ABSTRACT: Highly decayed coarse woody debris (CWD) is an important seedbed substrate in various forest ecosystems. In Europe, this particularly holds for spruce forests on shallow soils with insufficient water-holding capacity. The role of nurse logs in the recruitment of spruce seedlings is therefore mainly important on soils with limited water-holding capacity.

KEY WORDS: *Picea abies* L. Karst., downed logs, water content, natural regeneration, evapotranspiration

1. INTRODUCTION

Recent evidence shows that decaying logs acted as nurse logs for new seedlings as early as late Paleozoic (Césari *et al.* 2010). In Europe, this ecological strategy has been investigated mainly with regard to spruce (*Picea abies* L. Karst.). Hofgaard (1993) found that majority of saplings in a high-altitude boreal forest grew on substrates connected with tree-fall. Svoboda *et al.* (2010) reported that approximately one half of spruce seedlings were growing on dead wood substrates in a montane spruce forest. Also the survival of conifer species in a temperate zone subalpine forest was better on logs (Szewczyk and Sz-wagrzyk 1995), although *P. abies* grows very slowly on log substrates, achieving heights of 0.5 m after ca. 25 or more years (Zielenka 2006). It appears that highly decayed coarse woody debris (CWD) is an important seedbed substrate, mainly on shallow soils with insufficient water-holding capacity. However,
the regeneration ecology of trees on decayed wood is still limited (Brang et al. 2003, Baier et al. 2006), for instance with regard to light and substrate moisture conditions (Takahashi et al. 2000). In particular, CWD moisture differences may remain undetected under small seedlings (1 yr) due to their limited desiccation (Iijima et al. 2006). Therefore, our contribution investigates to what extent advanced spruce seedlings (higher than 20 cm) utilize available CWD water stores under field conditions. Our hypothesis was that if CWD provides moisture benefits for successful recruitment and further growth of spruce seedlings, CWD water content should be considerably reduced in nurse logs compared to logs devoid of older spruce seedlings.

2. MATERIAL AND METHODS

The study was conducted in a natural, subalpine spruce forest (*Picea abies* L. Karst.) located in the Zadná Polana massif (48°37’49”N, 19°27’50”E, 1351 m a.s.l.), Western Carpathians, Slovakia. The area is part of Polana Biosphere Reserve established within the UNESCO MAB program framework. It has an average annual temperature of 3.5°C, receives ca 1000 mm of precipitation, and the snow cover lasts approximately 190 days (Škvarenina et al. 2004). The local soil is Andic Cambisol (acc. to WRB; FAO 2006) from andesite. Tree species composition includes *Picea abies* (95%) accompanied by *Sorbus aucuparia* (5%). The concerned forest stand belongs to Piceion excelsae alliance with stocking and canopy closure around 0.7. Six downed logs with an average diameter of 0.4 m were selected in the forest. The logs were cut by chainsaw so as to obtain sections, ca. 4 m in length, from each log. All of them were positioned on the ground within the crown projections of mature spruce trees. CWD belonged to decay class 4 sensu Maser et al. (1979). The first three nurse logs sustained ca. 4–8 spruce seedlings per 1 m length. The majority of seedlings were 20–40 cm in height. The three remaining logs were covered by seedlings shorter than 10 cm, or they were devoid of seedlings altogether. All logs were covered by epiphytic lichens, bryophytes, *Vaccinium myrtillus*, *Oxalis acetosella* and other

Fig. 1. Moisture measurement set-up using Time Domain Reflectometry (TDR) in an individual downed log. TDR probes consisting of a plastic cylinder and stainless steel rods were installed into predrilled pilot holes.
Spruce seedlings utilize coarse woody debris water stores

herb species. By cutting the logs in the radial plane, surfaces perpendicular to the longitudinal axis were obtained. In each freshly cut log face, nine pairs of pilot holes, 2 mm in diameter, were pre-drilled in the axial direction to the depth of 20 cm. The pilot holes were prepared in positions No. 1–7, according to Figure 1.

Subsequently, TDR probes consisting of a plastic cylinder and two parallel stainless steel rods, running 16 mm apart, were installed into the pilot holes. CWD moisture and temperature readings were taken by connecting the probes to the TDR field operated meter (FOM/mts, Easy Test, Lublin, Poland) every two to three weeks during two vegetation periods (2007 and 2008). The actual moisture values were obtained using a species-specific TDR calibration relationship for spruce (Pi-}

chler et al. 2012). Throughfall precipitation was measured by portable ombrometers, one gauge placed at each log. Also, soil moisture was measured underneath each log by TDR probes inserted 5–10 cm below the lowest point of the log faces (i.e., perpendicular to it). Measurements were taken approximately every two weeks.

Kolmogorov–Smirnov test was used to assess whether measured CWD moisture data followed normal distribution. Differences between the moisture readings in logs with and without advanced spruce seedlings were tested separately for each CWD-layer by the Student $t$-test. Two-sample Kolmogorov-Smirnov test (Sokal and Rohlf 1995) was used in cases with bimodal distributions. All tests were performed using Statistica 9.0 (StatSoft 2009).

Table 1. Differences between average volumetric moisture ($\theta$) of coarse woody debris (CWD) with and without advanced seedlings cover in positions according to Figure 1, during two vegetation periods (2007 and 2008), assessed by the $t$-test; $n$ (data per cell) represents the number of average CWD moisture values, calculated for the triplets of logs on a given day, and used for the $t$-test. SE – standard error, ** $P < 0.01$, * $0.01 < P < 0.05$.

<table>
<thead>
<tr>
<th>Position No.</th>
<th>Data per cell ($n$)</th>
<th>CWD moisture (m$^3$ m$^{-3}$)</th>
<th>Difference ($\Delta \theta = \theta_1 - \theta_2$)</th>
<th>$t$-statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>with seedlings</td>
<td>without seedlings</td>
<td>Mean ($\theta_1$)</td>
</tr>
<tr>
<td>1</td>
<td>15</td>
<td>0.28</td>
<td>0.02</td>
<td>0.41</td>
</tr>
<tr>
<td>2</td>
<td>15</td>
<td>0.28</td>
<td>0.02</td>
<td>0.43</td>
</tr>
<tr>
<td>3</td>
<td>15</td>
<td>0.28</td>
<td>0.02</td>
<td>0.39</td>
</tr>
<tr>
<td>4</td>
<td>15</td>
<td>0.45</td>
<td>0.02</td>
<td>0.57</td>
</tr>
<tr>
<td>5</td>
<td>15</td>
<td>0.32</td>
<td>0.01</td>
<td>0.38</td>
</tr>
<tr>
<td>6a, b</td>
<td>30</td>
<td>0.36</td>
<td>0.02</td>
<td>0.39</td>
</tr>
<tr>
<td>7a, b</td>
<td>30</td>
<td>0.35</td>
<td>0.02</td>
<td>0.40</td>
</tr>
</tbody>
</table>

Fig. 2. Histograms of throughfall (A), and soil water content (SWC) (B), obtained from data collected at logs with and without seedlings during 2007 and 2008 vegetation periods.
Fig. 3. Histograms of volumetric moisture ($\theta$) inside decayed coarse woody debris (CWD) with and without seedlings, in positions according to Figure 1, obtained from downed logs in the Poľana massif during 2007 and 2008 vegetation periods.
3. RESULTS

Two-sample Kolmogorov-Smirnov test was applied to data sets containing throughfall amounts recorded at logs with and without seedlings (Fig. 2A). While the absolute difference between throughfall totals was 40.5 mm, the maximum difference between the cumulative distributions, \( D \), was 0.12 with a corresponding \( P \) of 0.95. The result lends support to the null hypothesis that the two samples were distributed identically, including position and dispersion. Soil water content measured 0.05–0.10 cm below CWD was 0.25 and 0.35 underneath logs with and without seedlings, respectively (Fig. 2B). The difference was significant at \( P < 0.001 \) according to the \( t \)-test.

Figure 3 shows CWD moisture distributions during 2007 and 2008 vegetation periods. The average seasonal difference (\( |\Delta \theta_{\text{avg}}| \approx 0.09 \)) was significant at \( P = 0.02 \) (\( |t\text{–statistic}| = 2.70 \)). Results for individual positions are presented in Table 1: the maximum moisture differences were detected at positions No. 1–4; intermediate differences developed at the positions No 5 and 7a, b. In contrast, differences in the lateral position 6a,b were smaller and statistically insignificant.

4. DISCUSSION AND CONCLUSIONS

To draw any, even preliminary conclusions from our measurements, the equivalency of environmental variables in both groups of logs must be assessed. In this respect, we established that logs in both groups were wetted by practically identical amounts of water (2055.9 mm and 2015.5 mm). But because other factors that we did not measure could also be important (e.g. duration of direct lateral insolation of logs), the following assessment of the cumulative loss of water due to seedlings evapotranspiration, based on the parallel moisture measurements in the two triplets of logs, shall be viewed with the corresponding caution. From our data it appears that the seedlings intercepted and transpired an amount of water corresponding approximately to one fifth of the average log volume. For a 1 m log section (covering 0.4 m² in the horizontal plane on average), the evapotranspiration would thus have reached ca 0.73 mm day⁻¹ m⁻² of CWD surface (in the horizontal plane) during the period between mid-June and the end of September. This is comparable with 0.97 mm day⁻¹ in an area reforested with spruce seedlings and grass, but considerably less than 1.49 mm day⁻¹ in a mature spruce stand (Křeček and Hořická 2001).

Furthermore, leaning on the distribution of moisture differences at specific positions, we hypothesize that the localization of water losses within CWD may be related to the content of nutrients. This is based on the fact that spruce seedlings send their fine roots preferably to substrates rich in minerals (Jalovia et al. 2008). But while CWD interstitial water contains nutrient-rich organic compounds (Yavitt and Fahney 1985), Harmon and Sexton (1995) showed that especially the surface or near-surface CWD layers are subject to intense leaching. Resulting spatial distribution of nutrients within downed logs could explain intense desiccation not only on the surface zone.

In conclusion, seedlings established on decayed downed logs in a subalpine spruce forest appeared to utilize CWD water stores at a rate comparable with seedlings growing in soils. As a matter of fact, our data showed that during the vegetation period, the average moisture of downed logs covered by advanced seedlings was significantly lower than in bare logs or logs covered by small seedlings (shorter than 10 cm). Also, the biggest moisture differences were spatially concentrated within CWD top and inner segments containing significant water stores. Because soil water content underneath logs with seedlings was lower than underneath logs without seedlings, moisture differences were probably caused through the desiccation by seedlings and not by CWD leaching.

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5. REFERENCES


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