Wind and gravity in shaping *Picea* trunks

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Abstract

Understanding why trunks (tree stems) are the size that they are is important. However, this understanding is fragmented into isolated schools of thought and has been far from complete. Realistic calculations on minimum trunk diameters needed to resist bending moments caused by wind and gravity would be a significant step forward. However, advancements using this biomechanical approach have been delayed by difficulties in modelling bending of trunks and wind gusts. We felled and measured five Norway spruces (*Picea abies*) in an unthinned monoculture in southeastern Finland planted 67 years earlier. We focused on forces working on storm-bent (maximally bent) trees caused by gravity and the strongest gust in a one-hour simulation with a large-eddy simulation model. The weakest points along the trunks of the three largest trees resisted mean above-canopy wind speeds ranging from 10.2 m s^{-1} to 12.7 m s^{-1} (3.3-fold in the strongest gust), but the two smallest were well protected by a dense layer of leaves from the bending tops of larger trees, and could have resisted stronger winds. Gravity caused approximately one quarter of the critical bending moments. The wind that breaks the trunks in their weakest points is close to breaking them in other points, supporting importance of bending moments caused by wind and gravity in evolution of trunk taper. This approach could also be used to model tree biomasses and how those may change with changing climate.

Introduction

Understanding why trees and their trunks (stems) are the size that they are is important for evaluating the potential of forests to mitigate climate change and produce timber. Therefore it is surprising that that the scientific understanding of tree height and diameters along the trunk is fragmented. For example, a question concerning the dimensional determinants of a particular tree trunk may cause surprise and be considered too general by experts in narrow fields, even though understanding trunk dimensions should be considered one of the largest questions in applied ecology.

Research on trunk dimensions can be classified in two ways. Firstly, the classification can be based on the object of the study, i.e. the condition of the forest. Some studies focus on those experiencing natural successions (Anderson-Teixeira et al., 2013), others on tallest old-growth forests (Van Pelt et al., 2016), on plantations subject to self-thinning (Yoda et al., 1963) or silvicultural treatments (Bianchi et al., 2020). Secondly, the classification can be based on whether the approach is descriptive or theoretical. The majority of research on trunk dimensions in forest sciences and research related to forests' role in climate change mitigation is mainly descriptive (e.g. Chave et al., 2014), while much of the physiological and ecological research attempts to explain the causes of the described patterns based on theories. These theories may be grouped based on the function on which the focus is: transport, storage or biomechanical support as explained in the following paragraphs.

Trees passively transport sap (water) up in the sapwood, and the resistance caused by length of the path or need to lift sap against gravity has been used as the basis for modelling maximum tree height (Koch et al., 2004) and growth deceleration in plantations (Ryan and

Yoder, 1997). However, as the heartwood is not contributing to sap transport, diameters

along the trunk cannot be understood based on sap transport only, unless heartwood is

considered a waste produced e.g. because of ageing (Collalti et al., 2019) or difficulties in

using the same sapwood when branches die and grow (Chiba et al., 1988). Phloem transport

down the trunk may be similarly limiting tree height due to path length (Woodruff, 2013), but

does not explain diameters, unless trunk circumference needs to be increased to increase

transport capacity.

Trees are dependent on the storage of water (Scholz et al., 2011) and energy (Schiestl‑Aalto

et al., 2015) in their woody tissues and this is likely to influence trunk dimensions in certain

conditions. For example, baobab (*Adansonia digitata*) trees probably have unusually fat

trunks to store water needed to level out seasonal variation in water availability (Chapotin et

al., 2006), and lignotubers located at the trunk base can store energy and nutrients enabling

rapid sprouting (Canadell and López‑Soria, 1998). Trunk dimensions are therefore

potentially influenced by storage needs, but this is unlikely to be common and may be

restricted to the rare trees that do not form metabolically dead heartwood and therefore

cannot increase sapwood volume by adjusting the sapwood-to-heartwood-ratio such as the

above-mentioned baobabs (Patrut et al., 2010).

The third general function of trunks in addition to transport and storage, and the only for

which heartwood is useful, is to biomechanically support the leaves, branches and trunk

sections above the height at which the focus is. Common sense tells that trees exposed to

wind or heavy loads need to have thicker trunks for a given height and crown size. These

mechanism have been studied experimentally for over two centuries (Telewski, 2016), and

the term "thigmomorphogenesis" has become established in the recent decades to describe

the responses of plants to mechanical stimuli (Pruyn et al., 2000). Two very different

mechanisms may serve as a basis for modelling trunk dimensions biomechanically. Elastic

buckling (Euler buckling) can permanently bend trunks if the tree fresh mass and permanent

loads, such as epiphytes and lianas, exceed the limit that the trunk can support. Modelling can

be performed easily (McMahon, 1973), and normally a "safety factor" is computed

describing how far the height of the tree is from a height that leads to buckling. This approach

has been used in well-known modelling approaches (e.g. West et al., 1999). However, most

trees, with the exception of certain rainforest understorey trees, are far from elastic buckling.

For example, Niklas (1994) reported an average safety factor of four. Because of non-

linearities, a safety factor of four implies that plants weight is only 1.6% of the weight that

would lead to elastic buckling. Furthermore, the safety factor is a misleading concept and

should not be interpreted as an indication of biomechanical safety. A safety margin is needed

for engineer-designed structures, as they are built and then need to resist variable forces

without subsequent adjustments to the structure. However, trees can tune their structure

(Bonnesoeur et al., 2016) and a small safety factor is therefore not dangerous, as supporting

tissue can be increased according to demand from the increasing height or weight. The wide

usage of the theory on elastic buckling shocked Mattheck (2012) and he wrote: "Much to the

surprise of the author, failure by buckling has nevertheless been discussed by McMahon

(1973), and comparisons have been made between measured height-diameter relations and

relations calculated from Euler's buckling theory." The other, more useful, biomechanical

approach is based on trunks breaking. Brief buckling e.g. due to a temporary load of snow

may not be a problem for the tree if it recovers and is erect most of the time. However, when

modelling trunk breakage, even a short period to which the tree has not been able to

acclimatize may be fatal. This modelling approach is challenging to follow, as wind speeds

are variable in space and time, and trunks, branches and leaves streamline in wind. In both

115   buckling and breaking approaches, diameters needed along the trunk for a given height and

116   other characteristics can be computed based on biomechanics. However, these approaches do

117   not limit height if the diameters are not limited.

118

119   All trees need trunks to transport, to provide biomechanical support and probably also to

120   store, and theories and modelling to understand trunk dimensions should ideally incorporate

121   all of these with appropriate weights. However, in practice realistic modelling of even one of

122   these aspects at a time is challenging. Therefore, it is useful to consider their relative

123   importance. One challenge is that scientists are often experts on only one of these three

124   functions and may therefore overestimate its importance, even though some reviews on all

125   them are available (Badel et al., 2015). Secondly, if building or maintaining a trunk that is

126   superior in any of the three functions causes an energetic cost, all functions would evolve

127   close to the needed level even if the cost improving it relative to the others would be

128   minuscule. An example with an engineer-designed product demonstrates this issue well. An

129   expert focusing on tires may conclude that a given car cannot go faster than e.g. 50 m s^{-1}

130   because of the speed rating of the tires. According to an expert on engines the top speed of

131   the same car is restricted by engine power. Both would be technically correct, but to

132   understand the main reason why markets set the top speed at its level, the challenges in

133   designing, manufacturing, maintaining and operating engines and tires that allow faster

134   speeds must be considered. This reveals that, as improving the speed rating of tires is very

135   easy relative to designing and building a more powerful engine, it makes normally more

136   sense to say that the car does not go faster because the engine is not more powerful and not

137   because of its tires. Similarly, demonstrating that e.g. transporting sap higher than the current

138   height of the tallest trees (Koch et al., 2004) does not necessarily mean that sap transport is

139   the main factor determining maximum heights. Instead, in evolutionary time scales for

140 example sap transport capacity could improve to a height determined mainly by the

141 biomechanics and energetics of maintaining the living biomass.

142

143 We did not properly assess the relative importance of how the functions of trunks influence

144 their dimensions, as that would need to be done by incorporating them into one model. In this

145 paragraph, we just note a few pieces of evidence that indicated to us the direction to take.

146 One approach is to consider the marginal construction and maintenance costs of increasing

147 capacity. Tissue suitable for storage or sap transport may be increased by increasing sapwood

148 to heartwood ratio. Furthermore, sap transport efficiency may be boosted by increasing the

149 density of conduits in angiosperm wood, probably with little or no additional construction

150 costs (Larjavaara, 2021) . However, significant strengthening of the trunk is not possible

151 without substantial additional construction costs, either by increasing diameters or wood

152 density (Larjavaara and Muller-Landau, 2012). Another approach to know about the relative

153 importance of factors influencing trunk dimensions is to compare them in variable

154 environmental conditions that demand for variable transport, storage and biomechanical

155 support needs. This approach underlines the importance of sap transport if height and

156 diameters along the trunk vary according to water availability. The very tallest trees would

157 then be expected to be found in climates and soils with most abundant water, which is not the

158 case, even though the driest climates have a low canopy height (Klein et al., 2015). If storage

159 function was critical in determining trunk dimensions, then seasonality should increase trunk

160 volumes relative to leaf area, which may be the case (Chapotin et al., 2006) but probably only

161 in the case of exceptional species. Finally, with biomechanical support being the most

162 significant, tree heights and forest biomasses should vary depending on winds. This is the

163 case for example with variable distances from the edge and therefore variable wind regimes

164 (Brüchert and Gardiner, 2006). Another perspective on the importance of biomechanics is

165   provided by comparing trees to lianas, which do not have the same biomechanical support

166   needs. Lianas have similar transport and storage needs as trees, and much higher leaf area for

167   a given stem basal area (Ichihashi and Tateno, 2015), which is very likely due to differing

168   biomechanical needs, highlighting their importance to trunk diameters. These considerations

169   led us to explore the role of wind forces and gravity as key determinants of trunk diameters,

170   which is the focus of this article.

171

172   The importance of wind and gravity as a cause of trunk breakage is perhaps what common

173   sense would suggest to be the main factor explaining trunk dimensions. This approach was

174   pioneered in the 19th century (Metzger, 1893) and regularly discussed (Mäkelä, 2002).

175   However, we argue that it still remains underrepresented and that this is probably due to

176   methodological challenges from variable winds. In addition, the streamlining mentioned

177   above and the rarity of the strongest storms that are critical for tree survival and therefore

178   probably drive evolution cause extra challenges. Interesting studies are available on small

179   trees secured on the roof of a moving car (Butler et al., 2012) and medium-sized trees during

180   the leafless period (Niklas and Spatz, 2000), but small (Larjavaara, 2015) and leafless

181   (Mattheck, 2000) trees have different biomechanical constraints than large foliated trees.

182   Large foliated trees have also been examined in impressive studies representing simple

183   (Morgan and Cannell, 1994), more realistic (Spatz and Bruechert, 2000) or excellent detail in

184   tree dimensions (Jackson et al., 2019). However, none of these studies focused on maximally

185   bent trees.

186

187   The objective of this study was to increase our comprehension of determinants concerning

188   tree size and trunk taper, as modified by selective pressures caused by exposure to storm-

189   strength winds, and to examine whether trees are adapted and acclimatized to those. To this

190 end, we modelled wind in a canopy of a mature storm-bent stand and computed gravity- and

191 wind-caused forces on segments along the trunks based on destructive sampling of *Picea*

192 *abies* [L.] Karst. trees (Norway spruces). We then focused on the winds that break the trunks

193 at their weakest segment and expected diameters at other segments to be only slightly larger

194 than what was needed to resist the bending moments caused by this wind and gravity.

195

196

197 **Methods**

198

199 *Picea abies* is a common tree species in its natural range of Northern Europe and Central

200 European mountains and is also planted widely in Central European lowlands and North

201 America (Caudullo et al., 2016). In Finland, *Picea abies* trunk volumes make up 30% of all

202 tree trunk volumes and the volume of harvested trees is 38% of total (Peltola, 2014). It

203 regenerates in intermediate or fertile soils, is the most shade tolerant of the main tree species

204 in Finland and will therefore invade all but the most infertile sandy or peat soils when

205 sufficient time since disturbance has passed (Kuuluvainen and Aakala, 2011). *Picea abies*

206 trees have a straight trunk and long conical crown often reaching the ground. In Finland, the

207 lower branches shed from the lower crown layers in the deep shade of conspecifics. New

208 branches develop annually, forming whorls of branches. Its wood is of low density at 374 kg

209 m^{-3} (Kantola and Makela, 2006) especially when compared to angiosperms (Chave et al.,

210 2009).

211

212 We based our study on data collected in 2001 to investigate crown development in three sites

213 around southern Finland in stands after canopy closure (Kantola and Mäkelä, 2004).

214 However, to reduce the complexity of wind gust-related analysis, only a single plot featuring

215 flat terrain is included in this study. The other plots were excluded because of hilly terrain,

216 which alters low-altitude winds in a complex manner (Gardiner et al., 2016). The included

217 plot, described in more detail by Kantola and Mäkelä (2004), was located in Punkaharju at

218 61°49'N, 29°19'E, now part of Savonlinna in southeastern Finland. The local climate is

219 conducive to tree growth, as abundant lakes level out temperature fluctuations during the

220 growing season. The soils in the plot are well above average fertility for the region, classified

221 as *Oxalis*-type (Cajander, 1949), leading to a site index, H_{100} of 32 m. The monoculture of

222 *Picea abies* trees was planted 67 years prior to data collection.

223

224 Three stands with varying thinning histories were studied in the plot but two were excluded

225 from our study because of thinnings, as explained below. The included unthinned stand had a

226 basal area of 44 m^2 ha^{-1} and stand density of 805 ha^{-1}. Five sample trees representing various

227 canopy layers were felled, and their trunks, branches and leaves (i.e. needles) were measured

228 and weighed as described in detail by Kantola and Mäkelä (2004). In summary, trunk

229 diameters were measured below each whorl of branches, and all branches were cut and

230 measured and a subset of them taken to a laboratory for more detailed measurements. The

231 heights and diameters of the five trees at a 1.3-m height ($d_{1.3}$) can be seen in Fig. 8 in the

232 Results section. The percentage of the trunk with living branches of the five sample trees

233 differed between 42–63, being greatest for dominant trees and smallest for trees grown in

234 more suppressed positions. And further, the more suppressed, i.e. thin, trees also had the

235 lightest-weight crowns compared to more dominant ones, which was consistent with the pipe

236 model theory (Kantola and Mäkelä, 2004).

237

238 For this study, we divided the five tree trunks into "segments" and estimated their angle

239 relative to vertical and location relative to the base based on bending and length of all

240   segments below. From the angle relative to vertical we computed their projected area

241   perpendicular to wind direction (i.e. frontal area) and fresh mass based on volumes. We

242   assumed the centre of each segment to be in the whorl of branches and extremes to be located

243   half way between neighbouring whorls. We divided the unmeasured lower branchless trunk

244   into four segments, with the lowest centred at a height of 1.3 m, the remaining three at regular

245   intervals between 1.3 m and the lowest whorl and assumed diameter to simply change

246   linearly, as we anticipated this lowest part of the trunk to contribute only little to the bending

247   moments or to the bending of the trunk.

248

249   The streamlining of trees is complex, and therefore the common approach is to simulate

250   upright trees but with reduced wind drag estimated with a coefficient (Gardiner et al., 2016).

251   We instead focused on the strongest gust and "storm-bent" trees, i.e. trees bent along their

252   trunks as much as they can without breaking (see Fig. 6). This focus was based on the

253   reasoning that even though acclimation is likely to be mainly driven by signals from normal

254   wind speeds (Bonnesoeur et al., 2016), trunks are probably tuned to resist the strongest gusts

255   based on normal winds. Maximum strain in both compression and tension may be assumed to

256   equal the ratio of modulus of rupture and modulus of elasticity. In a bending segment or

257   cylinder, the maximum tension occurs in the outermost fibres of the convex side and

258   maximum compression on the opposite side. However, to simplify the calculations, we

259   assumed rigidity of the segments (as can be seen in Fig. 3) and bending was realised by

260   assuming a change (α) in the deviation of the axis of the segment relative to the segment

261   below:

262

$$\alpha = sin^{-1} \frac{2l\sigma}{dE} \tag{1}$$

263

264 where l is the length of the segment, σ the modulus of rupture obtained from tree-pulling

265 experiment is 36.26 Mpa (Peltola et al., 2000), d the diameter of the segment at its centre and

266 E the modulus of elasticity is 7730 Mpa (Peltola et al., 2000).

267

268 We used the projected area of trunks, branches and leaves (we call their sum "sail area") first

269 for estimating wind speeds and then to compute wind-caused horizontal forces (Online

270 Resource 1).

271

272 In addition to the five felled trees, we measured the $d_{1.3}$ of all trees less than seven metres

273 away from the felled ones. We estimated their sail area and its vertical storm-bent distribution

274 by fitting two simple linear regressions to the variables. We then first computed the storm-

275 bent height based on the model in Fig. 1 and then its sail area based on the model in Fig. 2, in

276 which a linear relationship was expected based on biomechanics, as the bending moment is

277 expected to scale roughly with the product of the sail area and the length of the lever (tree

278 height) and the strength of the trunk with the cube of its diameter (Ennos, 2012). We plotted

279 these models for all three stands, but observed the fit to be tight in the unthinned plot only.

280 We surmised that as the previous thinning occurred only 14 years prior to the measurement,

281 the trunk dimensions relative to the sail area (Online Resource 1) were possibly still

282 unbalanced because of too little time since the thinning. We therefore excluded these stands

283 from the analysis.

284

285 The mean $d_{1.3}$ of the five felled trees was 0.272 m and they ranged from 0.213 m to 0.328 m,

286 while the surrounding trees around these five had a mean of 0.260 m and a range from 0.167

287 m to 0.382 m. Because of the tight fit of models in Fig. 1 and Fig. 2, we do not think that

288 extrapolating to some distance out of the range was likely to cause a significant bias.

12

289

290   We wanted to focus on strongest wind gusts that the trees can stand and therefore used

291   turbulence resolving large-eddy simulation (LES) model to describe wind behaviour above

292   and within forest canopies. Because of significant horizontal movement of trees in gusts we

293   had to assume that the forest canopy had a horizontally homogenous sail area and therefore

294   sail area per unit volume (i.e. plant area density) for each 1.5-m thick layer. The large-eddy

295   simulation model PALM (Maronga et al., 2015) was employed to obtain a time-accurate and

296   spatially resolved description of fully developed boundary layer turbulence over continuous

297   forest canopy. The PALM model is specifically tailoured for atmospheric boundary layer

298   turbulence applications and has been optimized for massively parallel supercomputing

299   environments. The model implements the conservation equations governing atmospheric

300   boundary layer turbulence employing finite-difference discretization on a staggered Cartesian

301   grid. The system of equations is solved using a third-order accurate Runge-Kutta time-

302   stepping scheme and fifth-order accurate upwind biased spatial discretization scheme

303   (Wicker and Skamarock, 2002). The forest canopy is modelled assuming a porous

304   homogenous medium within each 1.5-m layer, whose porosity varies according to the

305   measured vertical sample-averaged plant area density distribution of the trees.

306

307   A vast majority of the drag caused by the forest canopy was assumed to be pressure drag, and

308   therefore the drag force (*f*) is implemented in PALM as:

309

$$\vec{f} = C_d P |\vec{u}| \vec{u}, \tag{2}$$

310

311   where C_d is the drag coefficient for forest canopy, P is the vertical plant area density profile

312   of the forest, and $\vec{u}$ is the spatially and temporally resolved wind velocity vector whose

313   magnitude is denoted as $|\vec{u}|$. We set C_d at 0.2 as suggested by Katul (1998). The wind

314   simulations were performed on a rectangular domain with Lx of 3.84 km, Ly of 1.28 km and

315   Lz of 0.52 km as streamwise, lateral and vertical dimensions, respectively. Wind was driven

316   with a prescribed pressure gradient at z > 250 m, allowing the lower-altitude flow to attain a

317   constant momentum flux layer, which is characteristic for atmospheric boundary layer flows

318   (Stull, 2012). The magnitude of the pressure gradient was set sufficiently high to achieve very

319   high Reynolds number conditions, which ensures that the associated turbulence solution

320   attains a state that is independent of wind speed. That is, if the wind speed were further

321   increased, the turbulent structures and dynamics would remain statistically identical. This

322   Reynolds number independence allows one representative turbulent wind solution to be

323   freely scaled (especially upward) to represent other wind conditions. The simulation for the

324   (scalable) reference wind was initially run for one hour to allow the flow to reach a

325   statistically stationary state. The simulation was then continued for an additional hour during

326   which detailed wind velocity time series is collected every 3 s (at 1/3 Hz) across the entire

327   depth of the forest canopy from a 0.5-km^2 monitoring plane with 409 x 205 locations. This

328   time series contains a sample of 105.6 x 10^6 instantaneous wind events impacting the forest

329   canopy. As the main interest is on gusts whose duration is sufficient to cause further

330   displacements in the tree trunks, two consecutive wind events are averaged to yield a

331   conservative approximation for a 3-s gust. Thus, the time series contained approximately 50 x

332   10^6 gust events, which is considered a sufficiently large sample size to capture rare gust

333   events that impose the largest risk for trunk failure. The gust events causing the maximal

334   bending moments were searched by considering the forest canopy to contain trees with

335   uniform horizontal cross-sections (just for the sake of wind gust analysis). The bending

336   moment for each model tree was computed for all 3-s gust events and the maximum events

337   (time and location) were stored. The wind speed profile spanning across the tree height was

338 then obtained from this location and instance. The selected gust event provided the most

339 realistic estimation for the critical velocity distribution during a probable failure event.

340

341 In addition to the normal simulation named "Dense", we performed a second simulation with

342 half of the sail area removed from all heights above ground (i.e. "Thinned") and a third

343 simulation with trunks and branches remaining but leaves removed (i.e. "Leafless").

344 However, it is important to note that these two secondary simulations violate the basis of our

345 modelling of trees evolved to withstand a given above-canopy wind speed by equal strain

346 along the trunk, as a sudden thinning or defoliation would disturb the balance to which trees

347 have acclimated and trunks would therefore likely break from a severely underbuilt segment

348 before full bending is reached.

349

350 We computed the bending moments by adding moments from all segments and associated

351 branches and leaves above the segment in question (Fig. 3). We obtained the weights, i.e. the

352 vertical forces, by adding water contents of 0.79 for the trunk, 1.41 for the branches and 2.24

353 for leaves (Kantola and Makela, 2006; Kärkkäinen, 1985) to the dry masses (Kantola and

354 Mäkelä, 2004) and multiplying by the gravity constant (9.82 m s^{-2}). We did not take physical

355 contact between the trees into account.

356

357 The critical bending moment, i.e. the maximum bending moment that a cylindrical segment

358 can resist (m_r) is:

359

$$m_r = \frac{\sigma \pi d^3}{32}$$
(3)

360

15

361 where σ is modulus of rupture and d is the diameter of the segment (Ennos, 2012). The sum of

362 gravity- and wind-caused bending moments that cause this same m_r for the trunk segment is:

363

$$m_r = r^2 \sum m_u + \sum m_g, \qquad (4)$$

364

365 where $\sum m_g$ is the sum of all gravity-caused bending moments of all the segments and

366 associated branches and leaves above, $\sum m_u$ is the sum of all wind-caused bending moments

367 from segments and associated branches and leaves above in a reference above-canopy mean

368 wind speed and r is the ratio of the maximum and reference (to compute $\sum m_u$) mean above-

369 canopy wind speeds based on the wind profile obtained from the PALM model. These steps

370 are shown as a flow chart in Fig. 4.

371

372 We then computed critical wind speeds that break the trunks in their weakest segments and

373 compared diameters of other segments to those needed to resist this wind. We did not "tune"

374 the approach or parameters to obtain a desirable fit. Below, we report the results from the

375 analysis planned before beginning analysing the data with the exception of exclusion of

376 recently thinned plots.

377

378

379 **Results**

380

381 Most of the sail area of the five felled trees is caused by leaves and is located, once the trees

382 are storm-bent, at a height of 15–21 m (Fig 5a). When the surrounding trees are added, the

383 layer of dense sail area thickens, mainly upward (Fig 5b), but is still surprisingly thin for a

384 tree species having an unusually long crown. The lack of thinnings in the studied stand has

385 probably resulted in unusually small crown ratios and thin trunks enabling considerable

386 bending, both of which thin the layer of dense sail area in a storm-bent stand.

387

388 The gust wind speeds are weak below 8 m, and increase roughly linearly upwards through the

389 main sail area in Dense and Thinned stands (Fig. 5c). However gust wind is significant down

390 to the ground in the Leafless stand (Fig. 5c).

391

392 The weight of the branchless lower parts of the trunks of all five felled trees is important, but

393 they cause bending moments only to the lower segments of the trunk. These moments are

394 small, as the segments are nearly vertically aligned (Fig. 6). The weights from the upper

395 segments and associated branches and leaves that produce potentially more significant

396 bending moments are roughly evenly divided by those caused by the trunk, branches and

397 leaves (Fig. 6). The comparison between trees illustrates how trees with larger $d_{1.3}$ (Tree4 and

398 Tree5) have correspondingly heavier crowns but the differences are small. The differences

399 between the five trees are much more significant when the horizontal vectors caused by wind

400 are examined (Fig. 6). The smallest trees experience much greater forces caused by gravity

401 than wind, whereas both forces are of the same magnitude in the crowns of the largest trees.

402 However, the wind-caused forces act higher up along the trunk and their direction also causes

403 greater strengthening requirements for the lower trunk. Because the top of storm-bent Tree1

404 is only at a height of 16.1 m, it is well protected by more rigid taller trees (Fig. 6).

405 Interestingly, because the shorter trees bend more, the horizontal displacement caused by

406 wind is approximately the same for all five trees, ranging from 12.7 m (Tree5) to 14.3

407 (Tree3).

408

409   Gravity from all segments and associated branches and leaves above the height at which the

410   focus is 18–27% of the bending moment that breaks a tree at a height of 1.3 m (Fig. 7). This

411   proportion increases upwards to a height of 12–15 m with the lowest branches and then

412   decreases down to a rounded 0% for the tops of the trees. However, as bark is included in the

413   used d and the wood characteristics are unusual for the topmost segments, the estimated

414   proportion is likely to be a severe underestimation. Nevertheless, the proportion of gravity

415   relative to the critical bending moment clearly decreases upwards in the canopy.

416

417   Fig. 8 demonstrates the dimensions of the five felled trees without wind and in addition to the

418   measured diameters, the diameters needed to resist an above-canopy mean wind of 10.2 m s^{-1},

419   which is the speed that is at the limit of breaking Tree4. This can be seen from the dotted red

420   line contacting the solid black line at a height of 13.9 m. Tree3 and Tree5 are able to resist

421   similar mean above-canopy wind speeds (12.7 m s^{-1} and 11.3 m s^{-1}), and therefore the

422   modelled taper is similar to the measured taper (Fig. 8). However, for Tree2 and especially

423   Tree1, a significantly thinner trunk would be sufficient to withstand the simulated gust with

424   an above-canopy mean wind of 10.2 m s^{-1}. The simulated gust increases wind speeds

425   considerably, reaching 34.2 m s^{-1} above-canopy (height of 29.25 m) and decreasing

426   downwards as shown in Fig. 5c, with a speed of 25.9 m s^{-1} in the upper part (height of 21.75

427   m) of the storm-bent main canopy and 5.6 m s^{-1} in the lower part (height of 12.75 m).

428

429   The above-canopy mean wind speed in the thinned stand is surprisingly similar to that above

430   the dense stand, and rounds to the same 10.2 m s^{-1} in the equivalent meteorological situation

431   and is slightly weaker in the strongest gust at 33.2 m s^{-1}. However, the winds are stronger

432   within the canopy, and for all except Tree1, greater diameters would have been needed to

433   resist breaking (Fig. 8), indicating that thinnings increase the risk of stem breakage.

434

435   The wind simulation for a leafless stand resulted in an above-canopy mean wind speed of

436   14.6 m s^{-1} (gust 36.3 m s^{-1}) in the same meteorological situation as discussed above and the

437   wind penetrated the stand with much more force (Fig. 5c). A significantly smaller diameter

438   for all trees and along all heights would be sufficient in this situation (Fig. 8), as sail areas of

439   the trees decreased.

440

441

442   **Discussion**

443

444   We developed a novel approach to model bending moments of storm-bent trees caused by

445   wind and gravity and applied this to an unthinned middle-aged *Picea* stand originated from

446   planted seedlings. We focused on winds that break the weakest segments and observed a

447   close match of modelled and the actual diameters along other segments their trunks for most

448   of the trees (Fig. 8). Therefore, we may conclude that these bending moments are probably

449   important in determining trunk diameter and shape, but we are unable to compare importance

450   of alternative determinants of tree size such as sap transport. The relatively small contribution

451   of a tree's own mass (Fig. 7) indicates that, if to simplify only gravity or wind can be

452   included in the modelling, wind would probably be a better choice, even in a dense unthinned

453   stand (e.g. Larjavaara, 2010) with small sail areas relative to fresh masses. The studied trees

454   where probably much closer to elastic buckling than plants in the dataset of Niklas (1994)

455   and may be close to bending due to the extra weight of snow.

456

457   Our simulated winds may be compared to those within (at a height of 9 m) and above (at a

458   height of 23 m) a 16-m tall *Pinus sylvestris* stand during a summer microburst that toppled

19

459   over trees approximately 300 m from the wind measurements (Järvi et al., 2007). The

460   microburst caused one-minute mean wind speeds of ca. 14 m s^{-1} above and 5 m s^{-1} within the

461   canopy. The above-canopy speed is close to the winds that our five trees can resist, with the

462   exception of Tree1 (Fig. 8). Furthermore, the wind speed within the relatively sparse *Pinus*

463   canopy corresponds to values that may have been expected based on our wind profiles (Fig.

464   5c). However, the variation in windspeed measured by Järvi et al. (2007) was much lower, as

465   their "instantaneous" above-canopy wind speeds peaked at only just above 20 m s^{-1}. This may

466   indicate that our biomechanical computations overestimated the resistance of trees to bending

467   forces. However, as the damaged *Pinus* trees were located some distance away from the

468   anemometers, it is likely they experienced much stronger wind speeds than recorded at the

469   specific location of the sensors.

470

471   Our objectives were to understand more about trunk taper based on wind and the risks that

472   trees potentially take, whereas the majority of research linking taper, wind and risks inversely

473   attempt to estimate risks from taper and winds (Gardiner et al., 2008). The demand for advice

474   from forest managers is substantial both in plantations (Gardiner et al., 2016) and urban

475   setting (Sæbø et al., 2003), and advances have been impressive (Gardiner et al., 2019).

476   However, a pessimist may argue that scientists will never be "wiser" than an acclimated tree

477   in understanding the local wind profile and risks caused by extreme gusts. From an

478   evolutionary perspective, trees balance between having their trunks breaking in a storm and

479   overinvesting in trunk tissue and being overtopped by their neighbours growing faster. A

480   winning strategy optimally balancing between the deadly "ditches" on both sides depends on

481   the position of the other ditch. Hence, in a situation with fierce competition and high

482   likelihood of being overtopped by neighbours, such as in middle-aged dense plantations, the

483   risk on trunk breakage in a storm is increased. Therefore, the most fruitful theoretical (not

484   just statistical and descriptive) way to estimate the risk of trunk breakage may be based on

485   competition for height from an evolutionary perspective. Physical modelling, such as that

486   used in this article but inversely, is more promising for trees in situations have not acclimated

487   to, e.g. after their neighbours have been harvested (e.g. Peltola et al., 1999).

488

489   In our simulation of the strongest gust, it is remarkable how a *Picea abies* monoculture,

490   characterised by long, conical, and slender crowns, forms a relatively thin layer of dense sail

491   area of sail area at approximately 18 m above ground during a gust. To support a larger leaf

492   mass, a tree needs to build a thicker trunk to resist the wind drag and gravity acting on this

493   additional mass. Even without additional height when unbent, the additional diameter reduces

494   bending and the storm-bent height increases. Because trees with thicker trunks are normally

495   also taller, they have greater wind drag caused by bending moments because of greater sail

496   area and this area being located in greater winds because of greater unbent height but also

497   reduced bending. The thicker trees in a stand are responsible for blocking wind and

498   protecting the smaller "biomechanical free-riders". This mechanism operates as a balancing

499   force, i.e. negative feedback, in stand development, thanks to which height growth of shorter

500   trees is boosted.

501

502   Tree1 is much thicker and Tree2 is to some extent thicker than they need to be to resist the

503   modelled gust. Their positions in the canopy may have weakened rapidly, leaving their

504   thicker trunks as a legacy of a time when they needed strength for a larger leaf area, but

505   biomechanically they would not then need new diameter growth. Also the transport-focused

506   perspective offers an alternative explanation. When trees become suppressed in the canopy,

507   they rapidly lose their lower branches and their crown length grows more slowly than their

508   height, reducing their crown ratio. This change in growth pattern may be regarded as an

509 evolutionary response to competition for light (e.g. Mäkelä, 1985). In this process, active

510 wood, i.e. sapwood, related to the receding branches loses its connection to the foliage and

511 gradually turns into inactive heartwood. Empirical evidence and eco-evolutionary balance

512 theories suggest that active wood area and foliage area are in balance with each other (Chiba

513 et al., 1988; Mäkelä and Valentine, 2006; Shinozaki et al., 1964). Losing the active wood

514 related to the receding branches therefore creates a need for new diameter growth to build

515 new sapwood, as the existing inactive wood can no longer be used for water transport. If we

516 assume that all these selective pressures, related to biomechanics, water transport, and

517 competition for light, are present in the tree population, then our results suggest that

518 biomechanics dominate trunk dimensions of dominant trees (see also Mäkelä and Valentine,

519 2006), while with suppressed trees the balance has possibly shifted from biomechanics

520 towards sap transport. Another reason for our result that smaller trees have larger diameters

521 than apparently necessary may be that our wind model severely overestimates the steepness

522 of the vertical wind profile. It is also possible that supressed trees occasionally experience

523 unusually strong gusts that penetrate the canopy but which was not our "strongest gust" due

524 to our sampling, and are therefore seemingly overbuilt. If suppressed trees are

525 biomechanically overbuilt because of sap transport, they would be expected to survive storms

526 more likely than dominants, but if they are not biomechanically overbuilt, due to problems in

527 our wind modelling, they are likely on the contrary be more vulnerable due to greater risk-

528 taking. However, survival of suppressed trees could also be due to their strategy to benefit

529 from the failure of their supressors.

530

531 The tops of all five trees appear overbuilt. We can try to understand this by comparing small

532 trees of the same height that may initially seem to have nearly identical biomechanical

533 constraints. Coincidentally, both small *Picea* trees and residue treetops have commonly been

22

534 used as Christmas trees in Finland and are easy to differentiate even from a distance. Treetops

535 need to resist much stronger winds but can streamline easier, as their bases are tilted thanks to

536 the bending lower trunk. Probably most importantly, treetops cannot rely on the "shrub

537 strategy" of bending all the way to the ground to remain unharmed (Larjavaara, 2015). This

538 makes small trees resistant to the strongest winds and heaviest snowloads, as they can bounce

539 back after a gust has passed or the snow has melted. Treetops however, cannot rely on ground

540 support during gusts, but this is probably not a problem for the well-streamlined tops of *Picea*

541 *abies* (Fig. 6). Snow weight, which may be significant in the region, is a possible reason for

542 the seemingly overbuilt tops in our dataset (Peltola et al., 1999), especially when

543 temperatures are close to freezing or when direct condensation occurs on trees.

544

545 We focused on an unthinned boreal monoculture, i.e. nearly the simplest stand imaginable –

546 only treetops could potentially have been easier to understand in an ice-free climate. We

547 nevertheless had to make many simplifying assumptions. The risk of resonating with the

548 wind is a serious concern in designing structures, such as bridges, and the risk of trees

549 swaying with a pulsing wind has often been the focus of trunk breakage literature (Niklas and

550 Spatz, 2012). However, air flow modelling does not seem to create such winds (Gardiner et

551 al., 2019) and is rarely seen in dozens of videos found on the Internet that depict uprooting or

552 trunk breakage (ML personal observation). Similarly, torsional forces have attracted some

553 attention (Skatter and Kucera, 2000), but it is likely that strengthening the trunks to resist

554 twisting could be achieved by adjusting wood characteristics without increasing trunk

555 diameters. Uprooting possibly being more common than trunk breakage is one argument

556 against the biomechanical modelling of trunks, but this does not rule out the importance of

557 trunk dimensions on trunk failure. In their evolutionary history, trees have probably balanced

558 the risks of uprooting and trunk breakage depending on the level and variability of risks and

23

559   on the cost of strengthening them. Our assumptions that the same level of streamlining occurs

560   at all heights (Online Resource 1) and invariable, modulus of rupture (σ) and modulus of

561   elasticity (E), may be far from realistic but probably do not interfere significantly with our

562   comparison between trees and along the trunk of one tree, except perhaps in the tops which

563   may in reality be more flexible due to juvenile wood and therefore e.g. the relative

564   importance of gravity would be underestimated (Fig. 7). Choosing the value for drag

565   coefficient (C_d) was rather arbitrary as always. Furthermore, we did not attempt to include

566   physical contact with neighbours influencing the bending forces. Such canopy contacts may

567   be harmful, as tree tissue may be damaged, but on the other hand they may save a tree that is

568   supported by a neighbour in extreme winds.

569

570   Our greatest concern relates to dealing with streamlining and the homogeneousness of the sail

571   area. We assumed 50% streamlining for branches and none for leaves (Online Resource 1).

572   This is probably an underestimation (Peltola et al., 1999), but perhaps surprisingly it does not

573   strongly influence this kind of analysis related to trunk diameters, as despite streamlining

574   reducing wind drag caused by a given wind speed, it increases wind speeds within the stand.

575   For example, the Thinned simulation with half of the sail area removed corresponds to the

576   Dense simulation with streamlining reducing the projected area to half its original size. This

577   allows us to estimate the sensitivity of our results to assumptions on streamlining.

578   Interestingly, the wind-caused bending moments were larger for two of our five trees, with

579   50 % stronger streamlining, while they were smaller for three trees. This indicates that our

580   results are not very sensitive to streamlining, as the increasing wind speed due to streamlining

581   compensates for the reduced sail area. Similarly, the spatial grouping of sail area is probably

582   important and drastically influences both winds and the drags that they cause. However,

583   again it is possible that reduced winds for a given wind speed cause greater within-canopy

584 winds thanks to the clustering of sail area, and their impacts may roughly even out as with the

585 cause of streamlining.

586

587 Our approach could be utilized in several applications. Evolutionary simulations could

588 optimize trunk dimensions by considering the benefits of being a biomechanical free-rider

589 and relying on larger neighbour trees to withstand wind, but potentially face local extinction

590 if all canopy species or individuals take excessive risks and rely on trunks of others not

591 breaking. Other mechanistic modelling approaches (Kalliokoski et al., 2016), which are

592 potentially especially valuable when optimizing forest management in changed conditions,

593 may also benefit from incorporation of wind- and gravity-driven trunk diameter modelling,

594 e.g. by increasing detail in the direction pointed by Eloy et al. (2017).

595

596 **Availability of data and materials**

597 The dataset will be made available in a location specified later.

598

599 **Conflict of interest**

600 The authors declare that they have no conflict of interest

601

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604

605 **Author's contributions**

606 ML and AM developed the research idea, AK designed and implemented the data collection

607 procedure supervised by AM, MA performed the wind simulations and wrote the first draft of

608 its description, ML performed the other analyses, prepared the figures and wrote the first

609 draft of the other sections, and all authors participated in producing the final version of the

610 manuscript.

611

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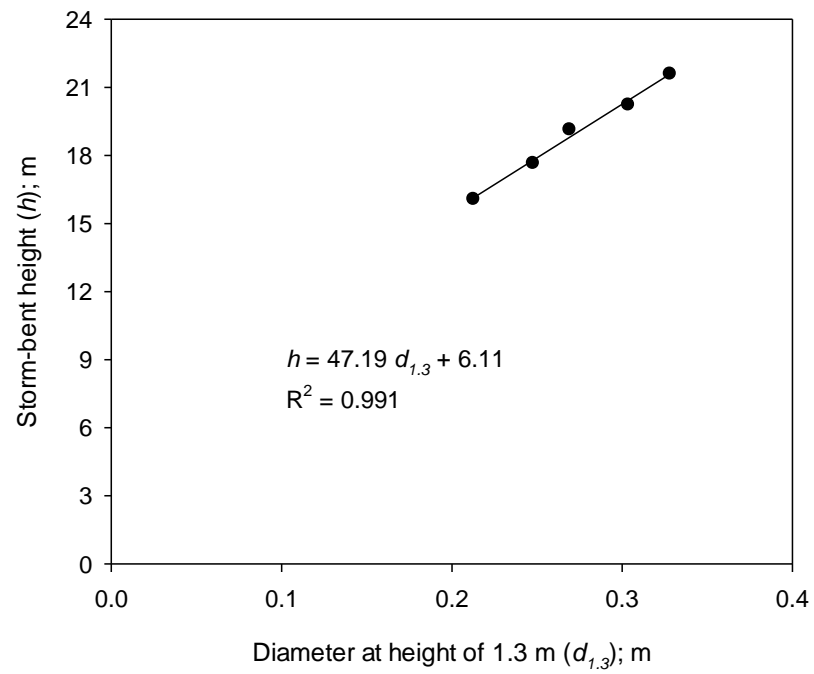758

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Figure captions

Figure 1. Storm-bent height of the five felled trees plotted against $d_{1.3}$ and a fitted linear regression model. R^2 is the coefficient of determination.
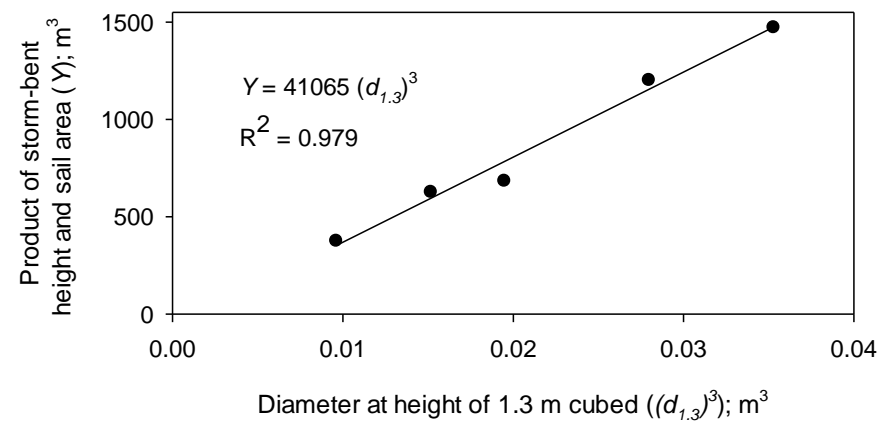

Figure 2. Storm-bent height of the five felled trees multiplied by their sail area (projected area of trunk, branches and leaves) plotted against the cube of $d_{1.3}$ and a fitter linear regression model. R^2 is the coefficient of determination.

Figure 3. An example of how we computed the bending moments from the forces caused by gravity and wind blowing from left to right. The "dashed" line represents storm-bent Tree3 with 18 uneven segments visible out of its 35 segments. The vectors show how we computed the moment caused by the 11th topmost segment to the 3rd lowest segment (both of which are highlighted with a thicker red line).

Figure 4. Calculation of bending moments on segments.

Figure 5. Sail area and winds in a gust at various heights in the canopy and just above.

Figure 6. The five felled trees shown as storm-bent. The number of the poorly visible topmost segments that have bent to horizontal ranges from 4 (Tree5) to 11 (Tree2). The green, red and blue horizontal lines represent force vectors caused by wind in the dense simulation on each segment, with the colour indicating whether the drag is caused by the trunk, branches or leaves. The vertical lines represent forces caused by gravity. The length of

784   vertical vectors from the lowest segments is not shown. The bottom end of a vector is -5.7

785   from the lowest segment of Tree5 with the same scale below the 0-level of the Y-axis as

786   above.

787

788   Figure 7. The relative importance of the bending moment caused by gravity acting on

789   segments and associated branches and leaves above the segment in question.

790

791   Figure 8. The dimensions of five felled tree trunks (solid black) and dimensions sufficient to

792   withstand wind and gravity (dotted and dashed lines) in a meteorological situation that

793   causes a mean wind above the canopy of the dense stand (w) of 10.2 m s^{-1}, which is the

794   critical speed that nearly breaks Tree4. The heights on vertical axis and diameters on the

795   horizontal axis are not proportional. Diameters at a height of 1.3 m are given in the bottom.

796   The critical above-canopy wind speed for the dense stand is indicated inside the trunks. The

797   lowest living branches were at heights of 11.2–14.5 m.

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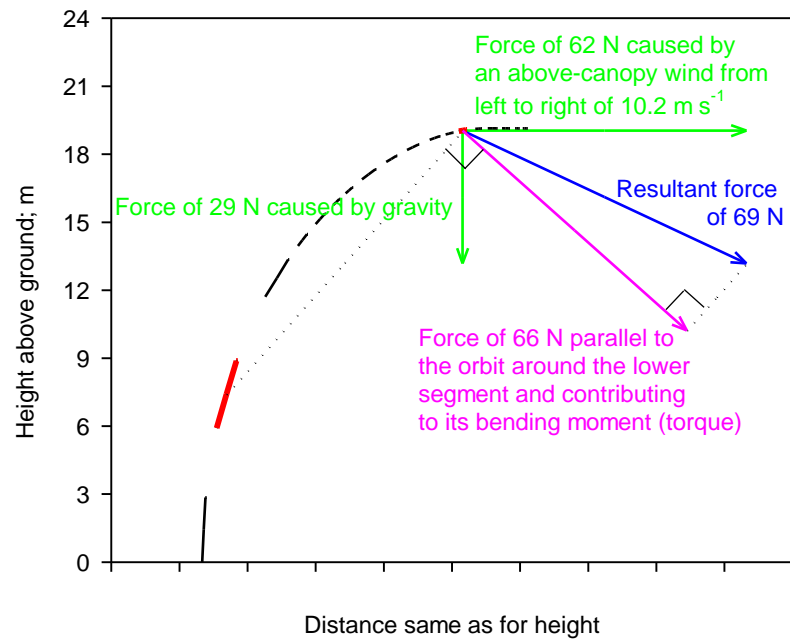
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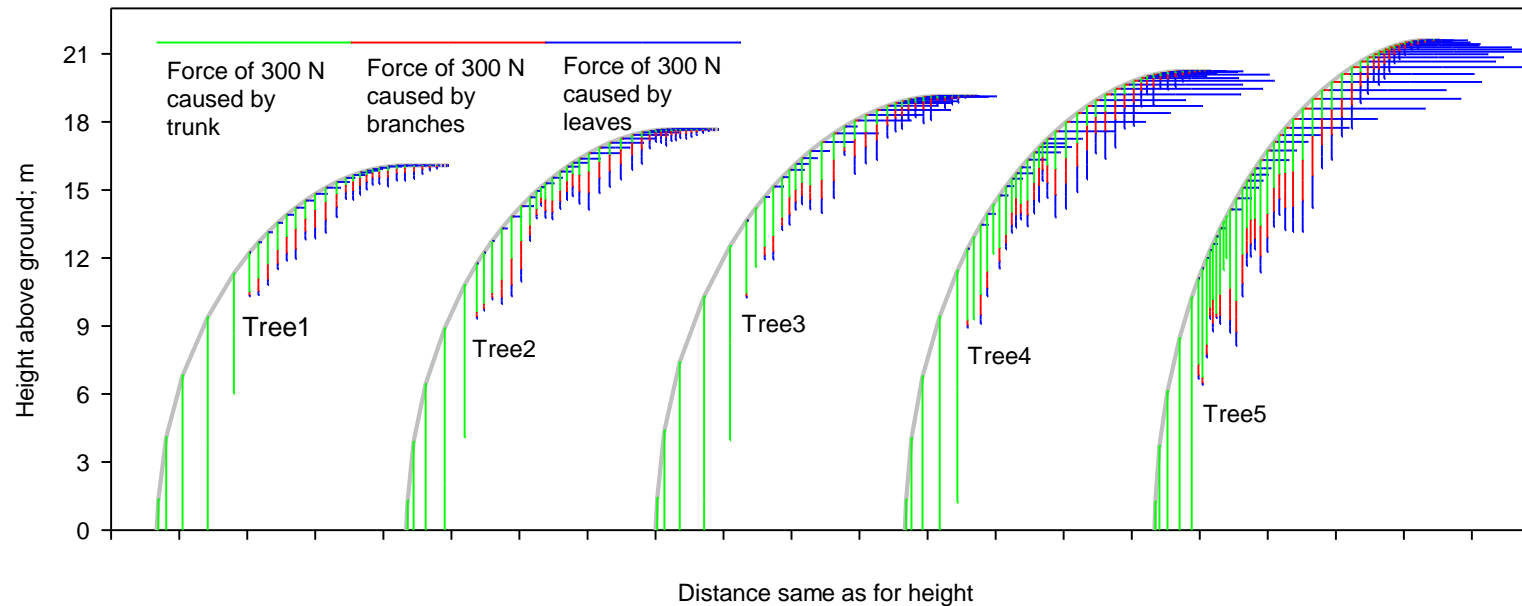
Figure 6. The five felled trees shown as storm-bent. The number of the poorly visible topmost segments that have bent to horizontal ranges from 4 (Tree5) to 11 (Tree2). The green, red and blue horizontal lines represent force vectors caused by wind in the dense simulation on each segment, with the colour indicating whether the drag is caused by the trunk, branches or leaves. The vertical lines represent forces caused by gravity. The length of vertical vectors from the lowest segments is not shown. The bottom end of a vector is -5.7 from the lowest segment of Tree5 with the same scale below the 0-level of the Y-axis as above.
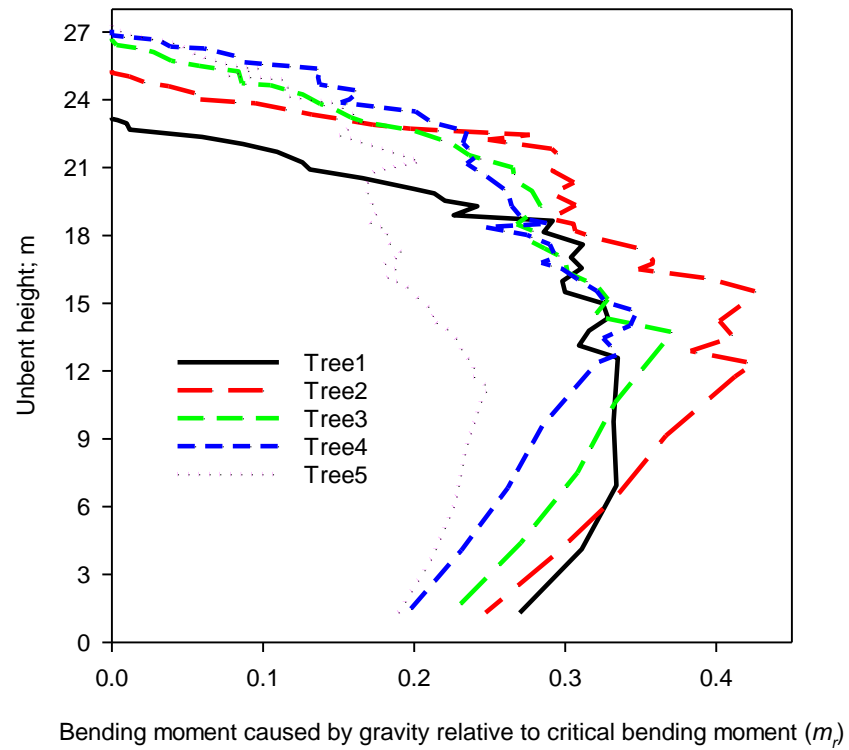
Figure 7. The relative importance of the bending moment caused by gravity acting on segments above the segment in question.
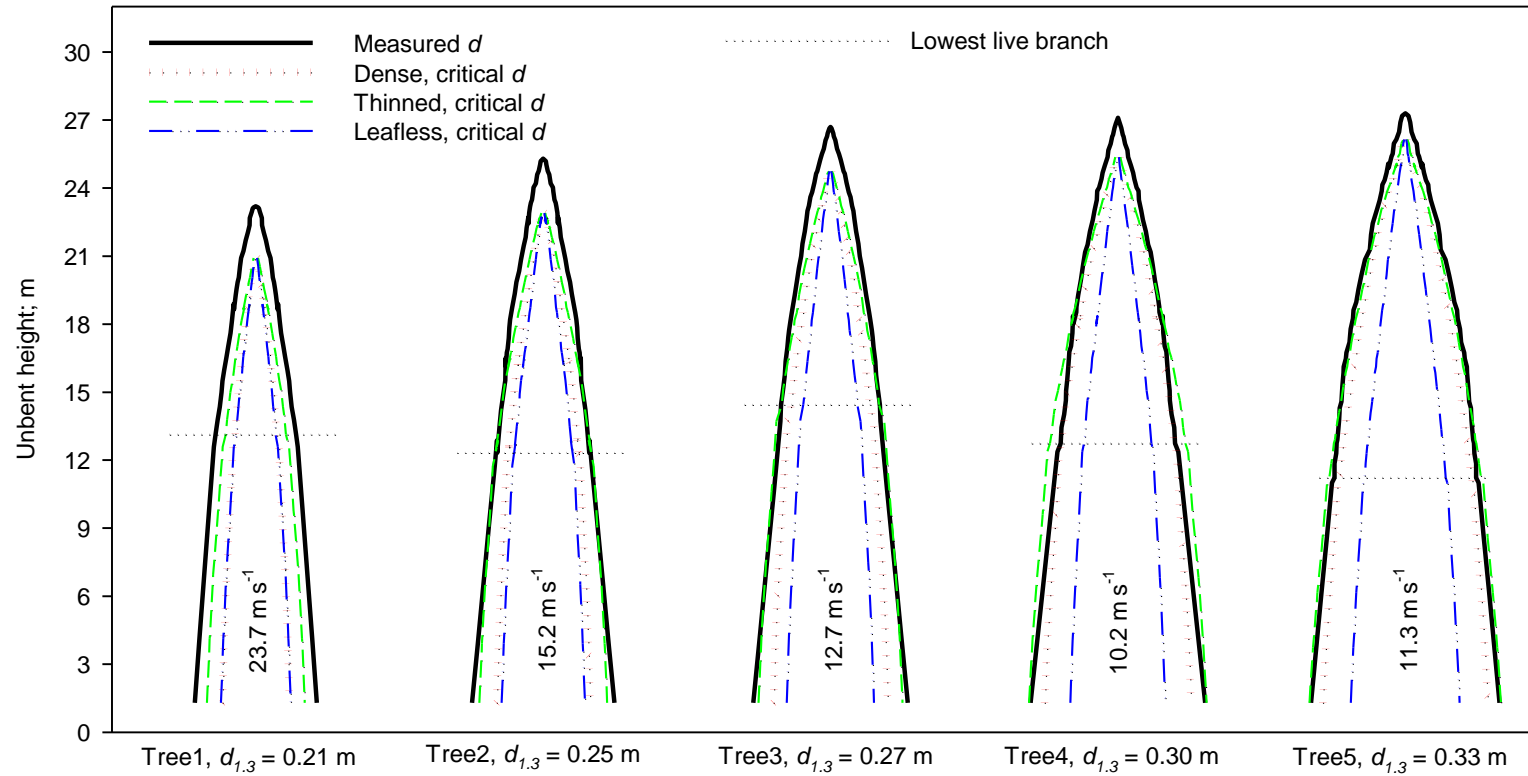
Figure 8. The dimensions of five felled tree trunks (solid black) and dimensions sufficient to withstand wind and gravity (dotted and dashed lines) in a meteorological situation that causes a mean wind above the canopy of the dense stand (w) of 10.2 m s^{-1}, which is the critical speed that nearly breaks Tree4. The heights on vertical axis and diameters on the horizontal axis are not proportional. Diameters at a height of 1.3 m

are given in the bottom. The critical above-canopy wind speed for the dense stand is indicated inside the trunks. The lowest living branches were at heights of 11.2–14.5 m.