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Development of species composition in long term simulations with an individual-tree growth simulator

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ABSTRACT: The spruce-fir-beech dominated forest stands in Litschau in the Austrian part of the Bohemian Massif were converted by former forest management practices into pure Norway spruce stands and are now discussed to be reconverted into the potential natural vegetation type. The targeted potential natural vegetation type is usually defined by experts in vegetation sciences. Because meanwhile individual-tree growth simulators are a well acknowledged tool for predicting future forest stand development, in this study we investigate if PrognAus can also be used to predict the redevelopment of managed forest ecosystems into natural forest ecosystems regarding species composition. The development of 23 stands in Litschau has been simulated over 1,000 years under the "no-management" option. Generally, the simulated species distribution agrees quite well with the expectations of the potential natural vegetation type. However, the predicted amounts of silver fir and maple species are lower than expected, which probably is due to browsing and management effects represented in the parameterization data for PrognAus.

Keywords: individual-tree growth model; potential natural vegetation type; forest stand development; species distribution

In many regions of Austria former forest management practices formed even aged pure Norway spruce stands. Due to different ecological as well as economical reasons, these stands are now discussed to be converted into mixed species stands according to potential natural vegetation type sensu Tüxen (1956). For Austrian forest sites the potential natural species distribution were described by Starlinger (in Lexer 2001). Another way to get an idea of the potential natural species distribution for a given stand could be the use of individual tree growth simulators under the non-management option. Such models can be used for long term simulations, if they – besides the individual tree growth models – contain a mortality model and a regeneration or ingrowth model. Since in the long run, without management, at least some uneven-aged stages will occur, there should be preferred simulators which do not rely on the concept of even-aged stands, i.e. such as the ones which do not use stand age or site index as input variables.

The objective of this study is to use the data of secondary conifer stands, apply the individual tree growth simulator PrognAus (Ledermann 2006) to predict the development of these stands under the no-management option for 1,000 years without considering any climate change, and see if the simulated development results in the potential natural species distribution, according to the expectations of Starlinger (in Lexer 2001).

MATERIAL AND METHODS

The study area

In the forest management district Litschau in Lower Austria, former stands of the spruce (*Picea abies* [L.] Karst.) -fir (*Abies alba* Mill.) -beech (*Fagus sylvatica* L.) ecosystem have been changed by large clear cuts, planting of Norway spruce, invasion of Scots pine (*Pinus sylvestris* L.) and litter raking. The

Table 1. Characterization of the experimental stands in 1982: Age, site class – mean annual increment at age 100 (m^3/ha) breast height diameter of tree with mean basal area (*dg* cm), number of trees (*N*/ha), basal area (*G* m^2/ha), volume (*V* m^3/ha) and the proportion of *Picea abies, Pinus sylvestris* and other tree species by volume (%). The soil types are marked with P for the substrate induced Podzol stands, with G for the Mollic and Umbric Gleysol stands and with gP for the gleyic variants of substrate induced Podzol. The amount of other tree species refers to *Abies alba* in stand number 12 (~) and to *Larix decidua* or broadleaf species in the other stands

No.	Soil type	Elevation	Age	Site class	*dg*	*N*	*G*	*V*	*Picea abies*	*Pinus sylvestris*	Other species
1	gP	450	25	17	11.2	2,572	25	164	81	18	1
2	P	550	110	10	35.5	397	39	466	51	49	0
3	P	550	95	9	32.1	425	34	397	44	56	0
4	P	550	52	11	19.1	1,335	38	360	73	25	2
5	P	550	85	7	24.3	816	38	359	45	55	0
6	P	450	55	12	22.4	862	34	347	49	51	0
7	P	550	50	14	18.9	1,099	31	278	46	48	6
8	P	550	90	9	29.8	495	35	395	68	25	7
9	P	550	65	13	23.1	990	41	449	51	49	0
10	P	450	35	18	17.2	1,483	34	305	73	27	0
11	gP	450	10	25	8.0	3,082	15	76	46	54	0
12	G	450	10	23	8.2	2,339	12	65	59	1	40~
13	P	550	110	9	35.4	414	41	497	30	70	0
14	P	550	95	9	29.1	603	40	445	56	44	0
15	P	450	90	9	30.6	511	38	443	49	51	0
16	P	550	35	14	13.3	2,402	33	238	72	20	8
17	G	450	105	9	30.8	615	46	530	44	56	0
18	P	450	90	9	28.8	658	43	486	45	55	0
19	P	550	15	17	7.0	4,139	16	66	98	2	0
20	P	550	30	16	11.5	2,523	26	181	74	26	0
21	P	550	10	18	6.4	3,589	12	41	93	6	1
22	P	550	20	17	9.1	2,566	17	75	64	36	0
23	P	550	100	11	32.5	519	43	506	30	70	0

mean annual temperature in this district is 6.6°C and the annual precipitation about 670 mm at an elevation of 505 m. The individual-tree and site specific input data for PrognAus had been determined in 23 sample plots in stands with different proportions of Norway spruce and Scots pine (Table 1), where diameter at breast height and tree height for every tree had been measured in 1982. The sites are located in the Austrian part of the Bohemian Massif, at an altitude ranging from 450 m to 550 m, on moist, substrate-induced Podzols and gleyic Podzols, except for two sites with Mollic and Umbric Gleysols, and on slopes from 0% to 20%.

The individual-tree growth simulator PrognAus

The parameterization of all models has been based on data of the Austrian National Forest Inventory (ANFI) (Forstliche Bundesversuchsanstalt 1981, 1986, 1992, cited in Monserud, Sterba 1996, 1999, and Ledermann 2002) for a simulation interval of 5 years.

Growth models

PrognAus comprises the individual-tree basal area increment model according to Monserud and Sterba (1996) (for coefficients confer Hasenauer

2000), the crown ratio model according to Hasenauer and Monserud (1996) and the individual-tree height increment model according to Nachtmann (2006). The 5-year basal area increment and the 5-year height increment is directly predicted by species specific functions of site factors, tree size factors and distance independent competition factors.

Mortality model

The individual-tree mortality model (Monserud, Sterba 1999; for coefficients confer Hasenauer 2000) allows directly predicting the probability (P) for mortality in a 5-year period:

$$P = \left(1 + e^{\left(b_0 + \frac{b_1}{dbh} + b_2 \times CR + b_3 \times BAL + b_4 \times dbh + b_5 \times dbh^2\right)}\right)^{-1} \quad (1)$$

where:

dbh – diameter (cm) at breast height (1.3 m),
CR – crown ratio,
BAL – basal area in larger trees (m^2/ha),
b_0–b_5 – species specific coefficients.

The *dbh* and *dbh*-square term in this function is only significant for Norway spruce, which results in continuously decreasing probability for mortality with increasing *dbh* for the other tree species, resulting in large trees never dying. Therefore the results of the long term simulations became unreliable. Thus, in this study, coefficients b_4 and b_5 of the Norway spruce model have been used also for the other tree species to get the expected *U*-shaped mortality rate over *dbh*.

Ingrowth model

Ingrowth in terms of ANFI means that trees exceed the 5 cm *dbh* threshold. The ingrowth model according to Ledermann (2002) consists of species specific sub-models for direct estimation of (*i*) the potential for ingrowth as well as (*ii*) the number of ingrowth trees for a 5-year period on the certain plot and (*iii*) the species, (*iv*) the *dbh* and (*v*) the height of every ingrowth tree. The coefficients in model (*iii*) have been corrected according to Ledermann (personal communication).

For the present study all models were used deterministically, except for sub-model (*iv*) of the ingrowth model, which is a transformation of the probability density function of the Weibull distribution. A uniformly distributed random number between zero and one is utilized to attribute a Weibull distributed *dbh* to each ingrowth tree. Tree volume has been calculated according to Pollanschütz (1974) and Schieler (1988).

Based on tree and site specific data of the 23 sample plots final simulation runs for 1,000 years without any management interventions were performed.

Table 2. The tree species proportion in percent of volume/ha for the experts expectation according to Starlinger (in Lexer 2001) and for the average volume/ha over the last 100 years in the simulations with PrognAus on moist substrate induced Podzol at 450 m a.s.l. (Plot 10), on moist substrate induced Podzol at 550 m a.s.l. (Plot 14), on very moist and gleyic substrate induced Podzol at 450 m a.s.l. (Plot 11) and on very moist Mollic and Umbric Gleysol at 450 m a.s.l. (Plot 17)

Species	Expectation	Plot 10	Plot 14	Plot 11	Plot 17
Norway spruce	> 40	16.8	18.6	40.7	22.6
Silver fir		1.9	3.7	0.0	0.0
European larch	< 20	0.6	0.6	1.2	0.8
Scots pine	< 20	0.7	0.6	6.0	10.5
Common beech	≥ 20	53.2	57.8	12.3	10.8
Common ash	< 25	6.0	5.5	11.5	9.5
Maple species	< 30	0.0	0.0	0.0	0.0
Birch species	< 5	2.0	1.8	3.0	2.3
Oak species		0.4	0.2	0.0	0.0
Common hornbeam		9.8	3.2	4.2	5.3
Alder species		8.6	8.0	21.1	38.1

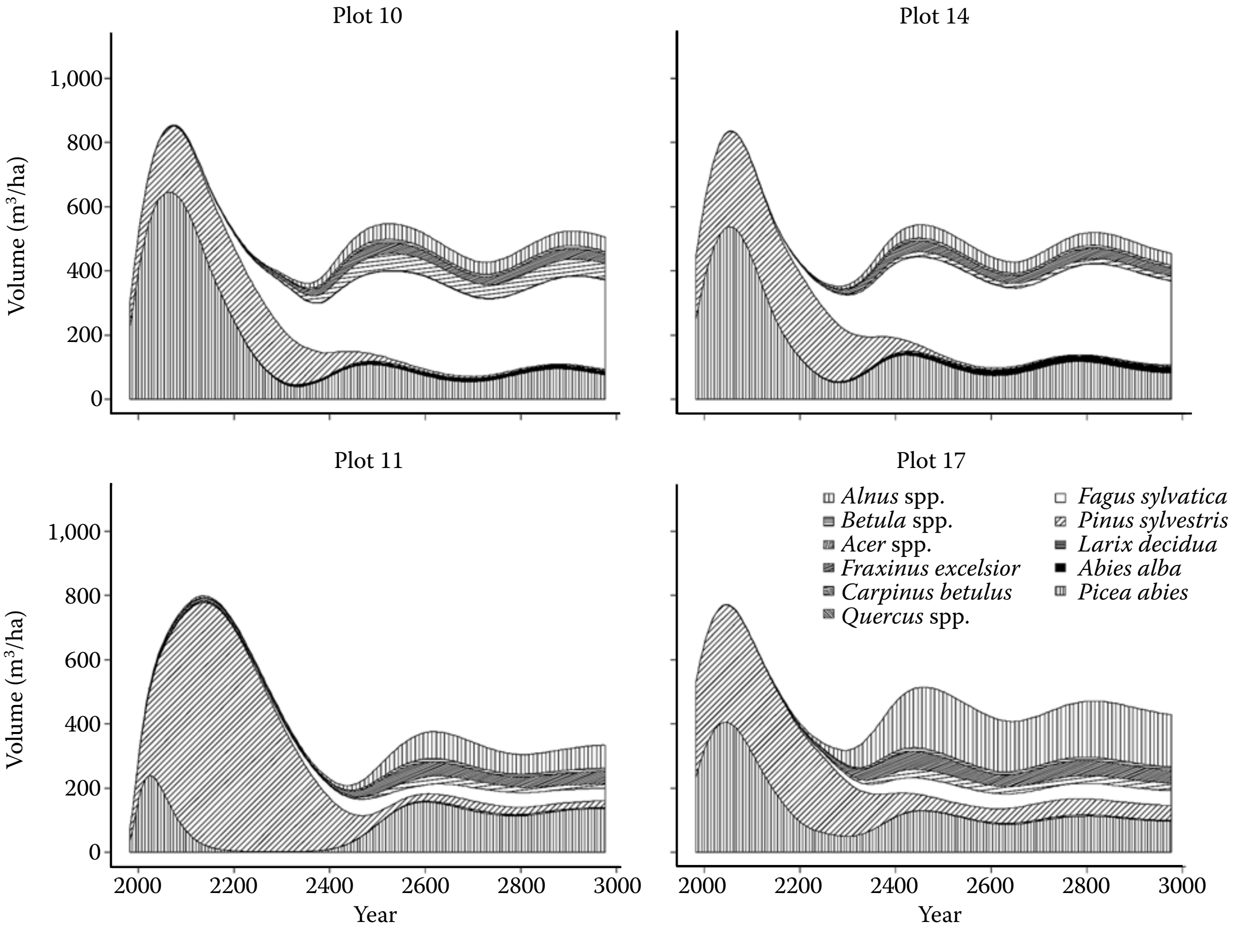

Fig. 1. Volume per hectare by species and year on moist, substrate induced Podzol at 450 m a.s.l. (top left), on moist substrate induced Podzol at 550 m a.s.l. (top right), on very moist and gleyic substrate induced Podzol at 450 m a.s.l. (bottom left) and on very moist Mollic and Umbric Gleysol at 450 m a.s.l. (bottom right)

RESULTS AND DISCUSSION

The simulations were run for all 23 plots, however, in Table 2 and Fig. 1 only 4 plots are highlighted as example for the rest of plots on similar site conditions and thus with very similar results.

Stand volume

The development of volume per hectare over time is shown in Fig. 1 for four different sample stands. All 23 stands show a maximum volume of 868 ± 98.7 m^3/ha after approximately 98 ± 26 years, correlating highly significant with the site class of Norway spruce (Marschall 1975) for the respective site as determined in 1982 (Fig. 2). Afterwards volume decreases within the next 260 ± 36 years to a minimum of 310 ± 61.5 m^3/ha and in the further development all plots show three waves in the volume trend and seem to oscillate around an equilibrium with a wavelength (distance in years between the last two volume peaks) of 367 ± 17 years and an amplitude (difference between the second peak and its subsequent low) of 160 ± 70.8 m^3/ha. The average volume over the last 100 years is between 327 m^3/ha and 573 m^3/ha, varying only marginally over the 100 years (standard deviations between 4.50 and 35.6 m^3/ha). The resulting volume development with a more or less constant volume over time is plausible, showing a "wave motion" like it is expected for the characteristics of stable ecosystems (Gigon 1982). The volume level of unmanaged forests ought to be higher and the wavelength (regeneration period) to be longer as for Plenter forests (Thomasius 1991). Mayer (1976) mentions a volume per hectare between 300 m^3/ha and 700 m^3/ha for Plenter forests in the Allgäu region in Germany, depending on site index. Compared to this, the simulation results would meet the expectation. Surprisingly, the average volume over the last 100 years occurs to be independent from site class of the respective stand (Fig. 2). However, it should be considered that site class was determined in 1982, when the stands were even-aged and contained only one or two species, whereas the stands in the simula-

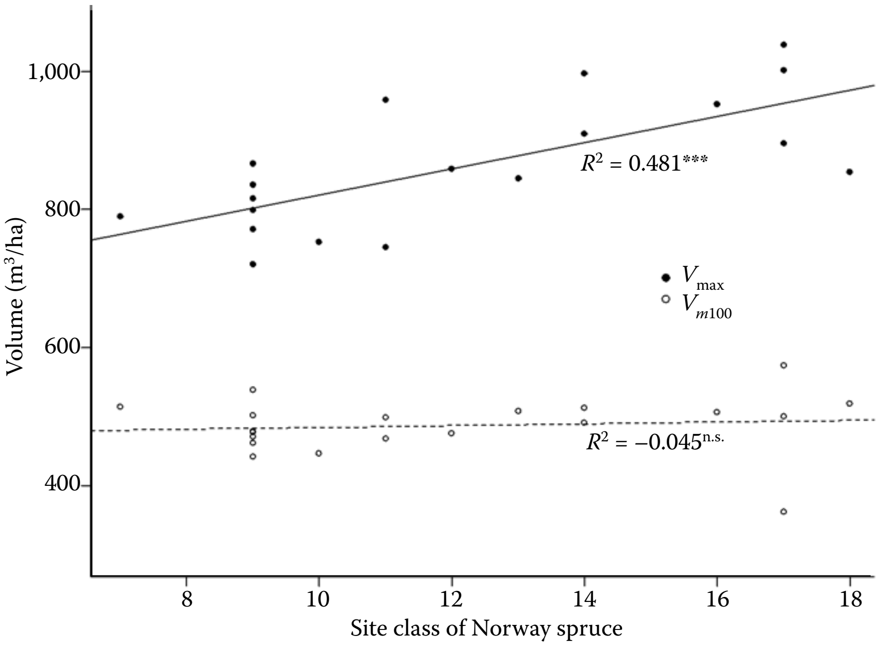

Fig. 2. Regression between the site class of Norway spruce (estimated mean annual increment at age 100, m^3/ha) and the maximum volume/ha (V_{max}) and the average volume over the last 100 years (V_{m100}) respectively. Stands with age under 25 have been omitted because of unreliable site class estimation

tion with PrognAus after 1,000 years are uneven-aged mixed-species stands.

Species composition

All plots show a steady state species composition after the year 2400, i.e. after 418 years. The species proportion in percent of the average volume per hectare over the last 100 years is given in Table 2 for four selected stands, in comparison with the expectations of Starlinger (in Lexer 2001). On substrate induced Podzol (Plot 10, Plot 14) common beech is predominant with an amount of more than 50%, followed by Norway spruce, alder species (*Alnus* spp.) and common ash (*Fraxinus excelsior* L.). Silver fir, common hornbeam (*Carpinus betulus* L.) and birch species (*Betula* spp.) are present with an amount smaller than 5%, except for the stand with lowest elevation (Plot 10), where the amount of common hornbeam is higher. European larch (*Larix decidua* Mill.), Scots pine and oak species (*Quercus* spp.) are present with a marginal amount smaller than 1%. Comparing different soil types and soil moisture classes, the amount of common beech is lower, that of Norway spruce, alder species, common ash and Scots pine is much higher at the very moist and gleyic Podzol stands (Plot 11). Silver fir as well as oak species are inexistent on these sites. On Mollic and Umbric Gleysol (Plot 17) alder species are predominant, followed by Norway spruce, common beech, Scots pine and common ash. Silver fir and oak species are inexistent again.

The potential natural vegetation type for the Litschau region is the sub-hercynic spruce-fir-beech forest with high proportions of Norway spruce (Kilian et al. 1994). Compared to the expectation of Starlinger (in Lexer 2001), the proportion of Norway spruce and silver fir would be too low and that of common beech would be too high in the simulation results with PrognAus. The expected proportions are given very generally for all spruce-fir-beech types in all growth districts and their altitudinal sub districts and thus characterized by a very wide range of soil conditions. A spruce-fir-beech forest as potential natural vegetation is the valid zonal forest type for the substrate induced Podzol, but for the Mollic and Umbric Gleysol an azonal forest type dominated at the given elevation in this growth district by common alder (*Alnus glutinosa* [L.] Gaertn.) is more plausible, which agrees with our simulation results. The generally low amount of silver fir could be due to browsing and the economical disadvantage of fir wood, reflected in forest management practice, as they are comprised in the parameterization database of PrognAus. This could be similarly true for European larch, whose amount in the species composition is lower than expected and maybe caused also by extinction of the natural occurrences of this species and miscarried crop growing because of wrong provenance selection. For Scots pine Mayer (1976) mentions a second ecological optimum in wet and acidic soil conditions which would constitute the increased amount of Scots pine at the stands stronger influenced by gley dynamics. The increased amount of ash species at the moister stands also reflects the species' ecological demands in site conditions. *Acer campestre* L., *Acer platanoides* L. and *Acer pseudoplatanus* L., the native maple species in Austria, have rather different demands in climatic site conditions but, due to the fact that *Acer pseudoplatanus* is the only species showing economical importance, the ANFI subsumed maple species. A generally small amount of maple in the species composition had been expected and is plausible because of intolerance of low soil pH values and the low frost resistance of all maple species. However, the reduced amount may also be due to the role of maple species as game forage. The ANFI also subsumed the native birch species *Betula pendula* Roth and *Betula pubescens* Ehrh. The presence of birch species in general is plausible due to its wide ecological range. The potential stronger presence of *Betula pubescens* at sites influenced by ground water may cause the slightly increased amount in the simulation results. Oak species are present in the resulting species compositions with only marginal amounts. The genus is dominant in eastern Austria together with common hornbeam and the oak-hornbeam forest is the potential natural vegetation type for the very south-eastern parts of the given growth district at elevations between 200 m and 400 m a.s.l. A remarkable amount of common hornbeam in the simulation results had been expected because of its less specific demands in site conditions, in comparison to oak species. The amount of common hornbeam is higher at dryer sites and sites at lower elevations.

CONCLUSIONS

Results of long term simulations with PrognAus meet the expectations for the given growth district and site conditions rather well. The steady state wave motion of the volume per hectare as well as its level is plausible. Regarding tree species the Podzol stands show a steady state composition dominated by common beech with admixed Norway spruce and the Mollic and Umbric Gleysol stands show a steady state species composition dominated by common alder with admixed Norway spruce, Scots pine and common beech. Other native tree species are present with amounts smaller than ten percent, depending on site conditions. The resultant species compositions approximately meet the expectations, but the amount of silver fir, European larch and maple species is surely too low, which is caused by the parameterization data of the ingrowth model in PrognAus, which represents the impacts of game animals and management practises.

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Vývoj druhové skladby v dlouhodobých simulacích stromového růstového simulátoru

ABSTRAKT: Porosty s dominancí smrku, jedle a buku v Litschau v rakouské části Českého masivu byly dřívější lesnickou praxí přeměněny na stejnorodé smrkové porosty a nyní je uvažováno o jejich přeměně na potenciálně přirozený typ vegetace. Cílový typ vegetace je obvykle definován experty na rostlinná společenstva. Pro předpověď budoucího vývoje porostů však začaly být mezitím používány i růstové simulátory. Ve studii jsme zjišťovali, jestli je model PrognAus také použitelný pro předpověď zpětného vývoje ekosystému hospodářských lesů na přírodní lesní ekosystémy ve vztahu k dřevinné skladbě. V Litschau byl simulován vývoj celkem 23 porostů v horizontu 1 000 let „bez zásahu". Simulovaná dřevinná skladba byla obecně v souladu s očekávanou potenciální přírodní vegetací. Simulované zastoupení jedle a javoru bylo nižší než očekávané, což bylo pravděpodobně způsobeno díky vlivu okusu a lesnického hospodaření. Tyto efekty jsou součástí parametrizace dat pro simulátor PrognAus.

Klíčová slova: stromový růstový model; potenciální přírodní typ vegetace; vývoj lesních porostů; druhová skladba

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