



Effect of different tree mortality patterns on stand development in the forest model SIBYLA

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Abstract

Forest mortality critically affects stand structure and the quality of ecosystem services provided by forests. Spruce bark beetle (*Ips typographus*) generates rather complex infestation and mortality patterns, and implementation of such patterns in forest models is challenging. We present here the procedure, which allows to simulate the bark beetle-related tree mortality in the forest dynamics model Sibyla. We explored how sensitive various production and stand structure indicators are to tree mortality patterns, which can be generated by bark beetles. We compared the simulation outputs for three unmanaged forest stands with 40, 70 and 100% proportion of spruce as affected by the disturbance-related mortality that occurred in a random pattern and in a patchy pattern. The used tree species and age class-specific mortality rates were derived from the disturbance-related mortality records from Slovakia. The proposed algorithm was developed in the SQLite using the Python language, and the algorithm allowed us to define the degree of spatial clustering of dead trees ranging from a random distribution to a completely clustered distribution; a number of trees that died in either mode is set to remain equal. We found significant differences between the long-term developments of the three investigated forest stands, but we found very little effect of the tested mortality modes on stand increment, tree species composition and diversity, and tree size diversity. Hence, our hypothesis that the different pattern of dead trees emergence should affect the competitive interactions between trees and regeneration, and thus affect selected productivity and stand structure indicators was not confirmed.

Key words: *Ips typographus*; dispersal pattern; empirical forest modelling; tree mortality

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1. Introduction

Models of forest dynamics have become important tools that supported forest management and increased our understanding of forest development under diverse management and natural conditions. Because forest damage is among the most important drivers of forest development with effect on the quality of ecosystems services provided by forests (Thom & Seidl 2015; Thom et al. 2016), a great deal of attention has been paid to the implementation of forest mortality processes into models (Pietsch & Hasenauer 2006; Merganičová & Merganič 2014; Seidl & Rammer 2016). At the same time, models were found highly sensitive to the mortality assumptions adopted (Bircher et al. 2015; Hlásny et al. 2014), which highlights the importance of proper implementation of algorithms driving the mortality-related processes. Despite these efforts and increasing complexity of models, Keane et al. (2001) and Bircher et al. (2015) argue that mortality algorithms implemented in models are generally based on simple assumptions and insufficient data.

Bark beetles of the genus *Ips*, and particularly the spruce bark beetle *Ips typographus* (L., 1758) (Curculionidae: Scolytinae), are the most damaging biotic agents in central European forest (e.g. Berec et al. 2013). Bark beetle-related tree mortality is a highly complex process that is driven by both the host susceptibility, bark beetle population size and diverse environmental perturbations (Wermelinger 2004; Hlásny & Turčáni 2013). Interactions between the host

tree distribution, tree susceptibility and density-dependent bark beetle dispersal capacity, generate specific patterns of infested trees. Such patterns might range from the scattered occurrence of infested trees, which is typical of small beetle densities, to patchy and even a large scale infestations that typically occur when the populations are in the outbreak phase (Hlásny & Turčáni 2013). Because tree mortality patterns might affect stand structure and the quality of ecosystem services in the period following the infestation, it is desired to include such information into forest models, which operate at a scale of trees.

Among such models, the forest model Sibyla (Fabrika & Ďurský 2005) has received an increased recognition in recent years (e.g. Vacek et al. 2013; Hlásny et al. 2011, 2014, 2016; Ambrož et al. 2015; Härtl et al. 2016). The model simulates mortality at a scale of trees and considers both the inherent tree mortality (Ďurský et al. 1996, 1997) and mortality related to disturbances (Fabrika & Vaculčíak 2009). Particularly the disturbance-related mortality shows significant differences between tree species, depending on tree species vulnerability to various disturbances. Hlásny et al. (2016) developed an application that simulates the disturbance-related mortality in the model Sibyla based on the species and age-specific mortality rates derived from the 10-year records on forest damage in Slovakia; this is the algorithm we use and evaluate in this study.

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Because the used mortality rates contain the cumulative effect of all damage agents (biotic and abiotic), each of them generating a specific pattern of tree mortality, the preference of any specific tree mortality pattern might be irrelevant. However, such an approach might generate biased outputs for regions, where mortality with patchy pattern, such as that related to bark beetle infestation, prevails. It is, however, not clear whether and how the consideration of such a mortality pattern might affect stand development in the period following the infestation.

To shed a light on this issue, we present a modelling exercise that evaluates in several virtual Norway spruce-dominated stands how biomass production, tree species and stand structure diversity can develop under the random and clustered mortality modes. We hypothesize that the appearance of clearings in response to the clustered emergence of dead trees could induce regeneration processes different from those induced by the random emergence of dead trees, and thus, in the long-run, affect tree species composition of the stands. Further, we hypothesize that the different patterns of dead tree emergence will affect the competition between trees and tree increment, and that such a difference will be translated from the tree scale to the stand scale. Finally, we hypothesize that mainly stand structure diversity will be affected by the tested mortality modes, while effect on biomass production will be less pronounced. Such a research is intended to contribute to mortality parameterization in tree-based forest models and to improve the reliability of forest development simulations.

2. Data and methods

2.1. Used model and simulation design

We used here the forest model Sibyla developed by Fabrika & Ďurský (2005) (available at <http://sibyla.tuzvo.sk>) and repeatedly used for research, for example, by Hlásny et al. (2011, 2014, 2016), Härtl et al. (2016) and others. Sibyla is empirical single-tree oriented climate sensitive forest model with a one-year simulation step, and the core components of the model are based on the Silva model (Pretzsch et al. 2002). A detailed description of the model can be found in the studies we referred to earlier.

We used three virtual forest stands with identical site conditions to secure the comparability of simulation outputs (Table 1). The used stand parameters represent the conditions in which spruce typically grows in Slovakia. The three stands were with a different share of Norway spruce (*Picea abies* L. Karst.). (Stand code: S100 – 100%; S70 – 70%; and S40 – 40%) and with a different admixture of other species (Table 2). The admixed species were European beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.), and Scots pine (*Pinus sylvestris* L.).

The inherent tree mortality (i.e. mortality related to competition) is implemented according to Ďurský et al. (1996) and Ďurský (1997). The disturbance module that is inherently implemented in the model (Fabrika & Vaculčíak 2006) was not used in this study, and we used an external module developed by Hlásny et al. (2016) instead. The latter module was developed in the Python and SQL languages, and the module allows flexible adjustments of a number of mortal-

ity settings. The disturbance mortality rates used here were specific to tree species and age class, and were parameterized based on the forest disturbance records for the period 1998–2009 using the data from the whole of Slovakia (Hlásny et al. 2016) (Table 3).

Table 1. Stand and site condition of the three simulated forest stands.

Stand and site parameters	Value
Elevation [m a.s.l.]	982
Soil type	Cambisol
Stand density	0.95
Initial age [years]	40
Mean air temperature during vegetation season [°C]	12.5
Precipitation totals during vegetation season [mm]	727

Table 2. Types of tree species composition in the three simulated forest stands.

Stand / species proportion [%]	Spruce	Fir	Beech	Pine
S100	100	0	0	0
S70	70	15	15	0
S40	40	25	25	10

Such initial rates were modified to consider the reduced susceptibility to infestation for stands with the admixture of non-spruce species based on Griess et al. (2012). The correction accounted for 3% for stands with spruce up to 80% and 15% with spruce below 60%.

Development of each stand was evaluated during a 200-year period, because the divergence of the tested stand development indicator is likely to occur in longer runs only. The simulations were run with the natural regeneration module activated (Merganič & Fabrika 2011). No management operations except for the removal of dead trees were applied. Each simulation was run ten-times to consider the variability related to the differences in the initial tree positions and stochasticity related to tree mortality and other model parameters.

Table 3. Tree species- and age class-specific mortality rates used to drive the forest mortality in the current study.

Tree species- and age class-specific mortality rates						
Age class	Spruce proportion in a stand [%]			Beech	Fir	Pine
	>80	60–80	<60			
<30	0.10	0.10	0.08	0.01	0.08	0.05
31–40	0.11	0.11	0.10	0.01	0.05	0.04
41–50	0.13	0.12	0.11	0.01	0.03	0.02
51–60	0.15	0.14	0.13	0.01	0.03	0.02
61–70	0.16	0.16	0.14	0.01	0.02	0.02
71–80	0.19	0.18	0.16	0.01	0.03	0.02
81–90	0.20	0.19	0.17	0.02	0.03	0.03
91–100	0.20	0.20	0.17	0.02	0.03	0.03
101–110	0.20	0.19	0.17	0.02	0.03	0.03
111–120	0.20	0.19	0.17	0.02	0.03	0.02
121–130	0.20	0.19	0.17	0.01	0.04	0.02
131–140	0.21	0.20	0.18	0.01	0.04	0.02
141–150	0.20	0.19	0.17	0.01	0.04	0.01
>150	0.17	0.16	0.14	0.01	0.03	0.00

2.2. Tested mortality patterns

Two mortality set-ups were tested – a random occurrence of dead trees driven by species- and age class-specific mortality only (Table 3, mode RAN) and a clustered occurrence of dead trees (mode CLUST), where mortality is also driven by the proximity of an evaluated tree to the trees that died in the

previous period. Hence, the CLUST mode generates the dead trees in a patchy pattern typical of bark beetle infestation in the epidemic phase.

In case for the RAN mode, a specific mortality rate from Table 3 is assigned to each tree in a stand based on the species and age class. Then, a real number in the 0 – 1 interval with the uniform distribution is generated for each tree to specify a threshold to which a mortality rate is compared. In case the threshold is exceeded a tree survives, otherwise a tree dies. Such a procedure is applied with a 10-year step.

In case for the CLUST mode, the procedure described above is modified based on the proximity of each tree to the trees which had died in the former simulation step. The literature review indicated that under high beetle densities (epidemic phase) most of beetles disperse over short distances (up to 100 m), and the dispersal (or the appearance of new infestation spots) disappears within 500 – 1,000 m from old infestations (Wichman & Ravn 2001; Kautz et al. 2011; Hlásny & Turčáni 2013; Stadelmann et al. 2014). Therefore, we modified the RUN algorithms so as we define the affinity of the newly infested trees to the trees infested in the previous period. The affinity with magnitude 1 causes that all new infestations might occur in trees adjacent to the old infestations, and the age effect does not apply in this case; however, the age threshold of 50 years is applied to avoid the infestation of trees, which are very unlikely to be infested. The 50-year age limit was applied though spruce bark beetle is thought to infest trees older than 70 years (Wermelinger 2004), but much younger stands have been recently found to be infested, for example, in the Czech Republic (J. Holuša, pers. comm.).

The affinity with the magnitude of 0 indicates no clustering effects and CLUST is equal to RUN. The transient affinity values can be applied to model various bark beetle dispersal patterns. The algorithm was developed in the SQLite using the Python language.

2.3. Evaluated stand development indicators

We evaluated effect of the two mortality setting on several production and stand diversity indicators. We evaluated the effect on volume increment of a stand ($\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$); species-specific relative standing volume (% of the total stand volume), which is indicative of tree species composition; volume of dead wood (m^3); tree species and tree size diversity. The true diversity index (Jost 2006), which is the exponential form of the Shannon's diversity index, is used as the indicator of tree species diversity; species-specific basal area is used as a weight. Tree size diversity index (H), which aggregates the diversity of tree heights and diameters (Staudhammer & LeMay 2001), is used as the indicator of stand structure diversity.

3. Results

3.1. Volume increment

Different species compositions and related mortality rates caused the mean stand volume increment ($\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$) to differ significantly between the simulated stands. While in

S40 the increment culminated at ca 90th year of the simulation (stand age 130) at $27 \text{ m}^3 \text{ha}^{-1} \text{year}^{-1}$, the increment was steadily declining during the whole simulation period in the two remaining stands (S70 and S100). Such a decline was primarily related to the progressive mortality of the dominating spruce trees, while such an effect was less pronounced in S40 and S70.

Although we assumed that the two tested mortality modes will affect the stand density differently, and this effect will result in a differential response of stand increment, our simulations showed almost no difference between the RUN and CLUST mortality modes during the whole simulation period; minor deviations of the two curves in Fig. 1 were in the range of the respective error bars.

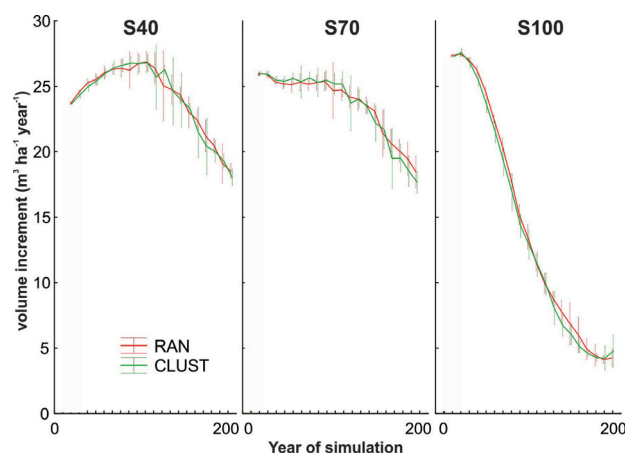


Fig. 1. Development of mean stand volume increment simulated with the random (RAN) and clustered (CLUST) occurrence of dead trees in three forests stands. Stand codes are explained in Table 2. The error bars show the 95% interval calculated based on 10 repeated simulation runs.

3.2. Relative standing volume

Relative standing volume was investigated as an indicator of the change in tree species composition. The simulations shows that fir was performing best and its volume was steadily growing during the simulation period (Fig. 2). The decrease of spruce was related to high mortality rates, while the decrease of beech was related to the unfavorable condition for beech growth in the elevation of 1,000 m a.s.l., where beech production and ability to compete with other species were not sufficient to persist.

As in the case of mean stand volume increment, the two tested mortality modes did not affect the per-species volume significantly during the whole simulation period.

3.3. Dead wood volume

Dead wood volume generated for each year of the simulation period directly reflects the species- and age-class specific mortality rates indicated in Table 3. Development of dead wood volume in all three stands shows the presence of damage culmination phase, where the proportion of spruce and/or other overmatured trees reached maximum (Fig. 3). In S40 the damage culmination occurred ca in year 70 of the simulation period, and then the damage decrease because

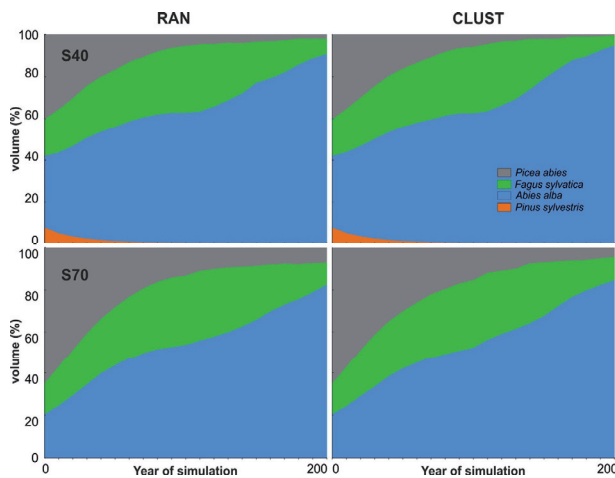


Fig. 2. Species specific standing volume calculated as the per cent of the total standing volume simulated with the random (RAN) and clustered (CLUST) occurrence of dead trees. Stand codes are explained in Table 2. Stand S100 was not presented because of the persisting dominance of spruce.

of the increase abundance of younger and less vulnerable spruce trees. In S40 and S70 the damage peaked in ca year 170 of the simulation period, though the peak in S40 was not as sharp as in the previous stands.

Because of the stochasticity in the algorithm, which is applied to evaluate whether or not a tree dies, the inter-simulation variability is largest of the all investigated indicators. As in the previous indicators, there was no difference between the RAN and CLUST modes. In case of this indicator, however, such an output could have been expected, because the used algorithm was designated so as it affects the distribution of dead trees in a stand, while the total number of dead trees remains equal.

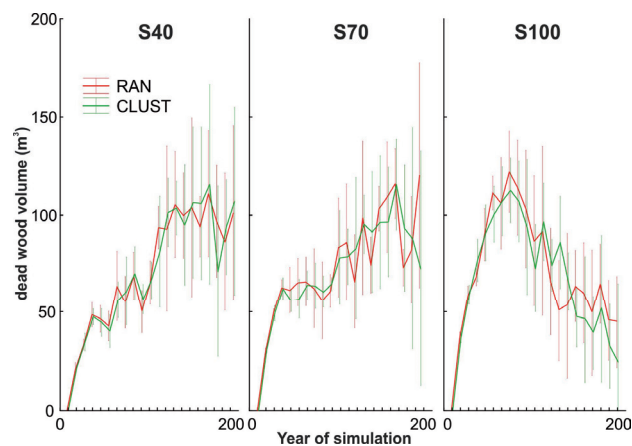


Fig. 3. Dead wood volume simulated with the random (RAN) and clustered (CLUST) occurrence of dead trees. Stand codes are explained in Table 2.

3.4. Tree species and tree size diversity

Tree species diversity was evaluated for stands S40 and S70 but not for S100, where only spruce could regenerate and thus the stand remained monospecific during the whole of the simulation period. In S40 the initial value of the used diversity index was significantly higher than in S70 because

of more equal proportions of tree species (Fig. 4). The diversity, however, sharply decreased as fir become to dominate in the stand.

Tree size diversity was increasing in all simulated stands, though the increase was rather erratic in S40. The increase was related to the occurrence of large overmatured trees, which have not died despite their high mortality rates (Table 1), as well as to the occurrence of smaller trees appearing in the new generation of the forest.

Tree species diversity shows minor differences between the development driven by CLUST and RAN mortality modes, the differences are, however, in the range of the variability related to the ten simulation runs. The difference between the mortality modes as well as the inter-run variability of the tree size diversity significantly increased after ca 150 year of simulation in S40, such a pattern, however, lacks interpretation.

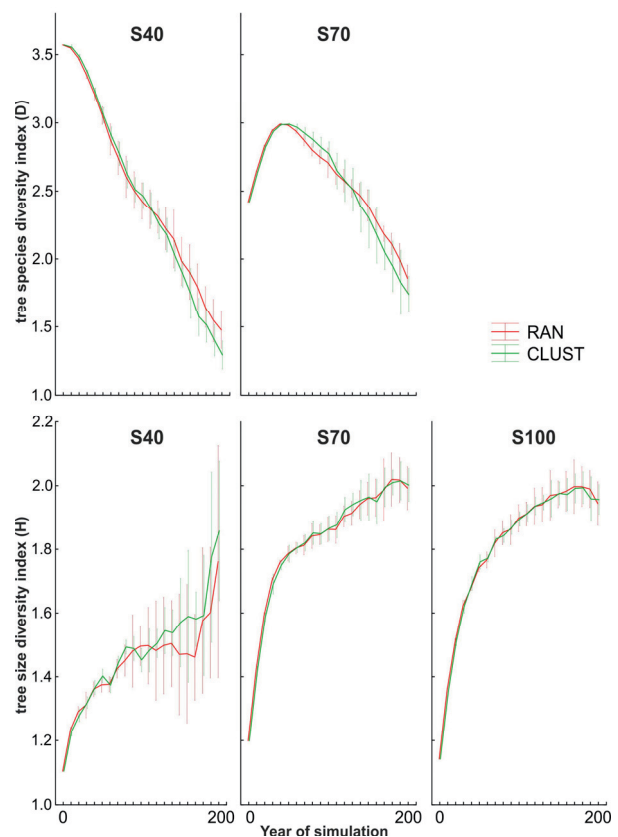


Fig. 4. Tree species (D) and tree size diversity index (H) simulated with the random (RAN) and clustered (CLUST) occurrence of dead trees. Stand codes are explained in Table 2.

4. Discussion

The model Sibyla represents a well-established forest model, which has been repeatedly used in the research of forest development driven by various management types, disturbances or by climate change (Hlásny et al. 2011, 2014, 2016; Vacek et al. 2013; Ambrož et al. 2015; Härtl et al. 2016). That the model operates at a scale of trees facilitated analyses that utilize tree positions, including the assessment of stand structure indicators or change in tree species composition. Still, there are limits in the understanding of model's behavior,

which should be explored to use the model more efficiently and support the proper interpretations of simulation outputs. We explored here how the spatially clustered occurrence of dead trees, which generates mortality patterns similar to those generated by spruce bark beetle, might affect selected stand structure and productivity indicators. Such a research might inform whether it is worth to consider the spatial distribution of dead trees in tree-based forest models, and how the selected indicators are sensitive to differences in the pattern of dead trees emergence.

We focused on three forest stands with different percentage of Norway spruce, which typically occur in central Europe. We found significant differences between the long-term developments of the three investigated forest stands, but we found very little effect of the tested mortality modes on stand increment, tree species composition and diversity, and tree size diversity. This was despite the pattern of dead trees distribution and the overall stand structure was rather different between the simulations driven by the two mortality modes (Appendix A). Hence, our hypothesis that the different pattern of dead trees emergence should affect the competitive interactions between trees and thus affect selected productivity and stand structure indicators was not confirmed.

Therefore, we suggest that different patterns of dead tree emergence might not be considered in tree-based forest model, when basic growth, yield and stand structure indicators are to be evaluated. Still, effect on specific indices of horizontal stands structure (e.g. Clark & Evans 1954, Stoyan & Stoyan 1992), which might be more sensitive to the modified distribution of trees, need to be explored.

There are some limits of the interpretation of our findings related to the used experimental design. We assumed that the prescribed degree of spatial clustering of dead trees remains constant during the whole simulation period. This is, however, not a realistic assumption because various transitions between random and patchy tree mortality patterns are typical of bark beetle population dynamics. Typically, small populations generate a scattered pattern because the beetles search for suitable hosts, while beetles in large populations tend to infest the trees in a closer vicinity (Kausrud et al. 2011; Hlásny & Turčáni 2013). Large populations might tend to collapse after a several-year period of the outbreak culmination because of the effect of diverse density dependent regulation mechanisms (Raffa et al. 2008). Therefore, the coefficient of affinity we used in the current study should change in time depending on a number of factors (e.g. stand age structure) to mimic the real bark beetle dynamics more reliably. We, however, argue that such a complex processes can be better addressed by models that specifically explore bark beetle dynamics (e.g. Netherer & Nopp-Mayr 2005; Jönsson et al. 2012) or process-based forest models (e.g. Seidl et al. 2012), while empirical growth and yield-oriented models, such as that used in the current study, might prefer a simplified design such as that we described here.

Another limitation relates to the technical implementation of our module in the model Sibyla. Because the source code of the model is not publicly available, the disturbance mortality module (including tree species- and age class-specific mortality probabilities described in the text, and the dead tree clustering module) were developed as an independent

application in the Python language. The application interrupts the forest development simulation, identifies the trees to die, and retrieves the output set-up to the model. Such an implementation is not that optimal, and it remarkably increases the computational time.

5. Conclusions

We presented here the testing of algorithm, which allowed to simulate various distributions of dead trees, which emerge during the development of spruce stands in the forest model Sibyla. Our study showed that the tested indicators of forest development were not sensitive to the altered distribution of dead trees in the stand and that the hypotheses on the effect of such an alteration on regeneration and increment were not confirmed.

Although the presented findings indicated that tree-based forest models might not consider specific patterns of dead trees emergence in forest stands, there are several limits related to the experimental design used in the current study, which require further investigation. These limits include, for example, the unknown sensitivity of the natural regeneration in the model to the modified stand density induced by the two tested mortality modes. Moreover, there are specific stand structure indicators, which can be more sensitive to tree distribution in a stand than the indicators evaluated here; the sensitivity of such indicators needs to be explored. Still, our study provided a new insight on the development of spruce forest stands in the forests model Sibyla and thus can support the optimized use of the model.

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Appendix A: Differences in the development of Norway spruce stand in the forest model Sibyla with the random and clustered occurrence of dead trees

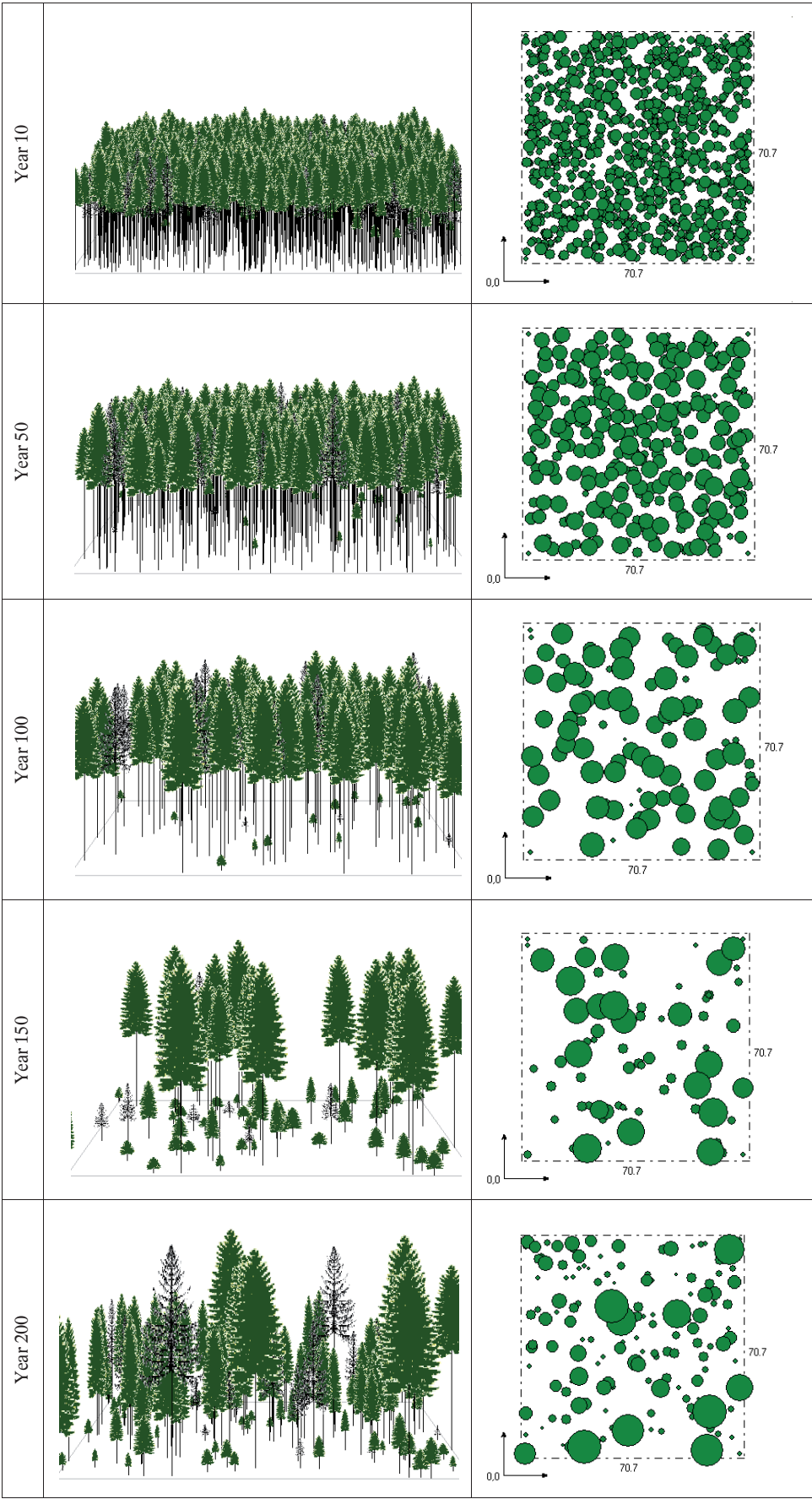


Fig. A1. Example of the development of spruce stand with the random occurrence of dead trees.

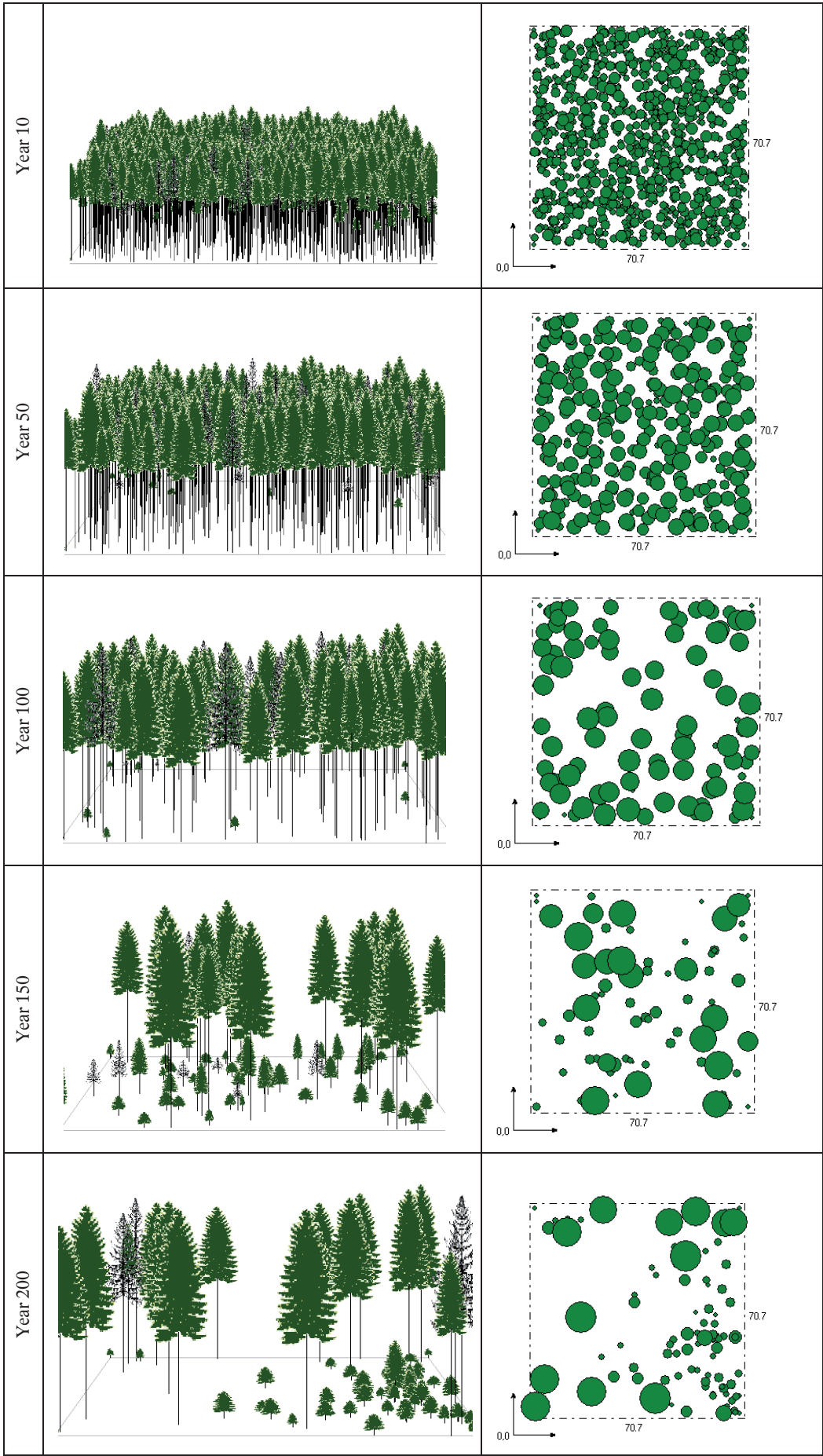


Fig. A2. Example of the development of spruce stand with the clustered occurrence of dead trees.