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Do individual-tree growth models correctly represent height:diameter ratios of Norway spruce and Scots pine?

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ABSTRACT

Height:diameter ratios are an important measure of stand stability. Because of the importance of height:diameter ratios for forest management, individual-tree growth models should correctly depict height:diameter ratios. In particular, (i) height:diameter ratios should not exceed that of very dense stands, (ii) height:diameter ratios should not fall below that of open-grown trees, (iii) height:diameter ratios should decrease with increasing spacing, (iv) height:diameter ratios for suppressed trees should be higher than ratios for dominant trees. We evaluated the prediction of height:diameter ratios by running four commonly used individual-tree growth models in central Europe: *BWIN*, *Moses*, *Silva* and *Prognaus*. They represent different subtypes of individual-tree growth models, namely models with and without an explicit growth potential and models that are either distance-dependent (spatial) or distance-independent (non-spatial). Note that none of these simulators predict height:diameter ratios directly. We began by building a generic simulator that contained the relevant equations for diameter increment, height increment, and crown size for each of the four simulators. The relevant measures of competition, site characteristics, and stand statistics were also coded. The advantage of this simulator was that it ensured that no additional constraint was being imposed on the growth equations, and that initial conditions were identical. We then simulated growth for a 15- and 30-year period for Austrian permanent research plots in Arnoldstein and in Litschau, which represent stands at different age-classes and densities. We also simulated growth of open-grown trees and compared the results to the literature. We found that the general pattern of height:diameter ratios was correctly predicted by all four individual-tree growth models, with height:diameter ratios above that of open-grown trees and below that of very dense stands. All models showed a decrease of height:diameter ratios with age and an increase with stand density. Also, the height:diameter ratios of dominant trees were always lower than that of mean trees. Although in some cases the observed and predicted height:diameter ratios matched well, there were cases where discrepancies between observed and predicted height:diameter ratios would be unacceptable for practical management predictions.

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1. Introduction

The height:diameter ratio is an important measure of tree and stand stability for conifers. Trees with higher ratios are more prone to snow and wind damage than trees with lower ratios. This was found for a variety of conifer species such as Norway spruce (*Picea abies*) (Pollanschütz, 1974; Merkel, 1975; Bentz and Schön, 1981; Rottmann, 1985), Scots pine (*Pinus sylvestris*) (Abetz and

Prange, 1976; Rottmann, 1985), ponderosa pine (*Pinus ponderosa*) (Powers and Oliver, 1970; Wonn and O'Hara, 2001), lodgepole pine (*Pinus contorta*) (Wonn and O'Hara, 2001), white fir (*Abies alba*) (Mangold and Spellmann, 1989), western larch (*Larix occidentalis*) (Wonn and O'Hara, 2001) and Douglas-fir (*Pseudotsuga menziesii*) (Bentz and Schön, 1981; Wonn and O'Hara, 2001). Trees with a height:diameter ratio of 80:1 or less (both measured in identical meter units) are considered stable (Abetz and Prange, 1976; Wonn and O'Hara, 2001). While this trend is relatively consistent among species, some variation does exist within species. For broadleaves, the effect of height:diameter ratio on tree stability is rarely considered. Under circumstance where the trees are liable to snow loading, broadleaves would be leafless.

Variations in height:diameter ratio are largely a result of spacing. Spacing trials and thinning experiments consistently show that

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as intertree spacing increases, height:diameter ratio decreases. Distinct differences were found for Norway spruce (Burger, 1936; Abetz, 1976; Bergel, 1982; Abetz and Unfried, 1983; Abetz and Feinauer, 1987; Röhle, 1995; Mäkinen and Isomäki, 2004) and Scots pine (Erteld, 1979; Mäkinen et al., 2005). The additional growing space provided through wider initial spacing or thinning (growing stock level trials) allows residual trees to maintain rapid diameter growth, thus increasing taper. The most extreme height:diameter ratios would be reached for open-grown trees and for trees at a maximum stand density. Furthermore, wide spacings or early thinnings provide the best means to reduce height:diameter ratios. Later thinnings are not as effective as heavy thinnings done early during stand development because the capacity to respond to release declines with age (Dimitri and Keudell, 1986; Wonn and O'Hara, 2001; Mäkinen and Isomäki, 2004).

On the stand level, a number of processes affect height:diameter ratios. First, the height growth of dominant trees is usually little affected by density. Subordinate members of the canopy, however, do experience height growth repression as competition increases with age and stocking (Abetz, 1976; Erteld, 1979; Mäkinen and Isomäki, 2004; Bevilacqua et al., 2005). In an attempt to maintain canopy position and better compete for light resources, intermediate and suppressed trees have less diameter growth for a given unit of height growth than more dominant trees. As stands differentiate, lower crown classes have smaller heights and disproportionately smaller diameters. Second, the absolute effect of thinning on basal area increment is highest for dominant trees because those trees have larger crowns and respond best to release (Mäkinen and Isomäki, 2004). The smaller trees cannot react to the increasing growing space as strongly as the larger ones. However, the relative increase in basal area increment (i.e. basal area increment/basal area at establishment) is higher for codominant and medium-sized trees (Assmann, 1961; Mäkinen and Isomäki, 2004). Third, self-thinning removes primarily lower crown classes from the stand. This process removes trees with high height:diameter ratios and has the effect of lowering the average ratios for the stand, even though all individual-tree height:diameter ratios might increase with time. The distribution is truncated on the left, which results in both an increased mean diameter and an increased skewness.

In model evaluation, it is important to analyse if model output is consistent with existing theories of forest growth (Vanclay and Skovsgaard, 1997). Even though many examples of an evaluation of individual-tree growth models exist (Pretzsch, 1992; Hasenauer, 1994; Kahn, 1995; Hasenauer and Monserud, 1996; Monserud and Sterba, 1996; Nagel, 1999, 2009; Kindermann and Hasenauer, 2005; Nachtmann, 2006; Froese and Robinson, 2007), it is rarely examined if individual-tree growth models conform to existing theories of forest growth. Two of the few examples are Pretzsch et al. (2002) and Monserud et al. (2005). Those papers examined if the models conform to self-thinning theory.

In this paper we examine if individual-tree growth models correctly represent the known principles on height:diameter ratios. Specifically, we want to examine the following hypotheses:

H1. Height:diameter ratios should not exceed that of very dense stands.

H2. Height:diameter ratios should not fall below that of open-grown trees.

H3. Height:diameter ratios should decrease with increasing spacing.

H4. Height:diameter ratios of suppressed trees should be higher than that of dominant trees.

2. Tree growth models

These hypotheses (H1–H4) will be tested using four widely used individual-tree growth models in Central Europe: *BWIN* (Nagel, 1999, 2009), *Moses* (Hasenauer, 1994; Kindermann and Hasenauer, 2005), *Prognaus* (Hasenauer and Monserud, 1996; Monserud and Sterba, 1996; Nachtmann, 2006) and *Silva* (Pretzsch, 1992; Kahn, 1995). These growth models were fit using data from permanent research plots in Central Europe, namely Lower Saxony (*BWIN*), Austria (*Moses*), and Bavaria (*Silva*), while *Prognaus* models were fit from the data of the Austrian National Forest Inventory.

The models have been evaluated on independent data and the nature of errors was analysed. Examples are Schröder (2004), Schmidt and Hansen (2007) for *BWIN*, Hallenbarter and Hasenauer (2003), Kindermann and Hasenauer (2007) for *Moses*, Sterba and Monserud (1997), Sterba et al. (2001) for *Prognaus*, Pretzsch (2002), Mette et al. (2009) for *Silva*. As a result, original coefficients published have sometimes been refit, using more extensive data (Pretzsch and Kahn, 1998) or more sophisticated statistical techniques (Hasenauer, 2000) and inappropriate models have been replaced (Nachtmann, 2006). Furthermore, these models represent different types of individual-tree growth models: models with and without an explicit growth potential and models with either distance-dependent or distance-independent measures of competition. Note that none of the four simulators predict height:diameter ratios directly.

Generally speaking, individual-tree growth models consist of functions for predicting diameter increment, height increment, crown size (e.g., crown ratio), and the probability of mortality for each tree over a given time period. A competition submodel is necessary to assess the competition situation of each tree within the stand. This competition measure can either be spatial (distance-dependent) or non-spatial (distance-independent). Although many additional submodels and features are often available (e.g., in growth routine, form factor functions, merchantable volume equations, insect damage, etc.), we will focus on the diameter and height increment functions and submodels for competition and crown ratio, which are the routines needed to predict height:diameter ratio. These functions usually are the core of the simulator.

Two general strategies exist for predicting growth: potential growth modifier functions, and direct functions. With the former, the growth rate of individual trees is the product of potential growth and a modifier (Newnham, 1964). For height increment, the theoretical maximum height growth rate attainable is most frequently estimated from height growth (site-index) curves of dominant trees at different ages for a given level of site productivity. Modifier functions may vary, but most contain crown ratio and some index of tree density or tree competition. The modifier will reduce height growth rate if a given tree is in a disadvantageous position within a stand. The growth models *BWIN*, *Moses*, and *Silva* use height increment models with a potential and modifier (see Table 1).

With the latter strategy, direct functions express diameter or height increment directly as a function of tree, stand, and site characteristics, including the competitiveness of a tree in a stand (Wykoff, 1990). Commonly used functions include the logistic, Chapman–Richards, or the Evolon model (Mende and Albrecht, 2001). *Prognaus* uses a direct functional approach (Table 1).

An advantage of models with a potential height increment is that height growth is reasonably bounded from above. In contrast, a model without growth potential might give unreasonable tree height increments if the underlying mathematical model is inappropriate or site conditions or the age span are an extreme extrapolation. A disadvantage of models with a potential height

Table 1
Height increment models of BWIN, Moses, Prognaus and Silva; see Table 4 for variables and their abbreviations.

BWIN	Model type	With potential from yield table, requires age, distance-independent competition
	Author	Original model: Nagel (1999); Coefficients: Nagel (2009)
Moses	Function	$h_{100} = a_0 + a_1 \cdot \ln(\text{age}) + a_2 \cdot \ln^2(\text{age}) + a_3 \cdot \text{SI} + a_4 \cdot \text{SI} \cdot \ln(\text{age})$ $ih_{\text{Pot}} = h_{100}(\text{age} + 5 \text{ years}) - h_{100}(\text{age})$ $ih = h \left(\frac{ih_{\text{Pot}}}{h_{100}} \right) + a_0 \cdot \left(\frac{h_{100}}{h} \right)^{a_1}$
	Model type	With potential from yield table, distance-dependent function
Prognaus	Author	Original model: Hasenauer (1994); Coefficients: Moses 3.0
	Function	$h_{100} = a_0 + a_1 \cdot \text{SI} + a_2 \cdot \text{SI}^2 \cdot \left(1 - e^{-\left(a_3 + a_4 \cdot \text{SI} + a_5 \cdot \text{SI}^2 \right) \cdot \text{age}^{(a_6 + a_7 \cdot \text{SI} + a_8 \cdot \text{SI}^2)}} \right)^{(a_9 + a_9 \cdot \text{SI} + a_{10} \cdot \text{SI}^2)}$ $ih = ih_{\text{Pot}} \cdot (cr^{a_0} \cdot (1 - e^{a_1 / (1 + a_2 \cdot \text{Cl}_{\text{Diff}})}))$
Silva	Model type	No explicit potential, Evolon model, Mende and Albrecht (2001)
	Author	Original model: Nachtmann (2006); Coefficients: Nachtmann (2006)
Silva	Function	$ih = c_0 \cdot h^k \cdot (B - h)^\lambda$ $\kappa = a_0 + a_1 \cdot \frac{h}{\text{hdom}} + a_2 \cdot \text{CCF} + a_3 \cdot \text{BAL} + z \cdot \text{Sitedummies}$ $B = b_0 + b_1 \cdot (\text{Elev} - s_x)^2 + b_2 \cdot \text{SL}^2 + b_3 \cdot \text{SL} \cdot \sin(\text{AZ}) + b_4 \cdot \cos(\text{AZ}) + z \cdot \text{Sitedummies}$ $\lambda = l_1 + z \cdot \text{Sitedummies}$
	Model type	Chapman–Richards function, with potential derived from site parameters, distance-dependent competition
Silva	Author	Original model: Kahn (1994); Coefficients: Pretzsch and Kahn (1998)
	Function	$h_{100} = A \cdot \left(1 - e^{-k \cdot \text{age}} \right)^p$ $ih_{\text{Pot}} = h_{100}(\text{age} + 5 \text{ years}) - h_{100}(\text{age})$ $ih = ih_{\text{Pot}} \cdot a_5 \cdot (1 - e^{-a_0 \cdot \text{CSA}}) \cdot e^{-a_4 \cdot (1 + \text{KMA})^{a_1} \cdot (1 + \text{NDIST})^{a_2} \cdot (\text{KKL} + a_3 \cdot \Delta \text{KKL})}$

increment is that the potential might be wrong. If the potential is too high (or low), then also the influence of competition would be overestimated (or underestimated) (Hasenauer, 2006).

Similarly, diameter increment models also use an approach with and without a growth potential. For diameter increment, the growth rates of open-grown trees provide useful empirical bounds for individual stand-grown trees (Smith et al., 1992). The potential growth is then again adjusted by a modifier accounting for competition. One possible concern is that open-grown trees become less and less analogous to forest-grown trees as the trees age and get larger. Models without a potential usually express increment as a function of size, site characteristics, and competition. *Silva* and *Moses* use a diameter increment model with a potential, *BWIN* and *Prognaus* use a diameter increment model without a potential. Model details are found in Table 2.

Crown size is an important measure of tree vigour. A tree's crown reflects the cumulative level of competition over the past and the potential for a released tree to utilize available resources such as increasing growing space. Accordingly, many single-tree growth models use crown size (usually crown ratio or crown length) as a predictor of height and diameter increment, as well as tree mor-

tality. Changing tree and stand characteristics over the course of a growth projection necessitates a model to update the estimate of crown size. The most common way is to use a function to estimate crown size directly using correlated tree size and stand characteristics. The advantage is that resulting relationship predicts the crown size for the next growing period from current tree and stand conditions. This procedure is appealing when only one-time observations of crown size are available, the usual situation with forest inventory data. If crown size has been observed repeatedly for at least two successive periods on the same individuals, then the change in crown size can be predicted directly, again relying on a relationship between crown increment and tree and stand characteristic (Hasenauer and Monserud, 1996). *BWIN*, *Prognaus*, and *Silva* use a model for crown size; change in crown size is used by *Moses* (Table 3).

A measure of competition is a surrogate for the ability of a tree to compete for scarce resources, such as light, water, and nutrients. A measure of competition or stand density is a key independent variable in most height and diameter increment functions, as well as the model for mortality. The competition measure can either include spatial information (distance-dependent) or not (distance-

Table 2
Basal area increment models of BWIN, Moses, Prognaus, Silva, see Table 4 for variables and their abbreviations.

BWIN	Model type	No explicit potential, distance-independent competition
	Author	Original model: Nagel (1999); Coefficients: Nagel (2009)
Moses	Function	$\ln(\text{bai}) = (b_0 + b_1 \cdot \ln(\text{CSA}) + b_2 \cdot \ln(\text{age}) + b_3 \cdot \text{c66} + b_4 \cdot \text{c66}_{\text{Diff}}) \times 10000$
	Model type	With potential–potential diameter increment: diameter increment a tree with maximum height increment would have, distance-dependent competition
Prognaus	Author	id _{Pot} : Stampfer (1995)
	Function	id: Original model: Hasenauer (1994); Coefficients: Moses 3.0 $id_{\text{Pot}} = a_0 \cdot (h + ih_{\text{Pot}})^{a_1} - a_0 \cdot (h)^{a_1}$ $id = id_{\text{Pot}} \cdot (cr^{a_0} \cdot (1 - e^{a_1 / (1 + a_2 \cdot \text{Cl}_{\text{Diff}})}))$
Silva	Model type	No explicit potential, distance-independent competition
	Author	Original model: Monserud and Sterba (1996); Coefficients: Hasenauer (2000)
Silva	Function	$\ln(\text{bai}) = a_0 + a_1 \cdot \ln(\text{dbh}) + a_2 \cdot \text{dbh}^2 + a_3 \cdot \ln(\text{cr}) + a_4 \cdot \text{BAL} + a_5 \cdot \text{CCF} + s \cdot \text{Site}$ Site = $s_0 \cdot (\text{Elev} - s_x)^2 + s_1 \cdot \text{SL}^2 + s_{1a} \cdot \text{SL} + s_2 \cdot \sin(\text{AZ}) + s_3 \cdot \cos(\text{AZ}) + s_4 \cdot F - \text{Humus} + s_5 \cdot H - \text{Humus} + z \cdot \text{Sitedummies}$ Dummy variables for soil type, soil moisture, soil depth, vegetation type, growth district, slope position
	Model type	With potential, derived from the 95th percentile of increment for a certain dbh class, distance-dependent competition
Silva	Author	Original model: Pretzsch et al. (2002); Coefficients: Pretzsch et al. (2002)
	Function	$id_{\text{Pot}} = a_0 \cdot (1 - e^{-a_1 \cdot \text{dbh}})^{a_2} \cdot a_1 \cdot a_2 \cdot e^{-a_1 \cdot \text{dbh}}$ $\text{bai} = \text{bai}_{\text{Pot}} \cdot \text{ESTO} \cdot a_5 \cdot (1 - e^{-a_0 \cdot \text{CSA}}) \cdot e^{-a_4 \cdot (1 + \text{KMA})^{a_1} \cdot (1 + \text{NDIST})^{a_2} \cdot (\text{KKL} + a_3 \cdot \Delta \text{KKL})}$ Esto: Aggregation of site variables for details see Pretzsch and Kahn (1998).

Table 3

Crown models of BWIN, Moses, Prognaus and Silva; see Table 4 for variables and their abbreviations.

BWIN	Model type Author Function	Base of live crown, crown width <i>Original model:</i> Nagel (1999); <i>Coefficients:</i> Nagel (2009) $cb = h \cdot (1 - e^{-abs(a_0+a_1 \cdot (h/dbh)+a_2 \cdot dbh+a_3 \cdot \ln(h/100))})$ $cw = (a_0 + a_1 \cdot dbh) \cdot (1 - e^{-(dbh/a_2)^{a_3}})$
Moses	Model type Author Function	Change of base of live crown <i>Original model:</i> Hasenauer (1994), <i>Coefficients:</i> Moses 3.0 $cb_{Delta} = a_0 \cdot h^{a_1} \cdot e^{(a_2 \cdot \sqrt{CI} + a_3 / CI_{Diff}) + a_4 \cdot dbh}$
Prognaus	Model type Author Function	Crown ratio <i>Original model:</i> Hasenauer and Monserud (1996), <i>Coefficients:</i> Hasenauer (2000) $cr = \frac{1}{1 + e^{(a_0+a_1 \cdot (h/dbh)+a_2 \cdot h+a_3 \cdot dbh^2+a_4 \cdot BAL+a_5 \cdot \ln(CCF)+a_6 \cdot Elev+a_7 \cdot Elev^2+a_8 \cdot SL+a_9 \cdot SL^2+a_{10} \cdot SL \cdot \sin(AZ)+a_{11} \cdot SL \cdot \cos(AZ))}}$
Silva	Model type Author Function	Base of live crown <i>Original model:</i> Pretzsch (1992); <i>Coefficients:</i> Pretzsch (2001) $cb = h \cdot (1 - e^{(a_0+a_1 \cdot (h/dbh)+a_2 \cdot dbh)})$ $cw = e^{a_0+a_1 \cdot \ln(dbh)+a_2 \cdot h+a_3 \cdot \ln(h/dbh)}$

independent). Some tree growth models explicitly include the change in the competition situation before and after thinning, to address an additional species-specific response to crown release. A distance-dependent measure of competition is used by *Moses* and *Silva*. Even though a distance-dependent variant of *BWIN* exists, our application of *BWIN* and *Prognaus* used distance-independent measures of competition. Details on the competition indices can be found in Table 4.

3. Data and methods

3.1. Data

The data for simulations in this study come from 69 permanent research plots that were established in pure and mixed stands of Norway spruce and Scots pine. Plots are located in two study areas in the northern (Litschau) and southern (Arnoldstein) part of Austria. In Litschau, 23 plots were observed for 30 years (1977–2007); in Arnoldstein, 46 plots were observed for 15 years

(1993–2008). The plots were established to provide a data basis for a distance-dependent tree growth model. In Litschau trees were released in 1982 using the A-value according to Johann (1982); thinning intensity varied from light to heavy thinning. Details can be found in Hasenauer et al. (1996). In Arnoldstein, five young plots were thinned in 1995, all other plots were left untreated.

Plots in Arnoldstein are located at an elevation of 550–650 m, on flat terrain. Arnoldstein has a temperate climate. Mean annual temperature at the nearest meteorological station is 8.2 °C, with a mean monthly temperature of −3.2 °C in January and +18.7 °C in July. Mean annual precipitation is 1075 mm, of which 564 mm falls from May–September. Plots are located at three different soil types: Fluvisols, heavy textured cambisols derived from moraine material, and leptosols. Each soil type encompasses a variety of age-classes and densities. According to the yield tables of Marshall (1992) mean annual increment at the age of 100 years range from 5 to 17 m³ ha^{−1} year^{−1} for Norway spruce and from 5 to 9 m³ ha^{−1} year^{−1} for Scots pine.

Table 4

Variables and abbreviations used in this paper.

Category	Abbreviation	Variable
Size	dbh	Diameter at breast height [cm]
	d_{mean}	Quadratic mean diameter [cm]
	h	Tree height [m]
	h_{100}	Dominant height [m], height of the 100 largest trees per hectare
	h_{mean}	Lorey's mean height [m], mean height weighted by basal area
Increment	age	Tree age [years]
	ih	Height increment [m/5 years]
	id	Diameter increment [m/5 years]
	id _{Pot}	Potential diameter increment [m/5 years]
Mortality	bai	Diameter increment of an open-grown tree of the same size
	p_{Mort}	Basal area increment [cm ² /5 years]
		Probability of mortality in a 5-year period
Tree crown	cl	Crown length [m]
	cb	Live crown base [m]
	cw	Crown width [m]
	cr	Crown ratio [%], $100 \times \frac{\text{crown length}}{\text{tree height}}$
	csa	Crown surface area [m ²]
Competition	BAL	Basal area of larger trees (Wykoff, 1990)
	CCF	Crown competition factor (Krajicek et al., 1961)
	CI	Competition index (Monserud, 1975)
		Modification of Bella (1971)
	CI _{Diff}	$CI_{Diff} = CI_{before \text{ thinning}} - CI_{after \text{ thinning}}$
	C66	Crown cross-sectional area at 66% of tree height (Nagel, 1999)
	C66 _{Diff}	$C66_{Diff} = C66_{before \text{ thinning}} - C66_{after \text{ thinning}}$
	KKL	Pretzsch (1995)
	KMA	$KMA = \frac{\text{crown surface area coniferous trees}}{\text{total crown surface area}}$
	NDIST	Horizontal distance of the center of gravity of competition to the stem center
Site	Elev	Elevation [m]
	SL	Slope [%]
	AZ	Aspect [°]
Other	lp	Length of the interval period, 5 or 6 years

Table 5

Number of observations, mean values, standard deviation, minimum and maximum for plot level variables at the beginning of the simulation period; see Table 4 for variables and their abbreviations.

Variable/Location		N	Mean	StdDev	Min	Max
Age [years]	Arnoldstein	46	48	24	18	111
	Litschau	23	60	37	10	110
h_{100} [m]	Arnoldstein	46	19.7	5.2	8.2	29.9
	Litschau	23	21.7	7.4	6.5	30.7
Stand density index	Arnoldstein	46	888	234	428	1348
	Litschau	23	749	89	578	932
d_{mean} [cm]	Arnoldstein	46	20.6	6.3	12.0	37.7
	Litschau	23	21.0	9.9	6.0	34.3
h_{mean} [m]	Arnoldstein	46	17.1	4.7	7.9	26.6
	Litschau	23	19.5	7.2	5.5	28.3
Spruce proportion [%]	Arnoldstein	46	65	37	0	100
	Litschau	23	53	20	0	100
Pine proportion [%]	Arnoldstein	46	32	38	0	100
	Litschau	23	44	23	0	100
Other species proportion [%]	Arnoldstein	46	3	6	0	30
	Litschau	23	3	9	0	45

Plots in Litschau are located at an elevation of 400–600 m. The climate is colder than in Arnoldstein. The mean annual temperature is 7.1 °C. January mean is again –3.2 °C but the mean temperature in July is only +16.2 °C. Mean annual precipitation is 707 mm, of which 416 mm falls from May–September. Soils are podzols, gleyic podzols, and mollic and umbric gleysols. According to the yield tables of Marschall (1992) mean annual increment at the age of 100 years range from 5 to 15 m³ ha⁻¹ year⁻¹ for Norway spruce and from 5 to 9 m³ ha⁻¹ year⁻¹ for Scots pine.

At plot establishment, all trees above a diameter at breast height (dbh) of 5 cm (Litschau) or 10 cm (Arnoldstein) were individually numbered and tree locations were recorded for each tree. For each tree, dbh, height, and height to the crown base were recorded at the first assessment. Dbh and heights were remeasured after 5 years. Height to the crown base was remeasured at longer intervals.

Stand characteristics of the research plots at the beginning of the simulation runs are given in Table 5. The stands are pure and mixed stands of Norway spruce and Scots pine. Stand age was 10–111 years at the first assessment. Dominant heights ranged from 6.5 to 30 m. A wide range of stand densities was found. The stand density index (Reineke, 1933) ranged from 428 to 1320.

To examine trends of age and density, we fit models of the form:

$$\frac{h}{d} = a_0 + b_0 \cdot \ln(A) + b_1 \cdot \text{SDI} \quad (1)$$

$$\frac{h}{d} = a_0 + b_0 \cdot \ln(A) + b_1 \cdot \text{BA} \quad (2)$$

where h/d : height:diameter ratio (m m⁻¹); $\ln(A)$: natural logarithm of age (year); SDI: stand density index; BA: basal area (m² ha⁻¹); a_0 , b_0 , b_1 : estimated parameters.

The variation in stand density is considerably higher in Arnoldstein than in Litschau (Table 5). Furthermore, the data in Arnoldstein are free of any trend of density with age. In addition, there is a sufficient variety of densities for all age classes in Arnoldstein. In Litschau, there is a nearly significant trend of density with age ($p = 0.0756$, $R^2 = 0.14$) and there is little variation within a given age class. This is probably an artifact of a smaller sample size ($n = 23$ plots).

3.2. Methods

The analysis was restricted to Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). These two species represent the most important conifer tree species in Central Europe. Accordingly, equations for predicting tree development for these two species had been fitted for all four growth simulators. Open-

grown tree relationships and maximum density relationships for these species have been published (Kramer et al., 1970; Stiefvater, 1982; Thren, 1986; Lässig, 1991; Stampfer, 1995; Hasenauer, 1997) and various spacing trials have been conducted for these species (Burger, 1936; Abetz, 1976; Erteld, 1979; Bergel, 1982; Abetz and Unfried, 1983; Abetz and Feinauer, 1987; Röhle, 1995; Mäkinen and Isomäki, 2004; Mäkinen et al., 2005). These two species provide an interesting comparison, because Scots pine is light demanding while Norway spruce is more tolerant of shade.

3.2.1. Open-grown trees

To simulate open-grown tree behaviour, we simulated planting 1 tree per hectare with a dbh of 10 cm on a good, average, and poor site. These three sites were defined by using the best, average, and worst site index at the age of 100 years according to the yield tables “Fichte Hochgebirge” and “Kiefer Litschau” (Marschall, 1992). This corresponded to site indices of 38 m, 26 m, and 14 m for spruce, and site indices of 30 m, 22 m, and 14 m for pine. For growth models that do not explicitly take a site index, we selected corresponding site parameters and re-ran the model until it yielded the desired site index. A maximum deviation of the desired site index of ±0.1 m was tolerated. To obtain initial height values for the 10 cm dbh tree, height values for the open-grown trees were calculated using the open-grown tree relationships of Stampfer (1995). This resulted in a tree height of 6.4 m for spruce and 5.6 m for pine. We selected the study on open-grown trees by Stampfer (1995) because dimensional relationships for open-grown trees were available for both Norway spruce and Scots pine, both young and old trees were included in the dataset, and the original data used to fit the relationship was available. Initial values that would have been obtained from other open-grown tree studies are comparable and ranged from 4.2 to 6.6 m (Kramer et al., 1970; Stiefvater, 1982; Lässig, 1991; Hasenauer, 1997) for spruce, and 6.0 m for pine (Thren, 1986).

For *Moses* and *BWIN*, the initial age was obtained by solving the top-height site-index equations for age. For the growth models *Prognaus* and *Silva*, which do not rely on yield tables, the age at the beginning of the simulation was assumed to be 15, 23, and 45 years for spruce and 12, 19, and 33 years for pine to correspond to good, average, and poor sites, respectively. This represents an average value for age of different yield tables. We then simulated open-grown tree growth until a dbh of 80 cm for spruce and 60 cm for pine was reached on all sites. From the simulation output we obtained the relationship between dbh and height:diameter ratio at all sites. Then we calculated the dbh, height, and crown ratio at an age of 100 years.

3.2.2. Simulation

We began by building a generic simulator that contained the relevant equations for diameter increment, height increment and crown size for each of the four simulators (*BWIN* (Nagel, 2009), *Moses* (Hasenauer, 1994; Kindermann and Hasenauer, 2005), *Prognaus*, (Hasenauer and Monserud, 1996; Monserud and Sterba, 1996; Nachtmann, 2006) and *Silva* (Pretzsch, 1992; Kahn, 1994)). The relevant measures of competition, site characteristics, and stand statistics were also coded.

The advantage of this simulator was that we could be sure that no additional constraint was being imposed on the growth equations. Output from each of the emulated simulators was checked against the respective original simulation model output to verify that the coding was correct. To ensure identical starting conditions, the same tree input data file was used by each of the four simulators. Site factors for *Prognaus* and *Silva* were assessed in the field or obtained from the nearest meteorological station. For *BWIN* and *Moses*, site index was calculated from the yield table of Assmann and Franz (1965) for spruce in Arnoldstein, from the yield table “Fichte Hochgebirge” (Marschall, 1992) for spruce in Litschau and from the yield table “Kiefer Südtirol” (Moling, 1993) for pine in Arnoldstein and from “Kiefer Litschau” (Marschall, 1992) for pine in Litschau. In order not to underestimate site potential in mixed stands, top height trees were selected independent of the species according to the recommendations of Sterba (1996). In stands where a species was present, but was not part of the top height trees, top heights were derived using equations from the Austrian National Forest Inventory that relate the top height of one species to that of another species (Vospernik, 2000).

Using each of the four simulators, we then simulated stand growth in Arnoldstein and Litschau for the length of the research plot measurements, 15 and 30 years, respectively. In Arnoldstein, a diameter threshold of 10 cm was used; in Litschau the diameter threshold was 5 cm. We used the observed removal and mortality and the observed ingrowth during the simulation on all plots to avoid any confounding of diameter increment, height increment, and crown models with further submodels.

We examined both individual tree values and stand values. For the stand values we compared observed and predicted height:diameter ratios of dominant trees (100 largest trees per hectare), and of the mean stem size (quadratic mean diameter and Lorey's mean height weighted by basal area) at the end of the simulation period.

4. Results

4.1. Simulations in Arnoldstein and Litschau

4.1.1. Individual-tree values

Tables 6–8 show the observed and simulated dbh, height, and height:diameter ratios of Arnoldstein and Litschau, their mean, standard deviation, and the minimum and maximum values observed and predicted by the growth simulators. Deviations of the average predicted dbh for each of the growth simulators from the observed dbh range from 0.2 to 4.1 cm, which corresponds to an underestimation/overestimation of 0.01–0.23 cm year⁻¹. Differences between observed and predicted values were mostly less than 2 cm. Higher values were found for *Moses* with Scots pine, for *Prognaus* with Scots pine in Arnoldstein and spruce in Litschau, and for *Silva* for both species in Litschau. Although not presented here, we plotted observed and predicted individual tree values for each plot and growth simulator. For spruce, *BWIN* and *Silva* in most cases underestimated the diameters of small trees and overestimated the diameters of large trees. For *BWIN* in particular, observed and predicted dbh matched quite well except that the very large trees

were considerably overestimated. In contrast, *Prognaus* and *Moses* overestimated the diameters of small trees and underestimated the diameters of large trees. Similarly for pine, all four growth simulators overestimated the size of small trees and underestimated the size of large trees.

Predicted heights deviated 0.3–3.5 m from observed values. This corresponds to 0.01–0.12 m year⁻¹. Observed and predicted height growth matched quite well in Arnoldstein, and there was little deviation between observed and predicted values for both mean and maximum values. In Litschau, however there was poor agreement with observed values, except for Scots pine height growth predicted by *Silva*. *Moses* overestimates the mean height but underestimates the maximum values. This seems to indicate that the shape of the height growth curve is inappropriate. Examining the plots of observed and predicted heights, we found that in Arnoldstein all four growth simulators for both species overestimated the height of small trees and underestimated the height of large trees. Patterns were less homogenous in Litschau. For pine, a pattern similar to that in Arnoldstein was prevalent, with an overestimation of small heights and the underestimation of large heights; for spruce the opposite was true except for *Prognaus*.

In many cases observed and predicted height:diameter ratios agreed fairly well. Within a plot low height:diameter ratios were overestimated and high height:diameter ratios were underestimated, except for predictions of spruce with the simulator *Silva* in Litschau. Height:diameter ratios are the result of the predictions of height and diameter increment. There are four different cases for the resulting height:diameter ratio: (1) increment and allometry correct, (2) height or diameter increment wrong, allometry distorted, (3) height and diameter increment wrong, allometry correct and (4) height and diameter increment wrong, allometry distorted. Indeed there were cases where neither model largely deviated, but the resulting height:diameter ratios were biased. Also, there were cases where both models deviated, but the resulting height:diameter ratio agreed fairly well with observed values. Compare, for example, the simulation results for Norway spruce in Litschau using *Moses* in Tables 6–8.

To examine height:diameter ratios in dense stands, we first examined the maximum values in Table 8. Because height:diameter ratios usually decrease with dbh, we further examined if height:diameter ratios were exceeded in any specific dbh class (Fig. 1). Our results indicate that the simulated maximum height:diameter ratios were lower than the observed maximum height:diameter ratio for all four growth models in Arnoldstein. Also, for a dbh <60 cm, the simulated height:diameter ratios did not exceed the observed maximum height:diameter ratios. In Litschau, the maximum values observed were exceeded by two models (*Silva* and *Moses*) for both spruce and pine. The examination with respect to dbh showed that the height:diameter ratios of a dbh of 5–40 cm were overestimated for spruce. The overestimation for Scots pine results from the fact that a number of trees were predicted to remain in the smallest diameter class by some growth models. The height:diameter ratios within a dbh class agree fairly well. For Scots pine there also seems to be a tendency to overestimate height:diameter ratios for large trees in *Prognaus*, *Silva* and *Moses*.

Average crown ratio values were predicted well by the four growth models. Deviations in average crown ratio were mostly less than 6%. However, *BWIN* did underestimate spruce crown ratio and *Moses* overestimated pine crown ratio by more than 6% (Table 9). The standard deviations in crown ratio predicted by *BWIN*, *Prognaus*, and *Silva* are considerably lower than the observed values, indicating too little variability in the predictions of crown ratio. This is also supported by the fact that the minimum values predicted by these three growth models are always higher than the minimum values observed, whereas the maximum values predicted are considerably lower than the maximum values observed. Only

Table 6
Observed and simulated dbh [cm] in Arnoldstein and in Litschau.

Location	Species	Model	N	Mean	StdDev	Min	Max
Arnoldstein	Norway spruce	Observed	1620	25.8	10.5	10.1	72.4
		BWIN	1620	25.6	11.0	10.6	76.4
		Moses	1620	24.7	9.7	10.3	66.9
		Proгнаus	1620	27.4	9.9	12.7	70.0
		Silva	1620	27.4	10.7	10.1	71.1
	Scots pine	Observed	613	29.1	8.9	10.9	62.1
		BWIN	613	28.4	8.7	12.9	59.8
		Moses	613	32.6	7.6	16.2	59.4
		Proгнаus	613	32.0	9.2	14.0	60.6
		Silva	613	27.9	9.2	10.4	57.8
Litschau	Norway spruce	Observed	725	24.9	11.2	6.0	64.6
		BWIN	725	25.9	10.5	6.1	69.7
		Moses	725	24.3	8.4	5.2	55.1
		Proгнаus	725	29.0	9.8	13.5	68.0
		Silva	725	29.0	12.3	5.1	67.8
	Scots pine	Observed	245	38.1	9.8	11.6	62.4
		BWIN	245	37.7	10.0	10.8	62.3
		Moses	245	41.8	6.9	11.6	60.2
		Proгнаus	245	38.8	10.2	11.6	62.1
		Silva	245	35.7	11.6	6.9	60.1

Table 7
Observed and simulated height [m] in Arnoldstein and in Litschau.

Location	Species	Model	N	Mean	StdDev	Min	Max
Arnoldstein	Norway spruce	Observed	1620	22.6	5.9	7.0	35.8
		BWIN	1620	21.3	5.6	4.6	35.2
		Moses	1620	21.8	5.1	6.8	33.8
		Proгнаus	1620	22.3	4.8	9.5	34.8
		Silva	1620	22.1	4.7	9.8	33.8
	Scots pine	Observed	613	22.8	4.0	9.7	31.7
		BWIN	613	21.0	3.8	9.5	31.7
		Moses	613	22.4	3.3	13.2	31.8
		Proгнаus	613	21.5	3.7	12.1	30.8
		Silva	613	21.2	4.0	11.2	31.0
Litschau	Norway spruce	Observed	725	22.8	7.1	6.3	38.7
		BWIN	725	23.2	6.0	4.7	36.2
		Moses	725	24.7	5.0	4.4	34.5
		Proгнаus	725	26.3	5.2	14.6	38.0
		Silva	725	25.5	7.0	5.4	39.0
	Scots pine	Observed	245	29.1	4.8	9.0	38.5
		BWIN	245	27.7	4.5	9.0	36.9
		Moses	245	29.4	3.6	9.0	35.2
		Proгнаus	245	26.6	4.7	9.0	34.3
		Silva	245	30.2	6.0	9.0	38.8

Table 8
Observed and simulated height:diameter ratios in Arnoldstein and in Litschau.

Location	Species	Model	N	Mean	StdDev	Min	Max
Arnoldstein	Norway spruce	Observed	1620	93.7	21.7	43.0	185.1
		BWIN	1620	88.9	19.8	38.7	153.9
		Moses	1620	93.8	19.8	42.4	152.3
		Proгнаus	1620	86.0	17.6	39.6	137.7
		Silva	1620	87.7	21.6	42.2	160.4
	Scots pine	Observed	613	83.3	21.6	40.0	156.0
		BWIN	613	78.1	18.0	40.3	133.2
		Moses	613	71.1	14.0	41.2	119.7
		Proгнаus	613	70.3	14.3	43.3	114.6
		Silva	613	81.1	19.2	44.6	150.4
Litschau	Norway spruce	Observed	725	98.5	20.6	54.7	181.3
		BWIN	725	95.5	18.0	39.2	152.8
		Moses	725	108.8	24.6	49.9	187.5
		Proгнаus	725	95.5	17.8	54.0	169.8
		Silva	725	98.1	28.5	53.9	184.1
	Scots pine	Observed	245	79.3	14.5	54.3	138.0
		BWIN	245	77.0	16.0	53.2	156.6
		Moses	245	71.2	8.9	51.2	94.7
		Proгнаus	245	70.9	10.6	51.8	107.1
		Silva	245	91.3	22.4	62.3	177.6

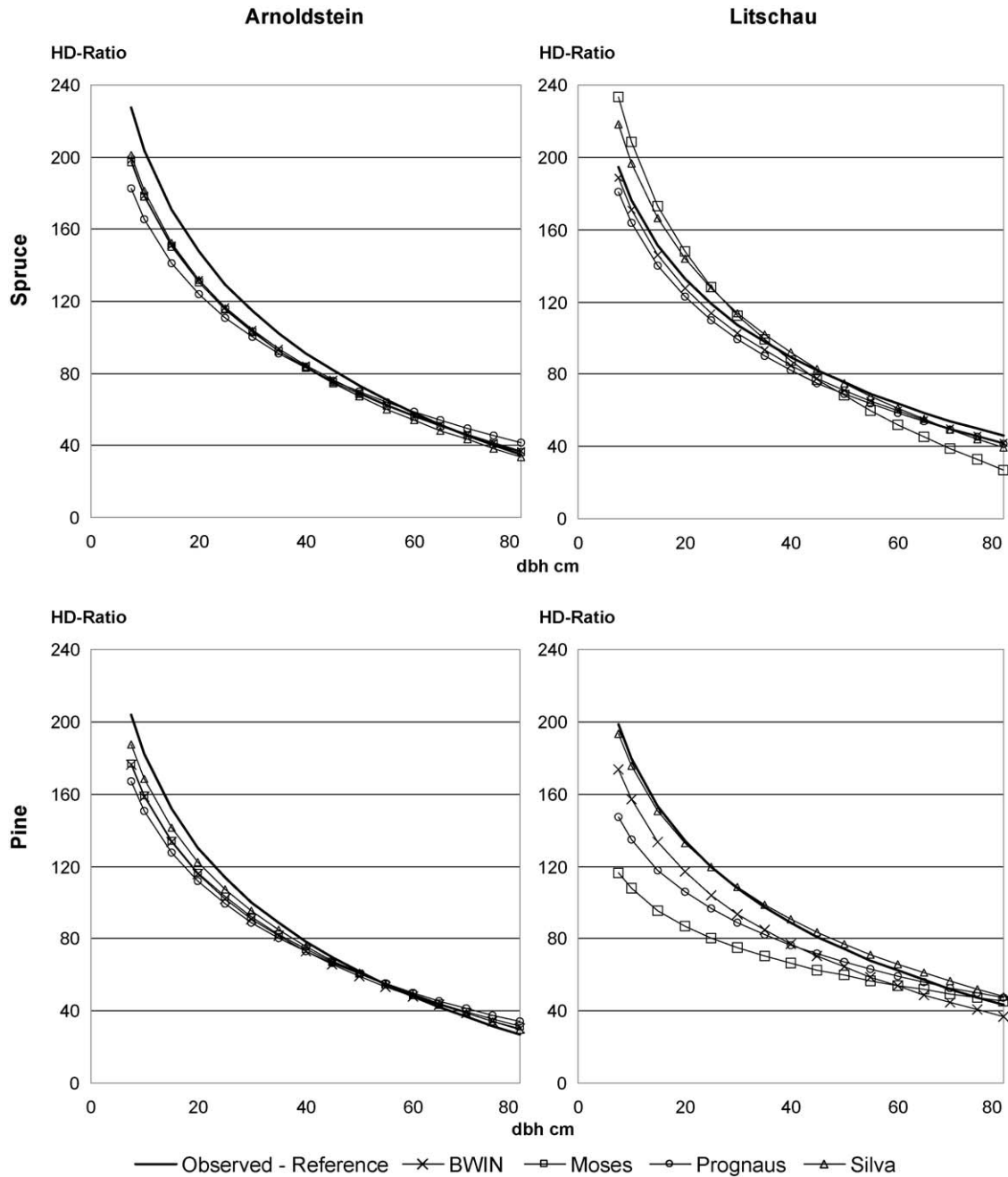


Fig. 1. Simulation output of height:diameter ratios at maximum density.

Moses, with its dynamic crown ratio model, reasonably depicts the variability in crown ratio. Prediction patterns within a stand are consistent for all four simulators for both species on both sites: small crown ratios are overestimated, whereas large crown ratios are underestimated.

4.1.2. Stand effects

To examine the effects of age, social position, and density on a stand level, we plotted the height:diameter ratios of dominant trees and mean trees in Litschau and Arnoldstein (Figs. 2a–5a). We then examined the effects of age and stand density in Arnoldstein. Two different models were calculated for Arnoldstein: a regression of height:diameter ratio on age and stand density index (SDI), and a regression of height:diameter ratios on age and basal area (see Eqs. (1) and (2) in Section 3.1). The fitted models for SDI for both dominant trees and mean trees are shown in Table 10. Although

not shown here, very similar results were obtained for basal area. Regressions for SDI resulted in a higher R^2 and a lower mean square error than for basal area.

There is a decrease of height:diameter ratios with age for both quadratic mean diameter and top height. The decrease is most pronounced in the observed data (Table 10, Figs. 2a–5a). In general, the very large height:diameter ratios of young stands are underestimated by the models (Figs. 2–5), except for BWIN and Silva for pine growing at Litschau (Fig. 5b, e). The regression coefficients and the plots indicate that the age trend for spruce in Arnoldstein is underestimated by Silva (Fig. 2e). On the other hand, both Moses (Arnoldstein and Litschau) and Prognaus (Arnoldstein) underestimate the age trend for pine (Figs. 3 and 5). All four models on both sites confirmed the hypothesis that dominant trees have lower height:diameter ratios than mean trees. The differences between height:diameter ratios of dominant and average trees are larger

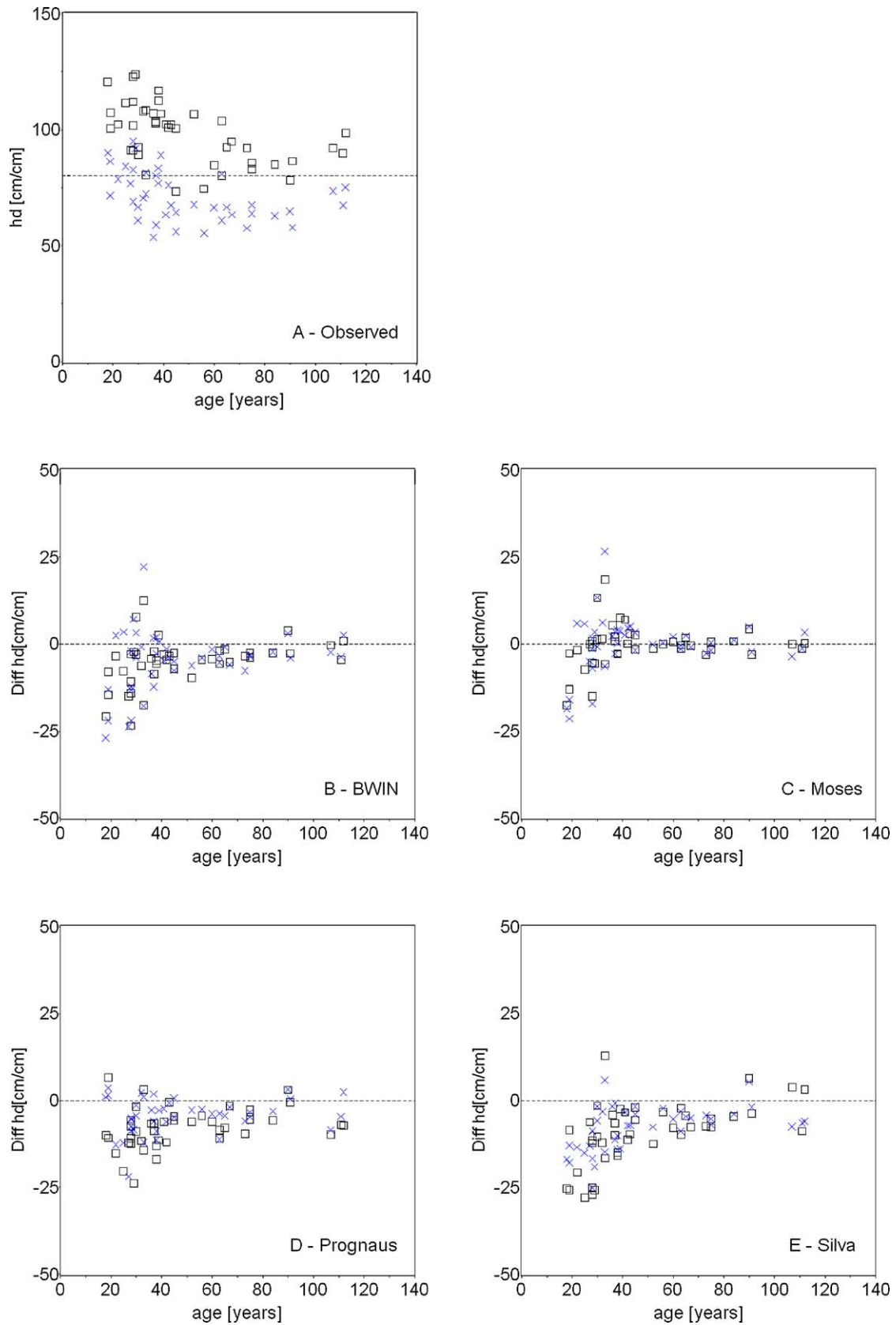


Fig. 2. Observed height:diameter ratios for *spruce* in Arnoldstein and differences between observed and predicted height:diameter ratios for the four simulators BWIN, Moses, Prognaus and Silva. Squares indicate mean trees, crosses indicate top-height trees.

Table 9
Observed and simulated crown ratios in Arnoldstein and in Litschau.

Location	Species	Model	N	Mean	StdDev	Min	Max
Arnoldstein	Norway spruce	Observed	1620	0.49	0.15	0.06	0.90
		BWIN	1620	0.38	0.06	0.25	0.68
		Moses	1620	0.46	0.11	0.07	0.89
		Prognaus	1620	0.48	0.09	0.25	0.75
		Silva	1620	0.44	0.08	0.23	0.64
		Silva	1620	0.44	0.08	0.23	0.64
	Scots pine	Observed	613	0.30	0.10	0.03	0.86
		BWIN	613	0.29	0.03	0.21	0.40
		Moses	613	0.52	0.15	0.19	0.92
		Prognaus	613	0.28	0.07	0.15	0.48
		Silva	613	0.36	0.04	0.25	0.50
		Silva	613	0.36	0.04	0.25	0.50
Litschau	Norway spruce	Observed	725	0.44	0.14	0.00	0.82
		BWIN	725	0.34	0.06	0.24	0.65
		Moses	725	0.38	0.09	0.07	0.74
		Prognaus	725	0.45	0.08	0.20	0.68
		Silva	725	0.41	0.09	0.19	0.58
		Silva	725	0.41	0.09	0.19	0.58
	Scots pine	Observed	245	0.30	0.07	0.10	0.62
		BWIN	245	0.26	0.03	0.15	0.48
		Moses	245	0.48	0.19	0.19	0.97
		Prognaus	245	0.31	0.04	0.22	0.48
		Silva	245	0.27	0.03	0.21	0.48
		Silva	245	0.27	0.03	0.21	0.48

for spruce than for pine for both observed and predicted values (Figs. 2–5).

With respect to the 80:1 reference line indicating stand stability, the following can be seen from the figures: for spruce in Arnoldstein (Fig. 2a), the dominant trees are almost all below the 80:1 threshold and the mean tree is above the threshold. This pattern is predicted well by all four growth models. A similar pattern is observed for spruce in Litschau, although here the deviations of the growth models from the observed values were larger (Fig. 4). Only *Prognaus* classifies the plots reasonably well with respect to the stability threshold (Fig. 4d). For pine, the performance of *BWIN* and *Silva* is good and many plots are correctly classified with respect to the 80:1 threshold. However, *BWIN* and *Silva* do tend to overestimate height:diameter ratios for stands 40-years and younger (Fig. 5b, e). *Prognaus* yields acceptable results, whereas *Moses* underestimates the height:diameter ratios, in particular those of young stands (Fig. 5c).

From Table 10 the following can be observed with respect to stand density: an increase of 100 units of SDI corresponds to an increase of height:diameter ratios of 4.9 and 7.9 for dominant trees and of about 20 units for mean stems for spruce and pine. Predicted effects range from 1.2 units and 26 units for dominant trees and from 9.5 to 32 units for the mean stem. For both spruce and pine,

BWIN and *Moses* overestimate the effect of density, while *Prognaus* and *Silva* underestimate the effect of density. For the mean stem, predicted effects are 0.5–2.0 times as high as the observed effects. For dominant trees, the predicted effects are 0.15–5.3 times as high as the observed effect.

4.2. Simulation of open-grown trees

Fig. 6 compares the height:diameter ratios predicted by the forest growth models to the reference equations of Stampfer (1995). The height:diameter ratios obtained from the forest growth models are in most cases higher than the reference equations. The largest discrepancies are found for spruce and pine on poor sites, where the height:diameter ratios predicted by *Silva* and *BWIN* are lower than the reference equations for almost all diameters. The differences between the shape of the relationship between dbh and height:diameter ratios are partly quite large. Whereas the open-grown tree relationship shows a monotonically decreasing form, this is only partially matched by the predictions of the individual tree growth models. In some cases there is a peak at the beginning of the simulation period, before height:diameter ratios decrease. The monotonically decreasing pattern was predicted by *Moses* and *BWIN* on all sites, except for pine on good-average sites

Table 10
Regression on age and stand density in Arnoldstein according to Eq. (1) in Section 3.1 (significance levels: * < 0.05, ** < 0.01, *** < 0.001).

	Species		a_0	b_0	b_1	R^2	Pr > F
Height:diameter ratio top height stem	Spruce	Observed	105.9***	-10.2740**	0.0049	0.24	**
		BWIN	62.4***	-4.9038	0.0261**	0.26	**
		Moses	77.2***	-6.9690*	0.0234**	0.29	***
		Prognaus	98.4***	-8.5772**	0.0012	0.18	*
		Silva	72.9***	-3.5043	0.0045	0.10	
		Silva	72.9***	-3.5043	0.0045	0.10	
	Pine	Observed	94.5***	-9.5694**	0.0079	0.26	*
		BWIN	86.6***	-8.9185**	0.0119*	0.38	**
		Moses	48.1***	-0.1258	0.0107*	0.16	
		Prognaus	68.0***	-3.2363	0.0012	0.06	
		Silva	86.7***	-6.9895*	0.0041	0.21	*
		Silva	86.7***	-6.9895*	0.0041	0.21	*
Height:diameter ratio mean stem	Spruce	Observed	134.4***	-14.2410***	0.0202**	0.42	***
		BWIN	98.4***	-8.7889***	0.0320***	0.54	***
		Moses	115.2***	-11.3370***	0.0291***	0.55	***
		Prognaus	121.3***	-10.6920***	0.0108	0.30	***
		Silva	85.9***	-3.3099	0.0179**	0.24	**
		Silva	85.9***	-3.3099	0.0179**	0.24	**
	Pine	Observed	112.7***	-13.2270***	0.0198*	0.47	***
		BWIN	105.4***	-12.4850***	0.0209**	0.51	***
		Moses	55.5***	-1.3183	0.0199***	0.38	**
		Prognaus	81.5***	-5.5884	0.0095	0.19	*
		Silva	105.9***	-10.0090**	0.0127	0.31	**
		Silva	105.9***	-10.0090**	0.0127	0.31	**

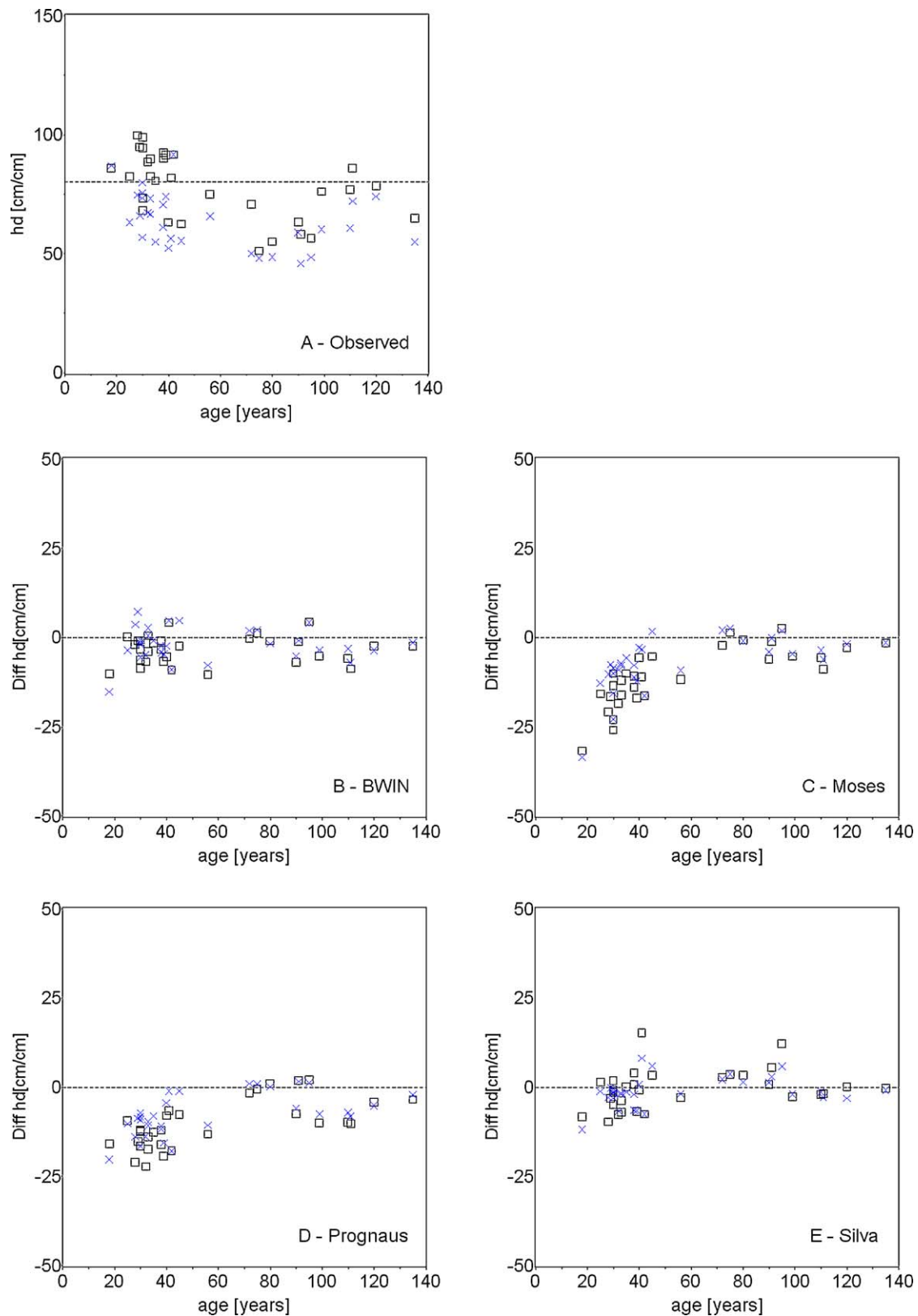


Fig. 3. Observed height:diameter ratios for pine in Arnoldstein and differences between observed and predicted height:diameter ratios for the four simulators BWIN, Moses, Prognaus and Silva. Squares indicate mean trees, crosses indicate top-height trees.

by *BWIN*. *Prognaus* correctly predicts open-grown tree patterns for spruce on poor sites and for pine on good sites. *Silva* predicts monotonically decreasing patterns for spruce on good and poor sites.

The dimensions of open-grown trees at the age of 100 years for different site indices for the four growth models are shown in [Table 11](#). Generally, predicted diameters are always higher on good sites than on poor sites for each of the simulators. On good sites the

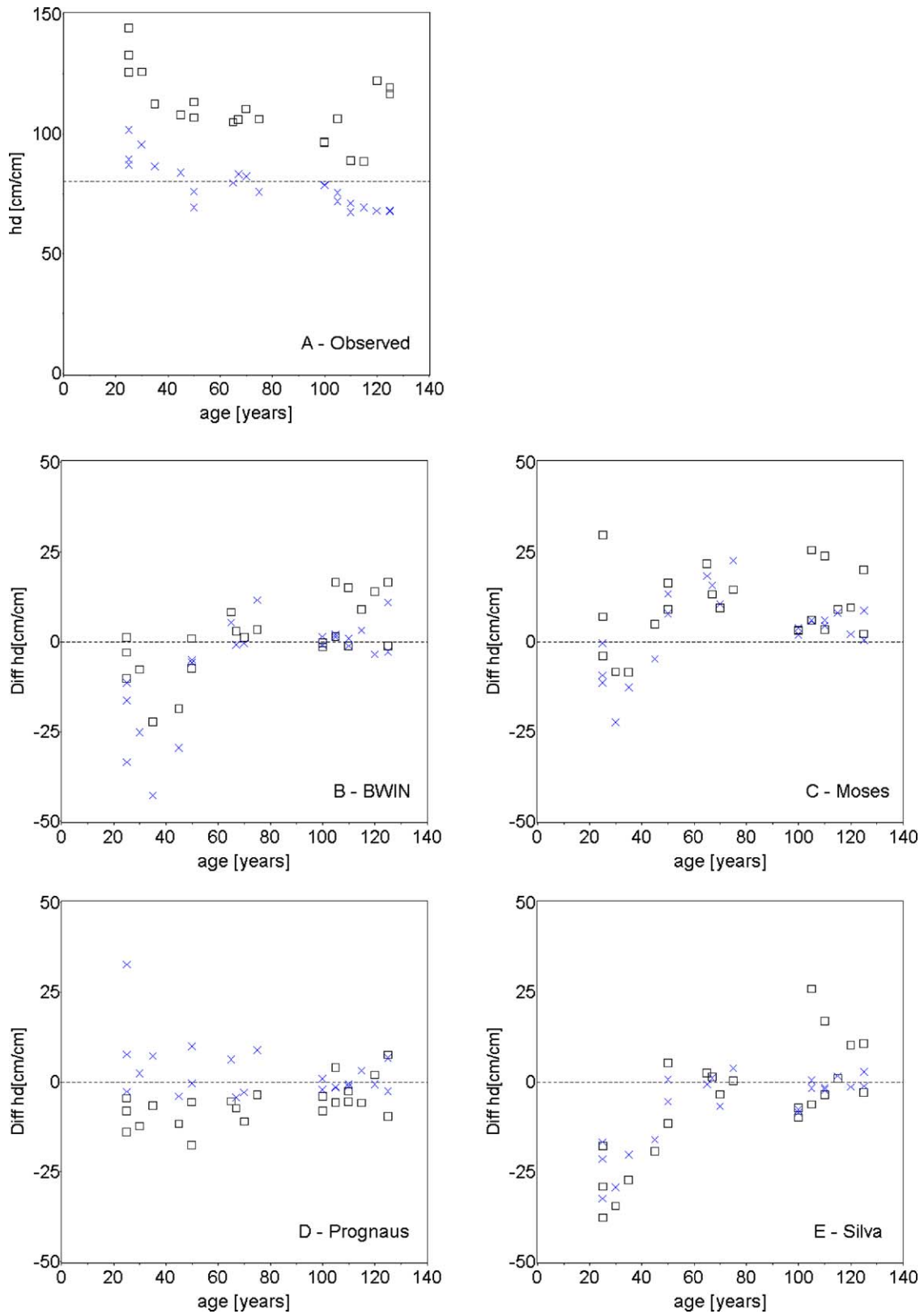


Fig. 4. Observed height:diameter ratios for spruce in Litschau and differences between observed and predicted height:diameter ratios for the four simulators BWIN, Moses, Prognaus and Silva. Squares indicate mean trees, crosses indicate top-height trees.

predicted diameters range from 68 to 245 cm for spruce and from 44 to 85 cm for pine. The diameter predicted by *BWIN* for spruce is considerably higher than the diameter predicted by the other simulators. On poor sites, predicted diameters for both spruce and

pine range from 24 to 42 cm. Please note that predictions of the four individual-tree growth models agree best for the average site.

Another detail regarding the predicted diameters deserves attention (Table 11): excluding *BWIN*, differences in the diameter

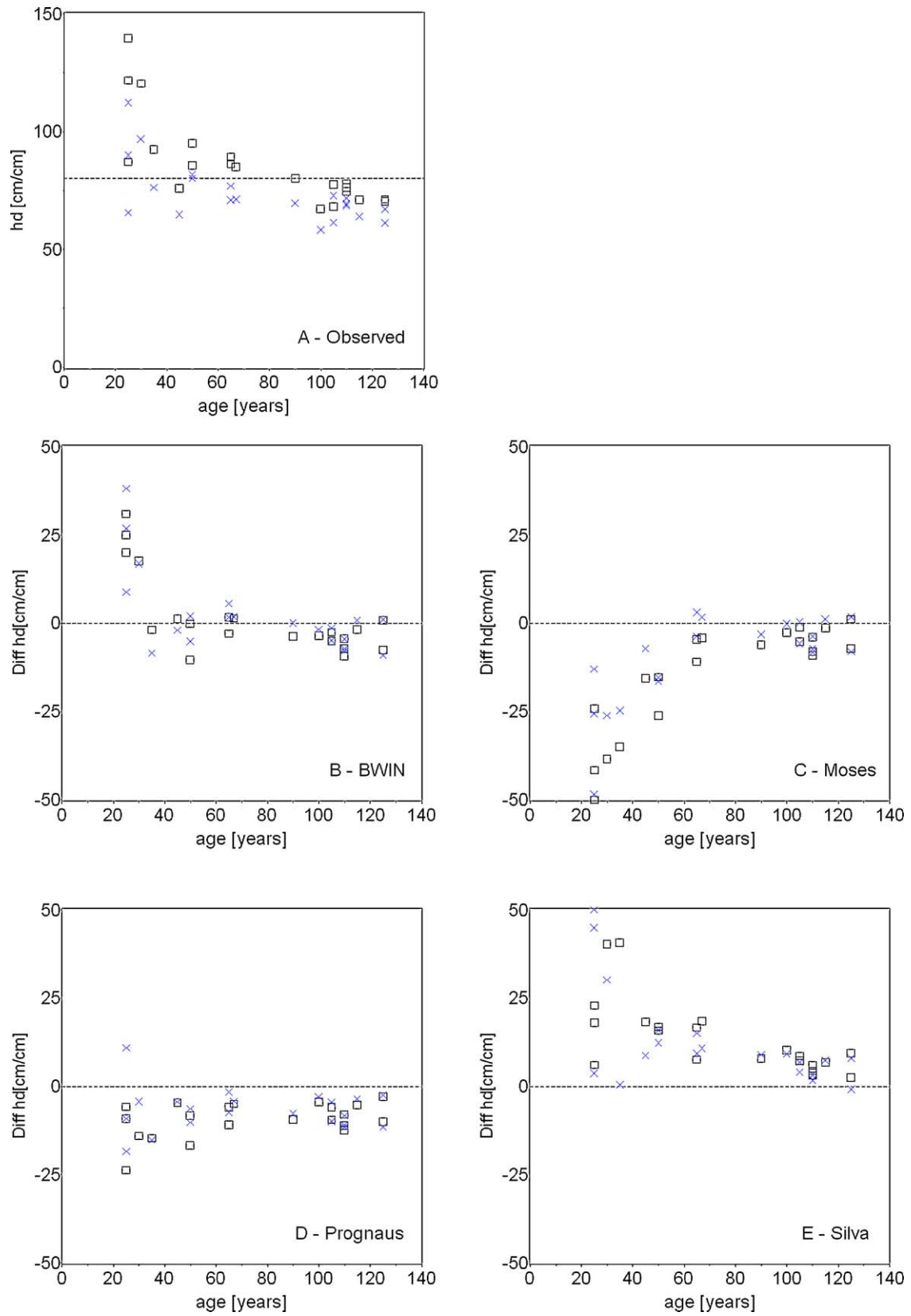


Fig. 5. Observed height:diameter ratios for pine in Litschau and differences between observed and predicted height:diameter ratios for the four simulators BWIN, Moses, Prognaus and Silva. Squares indicate mean trees, crosses indicate top-height trees.

Table 11
Dbh (cm) of an open-grown tree at the age of 100 years for different site indices [m] for the four forest growth models BWIN, Moses, Prognaus and Silva.

Species	Site	Site index	BWIN	Moses	Prognaus	Silva
Spruce	Good	38	245.4	107.6	99.1	68.1
	Average	26	133.9	65.8	53.7	59.4
	Poor	14	38.7	29.4	27.1	41.9
Pine	Good	30	54.0	66.9	85.8	43.8
	Average	22	47.4	47.1	50.0	41.7
	Poor	14	36.5	28.1	24.0	37.3

Site index is dominant height (100 largest trees) at an age of 100 years.

of an open-grown tree between good and poor sites can be as large as 78 cm and as small as 26 cm. Thus, the influence of site on diameter growth is clearly different among the different individual-tree growth models.

Crown ratios for open-grown trees can be found in Table 12. By constraint, *Moses* always yields a crown ratio of 1. *Prognaus* predicted a crown ratio for spruce >0.96 and a crown ratio for pine >0.67. Crown ratios obtained from *BWIN* and *Silva* were highly variable during the simulation period. For *BWIN*, they ranged from 0.39 to 0.99 for spruce and 0.3 to 0.81 for pine. For *Silva*, they ranged from 0.50 to 0.70 for spruce and from 0.28 to 0.67 for pine.

5. Discussion

5.1. Submodels

5.1.1. Diameter increment model

We found a bias of diameter increment that ranged from 0.01 to 0.23 cm year⁻¹ (absolute values) depending on the growth model and region. Our results do not indicate the superiority of any particular model, since it was the same growth model that had both the smallest and the highest bias. This prediction bias agrees well with results from numerous comparable studies, which report a bias of 0.002–0.273 cm year⁻¹ (absolute values) (Pretzsch and Dursky, 2001; Sterba et al., 2001; Pretzsch, 2002; Froese and Robinson, 2007; Schmidt and Hansen, 2007; Härkönen et al., 2010).

If bias exists, it can be temporal or spatial in nature. Temporal bias is frequently found in evaluations of forest growth models (Sterba and Monserud, 1997; Pretzsch and Dursky, 2001; Pretzsch, 2002). Temporal bias could arise from weather conditions that change from one growth period to another, or a gradual change in the soil system from nitrogen deposition, which may have interacted with a time lagged effect of abandoning litter raking (Sterba and Monserud, 1997). Pretzsch and Dursky (2001), for example, found a temporal trend with an overestimation in the first half of the century and an underestimation in the last half of the century. Also, hypothesized climate change recommends a test for temporal bias (Sterba and Monserud, 1997). Ideally, models should be based on data that can be regarded as the climatic mean for the evaluation period. Previous studies showed that temporal bias is smallest in the period that overlaps with the parameterization period (Sterba

and Monserud, 1997). Temporal bias can be exceedingly high if the evaluation period is shorter than 10–15 years (Pretzsch, 2002). Inferring from the data used for model fitting, temporal bias should be very small for the growth models *Silva* and *BWIN*, which were fit from long term research plots. Growth rates in these models can be interpreted as the long term climatic mean. In contrast, *Prognaus* was fit from a relatively short period, and temporal bias could be prevalent. The evaluation period of this study of 15–30 years should be sufficiently long to avoid excessive temporal bias.

Spatial bias also frequently occurs (Sterba and Monserud, 1997; Schmid et al., 2006; Froese and Robinson, 2007). Deviations are caused by site-specific variation not captured in the model (Sterba and Monserud, 1997). For example, this can be due to regionally variable trends between elevation and prediction accuracy or different ownership not accounted for by the model (Froese and Robinson, 2007). Spatial bias is an important problem, where the data used for model fitting are not spatially representative. It is the strength of inventory data to be spatially representative for a study area because national inventories are usually systematic samples covering the full range of conditions. Spatial bias is expected to be high for growth models fit from permanent research plots, because permanent research plots are often clustered at lower elevations on good sites; they rarely are representative of the site variation across a region. Spatial bias should therefore be relatively small for *Prognaus*, but higher for *BWIN*, *Moses* and *Silva*. This seems to be confirmed by evaluation results by Schmid et al. (2006). They found that *Silva* correctly predicted growth within the range of the parameterization data up to an elevation of about 1000 m, whereas at higher elevations there were notable deviations.

In addition to temporal and spatial deviations, other trends can be found in the evaluation data set. Often deviations with respect to size are found. In agreement with our results, most frequently there is an over-prediction for small trees and an under-prediction for larger trees (Sterba et al., 2001; Schmid et al., 2006; Froese and Robinson, 2007; Mette et al., 2009). Similarly, with respect to competition, an overestimation for low stand densities and an underestimation for high stand densities is often observed (Froese and Robinson, 2007; Schmidt and Hansen, 2007). As our results indicated, sometimes the opposite can occur. Such trends in the evaluation data set are difficult to account for, because they cannot simply be corrected by a plot-specific adjustment of the intercept term.

5.1.2. Height increment model

Height growth differences in this study ranged from 0.01 to 0.12 m year⁻¹. These results are consistent with similar research. Height increment bias previously reported ranged from 0.01 to 0.30 m year⁻¹ (Sterba et al., 2001; Härkönen et al., 2010). As with diameter increment, temporal or spatial trends or size effects can occur. Our results indicate that differing height growth patterns can partly be attributed to an incorrect shape of the site-index function. For example, the particularly good prediction results for spruce in Arnoldstein with the growth model *Moses* result from

Table 12
Minimum and maximum crown ratios of open-grown trees during the simulation for the four forest growth models BWIN, Moses, Prognaus and Silva.

Species	Site	Site index [m]	BWIN		Moses		Prognaus		Silva	
			Min	Max	Min	Max	Min	Max	Min	Max
Spruce	Good	38	0.39	0.94	1.00	1.00	0.96	0.98	0.54	0.57
	Average	26	0.77	0.99	1.00	1.00	0.97	0.99	0.50	0.64
	Poor	14	0.79	0.99	1.00	1.00	0.98	0.99	0.54	0.70
Pine	Good	30	0.3	0.81	1.00	1.00	0.67	0.86	0.28	0.67
	Average	22	0.37	0.81	1.00	1.00	0.76	0.87	0.34	0.67
	Poor	14	0.5	0.81	1.00	1.00	0.87	0.92	0.44	0.67

Site index is dominant height (100 largest trees) at an age of 100 years.

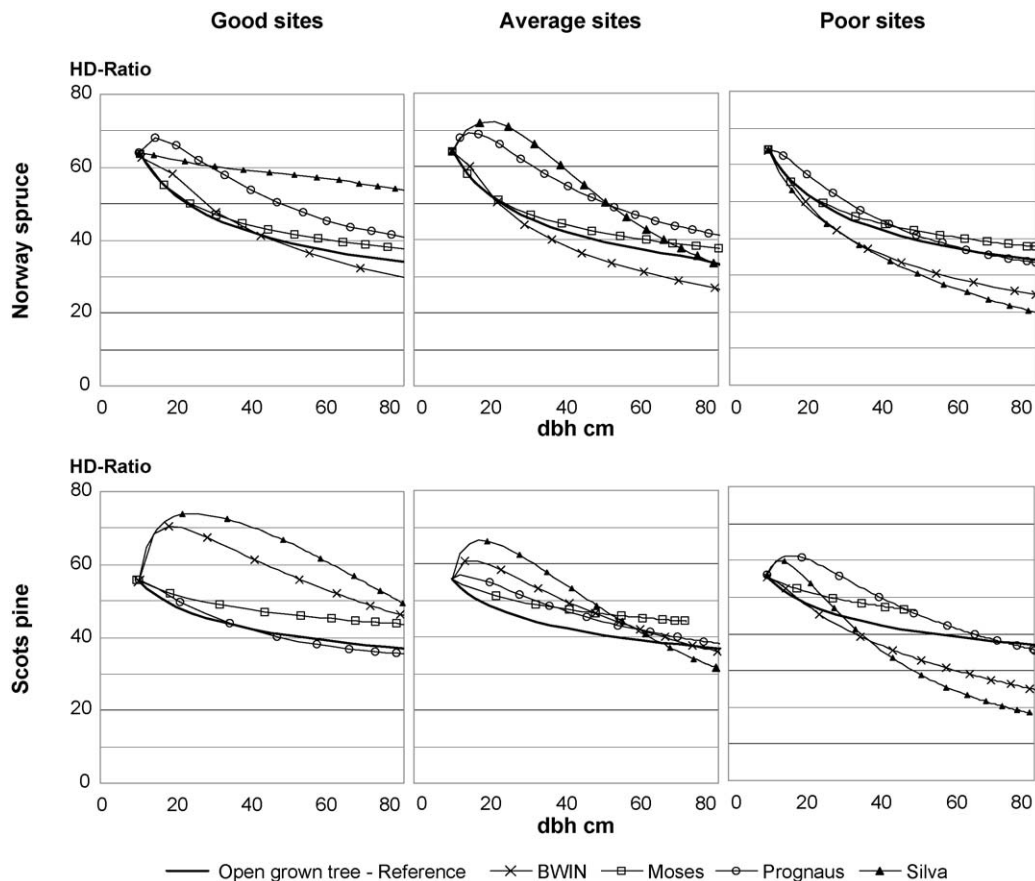


Fig. 6. Simulation output in comparison with an open-grown tree reference, Reference equations are taken from Stampfer (1995).

a run with the site-index functions of Assmann and Franz (1965). These site-index functions are known to very closely match the height growth patterns in Arnoldstein. In contrast, we did not find any spruce yield table that adequately represents dominant height growth in Litschau. Even though the model run with spruce “Hochgebirge” was better than with any other yield table, bias still remained. Another example is *Prognaus*: comparing the height growth patterns resulting from the *Prognaus* height increment model (Nachtmann, 2006) to the height growth patterns in Arnoldstein and to the yield tables of Assmann and Franz (1965) showed that the *Prognaus* height increment pattern was notably too steep at advanced ages, resulting in biased predictions. In contrast, observed and predicted height growth patterns for *Prognaus* were nearly identical in Litschau, resulting in a good performance.

Therefore, an appropriate curve form for a particular region is crucial to correctly predict height growth. Whereas the shape of the site-index curves is routinely examined before the application of a yield table for a region, evaluations of forest growth models so far have mostly focused on overall bias, ignoring shape. In individual-tree growth models that derive potential height increment from yield tables, often only one curve form per species is implemented (e.g. *BWIN*, and the first version of *Moses*). The assumption of one curve shape per species is certainly too stringent, since it is known that the pattern of height growth can vary considerably for different climatic regions, vegetation types, soils, or degrees of competition (Stage, 1963; Monserud, 1984; Sterba and Eckmüller, 2009). Here, a modification that allows for different site-index curves (e.g. Kindermann and Hasenauer, 2005) may help to solve this problem. Site-index functions developed from site factors appear flexible enough to represent different height growth patterns (*Prognaus* and *Silva*). Nevertheless, the pattern derived

from the site-index functions might or might not be appropriate for a new region.

5.1.3. Crown ratio model

The crown ratio model is an important submodel that influences the predictions of diameter increment. It is therefore interesting to know how well the predictions of this submodel agree with observed values. The highest crown ratios would be expected for open-grown trees. Typically, crown ratios of open-grown spruce range from 0.91 to 0.94 (Lässig, 1988; Stampfer, 1995), and crown ratio of open-grown pine is 0.86 (Stampfer, 1995). The light demanding pine trees can have a number of dying branches even on open-grown trees (Stampfer, 1995), due to self-shading. For stand grown trees, crown ratios would be high in sparse stands and low in dense stands. For open-grown tree, the simulated crown ratios of *Moses* (always 1.0) and *Prognaus* (>0.96 for spruce, >0.67 for pine) agree well with observations on open-grown trees. Crown ratios predicted by *BWIN* and *Moses* were more variable but they could be as low as 0.5 for spruce and 0.3 for pine. This is clearly too low for open-grown trees and rather corresponds to crown ratios of dominant stand grown trees. Abetz and Künstle (1982) reported crown ratios of 0.3–0.7 for dominant spruce. The high crown ratios of open-grown trees might be underestimated because sparse stands are often lacking in the data sets. *BWIN* and *Silva* were both fit from permanent research plots, which are usually fully stocked. On the other hand, *Prognaus* was fit from Forest Inventory data, which covers a larger variety of stocking degrees. *Moses* uses a function that forces a crown ratio of 1, if the competition index is 0. For stand-grown trees, the average crown ratios were predicted well by all four simulators, with deviations being mostly less than 0.06, and only in some cases as high as 0.22. This agrees well with differences

of 0.018, 0.02, and 0.246 in crown ratio after a 20-year simulation (Sterba et al., 2001). The variability in crown ratio is best predicted by a dynamic model, as implemented in *Moses*.

5.2. Hypotheses on height:diameter ratios

We expected that individual-tree growth models would correctly predict height:diameter ratios. The findings of our investigation generally support these expectations. Height:diameter ratios predicted by all four growth models are within the bounds defined by open-grown trees and very dense stands. Furthermore, all models show an increase of height:diameter ratios with increasing density, a decrease with age, and lower height:diameter ratios for dominant trees than for mean trees.

A word about misclassification costs: the cost of underestimating height:diameter ratios can greatly exceed costs of overestimation. Consider a collection of stands near the 80:1 threshold of stability. If a suite of thinning regimes are forecast by a simulator that consistently under-predicts height:diameter ratios, then management will be misled to expect a series of stable thinning regimes in the future, when the actual stand development could lead to an increase in the stand height:diameter ratio well past the threshold of stability. Furthermore, once management realizes that the ratio is 100:1 or even greater, then it is too late for reducing the ratio through thinnings. On the other hand, if thinning regimes are forecast by a simulator that consistently over-predicts height:diameter ratios, then management will be cautious regarding projections, only to find that the stands have remained in the zone of stability, which allows for future thinnings to maintain stand stability.

5.2.1. Maximum density

Height:diameter ratios of individual trees predicted by the four growth simulators never exceeded the maximum observed values in Arnoldstein, but they did exceed the observed maximum values in Litschau. We therefore compared the maximum values found in Litschau to maximum values observed by the Austrian National Forest Inventory. Note that we used only trees that were actually measured for height from the Austrian National Forest Inventory for this comparison. Predicted values did not exceed the values of the National Forest Inventory for any dbh class. We conclude that predictions for individual trees remain in a likely data range for very dense stands.

5.2.2. Open-grown trees

Our investigations showed that the simulated values are sometimes higher than the reference equations of Stampfer (1995). However, the values simulated are not unreasonably high. The entire curves are within the range of the open-grown tree values in the original dataset used by Stampfer (1995) and Lässig (1991). From our results for open-grown trees, there seems to be an illogical curve form for the growth models, except for *Moses*, on some sites. Height:diameter ratios first increase and peak and only monotonically decrease after some time (Fig. 6). The curve form does not correspond to the monotonically decreasing height:diameter ratios found in open-grown tree studies (Thren, 1986; Lässig, 1991; Stampfer, 1995; Hasenauer, 1997). A similar pattern was observed on permanent research plots for both dominant and mean trees planted at low densities (Busse and Weissker, 1931; Neumann, 1997), whereas monotonically decreasing patterns were found for young stands with high initial densities (Busse and Weissker, 1931). Similarly, for our simulations we found that the curve form was sensitive to starting values. If starting height:diameter ratios were high, then the ratios monotonically decreased over time; if the starting values were low, then there was a peak. The incorrect patterns predicted for open-grown trees might there-

fore be an artefact, because growth models were fitted from stand data.

We compared the simulated open-grown tree dimensions of the four forest growth models to values reported in the literature. There were few comparable studies, because most studies on open-grown trees do not include stand age (Stampfer, 1995; Hasenauer, 1997) or values are available only for young trees (<30 years) (Hartig, 1868; Kramer et al., 1970; Mäkinen and Hein, 2006) Where data are available, the studies are confined to good sites. Where no comparable studies are available, the growth of dominant trees is a useful lower threshold. Theoretically the diameter of an open-grown tree should be approximately twice as large as that of a mean stem at maximum density (Sterba, 1975). This is confirmed by comparisons between open-grown trees and stand-grown dominant trees (Lässig, 1991). For spruce on good sites (SI = 38 m), open-grown tree dbh of 68 cm, 99 cm, 107 cm, and 245 cm were simulated with *Silva*, *Prognaus*, *Moses* and *BWIN*, respectively.

Lässig (1991) reported a dbh of 91 cm for a reference open-grown spruce tree (constructed from stem analysis on 12 open-grown trees on 5 sites) at the age of 100. However, individual-tree diameters from stem analysis varied as much as 20 cm at the same age and site index. Gerecke (1991) investigated dominant trees on good sites (SI = 36 m). At a breast height age of 90 years (corresponding approximately to 100 years), he reported an average dbh of 58 cm. Thus, the simulated values for open-grown trees are all higher than observed values for dominant trees. Furthermore, the simulated diameters of *Silva*, *Prognaus* and *Moses* seem to be in good agreement with the results from Lässig (1991). *BWIN* clearly overestimates open-grown spruce growth. Open-grown trees on an alpine site were investigated by Rossi et al. (2008). He reported the average age, dbh, height, and standard deviation of his 5 sample trees. At an average age of 300 years, dbh was 81 cm, and average height was 23 m. The diameters observed compare surprisingly well to a 300-year simulation of a 14 m site index with *Prognaus*, *Moses* and *Silva*; predicted dbh was 86 cm, 98 cm, and 107 cm, respectively. In contrast, *BWIN* overestimates the dbh of open-grown spruce and predicts a dbh of 216 cm. The heights predicted by the growth models were 16, 28, 32, and 36 m for *Silva*, *Prognaus*, *BWIN*, and *Moses*, respectively. The height growth of *Silva* is lowest, because of a strongly curved site-index function for poor sites. The other growth models seem to over-predict the height growth, with values obtained from *Moses* being clearly too high. For pine, Thren (1986) reported an open-grown tree diameter of 57 cm for a site index of 22 m. The diameters simulated by all growth models are lower, but do not deviate more than 15 cm from Thren's (1986) results. Thus, open-grown pine growth is reasonably well predicted by all four growth models. Again, site has a different weight in the four models: differences in diameter between poor and good sites vary from 7 to 62 cm.

5.2.3. Stand density

All models predict an increase in height:diameter ratios with increasing stand density, which corresponds to results from growth and yield experiments. The observed effects of density are both overestimated and underestimated in Arnoldstein, depending on the growth simulator. The magnitude of the discrepancy was within a reasonable range.

Schmid et al. (2006) demonstrated that simulation output of *Silva* differed significantly depending on the method used to calculate missing heights. Performance was much better when calculating missing heights from the Swiss National Forest Inventory than when calculating heights with *Silva*'s internal routines.

Finally, problems in predicting the development of height:diameter ratios can arise from the form of the respec-

tive height and increment models, especially if there is a direct link between height growth and diameter growth models. Wonn and O'Hara (2001) reported a decrease in height:diameter ratios with increasing stand density for simulations with the growth model Prognosis (Wykoff et al., 1982). The cause was a diameter increment term in the height growth model of larger trees, which created positive feedback (Wonn and O'Hara, 2001).

5.2.4. Dominance

As expected, all four growth simulators predicted lower height:diameter ratios for dominant trees than for mean trees. Differences in height:diameter ratios were mostly reasonable. Relative deviations from observed values were largest in young stands. In our study we restricted simulations to the growth of trees with a dbh >5 or 10 cm, the minimum measurement diameter on the respective research plots. All four forest growth simulators are based on sufficient data for trees with dbh >5 cm.

The development of young stands is quite interesting for growth and yield simulations, because the capacity for young stands to respond to release is highest (Assmann, 1961; Dimitri and Keudell, 1986; Wonn and O'Hara, 2001; Mäkinen and Isomäki, 2004). In young stands, thinning can alter species mixture and stand stability, whereas at half of the rotation age most of the stand characteristics (e.g., species composition) have stabilized and there remains little possibility to influence stand development. This has led to recommendations that only low thinnings of little intensity should be done for spruce and pine after half of the rotation age has been reached (Pollanschütz, 1971; Abetz, 1976; Klädtke and Abetz, 2001).

The complex dynamics of young stands makes them difficult to predict. One methodological problem in young stands is the determination of site index, which is required for *Moses*. In young stands it is particularly difficult to determine site index because top-height curves are very close and steep, so that small height or age measurement errors can lead to large errors in site index (Sterba et al., 1990). As a consequence, site index in young stands is often considerably overestimated (Mantel, 1959).

5.3. Type of simulator

This paper compares simulation results for different individual-tree growth models employing different modelling strategies: models with and without a growth-potential formulation, and models with distance-dependent and distance-independent measures of competition. We did not find any particular modelling approach superior to the others. Also, we did not find a closer agreement between models of a similar subtype. This seems to be supported by the view of Wykoff (1990), who regarded the differences between an approach with potential and without a potential as mostly semantic, because either approach, if appropriately used, can produce acceptable predictions. Choice between the approaches may simply be a matter of preference or convenience or data availability. Similarly, no important differences were found between spatial and non-spatial models (Biging and Dobbertin, 1995; Windhager, 1999).

Nevertheless, some notable features emerged. Particularly good performance seems to coincide with strengths of certain models with respect to functional form or data used. For example, *Moses*, which uses open-grown tree relationships, performs particularly well for the prediction of open-grown trees. The strength of *Prognosis* is the prediction of poor sites, because it was fit from national inventory data. *Silva* and *BWIN* are considerably better in the prediction of pine than *Moses* and *Prognosis*, probably because pine is better represented in their datasets.

6. Conclusions

We found that the expected general patterns of height:diameter ratio development are predicted well by all four individual-tree growth models. This indicates that all four simulators were built using a general scientific concept that is logical and biologically reasonable.

However, the results are highly variable, depending on the geographic region. There is excellent fit in some areas, whereas the fit in other areas is rather poor. It is interesting to note that areas of good fit seem to coincide for all four individual-tree growth models (e.g., Arnoldstein), even though they use a different model structure and were fit from different data. Probably frequently occurring growth patterns are well represented, whereas patterns of local importance are not so well described.

Deviations in diameter increment models, height increment models, and crown ratio models are within a reasonable range for all four simulators. Model performance depends strongly on the region where it is applied (compare Arnoldstein vs. Litschau). Similarly, Schmid et al. (2006) found that efficiencies of the same model in different study areas can range from 0.583 (indicating very good model performance) to -0.911 (indicating bias). Coefficients of determination in their study between observed and predicted values ranged from 0.031 to 0.680, underlining highly variable performance.

Height:diameter ratios can be a rather sensitive measure, because moderate deviations in either the height growth model or the diameter growth model can cause comparatively large discrepancies. Differences between observed and predicted height:diameter ratios can be as much as 13 units on average. This is large, given that differences between light and heavy thinning in growth and yield experiments can be as little as 1.8 at the beginning of the experiment and are as large as 25.3 units at the end (Röhle, 1995). The discrepancies can be large when one submodel overestimates and the other submodel underestimates, and errors can cancel when both models overestimate or underestimate. Directly linking diameter and height increment models can cause feedback problems. Such a link can cause a reversion of observed dependencies of height:diameter ratios on density (Wonn and O'Hara, 2001). Furthermore, a bias in predicting height:diameter ratios can propagate into bias for volume increment predictions.

For management applications, the threshold of 80:1 is an important measure of tree and stand stability. For spruce in Arnoldstein, almost all plots are correctly classified with regard to the 80:1 threshold by all four simulators. In contrast, many spruce plots in Litschau are incorrectly classified, which could lead to incorrect management decisions.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.07.055.

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