Mortality, recruitment, and increment of trees in the Fagus-Abies-Picea stands of a primeval character in the lower mountain zone

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Abstract: From among three stands, situated in the lower mountain zone, and representing the association Dentario-glandulosae Fagetum, the Łopuszna I stand, being in the growing up stage and phase of selection forest, reached the highest increment (8.5 m³/ha/year, i.e. 1.3% of actual stand volume/ha measured at the end of the control period). Stands Łopuszna II, being in the stage of an intensive break-up, and Łopuszna III, being in the stage of an initial break-up, reached smaller increments (5.4 and 6.3 m³/ha/year respectively, i.e. each 0.9% of actual stand volume/ha). The greatest tree mortality occurred in stands Łopuszna II and III (14.1 and 10.5 m³/ha/year respectively), and the smallest in the stand Łopuszna I (4.8 m³/ha/year). The knowledge about the value of mortality, recruitment, and increment, expressed in the number of trees and in volume units, may greatly help in planning the amount of cut which would secure sustainability of the forest ecosystem in the layer of trees in the economic as well as in the protection forests, under similar stand and site conditions, managed by the selection cutting permitting to realize the conception of a close-to-nature silviculture.

Additional key words: Abies alba, Fagus sylvatica, development stages and phases, close-to-nature silviculture

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Introduction

A constant amount of organic substance of the over-ground part in the phase of a relative equilibrium is a feature of forests of a primeval character (Bormann and Likens 1979). This equilibrium, expressed by stand volume, is associated with three natural, separate, and partly antagonistic processes: tree mortality, recruitment, and increment (Dziewolski and Rutkowski 1987).

There are three basic causes of tree dying in primeval forests. The first cause consists of unfavorable light conditions and inadequate space for growth of trees from the lower, and possibly middle layer. This results in the process of natural stand thinning. The second cause, typical for primeval forests, is dying of trees due to physiological old age, i.e. reaching natural death by trees. The third cause is closely connected with the second one, because the trees reaching old age are frequently overturned or broken (Korpel 1989).

The process of recruitment is associated with reaching by trees of the young generation of a definite size, and passing over a certain d.b.h. threshold. Thus, including a part of tree population into the recruitment is of a conventional character.

While the volume increment of the stem of a single tree is the result of the increase in its height and diameter, and change of its form, the volume increment...
of a stand is connected not only with all these changes in tree dimensions, but also with changes in the number of trees forming the stand (mortality and recruitment). The process of increment and its value in primeval forests depends on several factors: species and condition of individual trees, site quality, age and structure of the stand, being characteristic for definite stages and phases of development.

The determination of mortality, recruitment, and increment is possible, in the first place, by carrying out two stand measurements in assumed control periods on permanent experimental plots. Data, also concerning the stand increment, for primeval stands of Bosnia (Peručica) were presented by Pintaric (1978), and of Slovakia by Korpel (1995). In stands of a primeval character in the Polish part of the Eastern Carpathians (the Bieszczady range) this problem was studied by Jaworski and Kolodziej (2002), who also determined the tree mortality. Data concerning exclusively the increment of the lower mountain zone natural stands of the Western Carpathians are a little more numerous. Similar studies were carried out by Dziewolski and Rutkowski (1987) in the Pieniny Mountains, and Jaworski and Paluch (2002) on Mt. Babia Góra. In the Gorce range this problem was studied by Dziewolski and Rutkowski (1991), and also by Przybylska et al. (1995). Outside the Carpathians the dynamics of changes in forest resources was investigated by other authors, e.g. Poznański (1998) in the Świętokrzyski National Park.

The purpose of this study was to determine the value of mortality (with description of dead trees), recruitment, and increment of stands, and to relate them to stages of stand development.

**Materials and methods**

The study plots were established in 1981 in the upper part of the lower mountain zone, in the “Dolina Łopusznej” reserve situated in the Gorce National Park (Fabijanowski and Jaworski 1989). This part of the reserve, representing the association Dentario glandulosae-Fagetum, was quite diversified in structure of stands. Taking into account the degree of human interference, the forest complexes investigated during this study were of a primeval, and in some places of a natural character, which was concordant with the definition of Schuck et al. (1994). The stages and phases of stand development in 1991 and 2001 are presented in table 1.

The initial measurements were completed in the field in August of 1991 (Jaworski and Skrzyszewski 1995), while the control measurements were carried out in 2001. They included the measurement of d.b.h. (≥ 6 cm) and height of all trees, with an exception of slanting ones. Trees with d.b.h. ≥ 8 cm were also classified according to the IUFRO classification (Leibundgut 1966) using its biological part:

- a – height classes: 100 – upper layer, 200 – middle layer, 300 – lower layer;
- b – vitality classes: 10 – luxuriant tree, 20 – tree normally developed, 30 – tree weakly developed;

<table>
<thead>
<tr>
<th>Study plot</th>
<th>Łopuszna I (s.p.I)</th>
<th>Łopuszna II (s.p.II)</th>
<th>Łopuszna III (s.p.III)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Geographic coordinates</td>
<td>49°32′21″N 20°07′54″E</td>
<td>49°32′14″N 20°08′12″E</td>
<td>49°39′17″N 20°07′56″E</td>
</tr>
<tr>
<td>Location (compartment)</td>
<td>72</td>
<td>71</td>
<td>72</td>
</tr>
<tr>
<td>Size (ha)</td>
<td>0.6</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>Exposure</td>
<td>SW</td>
<td>S</td>
<td>SW</td>
</tr>
<tr>
<td>Slope (°)</td>
<td>12–15</td>
<td>15–20</td>
<td>19</td>
</tr>
<tr>
<td>Altitude (m)</td>
<td>1025</td>
<td>990</td>
<td>1020</td>
</tr>
<tr>
<td>Species composition by volume 2001 (%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abies alba</td>
<td>8.1</td>
<td>23.7</td>
<td>12.7</td>
</tr>
<tr>
<td>Fagus sylvatica</td>
<td>83.6</td>
<td>23.6</td>
<td>81.0</td>
</tr>
<tr>
<td>Picea abies</td>
<td>8.3</td>
<td>52.7</td>
<td>6.3</td>
</tr>
<tr>
<td>Volume in 2001 (m³/ha)</td>
<td>641.58</td>
<td>601.78</td>
<td>714.01</td>
</tr>
</tbody>
</table>

Table 1. Location and general characteristics of study plots established in the “Dolina Łopusznej” reserve

<table>
<thead>
<tr>
<th>Forest site type</th>
<th>Mountain forest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage and phase of development</td>
<td>Dentario glandulosae-Fagetum</td>
</tr>
<tr>
<td>1991</td>
<td>growing up stage phase of selection forest</td>
</tr>
<tr>
<td>2001</td>
<td>growing up stage phase of selection forest</td>
</tr>
<tr>
<td>optimum stage phase of aging</td>
<td>intensive break-up stage</td>
</tr>
<tr>
<td>advanced phase of regeneration</td>
<td>advanced phase of regeneration</td>
</tr>
<tr>
<td>optimum stage initiation of phase of aging</td>
<td>initiation of break-up stage</td>
</tr>
<tr>
<td>optimum phase of regeneration</td>
<td>advanced phase of aging and regeneration</td>
</tr>
</tbody>
</table>

...
growth. In each plot the stage and phase of stand development was determined, using criteria assumed by Korpel (1989, 1995).

The stand volume and basal area per hectare were calculated using a computer program “Zasoby”, which was worked out by J. Ptak, and based on volume tables of Grundner – Schwappach (1952). Only trees of d.b.h. ≥8 cm were taken into account in this study.

To calculate stand volume in 1991 and volume of dead trees the height curve plotted on the basis of 1991 measurements was used, while stand volume in 2001 and volume of recruitment were calculated using the height curve plotted on the basis of 2001 measurements.

Calculations of the 10-year current volume increment comprised at first the control of the number of trees:

\[ N_{01} - N_{91} + N_L - N_R = 0 \]

where:
- \( N_{91} \) – number of trees at the beginning of the period (1991),
- \( N_{01} \) – number of trees at the end of the period (2001),
- \( N_L \) – number of trees that died (loss) during 1991–2001,

Volume increment \( I_V \) during 1991 – 2001 was calculated according to the formula:

\[ I_V = V_{01} - V_{91} + V_L - V_R \] (m³/ha/10 years)

### Results

#### Mortality, recruitment, and increment Łopuszna I

In this stand during the control period 32 trees per hectare (15 beeches, 15 firs, and 2 spruces) were lost due to mortality. Their volume was 48.39 m³/ha. There were 12 firs per hectare which grew up to d.b.h. ≥8 cm. Their volume was 0.19 m³/ha (Table 2). The greatest annual mortality in relation to the number of trees of a given species was found for fir (1.2%), then for beech (0.7%) and spruce (0.4%) (Table 3). Also the annual mortality expressed by volume in relation to volume of a given species was greater for fir (2.8%) than for beech (0.6%) and spruce (0.6%) (Table 3). The mean annual volume increment during the pe-

Table 2. Mortality, recruitment, and volume increment in 1991–2001

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</thead>
<tbody>
<tr>
<td></td>
<td>No. trees/ha</td>
<td>Volume V</td>
<td>No. trees/ha</td>
<td>Volume V</td>
<td>No. trees/ha</td>
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<tr>
<td></td>
<td>m³/ha</td>
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<td>m³/ha</td>
<td>m³/ha</td>
<td>m³/ha</td>
</tr>
<tr>
<td>Fagus sylvatica</td>
<td>243</td>
<td>496.91</td>
<td>228</td>
<td>536.52</td>
<td>15</td>
</tr>
<tr>
<td>Abies alba</td>
<td>132</td>
<td>56.25</td>
<td>129</td>
<td>52.11</td>
<td>15</td>
</tr>
<tr>
<td>Picea abies</td>
<td>55</td>
<td>51.54</td>
<td>53</td>
<td>52.95</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td>430</td>
<td>604.70</td>
<td>410</td>
<td>641.58</td>
<td>32</td>
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</table>

Łopuszna II

<table>
<thead>
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<tbody>
<tr>
<td></td>
<td>No. trees/ha</td>
<td>Volume V</td>
<td>No. trees/ha</td>
<td>Volume V</td>
<td>No. trees/ha</td>
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<tr>
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<td>m³/ha</td>
<td>m³/ha</td>
<td>m³/ha</td>
<td>m³/ha</td>
<td>m³/ha</td>
</tr>
<tr>
<td>Fagus sylvatica</td>
<td>68</td>
<td>162.71</td>
<td>88</td>
<td>142.15</td>
<td>8</td>
</tr>
<tr>
<td>Abies alba</td>
<td>48</td>
<td>139.93</td>
<td>50</td>
<td>142.38</td>
<td>2</td>
</tr>
<tr>
<td>Picea abies</td>
<td>196</td>
<td>384.92</td>
<td>144</td>
<td>317.25</td>
<td>58</td>
</tr>
<tr>
<td>Total</td>
<td>312</td>
<td>687.56</td>
<td>282</td>
<td>601.78</td>
<td>68</td>
</tr>
</tbody>
</table>

Łopuszna III

<table>
<thead>
<tr>
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</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. trees/ha</td>
<td>Volume V</td>
<td>No. trees/ha</td>
<td>Volume V</td>
<td>No. trees/ha</td>
</tr>
<tr>
<td></td>
<td>m³/ha</td>
<td>m³/ha</td>
<td>m³/ha</td>
<td>m³/ha</td>
<td>m³/ha</td>
</tr>
<tr>
<td>Fagus sylvatica</td>
<td>170</td>
<td>601.15</td>
<td>156</td>
<td>578.39</td>
<td>16</td>
</tr>
<tr>
<td>Abies alba</td>
<td>92</td>
<td>86.88</td>
<td>82</td>
<td>90.93</td>
<td>14</td>
</tr>
<tr>
<td>Picea abies</td>
<td>58</td>
<td>67.41</td>
<td>38</td>
<td>44.69</td>
<td>24</td>
</tr>
<tr>
<td>Total</td>
<td>320</td>
<td>755.44</td>
<td>276</td>
<td>714.01</td>
<td>54</td>
</tr>
</tbody>
</table>
Period of 10 years was 8.51 m³/ha (Table 2), which was 1.3% in relation to stand volume in 2001 (Table 3). The mean annual basal area increment during the control period reached 0.39 m²/ha (Table 4).

Łopuszna II

During 1991–2001 mortality amounted to 68 trees per hectare, mostly spruce (58 trees/ha) (Table 2). The greatest mean annual loss in the number of trees in relation to the number of living trees in 2001 occurred in the case of spruce (4.0%), then beech (0.9%) and fir (0.4%) (Table 3). The number of trees in recruitment reached 10 trees/ha (4 spruces, 4 firs, and 2 beeches) (Table 2).

Volume of mortality during the control period was 104.88 m³/ha, while that of recruitment only 0.11 m³/ha. Volume increment reached 6.33 m³/ha/year (Table 2), while that of basal area 0.34 m²/ha/year (Table 4). Mainly beech decided about increment (almost 83% in volume increment). The annual percent of stand volume increment during 1991–2001 reached the value of 0.9 (Table 3).

Characteristics of dead trees

Łopuszna I

Among dead trees (32 trees/ha) (Table 2), trees of diameter class I prevailed (37%) (Table 5). In the case of beech, these were usually the trees growing in the middle layer of the stand (56%), and among them specimens of a lowered vitality (67%) and a lower rate of growth (67%) prevailed. Among dead firs the majority was from the lower stand layer (56%), of a normal (44%) and lowered vitality (56%) and a lowered rate of growth (67%) (Table 5). The ratio between the number of dead beech trees (during 1991–2001) and the number of living ones was the greatest in the lower layer (23.1%), while in the case of fir and spruce it was the greatest in the upper layer (29.4% and 18.2% respectively) (Table 6).

Łopuszna II

In this stand, spruce dominated among dead trees (58 from among 68 trees/ha) (Table 2). Among dead spruces the trees of d.b.h. ≥36 cm prevailed (39%), and they were mainly from the upper stand layer.
Mortality, recruitment, and increment of trees in the Fagus-Abies-Picea stands... 19

(66%). These trees were chiefly of a normal (55%) and lowered (41%) vitality, and a normal (41%) and lowered (38%) rate of growth (Table 5).

The ratio between the number of dead beeches and spruces and the number of living ones was the highest in the middle stand layer (33.3% and 66.7% respectively), while dead firs occurred only in the upper layer, and their ratio between dead and living trees was 6.7% (Table 6).

Łopuszna III

During the control period spruce prevailed among dead trees (24 out of 54 trees/ha), while mortality of beech (16 trees/ha) and fir (14 trees/ha) was smaller (Table 2). Dead spruce trees were mostly from the diameter class IV (42%) and classes I and II (50% in total), from the upper (42%) and middle (33%) stand layers, of a normal (58%) and lowered (42%) vitality, and a normal (42%) and lowered (58%) growth tendency. Dead beech trees were from higher diameter classes (IV–VII) (75%), middle and upper stand layers (50% each), mainly of a lowered vitality (75%), and of a normal and lowered growth rate (50 and 38% respectively). Among firs, trees from the diameter class II (57%), from the lower and middle stand layer (43% each) prevailed, and all of them were of a lowered vitality and a lowered rate of growth (Table 5).

The ratio between the number of dead beeches and spruces and the number of living trees of these species was the greatest in the middle stand layer (36.4% and 133.3% respectively), while that for fir in the lower layer (25%) (Table 6).

Table 4. Mortality, recruitment, and increment expressed in m²/ha of basal area during 1991–2001

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1991 G₁*</td>
<td>2001 G₂*</td>
<td>G₁*</td>
<td>G₂*</td>
</tr>
<tr>
<td></td>
<td>m²/ha</td>
<td>m²/ha/10 years</td>
<td>%</td>
<td></td>
</tr>
<tr>
<td>Fagus sylvatica</td>
<td>34.26</td>
<td>34.96</td>
<td>2.22</td>
<td>2.92</td>
</tr>
<tr>
<td>Abies alba</td>
<td>5.67</td>
<td>5.01</td>
<td>1.38</td>
<td>0.08</td>
</tr>
<tr>
<td>Picea abies</td>
<td>4.62</td>
<td>4.69</td>
<td>0.25</td>
<td>–</td>
</tr>
<tr>
<td>Total</td>
<td>44.55</td>
<td>44.66</td>
<td>3.85</td>
<td>0.08</td>
</tr>
</tbody>
</table>

Łopuszna II

Fagus sylvatica | 11.12 | 10.27 | 2.00 | 0.21 | 0.94 | 24.9 |
Abies alba    | 8.92  | 9.25  | 0.73 | 0.03 | 1.03 | 27.2 |
Picea abies   | 26.14 | 21.12 | 6.88 | 0.05 | 1.81 | 47.9 |
Total         | 46.18 | 40.64 | 9.61 | 0.29 | 3.78 | 100.0 |

Łopuszna III

Fagus sylvatica | 38.02 | 35.63 | 4.60 | 0.01 | 2.20 | 64.3 |
Abies alba    | 7.16  | 7.50  | 0.68 | 0.02 | 1.00 | 29.3 |
Picea abies   | 5.36  | 3.61  | 1.99 | 0.02 | 0.22 | 6.4  |
Total         | 50.54 | 46.74 | 7.27 | 0.05 | 3.42 | 100.0 |

*See explanations in the text

Discussion

Processes of the mortality, recruitment, and increment of trees in the forest community correspond to the processes of death, birth, and growth of basic factors of the development of every complex ecological system (Dziewolski and Rutkowski 1987). The description of these phenomena and estimation of their value are the subject of research concerning natural forest ecosystems, and they constitute a measurable index of their stability. They may also have a significant importance for forestry based on principles of a close-to-nature silviculture (Vezina 1959, Leibundgut 1982, Schütz 1994). A quantitative expression of the processes taking place also permits to obtain a more detailed knowledge about stages and phases of development of the primeval forest described by Leibundgut (1959, 1982) and Korpel (1989, 1995).

It has been accepted that processes of natural mortality, recruitment, and increment in the investigated stands of the lower mountain zone were related to the stage and phase of stand development. The mortality process concerned trees of all diameter classes (Table 5, Figs. 1–4).

Tree mortality in our investigations had the smallest value in the growing up stage (plot I – 4.8 m³/ha/year), and the greatest in the stage of advanced break up (plot II – 14.1 m³/ha/year). In the study carried out in the Bieszczady Mountains the mortality of the smallest value occurred in the growing up stage, phase of a many-storied structure with symptoms of
Table 5. Characteristics of dead trees

<table>
<thead>
<tr>
<th>Species</th>
<th>Diameter class*</th>
<th>Stand layer</th>
<th>Vitality index</th>
<th>Index of growth tendency</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I   II  III IV V VI VII</td>
<td>100 200 300</td>
<td>Σ   10 20 30</td>
<td>Σ 1 2 3 4</td>
</tr>
<tr>
<td>Łopuszna I (0.6 ha)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Fagus sylvatica</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No.trees</td>
<td>2   1 2 2 2 2 2</td>
<td>9   5 2 9</td>
<td>3 6 9 1 2 6 9</td>
<td></td>
</tr>
<tr>
<td>%</td>
<td>22.2 11.2 22.2 22.2 22.2</td>
<td>100 22.2 55.6 22.2</td>
<td>100 33.3 66.7 100 11.1 22.2 66.7 100</td>
<td></td>
</tr>
<tr>
<td><strong>Abies alba</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No.trees</td>
<td>5   – 1 2 – 9 3</td>
<td>9   3 5 9</td>
<td>4 5 9 3 6 9</td>
<td></td>
</tr>
<tr>
<td>%</td>
<td>55.6 – 11.1 11.1 22.2</td>
<td>100 33.3 11.1 55.6</td>
<td>100 44.4 55.6 100 33.3 66.7 100</td>
<td></td>
</tr>
<tr>
<td><strong>Picea abies</strong></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>No.trees</td>
<td>– – – 1 – – 1</td>
<td>1   1 1 1</td>
<td>1 1 1 1 1 1</td>
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</tr>
<tr>
<td>%</td>
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<td>– – 100 – 100</td>
<td>– 100 – 100 – 100 – 100 – 100</td>
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</tr>
<tr>
<td><strong>Total</strong></td>
<td>7   1 3 4 4 19</td>
<td>19 6 6 7 19</td>
<td>8 11 19 1 6 12 19</td>
<td></td>
</tr>
<tr>
<td>%</td>
<td>36.8 5.2 15.8 21.1 21.1</td>
<td>100 31.6 31.6 36.8</td>
<td>100 42.1 57.9 100 5.2 31.6 63.2 100</td>
<td></td>
</tr>
<tr>
<td>Łopuszna II (0.5 ha)</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td><strong>Fagus sylvatica</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No.trees</td>
<td>– 2 2 2 – – 4 1</td>
<td>4   2 3 – 4</td>
<td>4 4 4 2 2 4</td>
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</tr>
<tr>
<td>%</td>
<td>– 50 50 50 – – 100 25</td>
<td>– – 100 100</td>
<td>– – 100 100 100 50 50 100</td>
<td></td>
</tr>
<tr>
<td><strong>Abies alba</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No.trees</td>
<td>– – – 1 – – 1</td>
<td>1   1 1 1</td>
<td>1 – 1 1 – 1</td>
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<td>%</td>
<td>– – – 100 – – 100</td>
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</tr>
<tr>
<td><strong>Picea abies</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No.trees</td>
<td>4 8 13 4 – – 29</td>
<td>29 19 10 – 29</td>
<td>1 16 12 29 6 12 11 29</td>
<td></td>
</tr>
<tr>
<td>%</td>
<td>13.8 27.6 44.8 13.8</td>
<td>100 65.6 34.4</td>
<td>100 3.4 55.2 41.4 100 20.7 41.3 38.0 100</td>
<td></td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>4 8 15 7 – – 34</td>
<td>34 21 13 – 34</td>
<td>1 17 16 34 6 14 14 34</td>
<td></td>
</tr>
<tr>
<td>%</td>
<td>11.7 23.6 44.1 20.6</td>
<td>100 61.8 38.2</td>
<td>100 2.9 50 47.1 100 17.6 41.2 41.2 100</td>
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<tr>
<td>Łopuszna III (0.5 ha)</td>
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<tr>
<td><strong>Fagus sylvatica</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No.trees</td>
<td>– 1 1 2 2 1 1 8</td>
<td>8   4 4 – 8</td>
<td>2 6 8 1 4 3 8</td>
<td></td>
</tr>
<tr>
<td>%</td>
<td>12.5 12.5 25.0 25.0 12.5 12.5</td>
<td>100 50.0 50.0</td>
<td>– 100 – 25.0 75.0 100 12.5 50.0 37.5 100</td>
<td></td>
</tr>
<tr>
<td><strong>Abies alba</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No.trees</td>
<td>1 4 – 2 – – 7</td>
<td>7   3 3 7</td>
<td>– 7 7 – 7 7</td>
<td></td>
</tr>
<tr>
<td>%</td>
<td>14.2 57.2 – 28.6 – – 100 14.2 42.8 42.8</td>
<td>100 – – 100 100</td>
<td>– – 100 100 100 100 100</td>
<td></td>
</tr>
<tr>
<td><strong>Picea abies</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No.trees</td>
<td>3 3 1 5 – – 12</td>
<td>12 5 4 3</td>
<td>12 – 7 5 12 – 5 7 12</td>
<td></td>
</tr>
<tr>
<td>%</td>
<td>25.0 25.0 8.3 41.7 – – 100 41.7 33.3 25.0</td>
<td>100 – – 58.3 41.7 100</td>
<td>– 41.7 58.3 100</td>
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</tr>
<tr>
<td><strong>Total</strong></td>
<td>4 8 2 9 2 1 1 27</td>
<td>27 10 11 6 27</td>
<td>– 9 18 27 1 9 17 27</td>
<td></td>
</tr>
<tr>
<td>%</td>
<td>14.8 29.7 7.4 33.3 7.4 3.7 3.7 100</td>
<td>37.0 40.8 22.2 100</td>
<td>– 33.3 66.6 100 3.7 33.3 63.0 100</td>
<td></td>
</tr>
</tbody>
</table>

*Diameter classes: I – 8.0–15.9 cm, II – 16.0–23.9 cm, III – 24.0–35.9 cm, IV – 36.0–51.9 cm, V – 52.0–71.9 cm, VI – 72.0–91.9 cm, VII ≥92 cm,

** See explanations in the text
Mortality, recruitment, and increment of trees in the Fagus-Abies-Picea stands...

aging (5.8 m³/ha/year), and of the greatest value also in the growing up stage, phase of a many-storied structure, but on another plot (7.6 m³/ha/year), while in the optimum stage, phase of aging, it was 7.1 m³/ha/year (Jaworski and Kołodziej 2002).

The above data indicate how diversified are the values expressing mortality of trees growing in different forest complexes.

The results, mentioned above, were based on a sample, too small to draw a far reaching conclusions concerning the relationship between the developmental stage and the value of tree mortality. Nevertheless, it may be concluded with a considerable probability that in order to fully describe a natural stand it is not enough to state the stage of its development, but also the phase and degree of its advancement should be given. Besides, the loss of trees does not only consist of their death due to reaching a physiological old age, which decides about the stage of break up, but it also is caused by biotic and abiotic factors that may disturb a natural cycle of development described by Korpe (1995) or Leibundgut (1959).

In studies on the dynamics of natural forests the mortality of trees may also be expressed by the ratio between the number of trees which died during the study period (control period) and the number of living trees at the end of the period (Table 3) or the number of trees at the beginning of the period (Szwagrzyk and Szewczyk 2001).

The annual tree mortality in our study calculated by the latter method was the smallest in the growing up stage (plot I – 0.7%), intermediate in the initial phase of the break up stage (plot III – 1.7%), and the greatest in the advanced stage of intensive break up (plot II – 2.2%). In a stable beech-fir-spruce stand of the lower mountain zone of Mt. Babia Góra the annual tree mortality was 1.25% (Szwagrzyk and Szewczyk 2001). The data presented above indicate that

![Fig. 1. D.b.h. distribution of living and dead trees for common beech](image)

![Fig. 2. D.b.h. distribution of living and dead trees for silver fir](image)
the stand is stable when tree mortality is about 1%, while if this index reaches 2% its break up begins. Authors of this paper are of the opinion, however, that mortality expressed by the per cent of dead trees alone (without giving their volume) does not fully characterize the processes taking place.

The study presented in this paper showed that the greatest increment was reached by the stand in the growing up stage, and the smallest in the break up stage (Table 2). Similar conclusions were drawn from studies carried out in the Bieszczady Mountains, Mt. Babia Góra, and Slovakia (Jaworski and Kołodziej 2002, Jaworski and Paluch 2002, Korpel 1995). While in the Pieniny Mountains the greatest current volume increment was found in a fir stand showing characters of the optimum stage, phase of aging, and a smaller one, although very diversified, was found in three fir-beech stands in the growing up stage (Jaworski and Podlaski – unpublished data). It may be supposed that increment depends on the developmental stage and phase to a lesser degree than on vitality of large trees, considerably contributing to volume and occupying much space in the stand. This to a certain degree was indicated by studies of Jaworski and Paluch (2002).

The investigated stands reached the annual volume increment close to the increments of stands of a primeval character in the Babia Góra National Park, Pieniny National Park and Gorce National Park (Władysław Orkan and Dolina Lopusznej reserves, as well as in the Peručica reserve (Sutjeska National Park of Bosnia), but it was smaller than in the Dobročsky Prales reserve in Slovakia (Table 7).

Fir in sample plot I and spruce in plots II and III was most severely affected by tree mortality during the period 1991–2001. This was expressed by the ratio between the number of dead trees and the number of living trees, and the ratio between volume lost due...
Table 6. Number and percentage of living and dead trees in respective stand layers

<table>
<thead>
<tr>
<th>Stand layer acc. to IUFRO classification</th>
<th>Species</th>
<th>Number of living trees 2001</th>
<th>Number of dead trees 1991–2001</th>
<th>Ratio between the number of dead trees of a given species and the number of living trees of this species (2001) in a layer</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>trees/ha %</td>
<td>trees/ha %</td>
<td>%</td>
</tr>
<tr>
<td>Łopuszna I</td>
<td>Fagus sylvatica</td>
<td>150 36.6</td>
<td>3 9.4</td>
<td>2.0</td>
</tr>
<tr>
<td></td>
<td>Abies alba</td>
<td>17 4.1</td>
<td>5 15.6</td>
<td>29.4</td>
</tr>
<tr>
<td></td>
<td>Picea abies</td>
<td>11 2.7</td>
<td>2 6.2</td>
<td>18.2</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>178 43.4</td>
<td>10 31.2</td>
<td>5.6</td>
</tr>
<tr>
<td>200</td>
<td>Fagus sylvatica</td>
<td>65 15.8</td>
<td>9 28.2</td>
<td>13.8</td>
</tr>
<tr>
<td></td>
<td>Abies alba</td>
<td>50 12.2</td>
<td>2 6.2</td>
<td>4.0</td>
</tr>
<tr>
<td></td>
<td>Picea abies</td>
<td>22 5.4</td>
<td>0 0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>137 33.4</td>
<td>11 34.4</td>
<td>8.0</td>
</tr>
<tr>
<td>300</td>
<td>Fagus sylvatica</td>
<td>13 3.2</td>
<td>3 9.4</td>
<td>23.1</td>
</tr>
<tr>
<td></td>
<td>Abies alba</td>
<td>62 15.1</td>
<td>8 25.0</td>
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<tr>
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<tr>
<td></td>
<td>Total</td>
<td>95 23.2</td>
<td>11 34.4</td>
<td>11.6</td>
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<tr>
<td>Total</td>
<td></td>
<td>410 100.0</td>
<td>32 100.0</td>
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<tr>
<td>Łopuszna II</td>
<td>Fagus sylvatica</td>
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<td>2 2.9</td>
<td>9.1</td>
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<td>2 2.9</td>
<td>6.7</td>
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<tr>
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<td>Picea abies</td>
<td>94 33.3</td>
<td>38 56.0</td>
<td>40.4</td>
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<td>Total</td>
<td>146 51.7</td>
<td>42 61.8</td>
<td>28.8</td>
</tr>
<tr>
<td>200</td>
<td>Fagus sylvatica</td>
<td>18 6.4</td>
<td>6 8.8</td>
<td>33.3</td>
</tr>
<tr>
<td></td>
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<td>10 3.6</td>
<td>0 0</td>
<td>0</td>
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<tr>
<td></td>
<td>Picea abies</td>
<td>30 10.6</td>
<td>20 29.4</td>
<td>66.7</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>58 20.6</td>
<td>26 38.2</td>
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<td>0 0</td>
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</tr>
<tr>
<td></td>
<td>Picea abies</td>
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<td></td>
<td>Total</td>
<td>78 27.7</td>
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<td>Total</td>
<td></td>
<td>282 100.0</td>
<td>68 100.0</td>
<td>24.1</td>
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<td>130 47.1</td>
<td>8 14.8</td>
<td>6.2</td>
</tr>
<tr>
<td></td>
<td>Abies alba</td>
<td>28 10.1</td>
<td>2 3.7</td>
<td>7.1</td>
</tr>
<tr>
<td></td>
<td>Picea abies</td>
<td>16 5.8</td>
<td>10 18.6</td>
<td>62.5</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>174 63.0</td>
<td>20 37.1</td>
<td>15.0</td>
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<tr>
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<td>22 8.0</td>
<td>8 14.8</td>
<td>36.4</td>
</tr>
<tr>
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<td>30 10.9</td>
<td>6 11.1</td>
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<td>8 14.8</td>
<td>133.3</td>
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<td>58 21.1</td>
<td>22 40.7</td>
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<td>24 8.7</td>
<td>6 11.1</td>
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<tr>
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<td>Picea abies</td>
<td>16 5.8</td>
<td>6 11.1</td>
<td>37.5</td>
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<tr>
<td></td>
<td>Total</td>
<td>44 15.9</td>
<td>12 22.2</td>
<td>27.3</td>
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<td>276 100.0</td>
<td>54 100.0</td>
<td>19.6</td>
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</table>
to mortality and volume of living trees (Table 3). In other Carpathian stands of a primeval character the greatest value of mortality was estimated for fir (Szwagrzyk et al. 1995, Jaworski 2004).

The results of this study may have a great practical importance.

The value of the current volume increment, determined in this study, is the index of a potential site productivity, and it may be used when this increment is being compared with increments of managed stands of the same species composition and growing under the same site conditions.

The natural mortality process in stands of a complex vertical structure seem to be similar, to a certain degree, to tree removal during selection cutting. It may be assumed that dead trees from the upper stand layer of 60–70 cm in d.b.h. correspond to “harvesting of the crop” (Table 5). The dead trees of smaller d.b.h. from this layer, and from lower layers, correspond with selection cuttings performed in all stand layers. The natural selection taking place in such stands somehow plays a role of selection cutting (Schütz 2001), but is mainly directed toward a negative selection. However, it is difficult to suppose that “cutting” performed by natural processes taking place in the stand could agree with aims of the forestry practice.

The volume loss due to mortality in the investigated stands was diversified (Table 2). In Łopuszna I (growing up stage, phase of selection forest) it was a little over 48 m³/ha/10 years (i.e. about 8% in relation to stand volume in 2001). This is a much smaller value than the value of volume increment (about 85 m³/ha/10 years) (Table 2). This volume loss, because it is smaller than increment, is comparable to volume harvested in selection cutting corresponding to a current volume increment. It is to be expected that this stand will be increasing its volume per hectare during transition from the growing up stage to the optimum stage.

In plots Łopuszna II and III the “cutting value” was 141 and 105 m³/ha/10 years (i.e. 23% and 15% of volume per hectare) respectively (Table 3), and it much exceeded allowable “harvesting”, which should not be greater than increment during the same period (54 and 63 m³/ha/10 years respectively). Such a volume loss disturbed the equilibrium of both stands, and this is why the break-up stage was reached there. Thus these “cuttings” were too strong to maintain a stable complex structure similar to the selection forest structure.

The stand break up found in plots II and III occurred over small areas, comprising only fragments of

<table>
<thead>
<tr>
<th>Area</th>
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<th>Stage and phase of development acc. to Korpel (1989, 1995)</th>
<th>Author</th>
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<td>Czarna Hala</td>
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<td>no data</td>
<td>Dziewolski and Rutkowski 1991</td>
</tr>
<tr>
<td>Dolina Łopusznej</td>
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<td>initiation of break-up stage, phase of aging and regeneration</td>
<td>Przybylska et al. 1995</td>
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<td>Badin</td>
<td>4.7</td>
<td>growing up stage</td>
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<td>8.6</td>
<td>advanced break-up stage</td>
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<td>Perućica</td>
<td>6.4–8.8</td>
<td>no data</td>
<td>Pintarić 1978</td>
</tr>
</tbody>
</table>
the plot area, and corresponded to a gap model (Shugart 1984), where gaps, in the opinion of many ecologists, decide about regeneration and formation of structure and dynamics of forest communities (Drössler and Lüpke 2005, Zeibig et al. 2005, Nagel et al. 2006). However, plots I and III, adjoining each other, and representing the growing up stage, the phase of a selection structure and the initial phase of the break up stage (Table 1), indicated that in the “Dolina Łopusznej” reserve the developmental stages of the primeval forest make a mosaic, which confirmed the correctness of conceptions of Leibundgut (1959) and Korpel (1995), concerning the development of the primeval forest, and based on developmental stages and phases.

Conclusions

1. The tree mortality process in the investigated stands of a primeval character included trees of all diameter and height classes.
2. In the investigated forests of a primeval character values of tree mortality and increment are connected with a stage of stand development. The growing up stage was characterized by a greater volume increment than increment in the break-up stage. The greatest loss due to mortality was found in the break-up stage.
3. The knowledge about mortality, recruitment, and increment, observed on a sufficiently large number of sample plots, and expressed in the number of trees and volume units, may be of help in planning of cutting extent in economic and protection forests managed according to the conception of a close-to-nature silviculture.

Acknowledgments

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References


