

1 **Cover page**

2 **Running title:**

3 Soil conditions affect belowground allocation in trees

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19 **Belowground allometric relations in Norway spruce are affected by**  
20 **soil waterlogging.**

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28

29 **Abstract**

30

31 An increasing importance is assigned to the estimation and verification of carbon  
32 stocks in forests. Forestry practice has several long-established and reliable methods  
33 for the assessment of aboveground biomass; however we still miss accurate predictors  
34 of belowground biomass. A major windthrow event exposing the coarse root systems  
35 of Norway spruce trees allowed us to assess the effects of contrasting soil stone and  
36 water content on belowground allocation. Increasing stone content decreases  
37 root/shoot ratio, while soil waterlogging leads to an increase in this ratio. We  
38 constructed allometric relationships for belowground biomass prediction and were  
39 able to show that only soil waterlogging significantly impacts model parameters. We  
40 showed that diameter at breast height is a reliable predictor of belowground biomass  
41 and, once site-specific parameters have been developed, it is possible to accurately  
42 estimate belowground biomass in Norway spruce.

43

44 **Key words:** belowground stump, coarse roots, *Picea abies*, soil stoniness, water-  
45 logging

46

47 **Introduction**

48 In terms of quantitative estimations of tree compartments, substantial interest of  
49 forestry research and practice was traditionally paid to the stem and its taper because  
50 of the importance of timber production (KOZLOWSKI & PALLARDY, 1997). Alongside  
51 the wood producers' interest in timber, tree physiologists and forest ecologists were  
52 interested in branches and mainly foliage (KONÓPKA *et al.*, 2000). Thus, while  
53 aboveground parts of trees have often been surveyed, information on below-ground  
54 compartments is less abundant. Lack of quantitative and qualitative parameters  
55 describing tree root systems has been mainly caused by the enormous time and labor  
56 demands involved in their excavation and, to some extent, an underrating of their  
57 significance (DANJON & REUBENS, 2008).

58 The root systems are important for tree anchorage, water and nutrients absorption  
59 from the soil, as a location for storing carbohydrate reserves and synthesizing growth  
60 hormones (KOZLOWSKI & PALLARDY, 1997). To ensuring all above-mentioned  
61 functions, trees must transfer a considerable proportion of assimilated carbohydrates  
62 into the root systems. As BRUNNER AND GODBOLD (2007) pointed out, estimation and  
63 modeling of belowground structures of trees and forests is particularly important for  
64 the calculation of carbon stock and its changes, as well as for understanding and  
65 predicting ecosystem functioning.

66 To avoid arduous work related to the excavation of root system, allometric  
67 relations based predominantly on diameter at breast height (DBH) or biomass  
68 expansion factors based on stem volume have been used by a number of authors  
69 (GREEN *et al.*, 2007; WIRTH *et al.*, 2004; ZIANIS *et al.*, 2005). KRANKINA AND  
70 HARMON (1995), LAIHO AND PRESCOTT (1999) and TOBIN *et al.* (2007a) all provide

71 examples of cases where this approach was used for the calculation of belowground  
72 necromass as part for carbon stock calculations. The fundamental issue when using  
73 these equation and factors is whether such species-specific models constructed for  
74 trees grown under particular conditions are applicable for individuals existing in  
75 different climate and soils (TOBIN *et al.*, 2007b). For instance, Bolte (2004) in their  
76 study concluded that the relationship between DBH and coarse root biomass was  
77 significantly modified by climatic and soil conditions, but less strongly in Norway  
78 spruce (*Picea abies*) than in European beech (*Fagus sylvatica*) stands.

79 SCHMIDT-VOGT (1977) wrote that the development of Norway spruce root system  
80 appeared to be optimal on deeply developed soils of coarse to medium textures, the  
81 species was also well adapted to grow on rock debris, as well as in the neighborhood  
82 of raised bogs in the uplands. Thus, a relatively large range of soil conditions may  
83 modify Norway spruce root system formation and growth. Several root system types  
84 can be determined and classified according to the root system architecture (KÖSTLER  
85 *et al.*, 1968). Norway spruce has often been categorised as a “surface-rooter”  
86 (STRASBURGER, 1983) or having a “plate-like” root system (STOKES *et al.*, 2007). This  
87 rooting habit is thought to be involved in stability and resistance weaknesses of  
88 Norway spruce in comparison with other species (e.g. vulnerability to windthrow,  
89 drought). For instance, KONÔPKA AND ŽILINEC (1999) compared root systems of  
90 Norway spruce and silver fir, two conifer species with very similar aboveground  
91 compartment allocation. While the root proportions of these two species in dystic  
92 cambisol did not differ, the maximum rooting depth was significantly larger in fir. On  
93 the other hand, PUHE (2003) in his review argues that several studies confirm no  
94 particular disadvantage of Norway spruce in terms of stability in respect to other tree  
95 species. Vertical root distribution of spruce can be considerably modified by inter-

96 specific competition with beech (SCHMID & KAZDA, 2002), but has been shown not to  
97 change in the presence of other tree species (KALLIOKOSKI, 2009).

98 Many studies investigate changes of the root/shoot ratio, considering it the  
99 simplest indicator of the relative biomass allocation between below- and above-  
100 ground compartments. A decrease of the ratio is generally associated with increasing  
101 soil moisture (KRAMER & KOZLOWSKI, 1979) and with increasing soil fertility  
102 (WARING & SCHLESINGER, 1985). On the other hand, the ratio tends to increase in  
103 stress conditions (PUHE, 2003). There is a considerable knowledge concerning shoot  
104 and root growth under contrasting soil moisture and nutrient levels, but the knowledge  
105 on biomass allocation in soils with varying stoniness (stones and boulders) content are  
106 rare. Similarly, comparative studies between tree stands grown on well-drained and  
107 water-logged sites are lacking at the present. Very often, soil stoniness and contrasting  
108 soil water conditions are omitted in tree biomass partitioning models (see for instance  
109 (BARTELINK, 1998).

110 To address the lack of information in this area, we utilized a major windthrow  
111 event which took place in the Tatra Mountains (Slovakia) on 19<sup>th</sup> November 2004,  
112 exposing a large amount of Norway spruce coarse root systems. The objectives of this  
113 study were: (1) to construct allometric relationships between stem parameters and  
114 below-ground compartment mass of Norway spruce and (2) to evaluate the effects of  
115 soil conditions, particularly soil stone content and water-logging, on the relative size  
116 of stem, stump and roots as well as on vertical coarse root distribution

117

## 118 **Materials and methods**

### 119 *Locations and sites*

120 All measurements were conducted in four uneven-aged Norway spruce stands in the  
121 High Tatra Mountains (northern Slovakia). The altitude of the stands ranged between  
122 897 and 1171 m above sea level. The climate is characterised by low average  
123 temperatures (annual mean of 5.8 °C) and ample precipitation (750 mm annually).  
124 Mean January temperature is -5.0 °C and the snow cover lasts approximately 114 days  
125 a year, while the summers are relatively mild with the mean of 14.7°C in July (data  
126 are from the nearest meteorological station in Stara Lesna, 49° 09' N, 20° 17' E). The  
127 prevailing bedrock is granodiorite.

128 We selected plots with decreasing stoniness: Koprova dolina (stand 1; coordinates:  
129 49° 09' 20" N, 19° 57' 58" E), Nad Podbanskym (stand 2; coordinates: 49° 08' 24" N,  
130 19° 55' 47" E ), Horny Smokovec (stand 3; coordinates: 49° 08' 40" N, 20° 14' 30" E ).  
131 In addition, we included another stand of similar stoniness to stand 2, but with  
132 different water regime: Kezmarske zlaby (stand 4; coordinates: 49° 11' 32" N, 20° 18'  
133 14" E). Soil stoniness was estimated by exposing and describing five soil profiles at  
134 each study plot according to (FAO, 1998). Average stoniness of the whole profile was  
135 estimated, rather than that of each horizon, since soil stone content is fairly well  
136 distributed due to the post-glacial origin of these soils. The soil of stand 4 was  
137 considered different from the other stands due to the presence of a stagnic horizon,  
138 suggesting water saturation for long periods. The main soil characteristics of all stands  
139 are shown in Table 1.

140 The stand ages were: Koprova dolina – 107 years, Nad Podbanskym – 65 years,  
141 Horny Smokovec – 60 years, Kezmarske zlaby – 53 years. All selected stands were  
142 partly damaged by the windstorm of 19th November, 2004. The highest intensity of  
143 wind damage was recorded within the stand Kezmarske zlaby with approximately  
144 90% of individuals heavily damaged, while the lowest intensity was recorded in stand

145 Koprova dolina approx. 35%. All stands originated as either planted or naturally  
146 regenerated clumps of spruce trees, which was therefore the dominant species in the  
147 canopy of all stands.

148

149 *Sampling and measurements*

150 During the summer of 2005, a total of 47 wind-uprooted spruce trees were randomly  
151 selected for stem and belowground compartment measurements. First, the branches  
152 were cut from the stem and the tree height was measured using a tape. Diameter  
153 measurements using calipers (two diameters perpendicular to one another) were taken  
154 from all sampled trees at the following positions: tree base (ground level, D0H), 20  
155 (D20H) and 130 cm (DBH) from the base, and also every 100 cm from the base to the  
156 top of the tree. A summary of measured stem parameters can be found in Table 2.

157 The position of the ground level was identified on each stem and the trees were  
158 then cut and separated into above- and belowground parts. Soil and stones still  
159 attached to the root systems exposed by windthrow were cleaned with the help of  
160 spades, picks and chisels. The original depth allocation of 0-30 cm, 30-60 cm and  
161 over 60 cm was marked out on all the roots. The exposed root plate were undisturbed  
162 by the windthrow, enabling a fairly accurate estimation of original root depth. Broken  
163 roots still in the soil were paired up with fresh root injuries on the exposed part of the  
164 root system, excavated manually and tagged. All roots under the diameter of 1 cm  
165 were cut off by secateurs and disposed of. Then, roots in each depth category were  
166 separated from the stump cylinder and classified into the following diameter classes:  
167 1.0-2.5 cm, 2.6-5.0 cm, 5.1-7.5 cm and so on until the maximum diameter of 30 cm.  
168 All of these observations were carried out on the exposed half of the root system,  
169 created by an imaginary horizontal plane drawn through the centre of the stump. As

170 the trees were mostly uprooted by northern, north-western and western wind,  
171 measured halves of the roots systems were always oriented to the north and the west  
172 of each stump. The prevailing wind direction and the direction of the windthrow were  
173 identical in all four compared stands, thus minimizing the error due to uneven root  
174 system development (DANJON *et al.*, 2005; TAMASI *et al.*, 2005).

175 At this point it is important to mention the existing inconsistency in terms of  
176 terminology and non-uniform specification of root system segments existing in the  
177 literature (TOBIN *et al.*, 2007a). The term “belowground biomass” is generally well  
178 defined and used to identify the belowground part of the stump and all roots. On the  
179 other hand, the meaning of “roots” and especially “root system” is not always uniform  
180 in the literature because of a facultative consideration of the stump. Definition of  
181 “coarse roots” is also not consistent, since different authors specify various diameters  
182 as the threshold between fine and coarse roots. The values most often used are 0.2 cm  
183 (e.g. BOLTE *et al.* (2004), 0.5 cm (e.g. CURIEL YUSTE (2004) or 1.0 cm (e.g. FINER *et*  
184 *al.* (1997). In this paper, the term “below-ground biomass” is used to describe the  
185 belowground part of the stump plus coarse roots with a minimum diameter of 1.0 cm.

186 A measurement of the diameter and length of all root segments was taken as they  
187 were removed from each depth class (0-30, 30-60 and 60+ cm). The diameter of the  
188 belowground portion of the stump was established at its top, middle and bottom. The  
189 volume of all root and stem segments was then calculated according to an equation for  
190 a frustum of a cone:

$$191 \quad V = \pi/3 * l * (r_1^2 + r_1 * r_2 + r_2^2) \quad (1)$$

192 where:

193 l – root or stem segment length

194 r – root or stem radius at the top ( $r_1$ ) and bottom ( $r_2$ ) end of a segment.



195 The total volume of stems and roots was then calculated by summing up the  
196 volumes of all stem and root segments. The volume of the below-ground portion of  
197 the stump was expressed by Newton's formula:

$$198 \quad V = \pi * l * (r_1^2 + r_2^2 + 4r_3^2) / 6 \quad (2)$$

199 where:

200  $l$  – stump length

201  $r$  – stump radius in top ( $r_1$ ), bottom ( $r_2$ ) and middle ( $r_3$ ) part of the stump.

### 202 *Biomass equations*

203 We tested two equations in order to develop a suitable model for belowground  
204 biomass prediction, and to test whether site conditions alter the model parameters.  
205 First, equation (3), presented by FINER (1989) and LAIHO AND FINER (1996) among  
206 others, was used with D20H and DBH to predict coarse root and total belowground  
207 biomass of spruce trees at every site.

$$208 \quad \text{Biomass} = B1 * X^{B2} \quad (3)$$

209 Subsequently, an equation (4) recently introduced by PETERSSON AND STAHL  
210 (2006) was tested for goodness of fit with D20H and DBH. This equation is meant to  
211 take into account the fact that root biomass is not zero when DBH or D20H have zero  
212 value.

$$213 \quad \text{Biomass} = e^{(B0+B1*X)} \quad (4)$$

214 Stem height and stem volume were also tested for their fitness as predictors of  
215 belowground biomass, a range of functions was tested including linear, exponential  
216 and polynomial equations.

### 217 *Analysis and statistics*

218 We constructed separate models for belowground biomass prediction for each stand.  
219 Resulting coefficients were then compared using extra sum-of-squares F test to test

220 for influence of soil conditions on belowground biomass prediction. Model fitting and  
221 statistical comparisons were done in SigmaStat 3.0 (Systat, California, USA) and  
222 GraphPad Prism 5 (GraphPad Software Inc., USA). All significances are reported at  
223  $P<0.05$ .

224

## 225 **Results**

226 Initial comparison of measured stem characteristics revealed that stand 1 (Koprova  
227 dolina) was different from all other stands. This was the case for diameter at 20 cm  
228 ( $P<0.002$ ), DBH ( $P<0.002$ ), stem height ( $P<0.007$ ) and stem volume ( $P<0.001$ ). The  
229 remaining three stands did not differ in any of these parameters (Table 2). Similarly,  
230 belowground biomass was higher in Koprova dolina compared to the other three  
231 locations ( $P<0.003$ ). The root/shoot ratio of sampled trees was also affected by the  
232 site conditions, stand 1 having significantly lower root/shoot ratio than stand 3 (Horny  
233 Smokovec,  $P<0.001$ ) and stand 4 (Kezmarske zlaby,  $P=0.005$ , Figure 1).

234 Using our observations of above- and belowground biomass we constructed  
235 biomass equations linking root and total belowground biomass to aboveground  
236 parameters. In general, both D20H and DBH are considered to be reasonably good  
237 predictors of coarse root biomass (e.g. TOBIN *et al.* (2007b)). The estimated values of  
238 parameters from equations (3) and (4) are detailed in Table 3. Both equations fit the  
239 data reasonably well, however equation (3) appears to be more accurate in predicting  
240 coarse root and total belowground biomass than equation (4).

241 To evaluate the effects of soil conditions, particularly soil stoniness and water-  
242 logging on the relationship between aboveground parameters and belowground  
243 biomass, we carried out a comparison of models resulting from our observations  
244 (Figures 2 and 3). There was no significant difference between the models due to the

245 stone content of the soil. Stand 1 (Koprova dolina) was only nearly significantly  
246 different from stand 3 (Horny Smokovec) when D20H was used to predict total  
247 belowground biomass ( $P=0.0650$  and  $P=0.0652$  for equations (3) and (4)  
248 respectively). However, we observed a very strong effect of soil water logging on  
249 model coefficients. The models for stand 4 (Kezmarske zlaby) with very high water  
250 table differed from all other stands regardless of which stem diameter or equation was  
251 used to predict belowground biomass ( $P<0.008$ ). For this reason, Table 3 reports the  
252 regression coefficients for stands 1, 2 and 3 pooled together and for stand 4  
253 separately.

254 Since stand 1 (Koprova dolina) was so different from the other three stands, to  
255 assess the effect of soil conditions on coarse root and belowground stump biomass we  
256 compared the relative sizes of biomass pools. Coarse root/stem biomass ratio was  
257 inversely related to the stone content in the soil. Coarse root biomass in the very stony  
258 soil of stand 1 did amount to 17% of stem biomass, while in stand 2 this increased to  
259 23% ( $P=0.056$ ) and in least stony stand 3 to 26% ( $P=0.002$ ). Similarly, high stone  
260 content negatively impacted on the volume of the belowground portion of the stump  
261 relative to the stem volume. Stand 3 had the highest ratio of 10%, significantly  
262 different from stand 2 (6%,  $P<0.001$ ) and stand 1 (5%,  $P<0.001$ ). The ratio between  
263 belowground stump and coarse root volume was also reduced by high stone content  
264 ( $P=0.0211$ ).

265 When comparing the root depth allocation in stands 1, 2 and 3, we did not  
266 observe any difference in the proportion of the root system in the 0-30cm soil depth  
267 ( $P=0.210$ ) or 30-60cm depth ( $P=0.365$ ). In the over 60 cm soil layer, a larger  
268 proportion of the root system was found in stand 1 with the highest stone content  
269 (Koprova dolina, 16%) than in stand 3 with the lowest stone content (Horny

270 Smokovec, 7%,  $P=0.015$ , Figure 4). We did not include stand 4 (Kezmarske zlaby) in  
271 this comparison, since 100% of coarse spruce roots in this water-logged location were  
272 found in the 0-30cm soil layer.

273

## 274 **Discussion**

### 275 *Soil stoniness*

276 The results show that a high proportion of boulders decreases the ratio between  
277 the belowground root system and the stem (root/shoot ratio), restricts the size of the  
278 belowground stump and increases the proportion of roots in the deepest soil horizons.  
279 Our results have to be interpreted with caution, mainly because stand 1 is somewhat  
280 older than the remaining stands. This should not have a significant influence on our  
281 observation, since the root/shoot ratio changes rapidly in young trees, but stabilizes  
282 fairly soon and does not change in mature trees (JOHNSON *et al.*, 2003; PAJTIK *et al.*,  
283 2008). Mechanical resistance and limited space within a soil profile with high boulder  
284 content do therefore influence biomass partitioning, as well as vertical root  
285 distribution in spruce trees. We attribute the increase in the coarse root biomass  
286 volume compared to the stump volume to the fact that the roots are more flexible in  
287 using the available space between the stones than the stump. Downwardly directed  
288 roots can deflect to horizontal growth along the surface of mechanical barriers, but  
289 turn back downwards if they encounter a cavity (DEXTER, 1986).

290 Our field observations also reveal (data not shown) that the stone content  
291 interferes with coarse root growth and alters not only the direction of growth, but also  
292 induces structural changes, such as root/stump ratio or root branching pattern. Greater  
293 presence of boulders in the soil places restrictions on root growth and functioning at  
294 depths where they are normally found. In order to explore a sufficient volume of soil,

295 spruce root systems in very stony soil had to extend into deeper soil horizons. This  
296 observation has potential bearing on the parameterization of biomass-partitioning  
297 models, carbohydrate cost of tree root system development and estimates of C storage  
298 in forest soil, a perspective that however still needs to be fully explored. Further  
299 studies in stands of comparable age need to be carried out, since it has been shown  
300 that vertical distributions of coarse roots may change with stand age (KALLIOKOSKI *et*  
301 *al.*, 2008). Root quantity, vertical distribution and morphological features are likely to  
302 be important for water and nutrient acquisition. Reduced root extension can result in  
303 low nutrient-uptake and increase susceptibility to water deficiency (PUHE, 2003).  
304 CANADELL *et al.* (1996) in his review pointed out the importance of deep roots,  
305 particularly for ecosystem water fluxes, as well as for carbon and nutrient cycling.

#### 306 *Waterlogging*

307 Waterlogged conditions increased the root/shoot ratio but, at the same time,  
308 drastically diminished root system depth and reduced the size of belowground stump  
309 relative to the stem. We expect the high value of this indicator to be linked to the  
310 limited root depth in the soil and consequently to lower nutrient availability. This  
311 view is supported by TOBIN *et al.* (2007b) who posit that trees growing on wet sites  
312 may need larger root systems for oxygen and nutrient uptake, or simply for anchorage.

313 Waterlogged soils are generally characterised by a lack of oxygen and high  
314 levels of CO<sub>2</sub> and ethylene (ARMSTRONG, 1982), creating conditions which explain  
315 decreased rooting depth and the existence of extremely shallow spruce root systems.  
316 Superficial root systems in waterlogged soils have been reported by a variety of  
317 authors (KONÔPKA, 2002; PYATT, 1966). At our site, spruce coarse root systems  
318 consisted of an extremely dense tangle, part of which was formed by root necromass,  
319 similar to those reported by COUTTS (1989). He stated that a zone of periodic death

320 and re-growth of roots (shaving brush roots) was often established in waterlogged  
321 soils since the positive geotropism of downward growing roots is never altered and  
322 seasonal fluctuations of water table kill off any new roots. Our results which indicate  
323 an increase in root/shoot ratio on a waterlogged soil are also in agreement with those  
324 of RAY AND NICOLL (1998), who indicated an increase of root biomass with  
325 decreasing total rooting depth. TOBIN *et al.* (2007b) stated that a positive feedback  
326 relationship might exist between root biomass quantity and anchorage; further  
327 biomass being required to support more extensively ramifying surface roots.

### 328 *Allometric relations in contrasting soil conditions*

329 Using the measurements in the Tatra Mountains, we have constructed allometric  
330 relations for belowground biomass prediction. We have compared two models  
331 (equation 3 and 4) available in the literature, finding no difference between the  
332 models regarding the effects of soil conditions on belowground biomass prediction.  
333 Perhaps surprisingly, given the response of biomass allocation ratios to increasing soil  
334 stoniness, there was no significant difference between the models fitted to the data  
335 from the sites with well-draining soil. All observations from stands 1, 2 and 3 were  
336 well captured with just a single model (Table 3). Waterlogging, on the other hand, had  
337 a strong impact on the model parameters, suggesting that it is this soil condition that  
338 has to be considered when constructing generalized belowground biomass allometric  
339 relations. Allometric relations are often thought to be modified by climatic or soil  
340 conditions (BOLTE *et al.*, 2004; WIRTH *et al.*, 2004). In our case, waterlogging did  
341 increase the belowground biomass relative to the stem.

342 Both stem diameters measured in this study, 20 and 130 cm above ground level  
343 (D20H and DBH, respectively), proved to be suitable parameters for estimates of  
344 belowground biomass. However, at the waterlogged site, we observed the formation

345 of large buttresses (as evidenced by the largest base shape ratio at this site, Table 2).  
346 Since the depth penetration of the stump was severely limited at this site, larger  
347 buttresses have probably developed to aid stability and resulted in uneven thickening  
348 of the stem base. As a result, cross-sections of stem bases at this site were irregular,  
349 resulting in higher variability of D20H values in comparison to DBH. Model fits  
350 based on DBH show higher coefficient of determination than those based on D20H at  
351 the waterlogged site (such differences were less clear in the other sites). Thus, DBH  
352 should be preferred to D20H as a predictor of belowground biomass at waterlogged  
353 sites.

#### 354 *Soil conditions and tree anchorage*

355 There are several important aspects worth considering in terms of tree resistance to  
356 uprooting and stand stability. Stokes (2002) stated that tree anchorage is mainly  
357 affected by root/shoot ratio, vertical root distribution, radial symmetry, as well as the  
358 spread and the shape of lateral roots, the latter demonstrated by NICOLL AND RAY  
359 (1996) and RUEL *et al.* (2003). Coutts (1989) noted that roots could be categorised  
360 into three principal groups: taproots, lateral roots and sinkers. Taproots, and especially  
361 sinkers, are believed to be the most important for anchoring (DANJON *et al.*, 2005),  
362 while the proportions of the particular type of roots can be considerably modified due  
363 to mechanical barriers or water-logging.

364 Theoretically, tree anchorage should improve with higher values of root/shoot  
365 (alternatively root/stem) ratio, root/belowground biomass ratio (discriminating the  
366 stump which is less important for tree anchorage than roots) and especially with  
367 increasing proportion of roots in deeper soil layers. However, it seems that for  
368 accurate evaluation of tree anchorage, the root system parameters must be combined  
369 with the soil property data (see also DUPUY *et al.* (2005). For instance, high root/shoot

370 ratio and high root/belowground biomass ratio could indicate good spruce anchorage  
371 at our waterlogged site. However, the stand at this site was completely uprooted by  
372 the windstorm. ROTTMANN (1989) stated that waterlogging worsens the coherence of  
373 soil and the root-soil friction, a confluence of which drastically lowers root anchorage.  
374 At the other extreme, low root/shoot ratio at our boulder site, on its own, would  
375 indicate low tree anchorage. However, a large part of this stand was left undamaged,  
376 many trees were broken at the stem rather than uprooted. We assume that the roots  
377 ingrown between stones were difficult to pull out from the soil and consequently did  
378 reinforce anchorage.

379

### 380 **Conclusion**

381 A severe windthrow event in forests dominated by Norway spruce has allowed us  
382 to assess the effect of soil conditions on coarse root and belowground stump biomass  
383 allocation. Increasing stone content of the soil had a negative influence on root/shoot  
384 ratio, while soil waterlogging resulted in the predomination of roots at the expense of  
385 shoots. We have shown that it is possible to construct reliable models predicting  
386 belowground biomass. DBH proved to be a stable and accurate predictor variable,  
387 across all site and soil conditions, however model coefficients have to be site specific,  
388 especially if they are to be applied to sites with contrasting soil water conditions.

389

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Table 1. Soil characteristics of the experimental plots

<b>Stand name and number</b>	<b>Soil type</b>	<b>Type of stones</b>	<b>Proportion of stones<sup>#</sup></b>	<b>Water regime</b>
Koprova dolina (1)	humic podzol	boulder	65%*	well drained
Nad Podbanskym (2)	cambic podzol	stony	45%*	well drained
Horny Smokovec (3)	haplic cambisol	moderate stony	25%*	well drained
Kezmarske zlaby (4)	stagnic pseudogley	stony	40%**	water-logged

**Notes:** # - on volumetric base

\* - at soil depth 0-100 cm

\*\* - at soil depth 0-30 cm (conforms with maximum rooting depth)

Table 2. Aboveground parameters of trees selected for root system measurements (D20H denotes stem diameter at 20 cm from the ground level, DBH is diameter at breast height, i.e. 130 cm from the ground level).

<b>Stand name and number</b>	<b>Number of trees</b>	<b>Height (cm) [ A ]</b>	<b>D20H (cm) [ B ]</b>	<b>DBH (cm) [ C ]</b>	<b>Slenderness ratio [ A/C ]</b>	<b>Base shape ratio [ B/C ]</b>
Koprova dolina (1)	11	2450	40.7	33.3	74	1.22
Nad Podbanskym (2)	10	1790	25.6	20.6	87	1.24
Horny Smokovec (3)	12	1650	22.8	19.5	85	1.17
Kezmarske zlaby (4)	14	1400	20.5	16.0	88	1.28

Table 3. Regression coefficients B0, B1, B2, their standard errors (S.E.), p-value (*P*), degrees of freedom (DF), coefficient of determination ( $R^2$ ), for equations (3) and (4) predicting coarse root and total belowground biomass from DBH and D20H respectively. Stands 1- 3 (Koprova dolina, Nad Podbanskym and Horny Smokovec) were estimated together since their separate model fits were not significantly different.

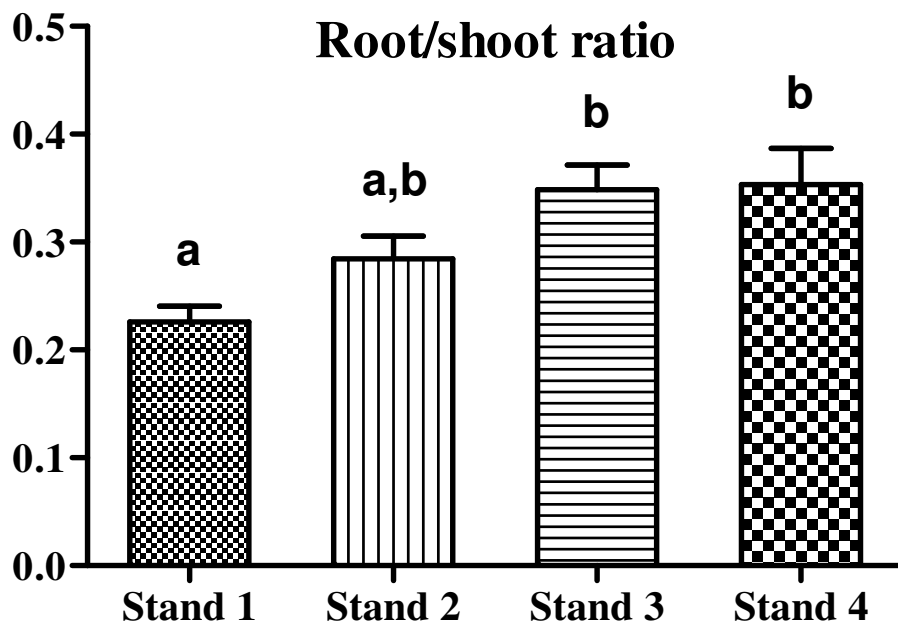
Equation	Model	Stands	B0 (SE) <i>P</i>	B1 (SE) <i>P</i>	B2 (SE) <i>P</i>	DF	$R^2$	
(3)	DBH – Coarse roots	1-3		0.000254 (0.0000933) 0.010	1.812 (0.101) <0.001	32	0.937	
		4		0.0000316 (0.0000401) 0.446	2.638 (0.385) <0.001	13	0.931	
	DBH – Belowground biomass	1-3		0.000258 (0.000102) 0.016	1.892 (0.108) <0.001	32	0.934	
		4		0.0000349 (0.0000353) 0.343	2.657 (0.314) <0.001	13	0.953	
	D20H – Coarse roots	1-3		0.0000615 (0.0000393) 0.127	2.105 (0.169) <0.001	32	0.905	
		4		0.000207 (0.000254) 0.431	1.876 (0.341) <0.001	13	0.867	
	D20H – Belowground biomass	1-3		0.0000486 (0.0000337) 0.160	2.247 (0.181) <0.001	32	0.906	
		4		0.000225 (0.000242) 0.369	1.898 (0.298) <0.001	13	0.897	
	(4)	DBH – Coarse roots	1-3	-3.900 (0.146) <0.001	0.0557 (0.00358) <0.001		32	0.897
			4	-5.075 (0.495) <0.001	0.126 (0.0193) <0.001		13	0.901
DBH – Belowground biomass		1-3	-3.668 (0.154) <0.001	0.0575 (0.00376) <0.001		32	0.896	
		4	-4.938 (0.419) <0.001	0.127 (0.0164) <0.001		13	0.927	
D20H – Coarse roots		1-3	-4.338 (0.196) <0.001	0.0579 (0.00426) <0.001		32	0.899	
		4	-4.246 (0.467) <0.001	0.0677 (0.0133) <0.001		13	0.795	
D20H – Belowground biomass		1-3	-4.163 (0.205) <0.001	0.0608 (0.00442) <0.001		32	0.904	
		4	-4.112 (0.423) <0.001	0.0685 (0.0120) <0.001		13	0.828	

**Figure 1.** Ratio of belowground biomass volume to stem volume in Koprova dolina (1), Nad Podbanskym (2), Horny Smokovec (3) and Kezmarske zlaby (4) [ $\pm$ SE], letters denote significant difference at  $P < 0.05$ .

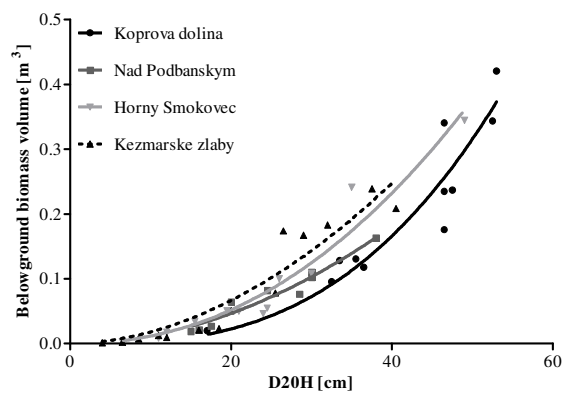
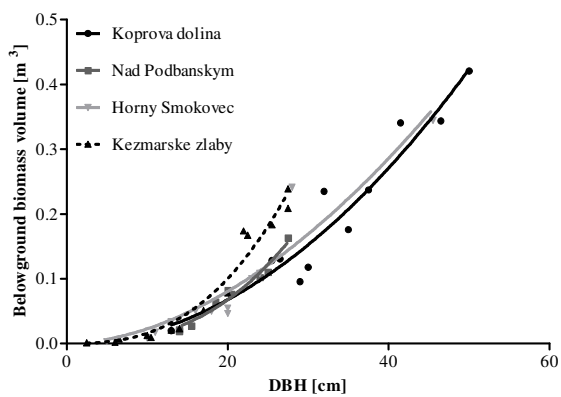
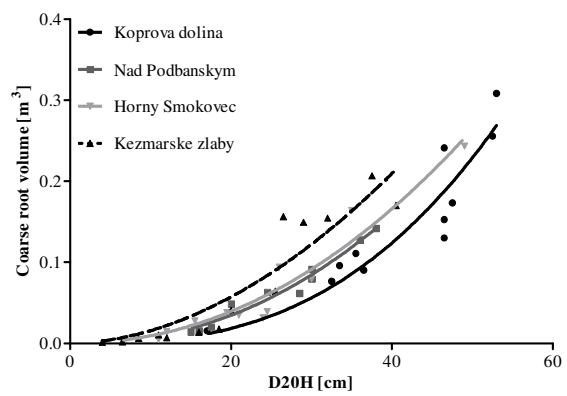
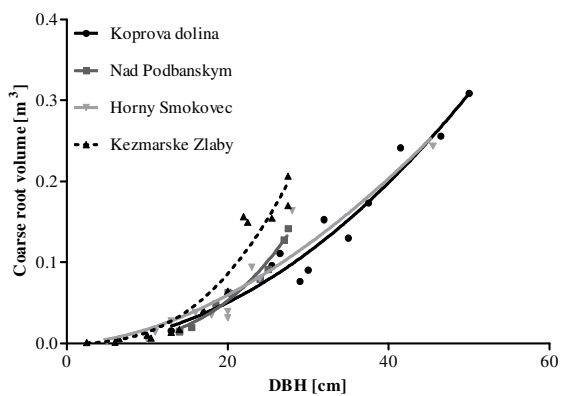
**Figure 2.** Coarse root volume and belowground biomass volume prediction curves based on equation (3).

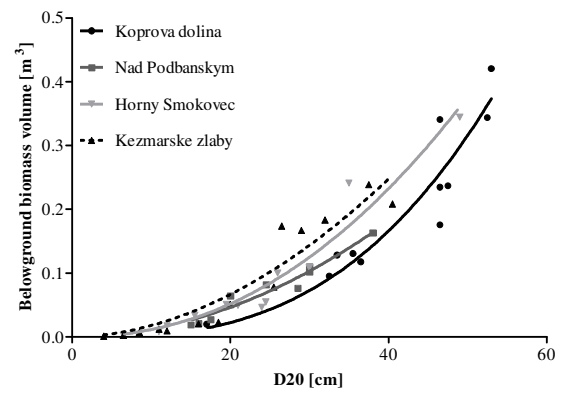
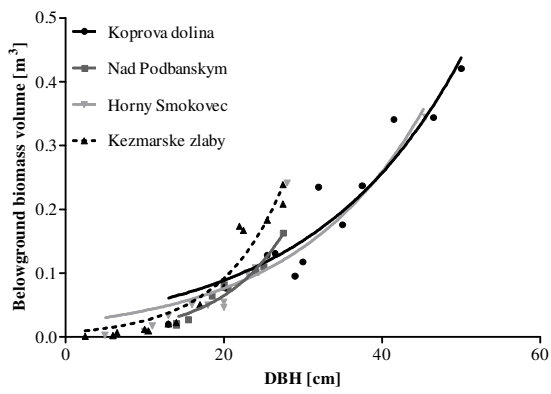
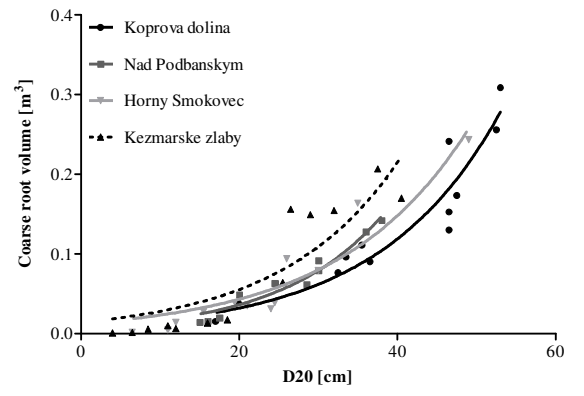
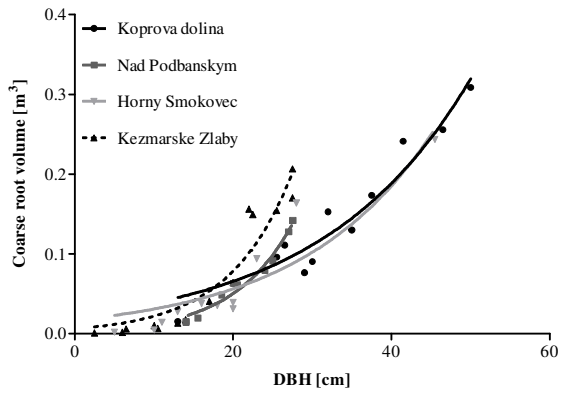
**Figure 3.** Coarse root volume and belowground biomass volume prediction curves based on equation (4).

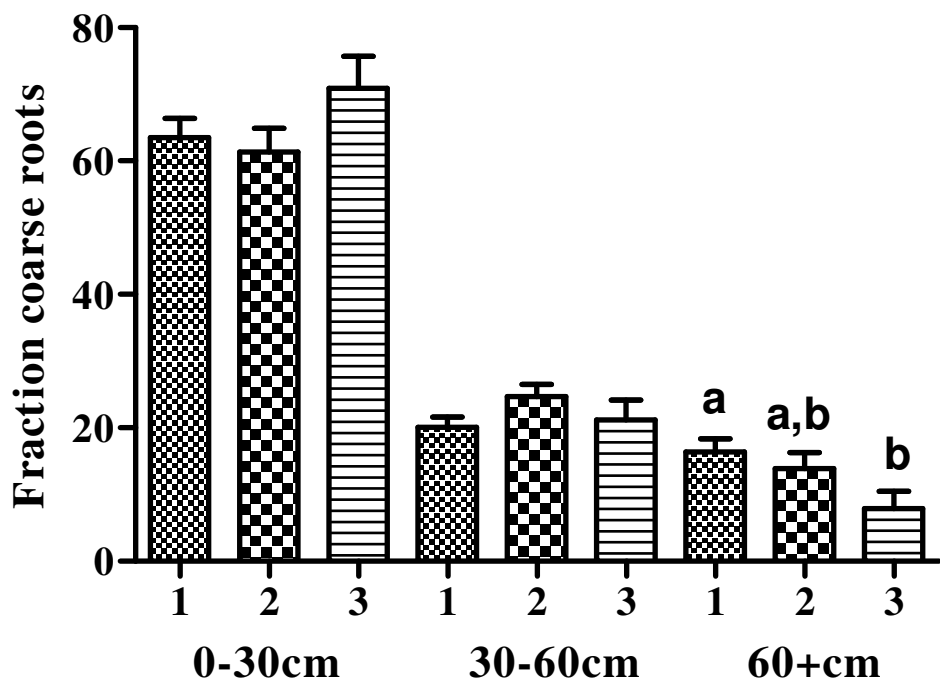
**Figure 4.** Proportion of coarse root volume in different soil depths in Koprova dolina (1), Nad Podbanskym (2) and Horny Smokovec (3) stands [%], letters denote significant difference at  $P < 0.05$ .











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