multiplier for the effect of aging are directly linked to quantum-use efficiency:

$$\alpha_{Cm(g)} = \alpha_C NR_{av(g)} f(\text{age}) \quad (13)$$

where α_C = quantum-use efficiency (default: 1.8 g C MJ^{-1} absorbed PAR); $\alpha_{Cm(g)}$ = actual quantum-use efficiency for species group g ; and $NR_{av(g)}$ = average nutrient response within species group g weighted with biomass shares.

Gross primary production is calculated with Equation 14. As proposed by Landsberg and Waring (1997), the NPP:GPP ratio is held constant at 0.45:

$$P_{G(g)} = \sum \Phi_{p.a.u.(g)} \alpha_{Cm(g)} \quad (14)$$

Following Landsberg and Waring (1997), the fraction of NPP allocated to aboveground growth is based on the ratio of absorbed and usable PAR as an index of environmental harshness for tree growth, and the nutrient supply index:

$$NPP_{ag(g)} = P_{N(g)} \left(1 - \frac{0.8}{1 + 2.5N_{av(g)} \left(\frac{\Phi_{p.a.u.(g)}}{\Phi_{p.a.(g)}} \right)} \right) \quad (15)$$

where $NPP_{ag(g)}$ = aboveground NPP of species group g ($g C m^{-2} year^{-1}$).

Assuming a carbon content of dry mass of 50%, the above-ground biomass increment for each species group is calculated as:

$$\Delta TDB_{ag(g)} = \frac{NPP_{ag(g)} 2area_{sim}}{1000} \quad (16)$$

where $TDB_{ag(g)}$ = top-down aboveground biomass increment for species group g ($kg_{DM} year^{-1}$).

Allometric estimates of aboveground biomass increments (Equation 5) are summed over all trees i within species groups g . The difference in top-down and bottom-up biomass increment is redistributed to all trees according to their estimated share in bottom-up total biomass growth (Equation 17), and the preliminary bottom-up state of biomass for the current year is updated accordingly:

$$d\Delta B(i, g) = \frac{\Delta BUB_{ag(i, g)}}{\Delta BUB_{ag(g)}} \quad (17)$$

$$(\Delta TDB_{ag(g)} - \Delta BUB_{ag(g)})$$

where $d\Delta B(i, g)$ = correction of bottom-up biomass increment for tree i of species group g (kg_{DM}); $\Delta BUB_{ag(i, g)}$ = bottom-up estimate of aboveground biomass increment for tree i of species group g ; and $\Delta BUB_{ag(g)}$ = bottom-up aboveground biomass increment for species group g (kg_{DM}).

Stand tree dimensions must be derived from the updated biomass estimates of all trees. By inverting Equation 5, the

DBH of all trees can be recalculated, and subsequently the diameter increment of the current year t :

$$\Delta DBH_{(i, g)t} = \sqrt[3]{\frac{Biom_{total(i, g)t}}{a}} - DBH_{(i, g)t-1} \quad (18)$$

For a consistent recalculation of the initial bottom-up height increment estimates, we use the strong relationship between tree stem volume (Equation 6) and tree biomass (Equation 5). For a given species, the ratio of Equations 6 and 5 can be expressed as a function of DBH and H . Once the final biomass of a tree for year t is known, the corresponding tree volume can be estimated by the parameterized function of the stem volume:tree biomass ratio, and H of a tree can be calculated from the inverted volume function (Equation 6) and DBH.

As an additional model component, a management module was included in PICUS v1.3 that allows for the definition of stand treatment programs. Based on five relative diameter classes (class width = $(DBH_{max} - DBH_{min})/5$), the relative removal with respect to volume or basal area in each DBH class can be specified for each tree species in any year of a simulation run. Stand initialization for a simulation is based on species-specific stem numbers (n) in diameter classes ($n ha^{-1}$) and a representative tree height per diameter class.

All other model formulations are as implemented in PICUS v1.2. The new model requires input of a time series of monthly climate data (mean temperature ($^{\circ}C$), precipitation (mm), incoming short wave radiation ($MJ m^{-2} day^{-1}$), vapor pressure deficit (kPa), and soil characteristics in terms of water-holding capacity (WHC; mm), pH and plant-available nitrogen ($kg ha^{-1} year^{-1}$)).

The current study was conducted with one general set of species parameters gathered in recent studies with PICUS v1.2 (see Lexer 2001, Lexer et al. 2001). The simulated stand area in all experiments is 1 hectare, and no site-specific tuning algorithms were applied.

Table 1. Characterization of the study sites. Abbreviations: Temp. = temperature; WHC = soil water-holding capacity; and N_{av} = plant-available nitrogen.

Site no.	Description	Abbreviation	Coordinate	Elevation (m)	Temp. ($^{\circ}C$)	Precipitation (mm year $^{-1}$)	Soil type (FAO)	pH	WHC (mm)	N_{av} (kg ha $^{-1}$ year $^{-1}$)
1	Wolschart-Wald	WW	E 14.37 N 46.78	550	7.6	1013	Eutric Cambisol	4.5	200	100
2	Sub-montane transect plot	T550	E 14.74 N 47.77	550	7.6	1313	Planosol	4.2	161	64.2
3	Montane transect plot	T950	E 15.24 N 47.32	950	5.4	1339	Dystic Cambisol	4.0	142	59.3
4	Sub-alpine transect plot	T1450	E 14.96 N 47.62	1450	2.7	1550	Cambic Podzol	3.9	139	55.3
5	Hirschlacke	HL	E 14.02 N 48.69	750	6.7	1146	Gleyic Cambisol	3.8	183	61.8
6	Lehrforst	LF	E 16.28 N 47.69	500	8.6	947	Cambisol	3.8	128	75.5

Data and study sites

To evaluate the performance of the hybrid model, several study sites across Austria were employed (Table 1). Climate data time series were provided by the Potsdam Institute of Climate Impact Research. For all sites, stochastic 100-year time series data based on the de-trended period 1961–1990 were available. In addition, for Sites 5 and 6, time series data spanning the duration of the growth records were provided. Soil parameters used in the simulation experiments are based on soil samples from Sites 1, 5 and 6, and estimated as the most frequently reported soil type for Sites 2, 3 and 4 along the elevation transect (e.g., Kilian et al. 1994). For the sites along the elevation transect, three soil fertility classes were defined to represent poor, intermediate and rich soil fertility conditions. Site 1 (Wolschart-Wald, hereafter “WW”) features highly productive conditions (mean total increment = $17 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$) with a 40-year-old pure Norway spruce stand with 992 stems ha^{-1} and a standing volume of $410 \text{ m}^3 \text{ ha}^{-1}$. The site was part of a network of study sites within the European Union Fifth Framework Program research project “SilviStrat.” For the productivity experiments, stands at the transect sites were initialized as a 9-year-old pure Norway spruce stand with 2300 stems per hectare. Sites 5 (Hirschlacke, hereafter “HL”) and 6 (Lehrforst, hereafter “LF”) are long-term observation sites of the Institute of Forest Growth Research/BOKU. The HL site in northeastern Austria was first measured in 1977 and features a Norway-spruce-dominated stand with admixed silver fir (*Abies alba* Mill.) and common beech (*Fagus sylvatica* L.) (the latter mainly in the understory), and single individuals of European larch (*Larix decidua* L.) and Scots pine (*Pinus sylvestris* L.). The main stand is older than 100 years with a standing volume of $725 \text{ m}^3 \text{ ha}^{-1}$ at the beginning of the observation period. In contrast, LF in the southeastern part of Austria is a mixed stand of Norway spruce, Scots pine and common beech with admixed fir, larch, oak (*Quercus* spp.) and other deciduous species. Initial measurement at LF was in 1980. Stand development for LF is recorded in a sample plot layout, resulting in a standing volume at trial start of $500 \text{ m}^3 \text{ ha}^{-1}$. At both HL and LF, the management regime focuses on continuous cover forestry with target diameter harvesting being applied at both sites over the course of the observation period.

Model evaluation experiments

The evaluation experiments comprised (a) tests of model response to environmental gradients, and (b) tests of model response to management.

Experiment A was designed to investigate climate sensitivity at Site 1. Simulations were initialized with a 40-year-old pure Norway spruce stand and run over 30 years without management interventions, with mean annual increment (MAI) as the target variable. We investigated a matrix of five changes in temperature (from +1 to +5 °C) and four changes in precipitation (from –20 to +20%) that were additively applied to the baseline climate. The layout is taken from a model study performed within the framework of the SilviStrat project (M. Lindner et al., European Forest Institute, Joensuu, Finland, unpublished manuscript). We compared the results of PICUS

v1.3 with those obtained with the detailed process-based production model BIOMASS (McMurtrie et al. 1990) that was applied in the same study (data from M. Freeman, Swedish University of Agricultural Sciences, Uppsala, Sweden, personal communication).

Experiment B was designed to examine model performance in simulating productivity along an elevation transect (Sites 2, 3 and 4) in terms of MAI of an unmanaged Norway spruce stand over a 100-year simulation period. Simulated response from the submontane to the lower subalpine vegetation belt was evaluated qualitatively, and also compared with results of an Austria-wide forest survey (Austrian Forest Damage Monitoring System (WBS); Herzberger 1996). To cover the possible range of varying site conditions, three soil fertility categories were defined for each transect plot.

Experiment C focused on a traditional strength of patch models. The three transect plots are complemented by HL and LF and used to simulate the equilibrium species composition (ESC) under current climate conditions. This experiment was designed to test whether the new model features affect the simulated long-term competitive relationship of tree species. Site properties are shown in Table 1. The simulation runs were initialized from bare ground, with 22 tree species potentially available for establishment, and run over 1000 years. The species-specific biomass shares averaged over the final 200 years were taken as the estimate of ESC (cf. Lexer 2001). Results are evaluated according to an expert assessment of the natural forest vegetation type as provided for Austrian eco-regions (Kilian et al. 1994), complemented with a classification scheme for ESC-types of the Austrian Forest Inventory (AFI) (F. Starlinger, Federal Forest Research Center, Vienna, Austria, unpublished manuscript).

Experiment D provided a test of model accuracy in predicting the growth of managed forests. Simulations aimed at reproducing the long-term growth and yield observation data at HL (Site 5) and LF (Site 6) were compared with available mensurational records over 20 and 21 years, respectively. Key variables in this assessment were growing stock and periodic volume increment, and structural stand features such as the development of the diameter distribution. The regeneration model of PICUS v1.3 was only deployed in Experiment C.

Results

Experiment A: Sensitivity to climate drivers

PICUS v1.3 shows a distinct response of productivity within the array of investigated changes in temperature and precipitation (Figure 1A). Substantial increment loss is predicted at high temperature and low precipitation. Higher temperatures yielded slightly higher increments only in scenarios with increased precipitation. Although model behavior under warmer and drier conditions matches general ecological expectations for Norway spruce, the relatively minor increase in the case of higher temperatures and increased precipitation was not expected. Apparently, the advantage of a longer vegetation period is offset by higher evapotranspiration demand, which feeds back through less favorable soil water conditions. The

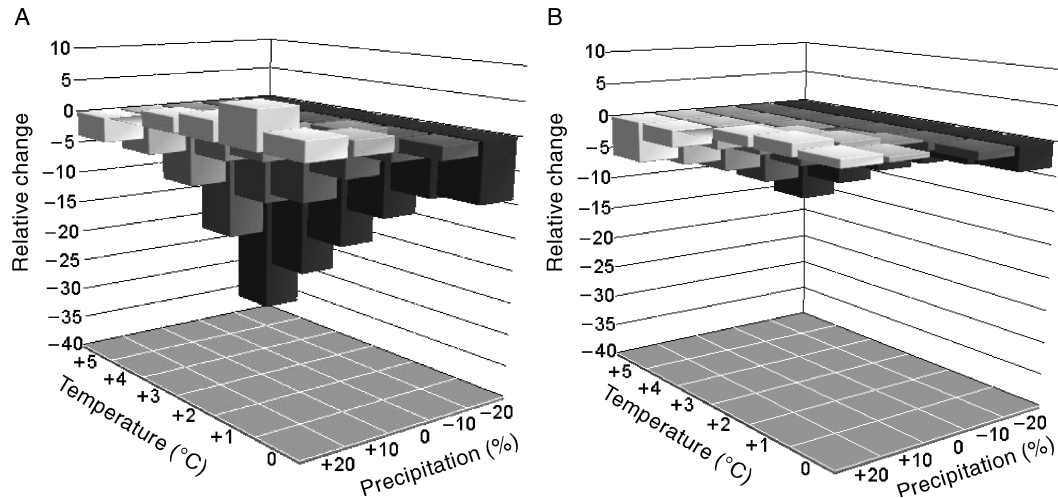


Figure 1. Results of the climate sensitivity simulation experiment at Site 1 (WW): A: PICUS v1.3. B: BIOMASS (M. Freeman, unpublished data). Target variable: relative change of mean annual increment.

model comparison with the BIOMASS model is therefore of particular interest because the two models operate on different levels of physiological detail and rely on different approaches to modeling forest production. Figure 1 shows that the simulated responses of the models are in good agreement ($r_p = 0.929$), with PICUS v1.3 yielding a similar pattern to that of BIOMASS, but being more sensitive overall, especially on the warm and dry end of the scenario matrix.

Experiment B: Productivity along an altitudinal gradient

The combined environmental effects of varying soil and climate conditions were investigated along an elevation transect (Sites 2–4). From Figure 2, it can be seen that varying soil fertility yields a generally distinct increment response, whereas the effect of climate (i.e., altitude) is strongest on fertile soils. The combined effect of soil and climate results in sensible esti-

mates of the mean annual increment at age 100 years (MAI_{100}) for the respective elevation. The simulations relate well to the records of WBS as the whole scatter of recorded site classes is covered by the model simulations. Furthermore, the regression slopes describing the effect of elevation for the three soil fertility classes (-0.0052 , -0.0011 and -0.0006 for rich, medium and poor soil fertility, respectively) are in reasonable agreement with the mean regression slope of -0.0050 reported by Herzberger (1996).

Experiment C: Equilibrium species composition

Along the altitudinal gradient, simulated ESC changes from beech-dominated at the submontane plot to spruce-beech (montane) and spruce (subalpine) (Figure 3). Although comparable quantifications at the species level have rarely been made in the ecological literature (cf. Lexer 2001), the simula-

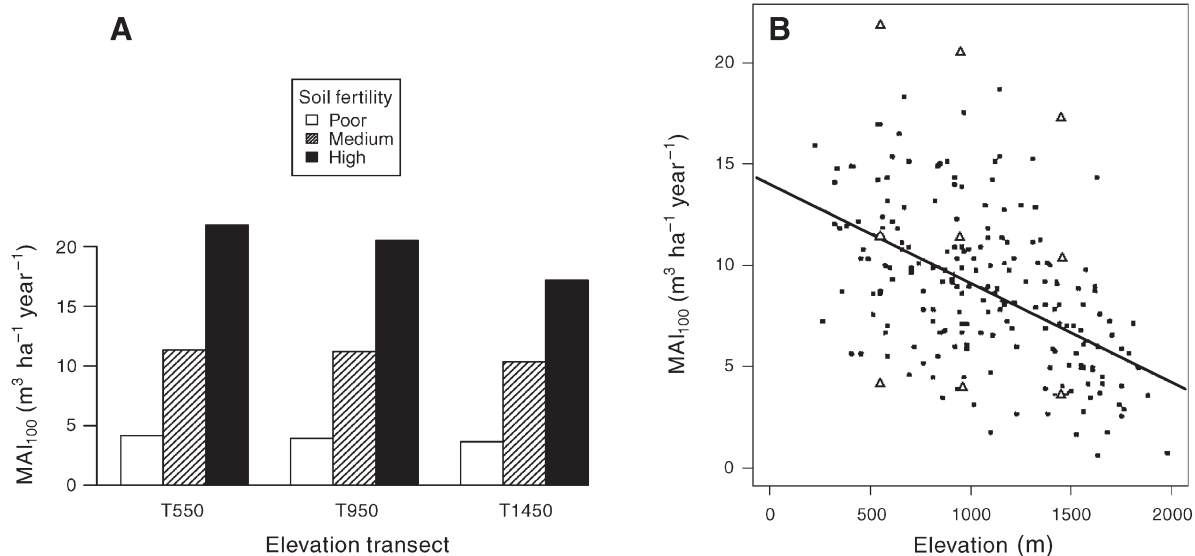


Figure 2. (A) Simulated Norway spruce productivity (MAI_{100} = mean annual increment over 100 years) along an elevation transect and three qualitative soil fertilities. (B) Simulation results (Δ) compared to records of the Austrian forest damage monitoring system (modified from Herzberger 1996).

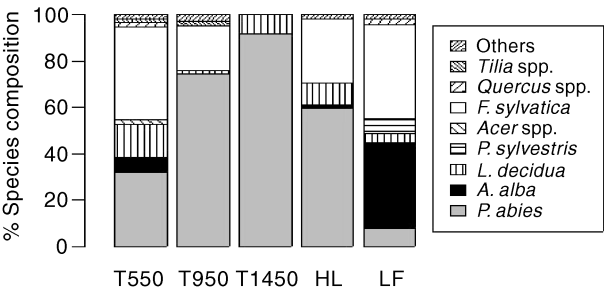


Figure 3. Simulated equilibrium species composition under current climate.

tion results correspond well to expert assessments of natural forest types as described by Kilian et al. (1994) and to the semi-quantitative classification scheme of the AFI, which explicitly breaks down forest types into possible species shares (Starlinger, unpublished data) (Table 2). Extending this assessment from the alpine transect, dominated by the altitudinal gradient, to two different eco-regions in the north (HL) and southeast (LF) of Austria, again demonstrated that PICUS v1.3 captures the realized niche of tree species well. The HL site is dominated by Norway spruce as a result of a harsh continental climate that limits the colonization by silver fir and deciduous species. At the milder LF site, where the occurrence of oak and pine reflect the warmer and drier conditions, beech is the most abundant species. The high proportion of silver fir at LF is unexpected; however, this species is frequently de-

scribed as an abundant admixed species in such communities (Kilian et al. 1994, Mayer 1974).

Experiment D: Evaluation against long-term growth and yield data

Detailed growth and yield measurements were related to model output at two sites offering detailed stand data records. The model tends to overestimate at LF, whereas at HL, the opposite is the case (Figures 4A and 4B). Regressions between observed and predicted increments yielded significant slope coefficients, whereas the intercept was not significantly different from zero at either site (Figure 4, lower panel). At LF, which is monitored by means of a sample plot layout, the simulation results are within the 95% confidence interval of the observed values. A review of the corresponding periodic increments reveals that at HL, the underestimation is mainly due to Norway spruce, whereas both Norway spruce and Scots pine are the major contributors to the overestimation of volume increment at LF. Predicted volume increment of beech is close to the 1:1 line in both stands (Figures 4C and 4D). At the stand level, mean annual increment (MAI) over the observation period is underestimated at HL (−15.8%) and overestimated at LF (+27.5%), likely reflecting the major role played by management in these stands, which were intensively managed throughout the observation period. The noticeable differences between observed and predicted values for harvested volume in turn interfered with predicted growing stock and volume increment. The total amount of removed volume (harvest plus natural mortality) is noticeably higher in the simula-

Table 2. Comparison of simulated equilibrium species composition to expert assessments of natural forest types for forest eco-regions. Species bounds for the respective forest type are given according to the classification scheme of the AFI (Starlinger, unpublished manuscript). Species with a share of less than 2% aboveground biomass are not shown.

Study site	Simulation		Expert assessment	
	Species	Share (%)	Forest type (Kilian et al. 1994)	Species abundance
T550	<i>F. sylvatica</i>	40.1	<i>F. sylvatica</i> forest, admixed	<i>F. sylvatica</i> + <i>Quercus</i> sp. > 50%
	<i>P. abies</i>	31.9	<i>A. alba</i> , <i>A. pseudoplatanus</i> ,	<i>F. sylvatica</i> > <i>Quercus</i> sp.
	<i>L. decidua</i>	14.1	<i>F. excelsior</i> , <i>P. abies</i> ,	<i>P. abies</i> + <i>A. alba</i> < 40%
	<i>A. alba</i>	6.7	<i>P. sylvestris</i> and <i>Quercus</i> sp.	<i>L. decidua</i> < 25%
	<i>Acer</i> sp.	2.1		<i>Acer</i> sp. < 30%
T950	<i>P. abies</i>	74.6	<i>P. abies</i> / <i>A. alba</i>	<i>P. abies</i> + <i>A. alba</i> > 40%
	<i>F. sylvatica</i>	19.3	<i>F. sylvatica</i> forest	<i>F. sylvatica</i> > 20%
	<i>Tilia</i> sp.	2.2		
T1450	<i>P. abies</i>	91.8	<i>P. abies</i> forest	<i>P. abies</i> + <i>L. decidua</i> > 70%
	<i>L. decidua</i>	8.2		<i>P. abies</i> > 35%
HL	<i>P. abies</i>	59.5	<i>P. abies</i> / <i>A. alba</i>	<i>P. abies</i> + <i>A. alba</i> > 40%
	<i>F. sylvatica</i>	27.7	<i>F. sylvatica</i> forest	<i>F. sylvatica</i> > 20%
	<i>L. decidua</i>	9.6		<i>L. decidua</i> < 20%
LF	<i>F. sylvatica</i>	40.7	<i>A. alba</i> / <i>F. sylvatica</i> forest	Forest type not classified
	<i>A. alba</i>	36.9	with admixed <i>Quercus</i> spp.,	
	<i>P. abies</i>	8.0	<i>C. sativa</i> and <i>P. sylvestris</i>	
	<i>P. sylvestris</i>	6.6		
	<i>L. decidua</i>	3.7		
	<i>Quercus</i> sp.	2.2		

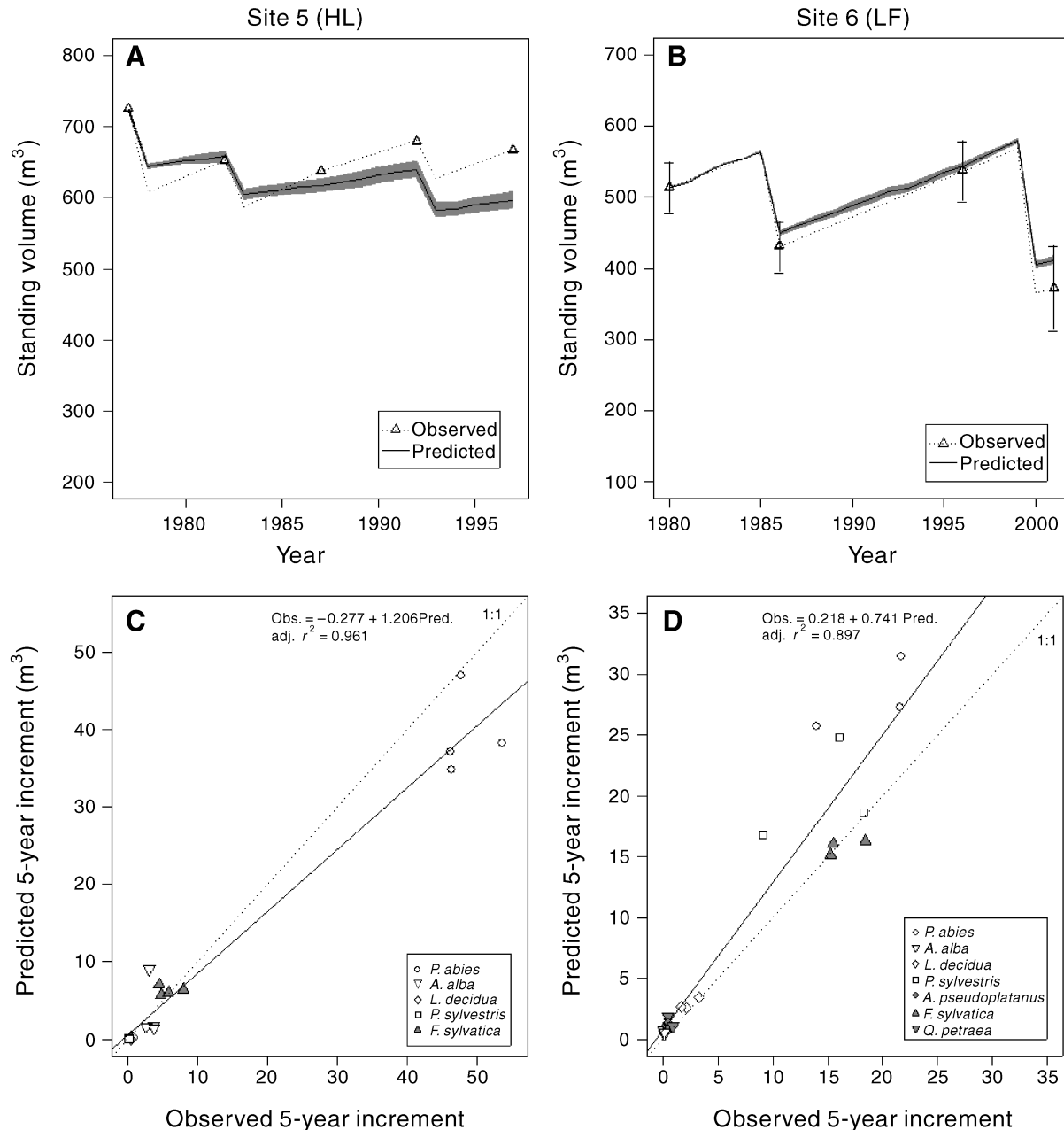


Figure 4. (A and C) Site 5 (HL) and (B and D) Site 6 (LF). A and B: Time-series of observed and predicted standing volume. Shaded area is the envelope of 10 model runs ($\alpha = 0.95$); error bars at site 6 represent the 95% confidence interval for observed volumes (sample plot inventory). C and D: predicted and observed 5-year volume increment in the observation periods.

tion than in the record (+13.1% at HL, +9.5% LF). However, observed versus predicted stem numbers are in good agreement at both sites, with differences smaller than $\pm 5\%$ at the end of the observation period. The comparison of predicted and observed diameter distribution over the observation period reveals that PICUS v1.3 is capable of simulating complex stand structures as represented by HL and LF sites over two decades (Figure 5). Kolmogorov-Smirnov statistics indicate no significant difference between observed and predicted DBH-distribution for all observation periods at both sites ($\alpha = 0.05$).

Discussion

We present a hybrid model that builds on a well-established three-dimensional forest patch model and integrates components of a process-based stand-level productivity model to assess model generality and accuracy. Although hybridization in general is seen as a promising technique to bridge the gap between detailed, parameter-rich process-based models and robust empirical models used in forest management (Mäkelä et al. 2000, Liu and Ashton 1995), the approaches and levels of hybridization are manifold. Whereas some hybrid forest mod-

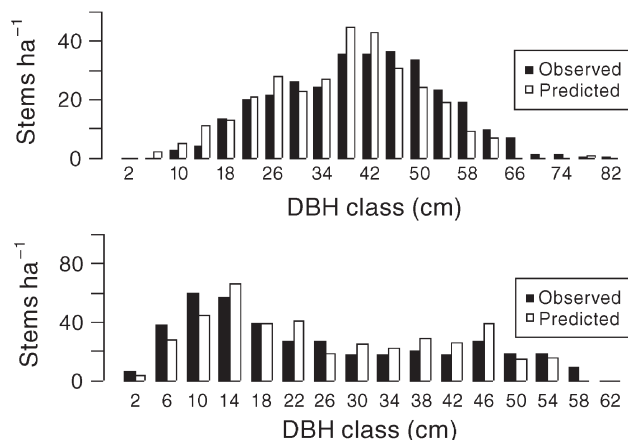


Figure 5. Diameter distribution at the end of the simulation experiment at Site 5 (HL) (upper) and Site 6 (lower). Kolmogorov-Smirnov tests yield *P* values of 0.982 (HL) and 0.941 (LF).

els are built from components of several models (e.g., Peng et al. 2002, Robinson and Ek 2003), in our approach hybridization was used to circumvent a specific deficiency of a former version of PICUS.

The study was partly motivated by the recognition that ecological models rarely satisfy the criteria of realism, generality and accuracy simultaneously (Levins 1966, Guisan and Zimmermann 2000), and by Yaussy (2000)'s model evaluation study, which questioned the application of any patch model. In this contribution, we use the term generality to denote the applicability of a model to a wide range of ecological conditions (site, stand, management) and a variety of target variables (species composition, structure, yield) without changes in model structure and parameters or tuning to site or stand conditions (cf. Battaglia and Sands 1998).

We tested the generality of the hybrid model with a climate sensitivity experiment extrapolating current temperature and precipitation regimes by magnitudes, estimated by the IPCC (2001), consistent with projections of a possible future climate change. We also evaluated the applicability of the general model over a wide range of environmental conditions in terms of two different target variables—productivity at the time scale of a rotation length, and ESC at a time scale of centuries. The same model parameterization was also applied to simulate growth and yield of two managed complex-structured mixed forests over two decades.

Reviewing the model's sensitivity to climate, plausible behavior of PICUS v1.3 is found with respect to Norway spruce productivity, showing that the species is sensitive to drought, and its productivity is optimum under the current climatic conditions of Site 1. This behavior conforms well with the potential niche of Norway spruce (e.g., Mayer 1974, Spiecker et al. 2004). The highly plausible result for the sensitivity of Norway spruce productivity to climatic changes is corroborated by the model comparison with BIOMASS (McMurtrie et al. 1990), which was run under identical experimental conditions (M. Freeman, personal communication). BIOMASS is a daily time-step model and includes a detailed crown architecture, a

radiation absorption model, and a model of leaf photosynthesis that distinguishes between sunlit and shaded foliage (e.g., McMurtrie 1993, McMurtrie and Wang 1993). The BIOMASS model has been applied successfully in several studies of forest productivity under conditions of climatic change (e.g., Berg et al. 1998, 2003, Hingston and Galbraith 1998). BIOMASS was not used to calibrate model formulations within PICUS v1.3.

In qualitative terms, the models showed virtually the same response in the climate sensitivity experiment, with PICUS simulating a more pronounced decrease in productivity at the most extreme combinations of higher temperatures and reduced precipitation. Detailed analysis indicated that the simple one-layer soil water model of PICUS might have overestimated drought conditions at Site 1, leading to more severe drought stress for Norway spruce, and consequently reduced biomass production. Although, overall, this is an encouraging result, it also highlights some deficiencies of the current model version. A further comparison with other process-based models over a range of ecological conditions (i.e., sites, species) would enhance model credibility during extrapolation in bioclimatic space.

Along environmental gradients as represented by the alpine transect, model results for productivity and equilibrium tree species composition (i.e., potential natural vegetation as defined by Tüxen (1956)) agree well with literature and ecological expert expectations. Simulated Norway spruce productivity (MAI_{100}) for the matrix of three synthetic soil fertility classes and three altitudes representing a mean annual temperature gradient from +7.6 to +2.7 °C was compared with findings from a study by Herzberger (1996), who determined MAI from yield tables, observed dominant height and stand age. The 100-year simulations did not include management interventions. According to Assmann (1961), volume productivity in unmanaged stands on sites of high soil fertility will be higher than in thinned stands, as is assumed by yield tables. The simulated MAI of about 16 m³ ha⁻¹ at altitudes of 1450 m a.s.l. in the best soil fertility scenario appears unrealistic; however, this is primarily due to the synthetically defined soil attributes, which are probably too favorable for the high altitude site compared with real site conditions. The productivity estimate of 21 m³ ha⁻¹ year⁻¹ in the best soil fertility scenario at the low-elevation site, which is outside the scatter of values as observed by Herzberger (1996), is well within the bounds of empirical observations for Austria (e.g., Unegg 1998). It may be worthwhile simulating productivity for all sites in Herzberger (1996) to compare simulated results with field data. However, the need to estimate climate data and soil parameters required to drive PICUS for all sites will introduce additional sources of error (cf. Lexer and Hönniger 2004).

Comparison of simulated ESC with expert reconstructions of potential natural forest vegetation (PNV) at five sites indicated that the well-known strength of the patch model version PICUS v1.2 has been successfully retained. It is acknowledged that matching simulated ESC and PNV does not represent direct empirical evidence. Rather, it resembles a model inter-comparison because expert reconstructions of PNV can

be viewed as “modeled” output. The use of empirical species composition data from virgin forests as an alternative to PNV would impose other serious difficulties that might hamper rigorous model evaluation (e.g., Badeck et al. 2001). In the current exercise, the ecological niche for species whose synecological behavior is difficult to mimic (such as *Abies alba* at site LF) is well captured by the model.

Besides having a weak physiological foundation, inaccurate growth and yield predictions are considered a major limitation of gap models (e.g., Yaussy 2000). Results of PICUS v1.3 were compared with long-term stand and tree growth data from two mixed stands managed under a continuous cover management regime. Although the model successfully predicted diameter distribution over time, there was a tendency to either overestimate (at site LF) or underestimate (at site HL) periodic volume increment for certain species. At site LF, simulated stand development was within the 95% confidence interval, whereas simulated growth of Norway spruce was apparently too low at site HL. This underestimation highlights the importance of accurate soil and climate data for process-based forest modeling. A sensitivity analysis along the altitudinal transect sites revealed that simulated productivity was sensitive to plant-available nitrogen (N_{av}) and soil pH. An increase in N_{av} by 10% resulted, on average, in an increase in MAI of Norway spruce over 100 years of 12.1%; a decrease in N_{av} by the same amount resulted in a mean decrease of 10.3%. This is relevant to the validation experiment because N_{av} is the only soil input that has not been directly derived from laboratory analysis, but was estimated from the total soil nitrogen pool by applying a temperature-dependent mineralization function (Paul 2001, Knoepp and Swank 2002).

A second limitation arose from the general nature of the data on timber harvests and mortality. The data records of most long-term growth and yield trials lack exact information about whether a tree was removed as a result of silvicultural intervention or died naturally. In our study, the “disappearance” of trees from both sites in periods without management intervention supports the assumption of natural mortality in the stands. For this proportion of the total removed volume, we lack both timing and amount, thus the mortality sub-model is deployed in the simulations. Although the mortality routine of the hybrid model realistically mimicked the self-thinning process in unmanaged stands (data not shown), in our managed stands, it led to an overestimation of mortality. Consequently, simulation of harvesting operations from data records is not straightforward and the pattern of implemented timber removals is likely to contribute to the deviation between simulated and observed results.

However, despite these deficiencies, simulation results deviate within reasonable bounds around measured values, if the accuracy demands of forest management and the precision of forest mensuration are taken into account (Battaglia and Sands 1998). It is interesting to compare the results of the validation experiment with similar studies. Sterba and Monserud (1997) applied the empirical, distance-independent, individual-tree-based growth and yield simulator PROGNAUS to predict growth of mixed stands of Norway spruce and Scots pine in

northeastern Austria over three 5-year periods and found coefficients of determination for the regression of predicted and observed increments in the range of $r^2 = 0.413$ to 0.813 . Merganicová et al. (2005) employed a species-specific variant of BIOME-BGC (Thornton 1998, Pietsch and Hasenauer 2002) to predict the development of Norway spruce stands managed under different timber harvesting regimes and found r^2 values for regressions between observed and predicted volume increment of between 0.17 and 0.65.

In response to Yaussy's (2000) criticism of forest patch models, we note that patch models can predict growth and yield with reasonable accuracy. Additionally, the proposed hybrid modeling approach improved the physiological foundation of the model and its robustness along environmental gradients and in extrapolated bioclimatic space. Moreover, the model evaluation exercises presented support the high degree of generality of the proposed hybrid modeling approach. The low input requirements of the model (4 climate variables, 3 soil variables, stem number in diameter classes) make it attractive for further application. Specific parameterization procedures as proposed, for instance, by Sands and Landsberg (2002) would further improve model performance.

A major criticism of the 3-PG model has been the simplifying assumption of a constant NPP:GPP ratio (e.g., Cannell and Thornley 2000, Mäkelä and Valentine 2001). This feature of 3-PG has been integrated in PICUS v1.3. Another limitation of the current model version is that it lacks a dynamic soil model. To tackle the challenges of sustainable forestry, the cycling of carbon and nitrogen as influenced by management and environmental conditions needs to be considered. A soil model that might fit well to the structural and temporal resolution of PICUS v1.3 has been presented by Currie et al. (1999). Future work will focus on the integration of such model components.

Acknowledgments

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