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ORIGINAL PAPER

European beech, silver fir, and Norway spruce differ in establishment, height growth, and mortality rates on coarse woody debris and forest floor—a study from a mixed beech forest in the Western Carpathians

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Abstract

• ***Key message*** **In mixed forests, coarse woody debris promotes the successful establishment and growth of conifers and beech. In contrast to beech and fir, older spruce seedlings were only present on coarse woody debris and not on the forest floor.**

• ***Context*** Coarse woody debris (CWD) is considered a suitable seedbed for small-seeded and light-demanding species. Its role in enhancing tree regeneration is well reported in boreal or subalpine spruce forests. Less is known about its role in the establishment, growth, and survival of other species, particularly in mixed forests.

• ***Aims*** We analyzed the role of CWD in seedling establishment, growth, and survival for European beech, silver fir, and Norway spruce.

• ***Methods*** We tracked the growth and survival of all germinants and seedlings over 5 years.

• ***Results*** Conifers were relatively more successful than beech at colonizing on CWD. The density of seedlings was variable in all CWD decay classes but was the highest on well-decomposed CWD. CWD supported the growth of all species. Beech cohorts and older seedlings had similar mortality rates on both microsites. Spruce germinants did not survive on the forest floor for more than a year, and older seedlings were only observed on CWD. Fir cohorts had similar mortality rates on both microsites, but older seedlings survived better on the forest floor.

• ***Conclusion*** Although the three species differed in their preferred microsite for establishment, CWD can be considered a suitable regeneration microsite for all three species by enhancing their growth and, in the case of spruce, both short- and long-term survival.

Keywords Regeneration · Colonization pattern · Decaying wood · Microsite

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Contribution of co-authors Olga Orman: gathering field data, data analysis, co-writing of the paper.
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1 Introduction

Coarse woody debris (CWD) (i.e., decaying logs, stumps, and the root plates of uprooted trees) is an important component of almost all natural forest ecosystems, influencing their functioning and biodiversity (Harmon et al. 2004; Pouska et al. 2010). During decomposition, CWD stores water, provides nutrients, significantly increases the abundance and diversity of saproxylic and epixylic species (Ódor et al. 2006; Stokland et al. 2012), and creates favorable seedbeds for seedling establishment by providing microsites of varying dimensions and properties (Baier et al. 2007; Simon et al. 2011).

Small-seeded species tend to establish themselves more successfully on CWD than do species that produce large seeds due to better seed interception and retention on logs (Christie and Armesto 2003; Lusk and Kelly 2003). Since CWD effectively retains water, it is thought to be responsible for better germination and can promote seedling establishment of small-seeded species (Mori et al. 2004; Mori and Mizumachi 2005; Iijima et al. 2006). Some studies have shown that CWD can be considered a good source of nutrients (Brunner and Kimmins 2003; Baier et al. 2006; but see Laiho and Prescott 2004); however, the physical and biochemical properties of logs and stumps change over time (Narukawa et al. 2003). In the case of some genera, such as *Picea* sp., the density of seedlings established on CWD can increase during decomposition and slightly decreases on the most decayed CWD (Mori et al. 2004; Zielonka 2006), but less is known about the colonization pattern of other species, such as broadleaves. Previous studies have shown that the enhanced growth and survival of conifers on elevated microsites may be attributed to less competition with shrubs and herbs (Zielonka 2006; Iijima and Shibuya 2010; Ota et al. 2012) and a better nutrient and moisture supply (Brunner and Kimmins 2003; Baier et al. 2006). However, in mixed broadleaf forests, these mechanisms may act differently for each species because large-seeded species are generally known to be more resistant to environmental stresses (Carlton and Bazzaz 1998; Moles and Westoby 2004).

Numerous studies have reported the positive role of CWD in the establishment of conifer species (Christy and Mack 1984; Ulanova 2000; Mori et al. 2004; Svoboda et al. 2010), but data for mixed and broadleaf forests are still lacking. Moreover, regeneration data show high interannual variability, which result in different seed retention rates, germinant and seedling abundances, and overall survival rates (Szwagrzyk et al. 2001; Bellingham and Richardson 2006). Thus, long-term data are required to obtain reliable results when considering seedling counts, mortality rates, and growth rates. We thus focused on a comparison between two conifer species and one deciduous species in the Carpathian mixed forest over a 5-year span. European beech, *Fagus sylvatica* L., is a dominant species in the Western Carpathian mixed forests, and silver fir, *Abies alba* Mill., and Norway spruce, *Picea abies* (L.) Karst., are two main codominants in these forests. Of these three species, Norway spruce is the most light-tolerant, and silver fir is the most shade-tolerant (Stancioiu and O'Hara 2006). Each species differs in seed weight. Norway spruce has the lightest seeds, and European beech has the heaviest seeds (the fresh weights of 1000 seeds of Norway spruce, silver fir, and European beech are 7.4, 55.8, and 212.7 g, respectively) (Grodziński and Sawicka-Kapusta 1970). Our study was designed to address the following questions: (1) are there differences in colonization patterns between European beech, silver fir, and Norway spruce on CWD and on the forest floor in this study stand?; (2) how do species vary in their establishment on different CWD decay classes?; (3) does seedling age correspond to survival patterns on CWD and on the forest floor?; (4) do growth rates differ between species growing on CWD and on the forest floor? A better understanding of these patterns would improve management strategies related to microsite selection for seedling establishment and growth in mixed forests.

2 Methods

2.1 Study area

The study site is located in a 112 ha old growth forest tract in the southern part of Gorce National Park, Western Carpathians, Poland (49° 32′ N, 20° 08′ E). Its elevation ranges from 1000 to 1050 m a.s.l., and it is located on both southern and southwestern-facing slopes. Dystric and eutric cambisols developed from sandstone (Carpathian flysh) comprise this area. At the highest peak (i.e., Turbacz) (1310 m a.s.l.), average annual temperatures range from 2.9 to 6.3 °C, and annual rainfall varies from 920 mm to over 1200 mm (Różański et al. 2006). Snow cover usually persists from mid-November to mid-April. The understory vegetation is characterized as a *Dentario glandulosae-Fagetum* plant community. The area contains a remnant old growth stand that has been strictly protected since 1970. No regular logging has ever been conducted at this site. The stand is composed of European beech, silver fir, and Norway spruce (hereafter, all species are noted by genus only), mixed in proportions of 63 %, 19 %, 18 % and 72 %, 14 %, 14 % based on tree number and basal area, respectively (Pawlaczek 2010).

The study was conducted from 2005 to 2009 on a 1-ha (100×100 m) site that was divided into twenty five 20×20 m^2. The data were collected simultaneously on two microsites (i.e., CWD and forest floor). Germinants and seedlings were counted and measured on CWD and in 40 small forest floor plots (approximately 1.9 m^2 each), covering a total of 75.4 m^2 along the forest floor. We chose five random intersections of the grid, where we established eight plots surrounding each intersection in a circle (Fig. 1).

2.2 CWD

All logs and their branches (at least 10 cm in diameter at the larger end with a minimum length of 1 m), stumps (heights lower than 1.3 m), uprooted trees, and uprooted tree plates found in the 100×100 m study site were measured, pooled, and referenced as one microsite type (i.e., CWD). We divided the CWD into five decay classes (DC). We used the same classification proposed by Szewczyk and Szwagrzyk (1996), which was based on a method used in old growth stands in the Pacific Northwest of the USA (Sollins 1982; Maser et al. 1988). Thus, we identified five DCs: DC 1—recently fallen trees or stumps with intact bark; wood solid and branches present; no vegetation or <10 % moss cover; DC 2—CWD with partially intact bark and partially decayed sapwood;

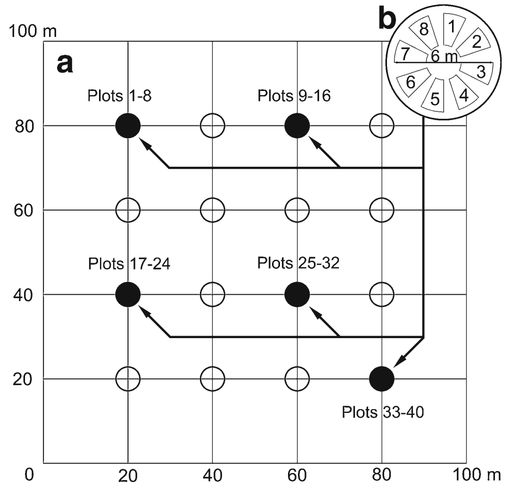

Fig. 1 **a** Plot design to sample forest floor (*dark circles*—randomly chosen five intersections of grid where we established groups of eight soil plots; 40 in total). **b** Design of single soil plots group

branches present and moss cover 10–25 %; DC 3—CWD without bark; wood soft with at least partially decayed heartwood and only large branches present; moss and herbs cover 25–75 %; DC 4—no branches present and logs still more or less round; wood soft; moss and herbs covering from 75 to 100 % of the CWD surface; and DC 5—logs flat, slightly distinct from the forest floor; wood soft and powdery structure; CWD completely covered with mosses and other vegetation.

We measured all CWD fragments above the minimum size threshold in 2005. We measured the lengths and diameters of whole logs and branches, and the diameters of dead stumps. In the case of uprooted trees, we also measured heights and root plate base diameters. Based on these measurements, we calculated the ground area covered by CWD. Whole log areas were calculated as trapezoids, stump areas were calculated as circles, and uprooted tree root plate areas were calculated as triangles. From 2006 onward, we measured newly fallen trees every year to obtain data regarding the area covered by CWD.

2.3 Regeneration

Regeneration measurements were conducted at the end of June every year. All germinants and older seedlings growing in the forest floor plots (hereafter referred to as forest floor) and on CWD were counted, recorded, and labeled so that we could track each individual during the 5-year study period. In 2006, we were unable to label all of the germinants on the forest floor; thus, their numbers were estimated later using the linear density relationship generated from previous years' data. Height and all visible annual height increments were measured. We estimated seedling age based on verticil or visible bud scar counts. Seedlings that showed signs of browsing damage were counted but excluded from the age and height analyses. Seedling survival was checked twice each year from 2005 to 2007 (at the end of June and at the end of September) and once each year from 2008 to 2009 (at the end of June).

2.4 Data analysis

We compared two microsites (CWD and forest floor) and each species separately for two regeneration types (germinants and seedlings). For each species, we calculated the following: the germinant and seedling density on CWD and on the forest floor in each year (i.e., the total number of germinants and seedlings found on each microsite divided by the total sampled area of the microsite), the average density across all 5 years (i.e., the average number of germinants and seedlings found on each microsite during the five study years divided by the total sampled area of the microsite), and the number of colonized dead wood pieces and colonized sample plots (i.e., fragments of CWD or the number of forest floor plots with at least one tree seedling of any species). The Chi-square test was used to compare the proportions of CWD and the sampled forest floor areas with the proportions of the numbers of seedlings growing on the forest floor and on CWD to the total number of seedlings on both microsites (for details, see Narukawa et al. 2003). This method was chosen because different areas were covered by CWD each year.

All data from the 5 years of our study were used to calculate average height growth rate estimations for beech and fir growing on CWD and on the forest floor. However, we were unable to calculate spruce growth rates on the forest floor due to an insufficient sample of spruce seedlings (n=1). We used the Mann-Whitney test to check for significant differences observed in height distributions between seedlings growing on both microsites. We compared each species in each age class.

We calculated the annual survival of beech, fir, and spruce germinants growing on CWD and on the forest floor (the ratio between initial germinant counts and surviving germinant counts) for each survey year. Average annual germinant survival rates (the ratio between the pooled number of germinants observed during our study and the number of germinants that survived until next year) were calculated for four time periods. We excluded 2006 data from our analysis because we could only estimate the number of germinants growing on the forest floor during this span. To assess long-term survival for all cohorts found during the study period, the relative percentage of seedling survival was calculated (i.e., the ratio between the number of observed seedlings and the total number of observed germinants in the year of cohort establishment). Long-term survival rates for older seedlings (≥6 years) observed in 2005 were calculated for each microsite separately.

3 Results

3.1 CWD

CWD fragments increased from 414 to 455 over the 5-year period. The area covered by CWD was 385 m^2/ha (3.9 % of total study area) in 2005 and increased by more than 15 % during the 5-year span, to 444 m^2/ha (Table 1). The area covered by CWD decreased steeply relative to decomposition class.

3.2 Colonization on CWD and on the forest floor via regeneration

The share of colonized CWD by germinants was highly variable among years (from 5.3 % in 2005 to 43.8 % in 2006; 18.6 % average over 5 years) though it was more stable in the case of seedlings (from 15.2 % in 2005 to 29.4 % in 2007; 21.2 % average over 5 years). Although CWD in DCs 1–3 covered larger areas, and thus had higher likelihoods of colonization, our results showed that the average percentage of CWD fragments colonized by fir and spruce germinants maximized in DC 4, and in DC 5 for beech (Fig. 2). The average share of CWD colonized by beech germinants was nearly ten times lower (4.4 %) than the percentage of colonized soil plots (42.0 %). Fir germinants established on 16.6 % of the CWD fragments and on 53.5 % of the soil plots, while spruce germinants colonized only 3.2 % of the CWD and 7.5 % of the soil plots (calculated as 5-year averages).

Table 1 Area covered by CWD in 1-ha study plot in the beginning (2005) and at the end of the study period (2009).

Decay class	Area covered by CWD (m^2/ha)			
	Beech	Fir	Spruce	Others[a]
2005				
1	85.2	34.8	55.2	0.0
2	35.5	35.8	41.0	2.2
3	19.5	17.1	17.6	4.8
4	9.0	6.1	11.3	5.3
5	0.1	2.2	0.7	1.8
Total	149.3	96.0	125.8	14.1
2009				
1	102.8	48.0	59.1	0.8
2	37.4	42.7	44.7	3.0
3	28.4	17.6	17.6	5.1
4	9.0	6.1	11.1[b]	5.9
5	0.1	2.2	0.7	1.8
Total	177.7	116.6	133.2	16.6

[a] Conifer wood of unidentified species

[b] Decrease due to fragmentation of single log

Beech and fir seedlings occupied, on average, 64.0 and 60.5 % of the forest floor plots, but fir was more successful in establishing seedling banks on CWD (Fig. 2). Fir seedlings colonized 16.7 % of CWD fragments, whereas beech seedlings colonized 9.9 %. Spruce seedlings established on 3.1 % of CWD and only on one forest floor plot, which comprised 2.5 % of the total number of forest floor plots.

3.3 Impact of CWD decay class on recruitment

Beech and fir germinants were generally more abundant on the forest floor (with average densities of 113 and 121 ind./100 m^2) than on CWD (with average densities of 11 and 60 ind./100 m^2). Spruce germinants were only observed on the forest floor in 2007 (32 ind./100 m^2). Germinant densities increased along the CWD decay gradient; the highest densities were found in DC 4 and DC 5 (Fig. 3).

Beech, fir, and spruce seedlings differed in microsite preference (Table 2). Spruce seedlings were much more abundant on highly decayed CWD in DCs 4–5 than on the forest floor, where we observed only one seedling ($p<0.0001$). The differences were also significant when comparing the densities on the forest floor and CWD in all DCs. Beech seedlings were much more numerous on the forest floor than on CWD ($p<0.0001$ for all 5 years). The comparison of beech seedling densities between CWD in DCs 4–5 and the forest floor also resulted in significant differences (except in 2007). Silver fir had less specific microsite requirements than the other species. In general, fir seedlings significantly preferred the forest floor (except in 2007). Though fir established more abundantly on CWD in DCs 4–5 than on the forest floor, the differences were not significant (Table 2).

Seedling density increased with an increasing degree of decay (Fig. 3). Beech and fir seedlings were present on CWD in all DCs and were densest in DCs 4–5. Spruce formed a stable seedling bank on CWD in DC 4 (Fig. 3).

3.4 Survival rates relative to seedling age

Beech germinants had very similar survival rates on CWD and on the forest floor (68 % for CWD and 67 % for the forest floor) (Table 3). Fir germinants had lower survival rates than beech germinants (the averages for CWD and the forest floor were 37 and 40 %, respectively). Spruce germinants had the lowest survival rates of all three species (the average for CWD was 20 %). We observed spruce germinants on the forest floor in 2007, but they did not survive until the next year.

The mortality rate for beech cohorts was slightly higher on the forest floor than on CWD, although the survival rate was low on both microsites. Fir cohorts established in 2006 had similar survival rates on the forest floor and on CWD. Fir cohorts established in 2007 survived slightly better on the forest floor. The only year when a spruce cohort appeared on

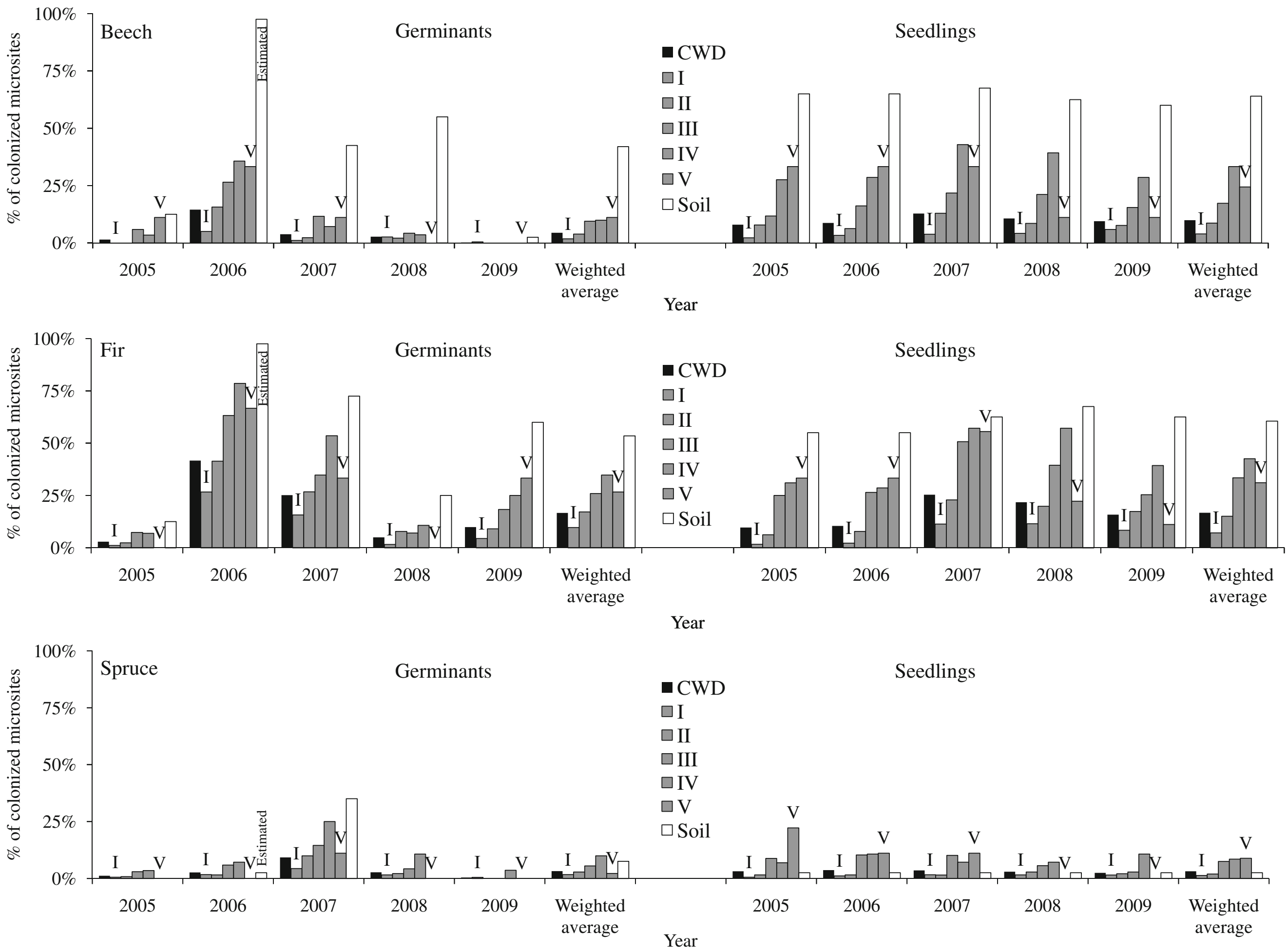

Fig. 2 Percentage of CWD pieces and soil plots colonized by germinants and seedlings in the years 2005–2009. *Gray bars* represent CWD in DCs 1–5 (from *left to right*), *black bars* represent the overall value calculated for CWD in all DCs

CWD was 2007, but only 10 % of these individuals survived until 2009 (Fig. 4).

We found several older seedlings (≥6 years) of beech and fir growing on CWD and on the forest floor in 2005 (6 ind./100 m^2 and 19 ind./100 m^2 for beech and 4 ind./100 m^2 and 8 ind./100 m^2 for fir). The oldest beech that we found on the forest floor was estimated as more than 10 years and on CWD as 9 years in 2005. The oldest fir that we found on the forest floor was more than 12 years old while the oldest fir on the CWD was more than 9 years old in 2005. We found several older spruce seedlings growing on CWD (4 ind./100 m^2) but not even a single one growing on the forest floor. The oldest individual growing on CWD was estimated to be more than 13 years old in 2005. The total survival rate (calculated across the 5-year period) of older beech seedlings was slightly higher on the forest floor than on CWD. Older fir seedlings had a higher survival rate than beech seedlings on the forest floor (83 % compared to 64 %) but lower survival rate than beech seedlings on CWD (44 % compared to 54 %) (Fig. 4). Older spruce seedlings had the highest survival rate of all species on the CWD (>71 %).

3.5 Height growth

Although the initial heights of beech and fir germinants were higher on the forest floor, the growth rates of both species' seedlings were higher on CWD (Fig. 5). The height distributions of beech germinants, seedlings older than 2 years, and of fir germinants, 1-, 2-, 3-year-old seedlings and seedlings older than 5 years were significantly different between microsites. We could not conduct tests for beech and fir seedlings older than 8 years because of their low abundances. Although we were unable to examine spruce height growth rates on either substrate, spruce exhibited the most dynamic height growth characteristics on CWD compared to other surveyed species.

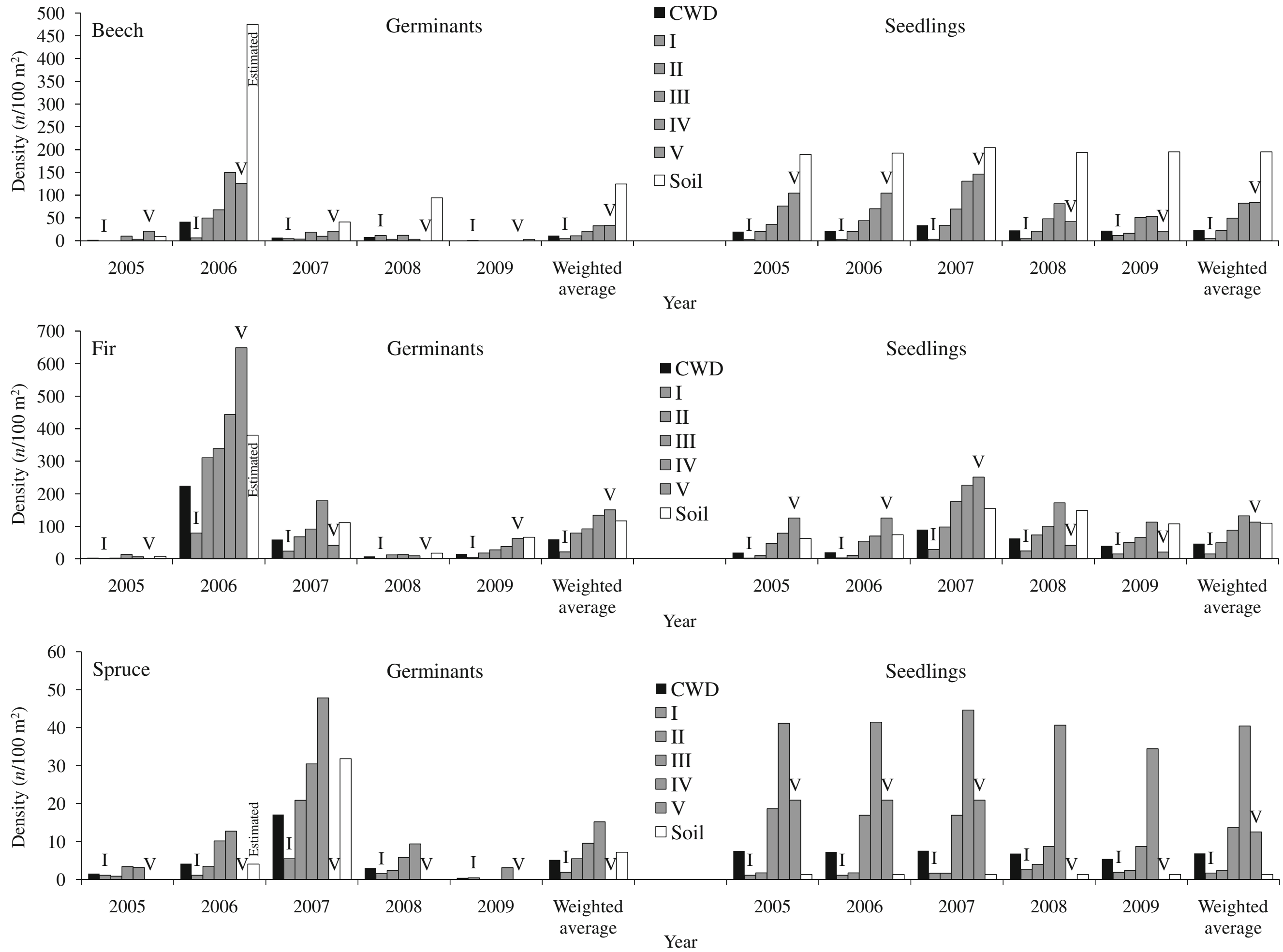

Fig. 3 Density of beech, fir, and spruce germinants and seedlings on CWD in DCs 1–5 and forest floor in the years 2005–2009. *Gray bars* represent CWD in DCs 1–5 (from *left to right*), *black bars* represent the overall value calculated for CWD in all DCs

4 Discussion

4.1 Regeneration and colonization patterns on CWD and on the forest floor

The importance of CWD as a regeneration microsite decreased with the seed weight of the three analyzed species. The higher density of beech on the forest floor indicates that the forest floor is the more favorable microsite for beech establishment, although this species was also quite successful in colonizing on CWD. CWD seems to be the most important substrate for spruce establishment considering the larger number of older spruce individuals growing on CWD in this forest stand. Fir was more successful in colonizing the forest floor and generally attained higher densities on this microsite, but its establishment was more successful on CWD in the most decayed classes. Similar regeneration patterns were shown in other studies conducted in old growth mixed beech forests (Szewczyk and Szwagrzyk 1996; Saniga et al. 2011). Previous studies from subalpine spruce forests have shown that better establishment of spruce on CWD was supported by more favorable light availability and moisture conditions (Zielonka and Niklasson 2001). CWD was also reported to be the preferred establishment microsite for *Abies sachalinesis*, *Picea jezoensis*, and *Picea glehnii* in boreal and subalpine forests in Japan (Narukawa et al. 2003; Noguchi and Yoshida 2004) and for *Picea engelmannii* in *Abies-Picea* forests in the USA (Knapp and Smith 1982).

The ability of seed interception and retention is strongly affected by decay stage of CWD (Szewczyk and Szwagrzyk 1996; Takahashi et al. 2000) and log size (Carlton and Bazzaz 1998; Ota et al. 2012). CWD in early decay stages lacks crevices that can act as seed traps (Zielonka 2006). Bače et al. (2011) demonstrated that some CWD types, such as stumps, may be preferred to logs for seedling establishment due to their better seed trapping abilities. In our study site, stumps were not abundant and CWD in DCs 1–2 dominated (Table 1); thus, colonization of CWD was unlikely (Fig. 2). Therefore, the overall share of CWD fragments occupied by germinants was low. We estimate that as the decay process

Table 2 Seedling densities on CWD and on forest floor in the years 2005–2009

Year	Microsite area (m^2)			Seedlings' density (n/100 m^2)								
				Beech			Fir			Spruce		
	Soil	CWD I–V	CWD IV–V	Soil	CWD I–V	CWD IV–V	Soil	CWD I–V	CWD IV–V	Soil	CWD I–V	CWD IV–V
2005	75.4	385.1	36.4	189.7	20.0***	79.7**	62.3	19.2***	85.2	1.3	7.5**	38.5***
2006	75.4	384.9	36.1	192.3	20.8***	74.8**	74.3	20.0***	77.6	1.3	7.3**	38.8***
2007	75.4	397.0	36.1	204.2	34.0***	133.0	155.2	89.7	229.9	1.3	7.6**	41.6***
2008	75.4	424.6	36.7	193.6	22.6***	76.3**	148.5	62.6*	155.3	1.3	6.8**	35.4***
2009	75.4	444.0	36.7	195.0	22.1***	49.0***	107.4	40.1**	100.8	1.3	5.4*	30.0***

Significant differences (Chi-test) between the densities on forest floor and on two categories of CWD (all DCs 1–5 and DCs 4–5) are marked with *p<0.05, **p<0.01, ***p<0.001

progresses at our study site, beech colonization patterns will become less variable while spruce and fir colonization patterns will become more pronounced.

4.2 Effect of CWD decay stage on seedling establishment

Beech seedlings were able to establish on CWD in all DCs (DCs 4–5 showed the highest density), though their abundances were significantly lower than those that established on the forest floor. The differences between fir seedlings' densities on CWD and on the forest floor were less pronounced than in the case of beech. Strongly decomposed wood, in particular, DC 4 seemed to be the most suitable substrate for fir recruitment. Spruce seedlings were most abundant on CWD in DC 4, and their abundance decreased thereafter. A similar pattern for spruce was reported in other studies (Mori et al. 2004; Zielonka 2006; Bače et al. 2012). Moreover, Hunziker and Brang (2005) found that *Abies alba* had less specific microsite requirements than *Picea abies*. The establishment of tree seedlings near ground level might be hindered by more competitive forest floor plants (Holeksa 2003). The previous studies explained the decrease in spruce seedling density in the most advanced stage of decay due to competition with mosses, herbs, and dwarf shrubs (Mori et al. 2004; Zielonka and Piątek 2004; Iijima et al. 2007). In our study, the establishment of fir was more successful than spruce on DC 5, but fir might also lose in competition with herbs. Similar results were found in Japanese mixed forests for *Abies veitchii* and *Abies mariesii* seedlings, which were most abundant in DCs 3–4 (Narukawa et al. 2003). Beech establishment may be hindered the least on the most decomposed CWD (DC 5).

4.3 Growth and survival of seedlings on CWD

CWD supported more height growth for all three species, but the annual increment on both microsites was relatively low due to partially closed canopy conditions. Bellingham and Richardson (2006) showed that in the cool temperate montane rain forest, the height growth rate of seedlings was higher on elevated microsites, such as CWD, and increased with canopy openness. Moreover, in the case of very strong competition with dwarf plants, positions situated higher on CWD are more beneficial for tree regeneration growth (Ježek 2004; Ota et al. 2012), although large-diameter logs and taller stumps are more prone to fragmentation, resulting in less seedling

Table 3 Germinant survival rates on CWD and on forest floor in the years 2005–2009

Year	Number/survival (%)					
	Beech		Fir		Spruce	
	CWD	Forest floor	CWD	Forest floor	CWD	Forest floor
2005	8/88 %	7/86 %	15/67 %	6/17 %	6/33 %	0/-
2006	161/43 %	No data	865/35 %	No data	16/31 %	No data
2007	27/63 %	31/68 %	236/32 %	84/44 %	68/18 %	24/0 %
2008	35/66 %	71/62 %	31/55 %	13/15 %	13/31 %	0/-
2009	1/100 %	2/100 %	67/42 %	50/42 %	2/0 %	0/-
Average survival[a]	67 %	66 %	37 %	40 %	20 %	0 %

[a] Calculated for the years 2005 and 2007–2009

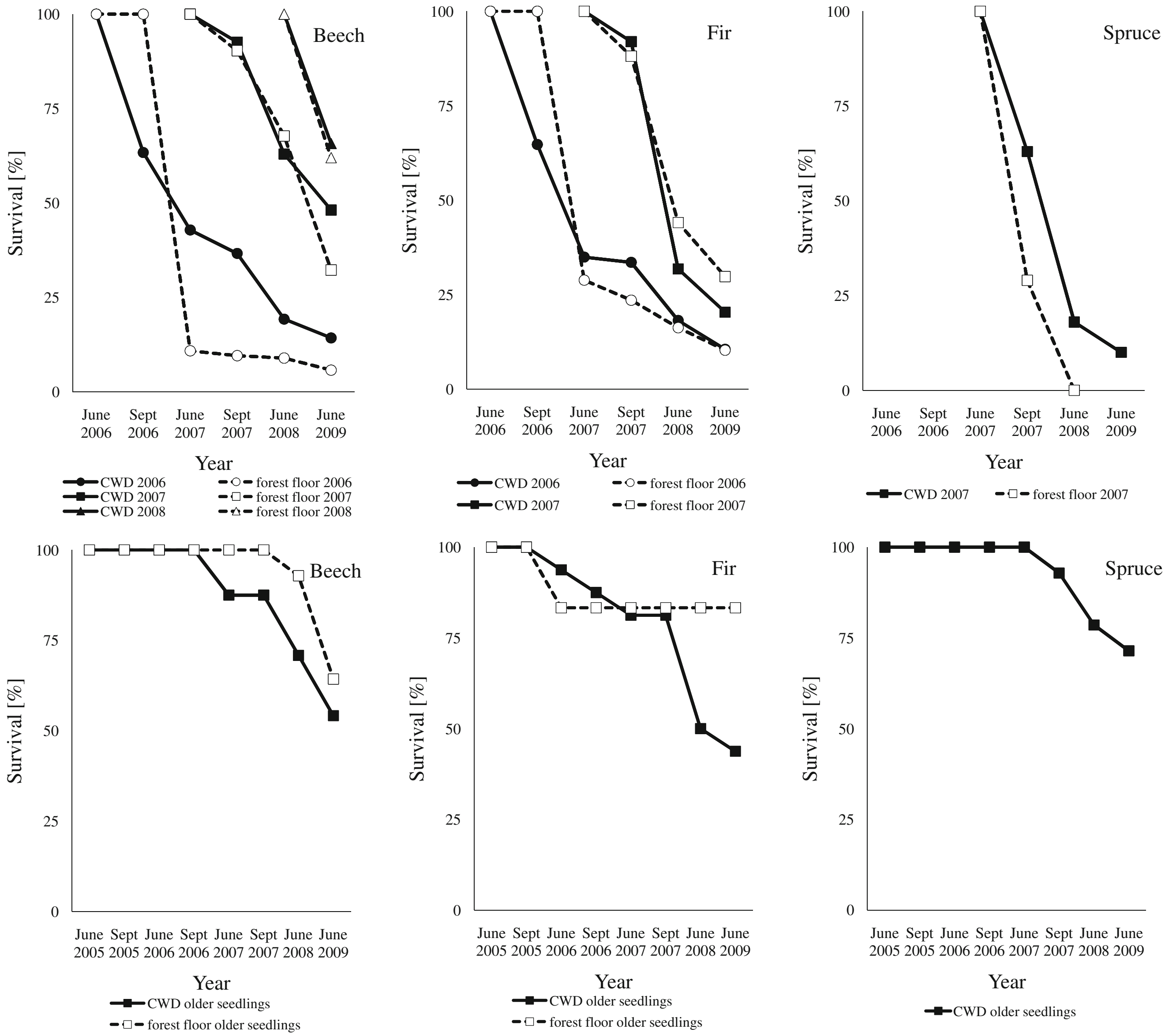

Fig. 4 Survival of beech, fir, and spruce cohorts and older seedlings (≥6 years) growing on CWD and on forest floor in the years 2005–2009. Initial number of germinants on forest floor in 2006 was estimated

establishment time and an increase in the probability of seedling mortality (Harmon 1989a). In our study, spruce showed the most dynamic growth of all species. Baier et al. (2006) demonstrated that spruce seedlings growing on CWD have longer roots, more root tips and forks per root, and a higher mean number of mycorrhizal root tips per root. Moreover, nutrient element ratios were more balanced in seedlings growing on CWD.

Among the three species, spruce seems to survive better on CWD over both short- and long-term spans. In our study, all individuals that germinated on the forest floor did not survive through the following year, and we could not find well-established older seedlings on this microsite. The higher survival rate of spruce on CWD is considered to be the main factor that determines a spruce's ability to use decaying logs as establishment sites (Mori et al. 2004; Bače et al. 2012), but the mechanisms of this phenomenon are still not clear. A recent study by Bače et al. (2012) suggests that the presence of some fungi species (*Phellinus nigrolimitatus*) in decomposing logs impacts the survival of spruce seedlings in subalpine forests, although it is unclear whether the same mechanism could also relate to spruce establishment in mixed forests. Beech cohorts and older seedlings had similar survival rates on both of our microsites. The higher abundance of older beech seedlings on the forest floor may be a result of differences in interception abilities between CWD and the forest floor, not better long-term survival rates on the forest floor. Young fir seedlings had similar mortality rates on CWD and on the forest floor, but older seedlings had higher mortality rates on CWD. However, this latter result may not be a

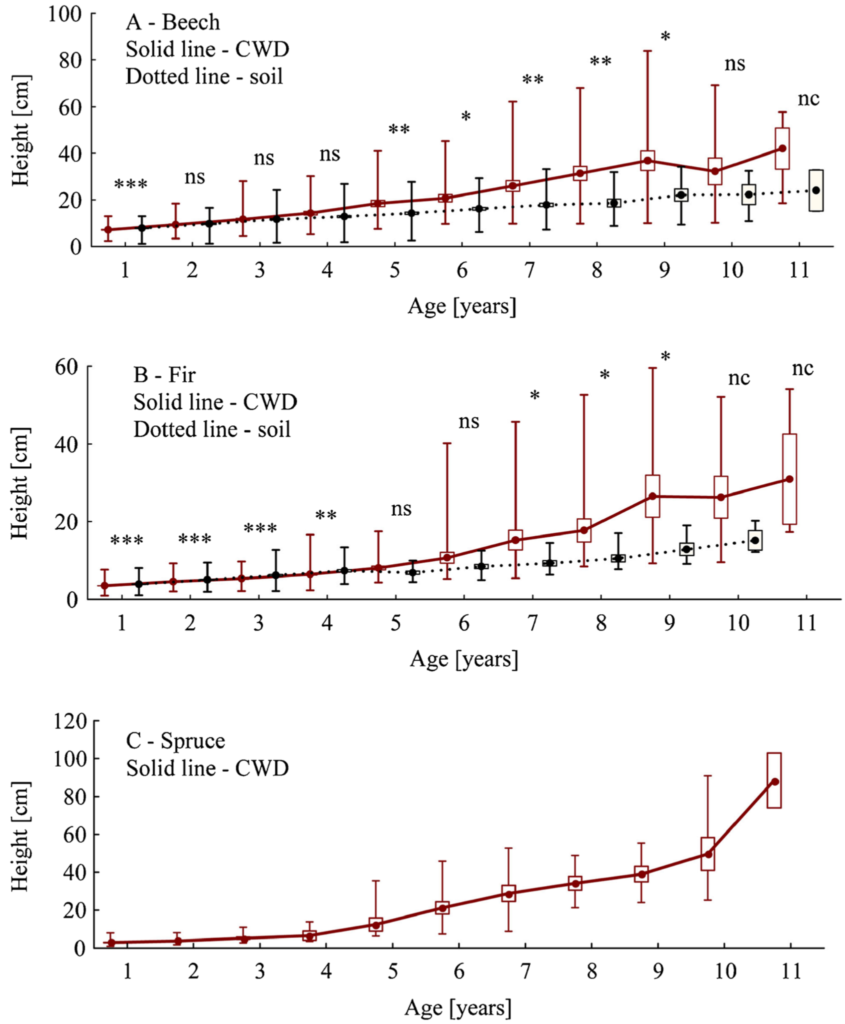

Fig. 5 The height growth of beech, fir, and spruce on CWD and on forest floor (all individuals damaged or browsed were excluded). *Lines* represent average heights, *boxes* standard errors, and *whiskers* minimal and maximal values. The results of Mann-Whitney test for differences between seedling heights on both microsites: $*p<0.05$, $**p<0.01$, $***p<0.001$, *ns* not significant, *nc* insufficient sample of seedlings to conduct the test

microsite effect but an effect of some other unidentified factor, responsible for a big mortality peak which occurred only on CWD in winter 2007/08. Although studies have shown (Narukawa and Yamamoto 2002; Baier et al. 2007) that the thick organic layer on the forest floor is a good seedbed for conifer establishment, mixed forests dominated by broadleaf species, where thick leaves tend to accumulate, may negatively effect germination and survival on the forest floor for such species as *Picea abies* or *Abies* sp. (Parent et al. 2006; Simon et al. 2011). Litter on the forest floor at our study site was often composed of a thick layer of beech leaves, which may bury or smother small spruce germinants. Harmon (1989b) reported that logs in the advanced decay stage retain as much litter as seeds. Although this is true for conifer needles, leaves are more likely to dispersed by wind, thus removing them from CWD surfaces. Some studies have shown that CWD, due to its somewhat round shape, does not effectively accumulate a thick litter layer (Christy and Mack 1984; McKenny and Kirkpatrick 1999). As beech increasingly dominates the Carpathian mixed forests (Vrška et al. 2009), the role of CWD in the establishment and survival of conifer species might be more pronounced in the future.

5 Conclusion

In our study, European beech, silver fir, and Norway spruce were successful in colonizing CWD, although they differed in their preferred microsites for establishment. Seedling density was variable within all decay classes. Beech density peaked on CWD in DC 5 while spruce and fir density peaked in DC 4. CWD correlated to the more pronounced height growth in all observed species. In contrast to beech and fir, older spruce seedlings were only found on CWD, with a relatively high survival rate.

This study shows that CWD can be an effective regeneration microsite for light-demanding and small-seed species, such as spruce, and can provide a suitable seedbed for the establishment and growth of other species, such as fir and beech, in the Carpathian mixed beech forests. Well-decomposed CWD, particularly in DC 4, is recommended for successful fir and spruce regeneration. This decay stage should be utilized to improve spruce establishment, growth, and survival over both short-term and long-term spans. Thus, the amount of CWD that can ensure successful regeneration should be the focus of future studies. Nonetheless, the relative importance of CWD as a regeneration microsite might be site specific and shifted by single events (such as a hot summer). For further studies, a longer study period comprising different weather conditions would be necessary to asses a long-term survival and growth on CWD.

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