



Light-growth responses of Sitka spruce, Douglas fir and western hemlock regeneration under continuous cover forestry

Bianchi, Simone; Hale, S.; Cahalan, Christine; Arcangeli, Catia; Gibbons, James

Forest Ecology and Management

Published: 15/08/2018

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):

Bianchi, S., Hale, S., Cahalan, C., Arcangeli, C., & Gibbons, J. (2018). Light-growth responses of Sitka spruce, Douglas fir and western hemlock regeneration under continuous cover forestry. *Forest Ecology and Management*, 422, 241-252.

Hawliau Cyffredinol / General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Light-growth responses of Sitka spruce, Douglas fir and western hemlock regeneration under continuous cover forestry

Authors

Simone Bianchi^{1,4}, Sophie Hale², Christine Cahalan¹, Catia Arcangeli³, James Gibbons¹

¹ School of Environment, Natural Resources and Geography, Bangor University, Bangor, Gwynedd, UK

² Northern Research Station, Forest Research, Roslin, Midlothian, UK

³ Alice Holt Lodge, Forest Research, Farnham, Surrey, UK

⁴ Correspondence: simonebianchi79@gmail.com

Abstract

Natural regeneration is crucial for silvicultural approaches based on the continuous presence of a forest cover, or Continuous Cover Forestry (CCF). Light is considered one of the most important factors affecting regeneration growth under canopy cover. Sitka spruce, western hemlock and Douglas fir are important forestry species both in Europe and in North America with potential to be used together under CCF management. Our aim was to develop predictive early-growth models for these species growing beneath forest canopies, and to investigate species differences in terms of shade tolerance.

We sampled regenerating trees growing under canopy cover at multiple sites in the UK. We compared alternative asymptotic non-linear models as a function of light availability to

22 simulate the height growth for all species and the diameter growth for Sitka spruce and western
23 hemlock only. We included tree size and intra-regeneration competition as predictors, which
24 affected the asymptotic growth at full light and/or the growth rate at which such asymptote was
25 reached. We also calibrated models of apical dominance ratio (ADR, for all species) and live
26 crown ratio (LCR, for Douglas fir and Sitka spruce only) as a function of light availability, tree
27 size and intra-regeneration competition.

28 Species-specific non-linear models best simulated the light-growth responses (3-points
29 Logistic for Sitka spruce, Michaelis-Menten for western hemlock, asymptotic with offset for
30 Douglas fir). Tree size in all cases increased the asymptotic growth and in two cases also the
31 growth rate. Competition significantly reduced the growth for Sitka spruce and western
32 hemlock, with the diameter growth reduced more than height growth. Both the ADR and the
33 LCR increased with light availability, with species-specific differences for LCR but not for
34 ADR. For Sitka spruce an apical dominance ratio of 1.5 can be used in the field to identify
35 adequate growing conditions. An increasing shade tolerance ranking was found as Douglas fir
36 \leq Sitka spruce $<$ western hemlock.

37 We conclude that modelling light-growth requires species-specific non-linear functions and
38 that predictions are improved by including size and competition. The developed predictive
39 models for height and diameter growth will allow accurate modelling of the study species in
40 CCF management.

41 **1.1 Introduction**

42 Continuous cover forestry (CCF) is a range of silvicultural approaches involving uninterrupted
43 maintenance of forest cover and avoidance of clearcutting (Pommerening and Murphy, 2004),
44 is becoming increasingly important worldwide (Schütz et al., 2011). Mason et al. (1999)
45 indicated the following principles for CCF: management of the forest ecosystem rather than

46 just the trees; use of natural processes as the basis for stand management; adaptation to site
47 limitations; and creation of a diverse stand structure with a range of species. Amongst the
48 consequences of those principles, there is an increasing focus on the use of natural regeneration
49 to develop uneven-aged and mixed-species stands (Pommerening and Murphy, 2004).

50 Light is considered one of the main factors affecting tree regeneration under forest cover
51 (Lieffers et al., 1999; Oliver and Larson, 1996). Measurements of the light regime under
52 canopy have been widely used as main inputs for regeneration growth models, especially in
53 uneven-aged and mixed-species stands (Duchesneau et al., 2001; Finzi and Canham, 2000;
54 Grassi and Giannini, 2005; Ligot et al., 2013; Pacala et al., 1996; Wright et al., 1998). Canopy
55 characteristics, and in turn light analysis based on those characteristics, are better predictors
56 for regeneration growth models than traditional stand parameters, such as stem density or tree
57 volumes, especially in uneven stands (Chrimes and Nilson, 2005; Peng, 2000).

58 We focus here on three important forestry species in Europe and North America with potential
59 to be used together in CCF systems. Sitka spruce (*Picea sitchensis* (Bong.) Carr.) is an
60 important forest species in its original range, the Pacific North-West of America, and it is the
61 most common introduced non-native tree species in Atlantic Europe, covering about 1.3
62 million hectares (Mason et al., 2011; Nygaard and Øyen, 2017). In the United Kingdom (UK)
63 it is the main commercial tree species, comprising alone about a quarter of the total forest cover
64 (Forestry Commission, 2017). Sitka spruce reproduces abundantly across all the UK (Nixon
65 and Worrell, 1999) and its potential for CCF management has already been positively tested in
66 many experiments (Mason, 2015). Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and
67 Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), both associates of Sitka spruce in its
68 natural range, are other successfully introduced coniferous species in the UK that could be
69 adequate companions of Sitka spruce in mixed-species, uneven-aged forests (Cameron, 2015).
70 Mixed regeneration of these species is already found occurring naturally in the UK. However,

71 there are no general predictive models of the early growth of these species growing under the
72 range of light regimes encountered in CCF systems.

73 Interspecific differences in shade tolerance significantly affect stand dynamics (Finzi and
74 Canham, 2000). For Sitka spruce, Mason (2015) indicated that in the United Kingdom
75 regeneration under canopy cover requires at least 20-25% of full light for a growth about half
76 that under full sunlight. Carter & Klinka (1992) in British Columbia (Canada) found that for
77 Douglas fir that happened at 20-40% of full light, and for western hemlock at 10-20% of full
78 light. Generally, western hemlock was considered the most shade-tolerant of the three species
79 by all authors, while Sitka spruce was found to be either more than, less than or equally shade-
80 tolerant to Douglas fir (Malcolm et al., 2001; Mason et al., 2004; Minore, 1979). Shade
81 tolerance, the ability to grow and survive under low levels of light, is an elusive property;
82 ecologists have not yet agreed on a standardized method for its quantification (Lusk and
83 Jorgensen, 2013), and many characteristics have been used to define a shade tolerance ranking
84 amongst species. Shade-tolerant species usually show relatively faster growth at low light and
85 a slower growth at high light than less shade-tolerant species, although this trade-off is not
86 necessarily clear-cut (e.g. Pacala et al. 1996). Usually, shade-tolerant species show a
87 complementary trade-off between higher capacity for surviving at low light with lesser growth
88 at high light (Kobe and Coates, 1997). Other authors define as more shade-tolerant the species
89 that reach the whole-plant compensation point at lower light levels (Lusk and Jorgensen, 2013).
90 Crown plasticity is another characteristic usually associated with shade tolerance. Shade-
91 tolerant trees growing under low light levels can modify their crown architecture to a more
92 efficient shape for light absorption, by expanding it more horizontally than vertically, and by
93 limiting the number of living lower branches, which are generally more shaded (Claveau et al.,
94 2002; Lieffers et al., 1999; Williams et al., 1999). In shade-tolerant trees this would result in a
95 reduction in the apical dominance ratio (ADR), the ratio between the length of the leader and

96 of the lateral shoots of the same year, and also a reduction in the live crown ratio (LCR), the
97 ratio between the height of the live crown and the tree height. In other words, shade-tolerant
98 trees tend to form an “umbrella-shaped” crown under low levels of light (e.g. O’Connell &
99 Kelty 1994), which allow them to survive long periods of shading from the overstorey. ADR
100 can be also used in the field as a quick tool for identifying whether a tree is growing under
101 sufficient light conditions (e.g. Page et al., 2001).

102 There is a growing consensus that theoretically-justified non-linear models are best suited to
103 describe plant growth (Paine et al., 2012). Such models are based on specific hypotheses
104 regarding the phenomenon to be described and use parameters that have a clear biological
105 meaning (Fekedulegn et al., 1999). In the case of the light-growth response of regenerating
106 trees, asymptotic non-linear functions have been commonly used, such as the Michaelis-
107 Menten and the Logistic (Ligot et al., 2013; Pacala et al., 1996; Paine et al., 2012): with
108 increasing values of input (light), the response (growth) increases but eventually saturates and
109 reaches a maximum value at a certain level of input. The two functions differ in the way the
110 growth rate reaches the asymptote. The Michaelis-Menten always has a concave-down shape
111 that passes through the origin (growth is zero at no light). The Logistic, in its “three-points”
112 form, has a sigmoid shape that confers better flexibility, but while it has a lower asymptote set
113 to zero, it is not constrained to pass through the origin (growth can be positive at zero light).
114 Ecological theory suggests that trees under low light levels could reach a “compensation point”
115 at which the photosynthesis equals the respiration costs, thus showing no growth at positive
116 light levels (Givnish, 1988). The asymptotic function with an offset (Pinheiro et al., 2016),
117 from here on called Asymptotic-with-offset, can resolve this issue: it is an always concave-
118 down function (in this regard similar to the Michaelis-Menten) but is not constrained to pass
119 through the origin. The growth can be equal to zero at a positive value of light, and the intersect

120 of the curve with the x-axis would be the compensation point as defined above. See Figure 1
121 for examples of the three different equations.

122 Most previous non-linear light-growth studies have assumed the same response curve for trees
123 of different size by using the relative growth rate, that is by scaling the absolute growth by the
124 tree size (e.g. (Pacala et al., 1996). However, relative growth rate usually decreases with
125 increasing tree size due to biological and geometrical issues (Paine et al., 2012). Photosynthetic
126 efficiency is also expected to change with tree height: taller trees can have an advantage in
127 better exploiting light resources, but that ability comes with higher respiration maintenance
128 costs (Givnish, 1988; King, 1990). Claveau et al. (2002) reported that the way in which tree
129 size affects light-growth responses has not been widely studied, and they suggested
130 incorporating it as a predictor in future studies.

131 The presence of intra-regeneration competition could be another factor significantly affecting
132 the light-growth response. Intra-regeneration competition was found to significantly affect
133 growth either only at higher light levels (Duchesneau et al., 2001); only the radial but not the
134 height growth (Collet and Chenost, 2006; van Couwenberghe et al., 2013); only if the trees
135 were overtopped (Hasenauer and Kindermann, 2002; Ligot et al., 2013); or not at all (Grassi
136 and Giannini, 2005; Monserud and Ek, 1977). As far as we are aware only Ligot et al. (2013)
137 used specific non-linear models where tree size and intra-regeneration competition were
138 included as additional variables modifying the asymptote of the functions, albeit not the growth
139 rate to reach it.

140 The general aims of this study were to expand the knowledge of the light-growth response of
141 Sitka spruce, western hemlock and Douglas fir in the understorey and to inform modelling for
142 forestry operators interested in CCF. To do so, we investigated regenerating trees growing
143 under canopy cover to evaluate:

- 144 1) The species-specific light-growth responses (in both height and diameter), under the
145 range of light regimes encountered in CCF systems, comparing different non-linear
146 models that include also tree size and intra-regeneration competition;
- 147 2) The species-specific crown plasticity (in terms of apical dominance ratio and live crown
148 ratio) under different light levels, how this process is affected by tree size and intra-
149 regeneration competition, and whether the apical dominance ratio can be an indicator
150 of the growth condition of the tree;
- 151 3) If the resulting light-growth and crown plasticity responses can be used to identify a
152 shade tolerance ranking.

153 **1.2 Methodology**

154 1.2.1 Data collection

155 The study areas included a wide range of forests across the UK, divided into various stands
156 dominated by different overstorey species (see Table 1 for more details). For each stand, we
157 laid out ten plots with a random-systematic approach. We drew random non-parallel transects
158 on a desktop map and placed on them evenly-spaced plots, later located in the field using a
159 GPS receiver. The distance between plots varied with the size of the stand. For each plot, we
160 selected the closest Sitka spruce (SS), western hemlock (WH) and/or Douglas fir (DF) naturally
161 regenerating tree, excluding trees with evident sign of browsing or other kinds of damage.
162 Trees were classified into broad height classes, and for subsequent plots we chose trees
163 belonging to a different class to ensure a balanced sample range. Recent silvicultural
164 management in each stand varied from no intervention to thinning of different intensity and
165 type, but purposely we selected no stand thinned in the last two years. We also relocated plots
166 that fell in areas with recent windblow events if possible; otherwise, we discarded them. While
167 all SS and WH seedlings were natural regeneration, one-third of the DF seedlings measured

168 were artificially under-planted (all those in Clocaenog and some of those in Wykeham). Data
169 collection was carried out from February to November 2016.

170 On each tree, we measured the height growth (Hg) as the length of the last complete leader
171 shoot, and the tree height previous to that growth (Hp) as the total height minus the height
172 growth. We calculated the apical dominance ratio for SS and DF (not for WH due to its different
173 canopy architecture) as the ratio between the corresponding leader and lateral shoots for both
174 the last complete vegetative season and the previous one (called respectively ADR and ADRp).
175 Note that we measured the largest and shortest one lateral shoot per tree and reached an
176 average. We calculated the live crown ratio (LCR) as the ratio between the length of the stem
177 from the top to the lowest live green branch and the total height. In all cases we discarded from
178 the measurements any incomplete shoots found if the survey was carried out during
179 spring/summer. The tree measurement schematics are displayed in the Supplementary
180 Information. For SS and WH trees, we collected a stem sample at 10 cm above the root collar,
181 unless the tree presented an evident swelling, a common occurrence for large regenerating
182 trees, in which case no sample was collected. For DF, we could not collect any stem samples
183 due to particular forest management prescriptions. For each stem sample, we measured with an
184 optical microscope the diameter growth (DRCg) as twice the width of the last tree ring, and the
185 diameter previous to that growth (DRCp), as the total diameter under bark minus the diameter
186 growth. We took all the measurements in two directions (the shortest and longest diameter for
187 each sample) and averaged the values. As above, we discarded from the measurements any
188 incomplete rings if the survey was carried out in spring/summer.

189 We assessed the intra-regeneration competition by counting the number of regenerating trees
190 of all species around the subject tree. If the subject tree was under 130 cm height, to count the
191 competition we used a circle of 80 cm radius from its stem (around 2 m²), if 130-250 cm height,
192 a circle of 120 cm radius (around 4.5 m²), and if above 250 cm height a circle of 160 cm (around

193 8 m²). We then added one and log-transformed the number, to create the variable *comp*,
194 indication of the competition at plot level, not transformed per area unit. While circular 2 m²
195 plots have been previously used for trees 20-180 cm tall (van Couwenberghe et al., 2013), we
196 decided to compensate for the increasing crown radius of bigger trees by using larger circles
197 based on empirical observations on the ground (i.e. a circle of radius 80 cm centred on a stem
198 of a 5 m tall tree in most cases did not extend beyond its crown).

199 1.2.1.1 Hemispherical photography

200 At the top of each tree, we took hemispherical photography (HP) images using a Nikon Coolpix
201 (4500 or 990 model), equipped with Nikon FC-E8 183° FOV Fish-Eye Converter Lens. We
202 carried out the circular HP image acquisition on windless days, under overcast sky conditions
203 or after sunset (Fournier et al., 1996). In stands with the presence of broadleaved trees, we
204 acquired the images during summer to have the full foliar development of the overstorey. We
205 positioned the camera on a telescopic pole, oriented to the North using a compass and upwards
206 to the zenith using a level. We took a picture using the automatic exposure and then more in
207 quick succession with reduced exposure bias to obtain at least one picture with good contrast
208 (Hale et al. 2009). For image processing, we used the protocol of Bianchi et al. (2017). We
209 automatically thresholded the pictures using the function *enhanceHemiphoto* of the package
210 *Caiman* (Diaz and Lencinas, 2015) from the R Statistical Software (R Core Team, 2017). Using
211 CIMES-FISHEYE (Gonsamo et al., 2011), we estimated: canopy openness (CO), the
212 unobstructed fraction of the sky hemisphere viewed from a single point (Gonsamo et al., 2011);
213 indirect site factor (ISF) and direct site factor (DSF), respectively the transmittance through the
214 canopy of the diffuse light from an overcast sky (considering a Standard Overcast Sky model)
215 and of the direct light from a clear sky (Hale et al., 2009). We calculated the global site factor
216 (GSF), the total radiation that comprises both those components, as shown in Equation 1 (Met
217 Office, 2006).

218 Equation 1 : $GSF = 0.65 * ISF + 0.35 * DSF$

219 1.2.2 Statistical analysis

220 We carried out all the analyses with the package *nlme* (Pinheiro et al., 2016) of the R Statistical
221 Software (R Core Team, 2017).

222 1.2.2.1 Height and diameter growth models

223 We modelled *growth*, either Hg (for each species) or DRCg (for SS and WH), as a function of
224 *light*, the GSF estimated from HP, comparing three asymptotic non-linear functions based on
225 the Michaelis-Menten (Equation 2), the 3-points Logistic (Equation 3), and the Asymptotic-
226 with-offset (Equation 4). Our rationale was to observe which function best fitted the growth
227 process in each case and then derive the corresponding biological implications.

228 Equation 2: $Growth = \frac{r + Asym * light}{xmid + light}$

229 Equation 3: $Growth = \frac{r + Asym}{1 + \exp^{(xmid - light)/scale}}$

230 Equation 4: $Growth = (r + Asym) * (1 - \exp^{-\exp(lcr) * (light - cp)})$

231

232 Where:

233 $Asym = (A + A2 * comp) * size^{Pa}$

234 $xmid = (K - K2 * comp) / size^{Pk}$

235 $lcr = (K + K2 * comp) * size^{Pk}$

236 $scale = S / size^{Ps}$

237 $cp = C / size^{Pc}$

238 In all equations, *Asym* indicates the asymptotic maximum growth that is reached at high light
239 levels, and *xmid* and *lcr* how fast the growth reaches this asymptote (i.e. the growth rate). In

240 Equation 2 and 3, *xmid* represents directly the value of light about which the growth is half of
241 the asymptotic growth, or simply half-maximum-growth. In Equation 4, *lcr* represents the
242 same, but after a transformation (see Supplementary Information). Then, *scale* in Equation 3
243 represents the steepness of the curve around the sigmoid inflection point, and *cp* in Equation 4
244 the compensation point, the level of light corresponding to zero growth. We included *size*,
245 either the height or diameter before the growth (*Hp* or *DRCp*), in each of those terms, with an
246 effect mediated by the coefficients *Pa*, *Pk*, *Ps* and *Pc*. We included competition (*comp*) only
247 in the terms related to the asymptotic growth and the growth rate, with an effect mediated by
248 *A2* and *K2*. We did not include a competition effect for *scale* in Equation 3 since it would not
249 have had any biological validity, or for *cp* in Equation 4 for computational simplicity. We
250 included *r*, a random factor at forest level affecting the value of asymptotic growth, to take into
251 consideration the possible auto-correlation of the plots in the same forest due to the site fertility
252 or local climatic conditions. It must be noted that the growth rate increases with lower values
253 of *xmid*, and the opposite for *lcr*. In other words, the asymptote is reached faster in Equations
254 2 and 3 for lower values of *xmid*, and in Equation 4 for higher values of *lcr*. The sign on the
255 *K2* parameter and the inclusion of *size* (as multiplier or dividend) were adjusted to ensure a
256 consistent direction of response for the *xmid* and *lcr* variables. The summary of the biological
257 implications of each coefficient is shown in the Supplementary Information. We also tested
258 equations in which *size* had opposite effects on *xmid/lcr*, *scale*, and *cp* than indicated on the
259 previous equations but the models did not fit.

260 For each combination of growth and species, we tested the three base functions, and all their
261 possible combinations where some or all the main coefficients (*A*, *K*, *S* and/or *C*) were not
262 affected by size (setting *Pa*, *Pk*, *Ps* and/or *Pc* to 0) or by competition (setting either *A2* and/or
263 *K2* to 0). Preliminary results showed that when the competition was affecting both asymptotic
264 growth and growth rate (by setting both *A2* and *K2* to non-zero values), it led to unrealistic

265 biological responses, so we discarded such models. There were 12 models belonging to the
266 family originated from the Michaelis-Menten function, and 24 each for the Logistic and
267 Asymptotic-with-offset, a total of 60. To consider the heteroscedasticity of the data, we
268 modelled the variance as a power of the fitted values, with the power determined during model
269 fitting. For each combination of species and type of growth, we pooled together all the models
270 belonging to the different families. We selected as candidates the model with the lowest Akaike
271 Information Criterion (AIC) and those within two AIC units. Then, in each case we chose the
272 best model as the one with the highest parsimony (fewest parameters affected by size and
273 competition), and in the case of a tie, with the best prediction performance (lowest AIC) and
274 better biological validity (by observing the simulated growth pattern). For each best model, we
275 calculated the Pearson's correlation coefficient r between simulations and observations, and
276 the simulation errors in terms of Root-Mean-Square-Error (RMSE), Mean Absolute Error
277 (MAE), and Mean Absolute Percentage Error (MAPE), that is the MAE relative to the observed
278 growth (Hyndman and Koehler, 2006).

279 To compare growth patterns across species, we also calculated the light level necessary to
280 obtain the half-maximum-growth for all best models. In case of the Michaelis-Menten and the
281 Logistic, that was directly equal to x_{mid} (calculated using the coefficient K and the influence
282 of K_2 and/or P_k), while for the Asymptotic-with-offset, it was estimated starting from lcr
283 (again accounting for the influence of K_2 and/or P_k).

284 1.2.2.2 Apical dominance ratio (ADR) and live crown ratio (LCR) analyses

285 Using a dataset where all species were combined, we calibrated Generalized Linear Mixed
286 Models (GLMMs) for ADR (only for SS and DF) and LCR. In both cases we used as predictor
287 variables: species, light (GSF), size (Hp) and competition (*comp*), including two-way
288 interaction terms between all variables. We included a random intercept effect at forest level
289 to account for spatial autocorrelation. After observations of the data distribution and

290 preliminary modelling results, we decided to use log-transformed GSF and Hp for a better fit.
291 From the global model with all variables, we then tested structures with fewer fixed effects,
292 and selected as the best model the one with lowest AIC. In the cases where models had
293 differences of less than 2 points, we chose the model with fewer explanatory variables.
294 We modelled the height growth (Hg) as a function of the previous year's apical dominance
295 ratio (ADRp) and tree height (Hp). After preliminary modelling, for both species we observed
296 better results in terms of AIC using a Logistic non-linear equation, as shown in Equation 5,
297 than a GLMM.

298 Equation 5:
$$Hg = \frac{r + A * Hp^{Pa}}{1 + e^{(K - ADRp)/S}}$$

299 **1.3 Results**

300 1.3.1 Growth models

301 For SS, we selected as best a model from the Logistic family for both height and diameter
302 growth; for WH, from the Michaelis-Menten again for both height and diameter growth; and
303 for DF/Height, from the Asymptotic-with-Offset. Table 2 presents the coefficient values of
304 those models, showing the main model components (asymptotic growth, growth rate, scale
305 and/or compensation point) affected either by the tree size (if Pa, Pk, Ps and/or Pc \neq 0) or by
306 the intra-regeneration competition (if A2 or K2 \neq 0). The estimated growth patterns for each
307 model versus the observations are shown in Figure 2. See Supplementary Information for the
308 AIC values of all the models fitted, and the confidence intervals of the predictions. In all cases
309 but for the WH/Height model, tree size affected the asymptotic growth (Pa > 0) and
310 consequently, the absolute growth was higher for bigger trees at all light levels. Absolute
311 growth was higher for taller trees also for the WH/Height model within the data range observed,
312 even if Pa = 0, due to the effect of Pk > 0. However, the analysis for western hemlock could
313 have been biased due to the lack of sampled trees growing at high light levels and of an

314 asymptote reached outside the data range. For SS/Height and WH/Height, tree size affected the
315 growth rate ($P_k > 0$): bigger trees had a higher growth rate than smaller trees, more markedly
316 at lower light levels. Only for DF/Height, tree of all sizes showed in the simulations a
317 compensation point above zero light (around GSF 0.08, the value of the coefficient C), due to
318 the Asymptotic-with-offset being chosen as base for the best model. Since both the WH models
319 were based on Michaelis-Menten, the compensation point was set at zero light for that species.
320 Sitka spruce, since Logistic was selected for both the height and diameter best models, had an
321 estimated positive growth at zero light. While the positive growth at zero light was almost
322 negligible in the SS/Diameter model, it was more evident in the SS/Height model (see Figure
323 2).

324 Table 2 presents the Pearson correlation coefficient between simulations and observations, and
325 the various measured errors. In Figure 3 the standardized residuals of the simulations are
326 plotted versus the observations, and the model predictors (tree size, light availability, and
327 competition, even if the latter was not included in all models). There were only minor signs of
328 heteroscedasticity in all models when the residuals were plotted versus the fitted values,
329 indication that it was properly corrected by using the power variance in the model. Considering
330 the residual distribution versus the model predictors, there were different patterns for each
331 model: a slight overprediction only for the largest trees for SS/Height; slight underprediction
332 for SS/Diameter and WH/Diameter at mid-light availability; and underprediction only towards
333 the end-range of light for WH/Height and DF/Height. The resulting values of Mean Absolute
334 Percentage Error (MAPE) were lowest for the western hemlock models (27% and 32% for
335 height and DRC), then higher for the Sitka spruce models (38-39% for height and DRC), and
336 highest for the Douglas fir height model (62%). It must be noted that the MAPE was influenced
337 in all cases by few but very large relative errors for the trees showing the smallest growth.

338 Intra-regeneration competition was included in three models, affecting the growth rate for the
339 SS/Height ($K_2 < 0$), and the asymptotic growth for the SS/Diameter and WH/Diameter models
340 ($A_2 < 0$) (see Figure 4). The resulting effect in the first model (SS/Height) was to decrease the
341 absolute growth especially at lower light levels, with a reduced impact as the light availability
342 increases, while in the last two models (SS/Diameter and WH/Diameter) the reduction was the
343 same in relative terms across all light levels.

344 The comparison of the species-specific absolute growth shows at low light a general advantage
345 of WH over SS, and of SS over DF, that is then reversed at high light, with some exceptions.
346 In Figure 5 (graphs a-d) we simulated growth values for medium-sized trees (height = 130 cm,
347 DRC = 12 mm) in the absence of competition (a and b), or under strong competition, 25 trees
348 per plot (c and d). For height growth, WH had the highest absolute values at almost all light
349 levels for both scenarios. In the absence of competition, for the height growth, SS had higher
350 values below GSF 0.2 than DF, while above it was the opposite; for the diameter growth, WH
351 had higher absolute values than SS below GSF 0.4, and the opposite above. With strong levels
352 of competition, at low light the advantage in height growth of SS over DF decreased markedly,
353 and at high light the advantage in DRC of SS over WH totally disappeared. For trees of
354 increasing sizes, SS had a slightly increasing advantage for growth at low light over DF (results
355 not shown).

356 Figure 5 (graph e) shows how tree size affected the growth rate in the height models for all
357 species, by plotting the light level necessary to reach the half-maximum-growth in the absence
358 of competition. For SS/Height and WH/Height, this light level decreased with increasing tree
359 size. For SS and WH, it decreased respectively from around GSF 0.25 and GSF 0.35 for a small
360 tree (20 cm height), to GSF 0.18 and GSF 0.22 for a big tree (400 cm height). For DF/Height,
361 it was GSF 0.29 for trees of all sizes. Again, the analysis for western hemlock, and partly for

362 DF, could have been biased due to the lack of sampled trees growing at high light levels. For
363 SS/Diameter and WH/Diameter, the light necessary for half-maximum-growth was
364 respectively GSF 0.37 and 0.17, in the absence of competition, for trees of all sizes. As
365 reference, we estimated that the study sites received a daily photosynthetic photon flux density
366 of around 53-56 moles per square meter (at the Earth surface), averaged during the vegetative
367 period from mid-April to mid-September, with little variation from the southernmost to the
368 northernmost site.

369 1.3.2 Crown plasticity analyses

370 Table 3 presents the best models describing ADR and LCR as a function of light. The final
371 model for ADR included only light availability with a positive effect (Figure 6, graph a). There
372 were no significant differences between SS and DF, so the same model was fitted to both
373 species. The threshold of 20-25% of full light indicated in the literature for good growth of
374 Sitka spruce would correspond to an ADR of 1.2-1.4 using such model. For the LCR model,
375 light availability again had a positive effect (Figure 6, graph b), but that was mediated by
376 species-specific differences (an interaction effect between light and species). WH had always
377 the highest LCR values, with LCR being almost unaffected by light. SS had significantly higher
378 LCR than DF, but the difference decreased towards higher light levels. Table 3 also presents
379 the details for the species-specific models simulating height growth as a function of the
380 previous year's apical dominance ratio (ADR_p). We could calibrate a model for both DF and
381 SS, however the fit was better for SS than DF (Figure 6, graph c and d). In both cases, the
382 height growth significantly increased with both ADR_p and tree height (Figure 6, graph d). The
383 model shows that for SS trees with an ADR_p around 1.2 (the value of the coefficient K) had
384 growth the following year equal to half the maximum growth observed in the field.

385 **1.4 Discussion**

386 The growth models presented here can be used to support planning in CCF management, by
387 simulating the potential growth response of natural regeneration to different levels of light
388 under a canopy, and for further prospective analyses. The use of light availability as the main
389 predictor makes these models well suited to describing the regeneration growth in those
390 uneven-aged, mixed-species forest stands that could be the result of continuous cover forestry
391 management in the UK. The simulated values of each model were biologically sound and fitted
392 well the observations, although in all models there was a tendency to under-predict the growth
393 of medium/large-sized trees growing at low/medium levels of light. We demonstrated that
394 different non-linear structures are best suited to simulating different species-specific light-
395 growth relationships. These relationships may also vary for the height and diameter growth in
396 the same species.

397 For western hemlock, and to some extent also for Douglas fir, there was lack of data on trees
398 growing at full light, which especially for the former may have affected the analysis. However,
399 we covered the critical range of low-medium light levels most likely to be encountered in
400 continuous cover forestry stands, and where the growth performance is more influenced by
401 light and less by other environmental factors (Carter and Klinka, 1992). It was observed in
402 other studies that the net photosynthesis in western hemlock and Douglas fir already reached
403 saturation towards light levels of 30-40% full sunlight (Carter and Klinka, 1992; Grossnickle
404 and Arnott, 1992; Leverenz and Jarvis, 1980). For the Sitka spruce height model only, the final
405 structure based on the Logistic function showed an unlikely positive growth at zero light, even
406 if it was very limited. We did not sample Sitka spruce trees growing at very low levels of light,
407 but due to the sampling design followed we cannot conclusively state that there were none
408 growing and surviving in those conditions. A more thorough sampling at those critical levels
409 of light would be necessary to improve the model, which showed an unrealistic positive growth

410 at zero light. With the data available, the Logistic model showed the best fit under all statistical
411 analysis. It must also be noted that hemispherical photography has been shown to be a poor
412 predictor of light transmitted through dense canopies, i.e. at values of GSF 0.1 and less (Hale
413 et al., 2009). Moreover, our study did not consider how light can vary throughout the years in
414 continuous cover forestry, and consequently how the trees react to a changing light
415 environment. For this reason, there may be the need to establish long-term field studies or
416 controlled shading experiment. Climatic variables were not considered, since collecting micro-
417 climatic information within the stands was not possible due to lack of time and resources. The
418 climate below a canopy can vary from open conditions according to the tree density (Sellars,
419 2005). Finally, some of the Douglas fir trees were underplanted (although not recently) and
420 may have had a different growth pattern.

421 The inclusion of tree size as an additional predictor always improved the fit. Tree size had a
422 significant effect in increasing the maximum growth in all models, both for height and
423 diameter. Larger trees as a consequence had a greater absolute growth at all light levels, due
424 mostly to an increased capacity for light absorption and partly to an increased efficiency of
425 light use (Binkley et al., 2013). We observed that for height growth in Sitka spruce and western
426 hemlock, bigger trees compared to smaller trees had a slight additional advantage at low light,
427 since they reached the half-maximum-growth at lower light levels (see Figure 5, graph e). It is
428 possible that larger regenerating trees are able to use their accumulated reserves to survive short
429 periods of reduction in light when compared to smaller ones (Delagrange et al., 2004), and this
430 could contribute to their growth advantage over small trees at low light (and maybe also
431 contributed to predict a positive growth at zero light, see before). Further work to analyse the
432 interaction between light availability and size for the growth processes may be necessary.

433 Intra-regeneration competition significantly decreased the growth in the Sitka spruce height
434 and diameter models, and in the western hemlock diameter model. The negative effect of

435 competition in the Sitka spruce height model decreased at higher light levels, consistent with
436 the findings of Hasenauer & Kindermann (2006) and Collet & Chenost (2006), while in the
437 diameter above root collar models for both Sitka spruce and western hemlock the growth was
438 reduced similarly at all light levels. The results suggest that height growth of regenerating trees
439 may be less affected by competition than diameter growth (Collet and Chenost, 2006; van
440 Couwenberghe et al., 2013). Trees growing in dense patches but with almost full sunlight above
441 them may have vertical growth that is not affected by competition while reducing their radial
442 growth. We are aware of studies where only the radial and not the height growth of trees was
443 affected by intra-regeneration competition (Collet and Chenost, 2006; van Couwenberghe et
444 al., 2013), but not of the contrary. On the question of why some combinations of species and
445 growth were affected by competition and others not, the results did not shed more light on the
446 already mixed review presented in the introduction. Further work, such as improving the
447 measure of competition by considering the size, distance and species of the competitors, is
448 needed to clarify the effects of intra-regeneration competition.

449 For Douglas fir and Sitka spruce, both the apical dominance ratio and the live crown ratio
450 increased with increasing light, with a pattern similar to that observed for other conifer species
451 by Duchesneau et al. (2001) and Grassi & Giannini (2005). This confirmed the ability of these
452 species to react to low light levels by changing their crown architecture. We did not observe
453 differences between Sitka spruce and Douglas fir when modelling the apical dominance ratio
454 as a function of light availability. However, there were significant differences in the live crown
455 ratio: Douglas fir maintained a shorter crown than Sitka spruce especially at lower light levels.
456 Conversely, western hemlock seemed almost unaffected by light availability and maintained a
457 full live crown at all levels of light. Grassi & Giannini (2005) suggested that the apical
458 dominance and live crown ratio patterns may shift as the trees gain in size, but this was not
459 observed in this study, consistent with the results of Williams et al. (1999). We found intra-

460 regeneration competition significant neither for the apical dominance nor for the live crown
461 ratio.

462 For both Douglas fir and Sitka spruce, we could fit models of height growth as a function of
463 the apical dominance ratio of the previous year, even if for the former the results were not very
464 accurate. For Sitka spruce, a value of apical dominance ratio of 1.2 corresponded to half of the
465 maximum potential height growth in the next year. This result is slightly higher to those of
466 Grassi & Giannini (2005) (for *Picea abies* and *Abies alba*) and Page *et al.* (2001) (for Sitka
467 spruce), who considered trees with an apical dominance ratio equal to or less than 1 to be “in
468 check”. The threshold of 20-25% of full light for good growth in Sitka spruce for the UK
469 (Mason 2015) applied to the model of apical dominance ratio as a function of light gives an
470 apical dominance ratio of 1.2-1.4. We thus suggest using as a quick assessment tool in the field
471 an apical dominance ratio of 1.5 (more conservative and simpler to measure) for identifying
472 Sitka spruce regenerating trees with an adequate growth potential.

473 Overall, observing all the parameters considered in this study, we define a shade tolerance
474 ranking as Douglas fir \leq Sitka spruce $<$ western hemlock, similar to the one identified by Mason
475 *et al.* (2004). However, considering only one parameter could be misleading. Douglas fir
476 compared to Sitka spruce had only slightly slower growth at low light but more evident faster
477 growth at high light. Western hemlock had the greatest height growth at all light levels, maybe
478 due to an intrinsic difference in the canopy architecture: a very thin, drooping, and elongated
479 leader, with no clear lateral shoots. Kunstler *et al.* (2005) also showed that a more shade-
480 tolerant species (*Fagus sylvatica* L.) had height growth higher at all light levels than a less
481 shade-tolerant one (*Quercus pubescens* Willd.). When comparing the diameter growth, the
482 higher shade-tolerance of western hemlock was evident: it had a faster radial growth than Sitka
483 spruce at low light and the opposite at high light, as observed in their natural range (Minore,
484 1979; Taylor, 1990). Similar to Petritan *et al.*, (2009), more shade tolerant species (western

485 hemlock and then Sitka spruce) had in this study higher live crown ratio, indication as high
486 tolerance to self-shading. The fact that under high intra-regeneration competition the Sitka
487 spruce advantage at high light disappeared may be another indication of higher shade tolerance
488 in western hemlock, which can better resist the lateral shading from other regenerating trees.
489 For the three species, the best growth models belonged to different families, reflecting their
490 different growth patterns. Only for Douglas fir was the Asymptotic-with-offset equation
491 selected, indicative of lower shade tolerance than Sitka spruce and western hemlock (even if,
492 as discussed already, some lack of sampling at very low light levels may have affected the
493 analyses). The identification of a compensation point above zero light for Douglas fir suggests
494 a lower capacity of this species to survive at low light when compared to both Sitka spruce and
495 western hemlock. Better studies of survivorship of these species at low light must be however
496 addressed to integrate the shade tolerance comparison carried out in this research.

497 We demonstrated that all the target species thrive relatively well at the light levels that can be
498 commonly achieved in conifer stands managed with shelterwood systems, and that can be used
499 as reference target by forest managers (GSF 0.20-0.30). Foresters aiming at mixed-species
500 stands in the UK could obtain an adequate regeneration growth of all these species at the same
501 time. For maintaining a viable presence of Douglas fir, however it seems likely that more
502 constant thinning will have to be carried out to keep the light always at around that level (and
503 at least above 10% of full light), while western hemlock, and to a lesser extent Sitka spruce,
504 will be able to keep growing for some periods also at higher shading. It is likely that
505 successional dynamics in a mixed-stand of species with such similar light requirements may
506 be affected more crucially by variations in regeneration occurrence and survival (Wright et al.,
507 1998), which could not be addressed in this study. The results show that is no need to release
508 the regeneration early, since all the target species could achieve a growth very similar to the
509 maximum at 50% of light. In addition, for the study species, this study did not show that trees

510 of bigger sizes require higher light availability and thus ever larger openings for their sustained
511 growth. For Sitka spruce only, the quick indicator of apical dominance ratio of 1.5 can be used
512 in the field to identify adequate growing conditions. For competition, the results showed that it
513 affects more the diameter growth than the height growth. However, in case forest managers
514 would be interested in higher diameter growth, the need to intervene with thinning of
515 regenerating trees (i.e. respacing) could be assessed only after studies of mortality and self-
516 thinning of the regeneration.

517 We conclude that modelling light-growth requires species-specific non-linear functions and
518 that predictions are improved by including size and competition. The developed predictive
519 models for height and diameter growth will allow accurate modelling of the study species in
520 CCF management.

521

522 **Funding information**

523 Funds for this study were provided by the Forestry Commission and the Scottish Forestry Trust.

524 **List of references**

525 Bianchi, S., Cahalan, C., Hale, S., Gibbons, J.M., 2017. Rapid assessment of forest canopy and
526 light regime using smartphone hemispherical photography. *Ecol. Evol.* 7, 10556–10566.

527 <https://doi.org/10.1002/ece3.3567>

528 Binkley, D., Campoe, O.C., Gspaltl, M., Forrester, D.I., 2013. Light absorption and use
529 efficiency in forests: Why patterns differ for trees and stands. *For. Ecol. Manage.* 288, 5–

530 13. <https://doi.org/10.1016/j.foreco.2011.11.002>

531 Cameron, A.D., 2015. Building Resilience into Sitka Spruce (*Picea sitchensis* (Bong.) Carr.)
532 Forests in Scotland in Response to the Threat of Climate Change. *Forests* 6, 398–415.

533 <https://doi.org/10.3390/f6020398>

534 Carter, R.E., Klinka, K., 1992. Variation in shade tolerance of Douglas fir, western hemlock,
535 and western red cedar in coastal British Columbia. *For. Ecol. Manage.* 55, 87–105.
536 [https://doi.org/10.1016/0378-1127\(92\)90094-P](https://doi.org/10.1016/0378-1127(92)90094-P)

537 Chrimes, D., Nilson, K., 2005. Overstorey density influence on the height of *Picea abies*
538 regeneration in northern Sweden. *Forestry* 78, 433–442.
539 <https://doi.org/10.1093/forestry/cpi039>

540 Claveau, Y., Messier, C., Comeau, P.G., Coates, K.D., 2002. Growth and crown morphological
541 responses of boreal conifer seedlings and saplings with contrasting shade tolerance to a
542 gradient of light and height. *Can. J. For. Res.* 32, 458–468. [https://doi.org/10.1139/x01-](https://doi.org/10.1139/x01-220)
543 220

544 Collet, C., Chenost, C., 2006. Using competition and light estimates to predict diameter and
545 height growth of naturally regenerated beech seedlings growing under changing canopy
546 conditions. *Forestry* 79, 489–502. <https://doi.org/10.1093/forestry/cpl033>

547 Delagrange, S., Messier, C., Lechowicz, M.J., Dizengremel, P., 2004. Physiological,
548 morphological and allocational plasticity in understory deciduous trees: importance of
549 plant size and light availability. *Tree Physiol.* 24, 775–784.
550 <https://doi.org/10.1093/treephys/24.7.775>

551 Diaz, G.M., Lencinas, J.D., 2015. Enhanced Gap Fraction Extraction From Hemispherical
552 Photography. *IEEE Geosci. Remote Sens. Lett.* 12, 1785–1789.
553 <https://doi.org/10.1109/LGRS.2015.2425931>

554 Duchesneau, R., Lesage, I., Messier, C., Morin, H., 2001. Effects of light and intraspecific
555 competition on growth and crown morphology of two size classes of understory balsam
556 fir saplings. *For. Ecol. Manage.* 140, 215–225. <https://doi.org/10.1016/S0378->

557 1127(00)00281-4

558 Fekedulegn, D., Siurtain, M. Mac, Colbert, J., 1999. Parameter estimation of nonlinear growth
559 models in forestry. *Silva Fenn.* 33, 327–336. <https://doi.org/10.14214/sf.653>

560 Finzi, A.C., Canham, C.D., 2000. Sapling growth in response to light and nitrogen availability
561 in a southern New England forest. *For. Ecol. Manage.* 131, 153–165.
562 [https://doi.org/https://doi.org/10.1016/S0378-1127\(99\)00206-6](https://doi.org/https://doi.org/10.1016/S0378-1127(99)00206-6)

563 Forestry Commission, 2017. Forestry Statistics 2017 [WWW Document]. URL
564 <https://www.forestry.gov.uk/forestry/inf-d-7aqdgc> (accessed 2.8.18).

565 Fournier, R.A., Landry, R., August, N.M., Fedosejevs, G., Gauthier, R.P., 1996. Modelling
566 light obstruction in three conifer forests using hemispherical photography and fine tree
567 architecture. *Agric. For. Meteorol.* 82, 47–72. [https://doi.org/10.1016/0168-](https://doi.org/10.1016/0168-1923(96)02345-3)
568 [1923\(96\)02345-3](https://doi.org/10.1016/0168-1923(96)02345-3)

569 Givnish, T.J., 1988. Adaptation to Sun and Shade: A Whole-Plant Perspective. *Aust. J. Plant*
570 *Physiol.* 15, 63–92. <https://doi.org/https://doi.org/10.1071/PP9880063>

571 Gonsamo, A., Walter, J.M.N., Pellikka, P., 2011. CIMES: A package of programs for
572 determining canopy geometry and solar radiation regimes through hemispherical
573 photographs. *Comput. Electron. Agric.* 79, 207–215.
574 <https://doi.org/10.1016/j.compag.2011.10.001>

575 Grassi, G., Giannini, R., 2005. Influence of light and competition on crown and shoot
576 morphological parameters of Norway spruce and silver fir saplings. *Ann. For. Sci.* 62,
577 269–274. <https://doi.org/https://doi.org/10.1051/forest:2005019>

578 Grossnickle, S.C., Arnott, J.T., 1992. Gas exchange response of western hemlock seedlings
579 from various dormancy-induction treatments to reforestation site environmental
580 conditions. *For. Ecol. Manage.* 49, 177–193. <https://doi.org/10.1016/0378->

581 1127(92)90134-U

582 Hale, S.E., Edwards, C., Mason, W.L., Price, M., Peace, A., 2009. Relationships between
583 canopy transmittance and stand parameters in Sitka spruce and Scots pine stands in
584 Britain. *Forestry* 82, 503–513. <https://doi.org/10.1093/forestry/cpp020>

585 Hasenauer, H., Kindermann, G., 2006. Modelling Regeneration in Even and Uneven-Aged
586 Mixed Species Forests, in: Hasenauer, H. (Ed.), *Sustainable Forest Management - Growth
587 Models for Europe*. Springer Berlin Heidelberg, pp. 167–194.
588 https://doi.org/https://doi.org/10.1007/3-540-31304-4_13

589 Hasenauer, H., Kindermann, G., 2002. Methods for assessing regeneration establishment and
590 height growth in uneven-aged mixed species stands. *Forestry* 75, 385–394.
591 <https://doi.org/10.1093/forestry/75.4.385>

592 Hyndman, R.J., Koehler, A.B., 2006. Another look at measures of forecast accuracy. *Int. J.
593 Forecast.* 22, 679–688. <https://doi.org/10.1016/j.ijforecast.2006.03.001>

594 King, D.A., 1990. The Adaptive Significance of Tree Height. *Am. Nat.* 135, 809–828.
595 <https://doi.org/https://doi.org/10.1086/285075>

596 Kobe, R.K., Coates, K.D., 1997. Models of sapling mortality as a function of growth to
597 characterize interspecific variation in shade tolerance of eight tree species of northwestern
598 British Columbia. *Can. J. For. Res.* 27, 227–236. <https://doi.org/10.1139/x96-182>

599 Kunstler, G., Curt, T., Bouchaud, M., Lepart, J., 2005. Growth, mortality, and morphological
600 response of European beech and downy oak along a light gradient in sub-Mediterranean
601 forest. *Can. J. For. Res.* 35, 1657–1668. <https://doi.org/10.1139/x05-097>

602 Leverenz, J., Jarvis, P.G., 1980. Photosynthesis in Sitka Spruce (*Picea Sitchensis* (Bong.)
603 Carr.): X. Acclimation to Quantum Flux Density Within and Between Trees. *J. Appl. Ecol.*
604 17, 697–708. <https://doi.org/https://doi.org/10.2307/2402648>

605 Lieffers, V.J., Messier, C., Stadt, K.J., Gendron, F., Comeau, P.G., 1999. Predicting and
606 managing light in the understory of boreal forests. *Can. J. For. Res.* 29, 796–811.
607 <https://doi.org/10.1139/cjfr-29-6-796>

608 Ligot, G., Balandier, P., Fayolle, A., Lejeune, P., Claessens, H., 2013. Height competition
609 between *Quercus petraea* and *Fagus sylvatica* natural regeneration in mixed and uneven-
610 aged stands. *For. Ecol. Manage.* 304, 391–398.
611 <https://doi.org/10.1016/j.foreco.2013.05.050>

612 Lusk, C.H., Jorgensen, M.A., 2013. The whole-plant compensation point as a measure of
613 juvenile tree light requirements. *Funct. Ecol.* 27, 1286–1294.
614 <https://doi.org/10.1111/1365-2435.12129>

615 Malcolm, D.C., Mason, W.L., Clarke, G.C., 2001. The transformation of conifer forests in
616 Britain — regeneration, gap size and silvicultural systems. *For. Ecol. Manage.* 151, 7–23.
617 [https://doi.org/10.1016/S0378-1127\(00\)00692-7](https://doi.org/10.1016/S0378-1127(00)00692-7)

618 Mason, B., Kerr, G., Simpson, J., 1999. What is continuous cover forestry? *For. Comm. Inf.*
619 Note.

620 Mason, B., Perks, M.P., Mason, W.L., 2011. Sitka spruce (*Picea sitchensis*) forests in Atlantic
621 Europe: changes in forest management and possible consequences for carbon
622 sequestration. *Scand. J. For. Res.* 26, 72–81.
623 <https://doi.org/10.1080/02827581.2011.564383>

624 Mason, W.L., 2015. Implementing Continuous Cover Forestry in Planted Forests: Experience
625 with Sitka Spruce (*Picea Sitchensis*) in the British Isles. *Forests* 6, 879–902.
626 <https://doi.org/10.3390/f6040879>

627 Mason, W.L., Edwards, C., Hale, S.E., 2004. Survival and Early Seedling Growth of Conifers
628 with Different Shade Tolerance in a Sitka Spruce Spacing Trial and Relationship to

629 Understorey Light Climate. *Silva Fenn.* 38, 357–370.
630 <https://doi.org/https://doi.org/10.14214/sf.404>

631 Met Office, 2006. Met Office Land Surface Stations Data (1900-2000). NCAS British
632 Atmospheric Data Centre [WWW Document]. URL
633 <http://catalogue.ceda.ac.uk/uuid/ea2d5d8bce505ad4b10e06b45191883b> (accessed
634 10.14.16).

635 Minore, D., 1979. Comparative Autecological Characteristics of Northwestern Tree Species -
636 A Literature review. USDA Forest Service, Pacific Northwest Forest and Range
637 Experiment Station, Portland, Oregon.

638 Monserud, R., Ek, A., 1977. Prediction of understory tree height growth in northern hardwood
639 stands. *For. Sci.* 23, 391–400.

640 Nixon, C.J., Worrell, R., 1999. The Potential for the Natural Regeneration of Conifers in
641 Britain. *Bullettin*.

642 Nygaard, P., Øyen, B.-H., 2017. Spread of the Introduced Sitka Spruce (*Picea sitchensis*) in
643 Coastal Norway. *Forests* 8, 24. <https://doi.org/10.3390/f8010024>

644 O’Connell, B.M., Kelty, M.J., 1994. Crown architecture of understory and open-growth white
645 pine (*Pinus strobus* L.) saplings. *Tree Physiol.* 14, 89–102.
646 <https://doi.org/10.1093/treephys/14.1.89>

647 Oliver, D.C., Larson, B.C., 1996. *Forest stand dynamics*. Wiley, New York.

648 Pacala, S.W., Canham, C.D., Saponara, J., Silander Jr., J.A., Kobe, R.K., Ribbens, E., 1996.
649 Forest models defined by field measurements: estimation, error analysis and dynamics.
650 *Ecol. Monogr.* 66, 1–43. <https://doi.org/https://doi.org/10.2307/2963479>

651 Page, L.M., Cameron, A.D., Clarke, G.C., 2001. Influence of overstorey basal area on density

652 and growth of advance regeneration of Sitka spruce in variably thinned stands. *For. Ecol.*
653 *Manage.* 151, 25–35. [https://doi.org/10.1016/S0378-1127\(00\)00693-9](https://doi.org/10.1016/S0378-1127(00)00693-9)

654 Paine, C.E.T., Marthews, T.R., Vogt, D.R., Purves, D., Rees, M., Hector, A., Turnbull, L.A.,
655 2012. How to fit nonlinear plant growth models and calculate growth rates: An update for
656 ecologists. *Methods Ecol. Evol.* 3, 245–256. <https://doi.org/10.1111/j.2041->
657 [210X.2011.00155.x](https://doi.org/10.1111/j.2041-210X.2011.00155.x)

658 Peng, C., 2000. Growth and yield models for uneven-aged stands: past, present and future. *For.*
659 *Ecol. Manage.* 132, 259–279. [https://doi.org/10.1016/S0378-1127\(99\)00229-7](https://doi.org/10.1016/S0378-1127(99)00229-7)

660 Petritan, A.M., von Lüpke, B., Petritan, I.C., 2009. Influence of light availability on growth,
661 leaf morphology and plant architecture of beech (*Fagus sylvatica* L.), maple (*Acer*
662 *pseudoplatanus* L.) and ash (*Fraxinus excelsior* L.) saplings. *Eur. J. For. Res.* 128, 61–74.
663 <https://doi.org/10.1007/s10342-008-0239-1>

664 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Team, R.C., 2016. nlme: Linear and Nonlinear
665 Mixed Effects Models.

666 Pommerening, A., Murphy, S.T., 2004. A review of the history, definitions and methods of
667 continuous cover forestry with special attention to afforestation and restocking. *Forestry*
668 77, 27–44. <https://doi.org/10.1093/forestry/77.1.27>

669 R Core Team, 2017. R: A language and environment for statistical computing.

670 Schütz, J.P., Pukkala, T., Donoso, P.J., von Gadow, K., 2011. Historical Emergence and
671 Current Application of CCF, in: Pukkala, T., von Gadow, K. (Eds.), *Continuous Cover*
672 *Forestry*. Springer Science & Business Media, pp. 1–28.

673 Taylor, A.H., 1990. Disturbance and persistence of sitka spruce (*Picea sitchensis* (Bong) Carr.)
674 in coastal forests of the pacific Northwest, North America. *J. Biogeogr.* 17, 47–58.
675 <https://doi.org/10.2307/2845187>

676 van Couwenberghe, R., Gégout, J.C., Lacombe, E., Collet, C., 2013. Light and competition
677 gradients fail to explain the coexistence of shade-tolerant *Fagus sylvatica* and shade-
678 intermediate *Quercus petraea* seedlings. *Ann. Bot.* 112, 1421–1430.
679 <https://doi.org/10.1093/aob/mct200>

680 Williams, H., Messier, C., Kneeshaw, D.D., 1999. Effects of light availability and sapling size
681 on the growth and crown morphology of understory Douglas-fir and lodgepole pine. *Can.*
682 *J. For. Res.* 29, 222–231. <https://doi.org/10.1139/cjfr-29-2-222>

683 Wright, E.F., Coates, K.D., Canham, C.D., Bartemucci, P., 1998. Species variability in growth
684 response to light across climatic regions in northwestern British Columbia. *Can. J. For.*
685 *Res.* 28, 871–886. <https://doi.org/10.1139/x98-055>

686

687

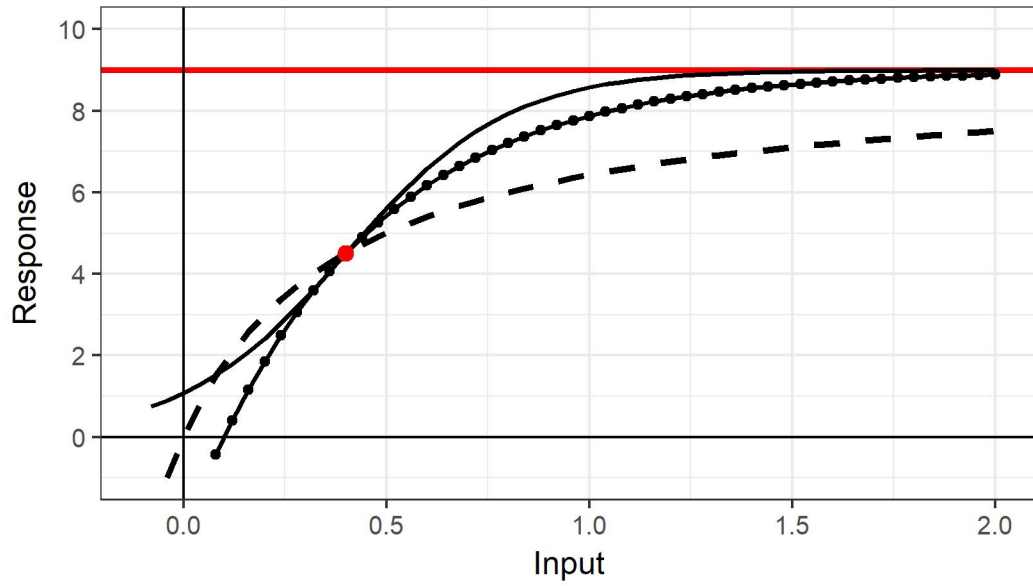


Figure 1. Examples of a Michaelis-Menten (dashed line), Logistic (continuous line) and Asymptotic-with-offset (dotted-continuous line) functions. All the functions were set to reach the same asymptotic response towards high values of input (represented by the red continuous line, response = 9). Note the Michaelis-Menten will reach it at higher values of input outside the graph. The growth rate parameter in all functions controls the value of input about which the response is half of the asymptote (represented by the red dot), and it was set equal for all of them (input = 0.4). Note also the different behaviour at zero input.

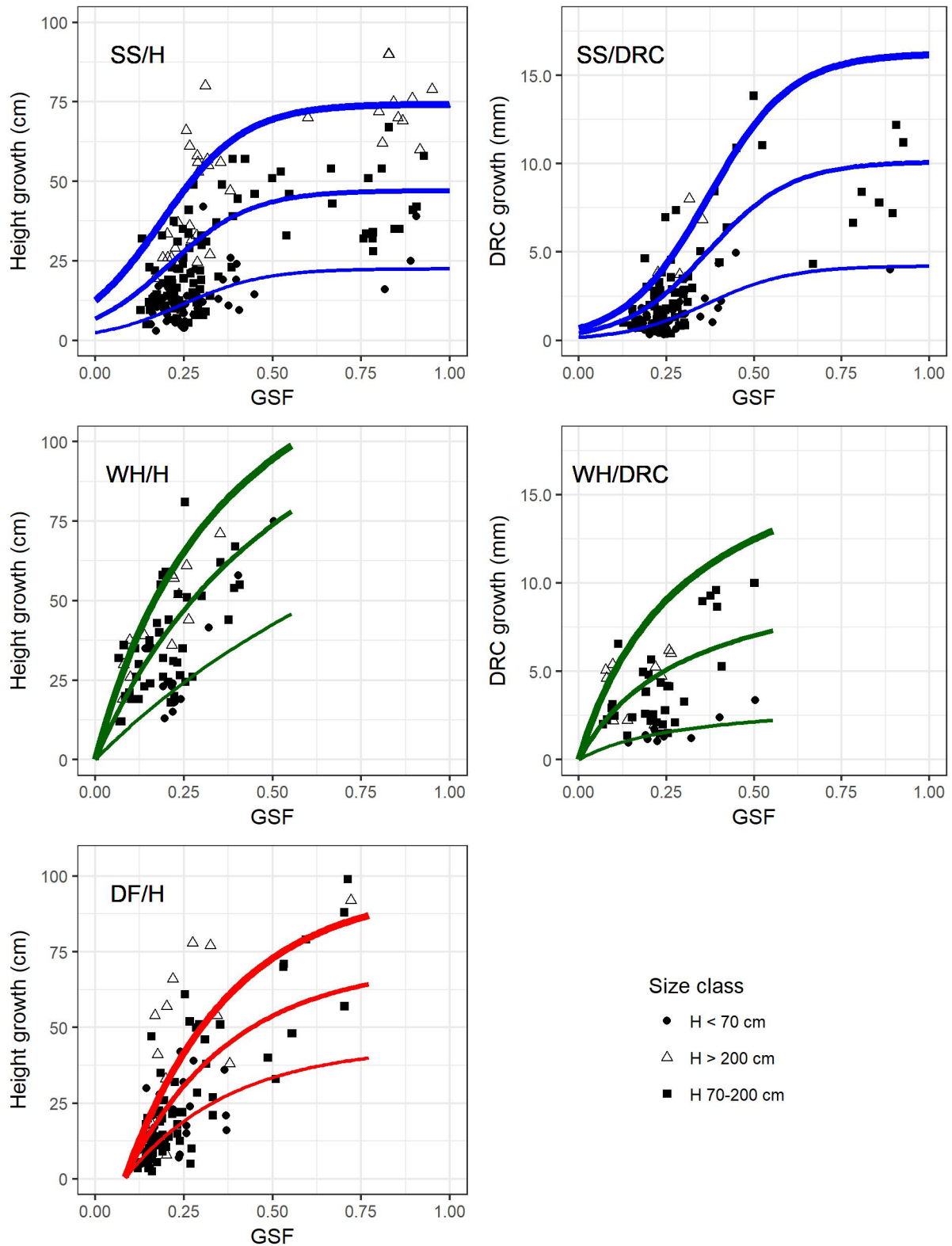


Figure 2. Simulated (lines) and observed (points) growth as function of light (GSF, Global Site Factor), for trees of different sizes, in absence of competition. SS, Sitka spruce; DF, Douglas fir; WH, western hemlock; H, Height; DRC, Diameter above Root Collar. In each graph: top line, simulated growth for a tree having size (height or diameter) equal to the 95% quantile of the population, medium line, to the mean, and bottom line, to the 5% quantile.

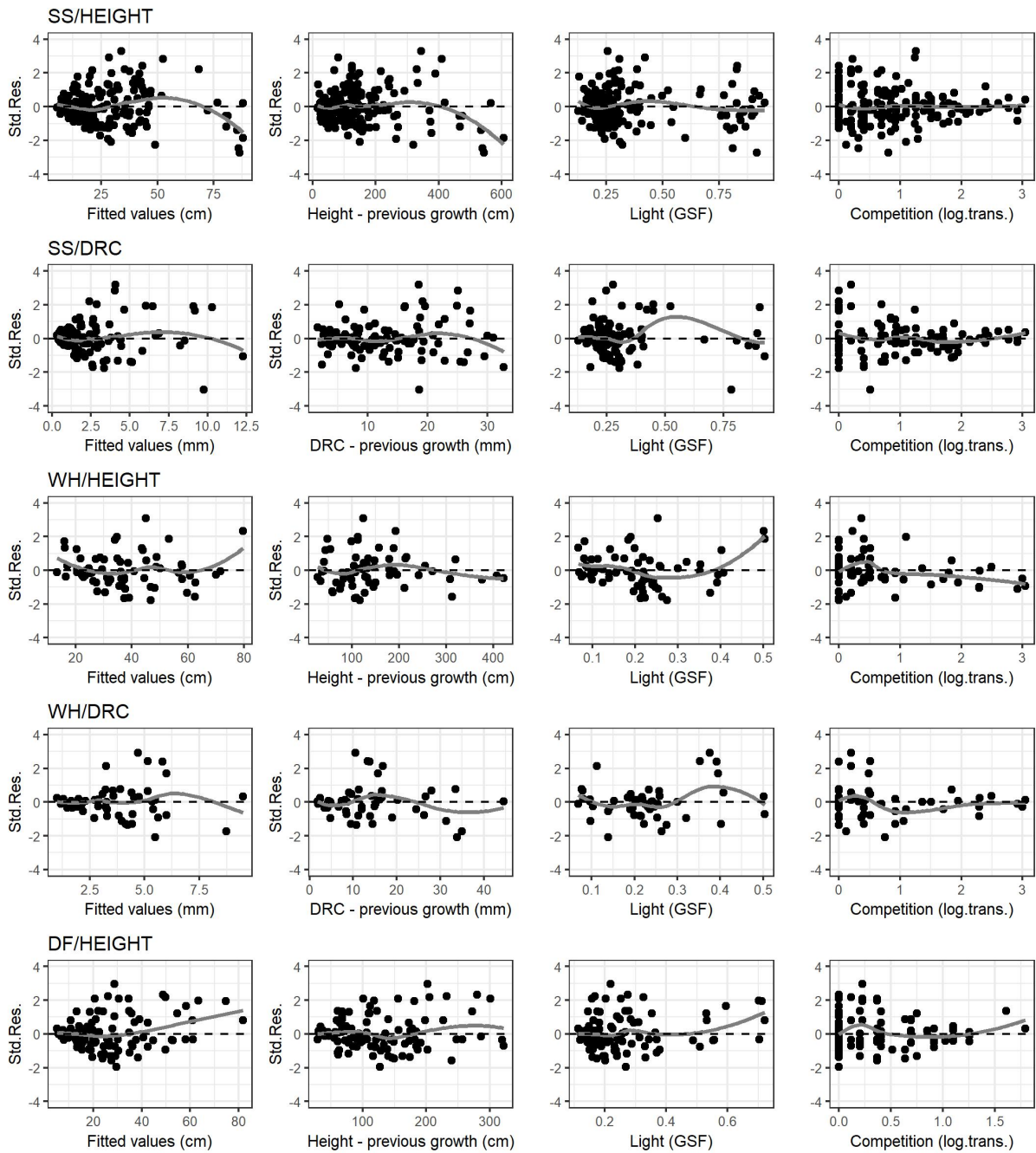


Figure 3. Standardized residuals plotted against the observed growth, the size previous the growth, the light availability (GSF, Global Site Factor) and the intra-regeneration competition (log-transformed plus 1). SS, Sitka spruce; DF, Douglas fir; WH, western hemlock; DRC, diameter above root collar. Continuous lines, LOESS (locally weighted scatterplot smoothing) curves.

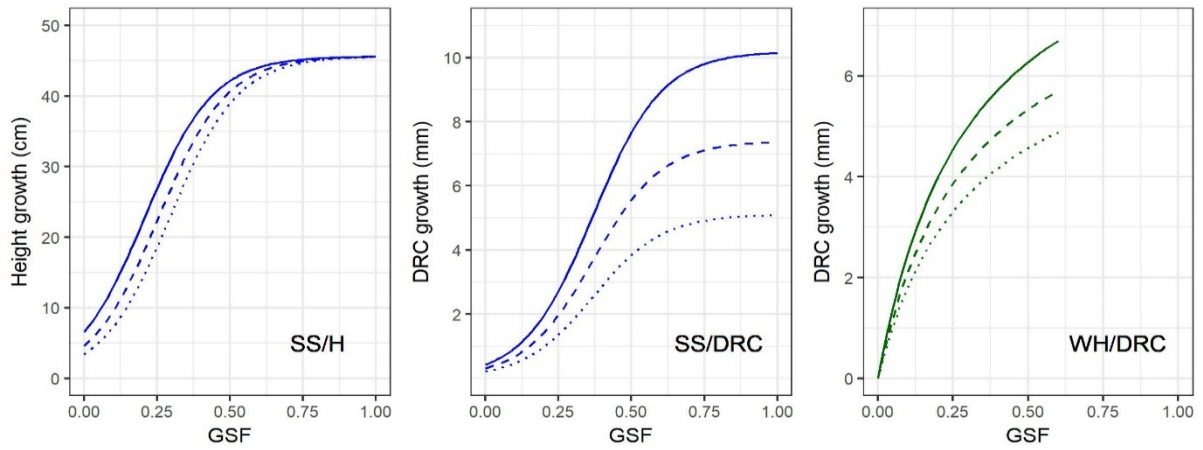


Figure 4. Simulated growth as function of light (GSF, Global Site Factor) under different competition levels. SS, Sitka spruce; WH, western hemlock; H, Height; DRC, Diameter above Root Collar. For height growth, a tree of height 130 cm was considered; for DRC growth, of DRC 12 mm. Continuous lines, no competition; dashed lines, low competition (5 trees/plot); dotted lines, high competition (25 trees/plot).

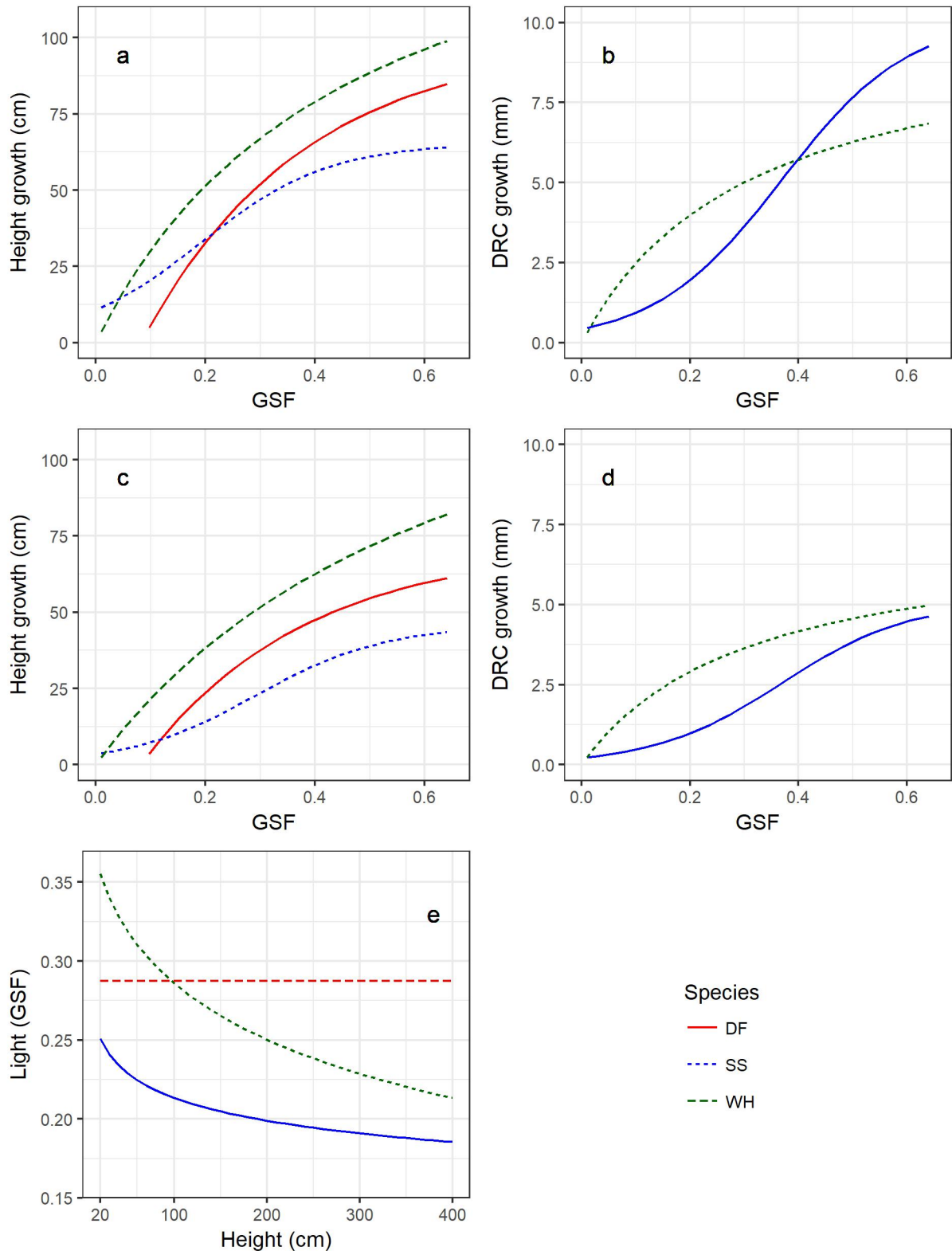


Figure 5. Graphs a-d. Comparison of species-specific simulated growth as function of light (GSF, Global Site Factor), in absence of competition (a and b) and under strong competition (25 trees/plot, c and d). DF, Douglas fir; SS, Sitka spruce; WH, western hemlock. The height growth was simulated for trees of 130 cm height; the diameter above root collar (DRC) growth for trees of DRC 12 mm. Graph e: light level necessary for height growth equal to half the maximum growth at full light, as function of tree size.

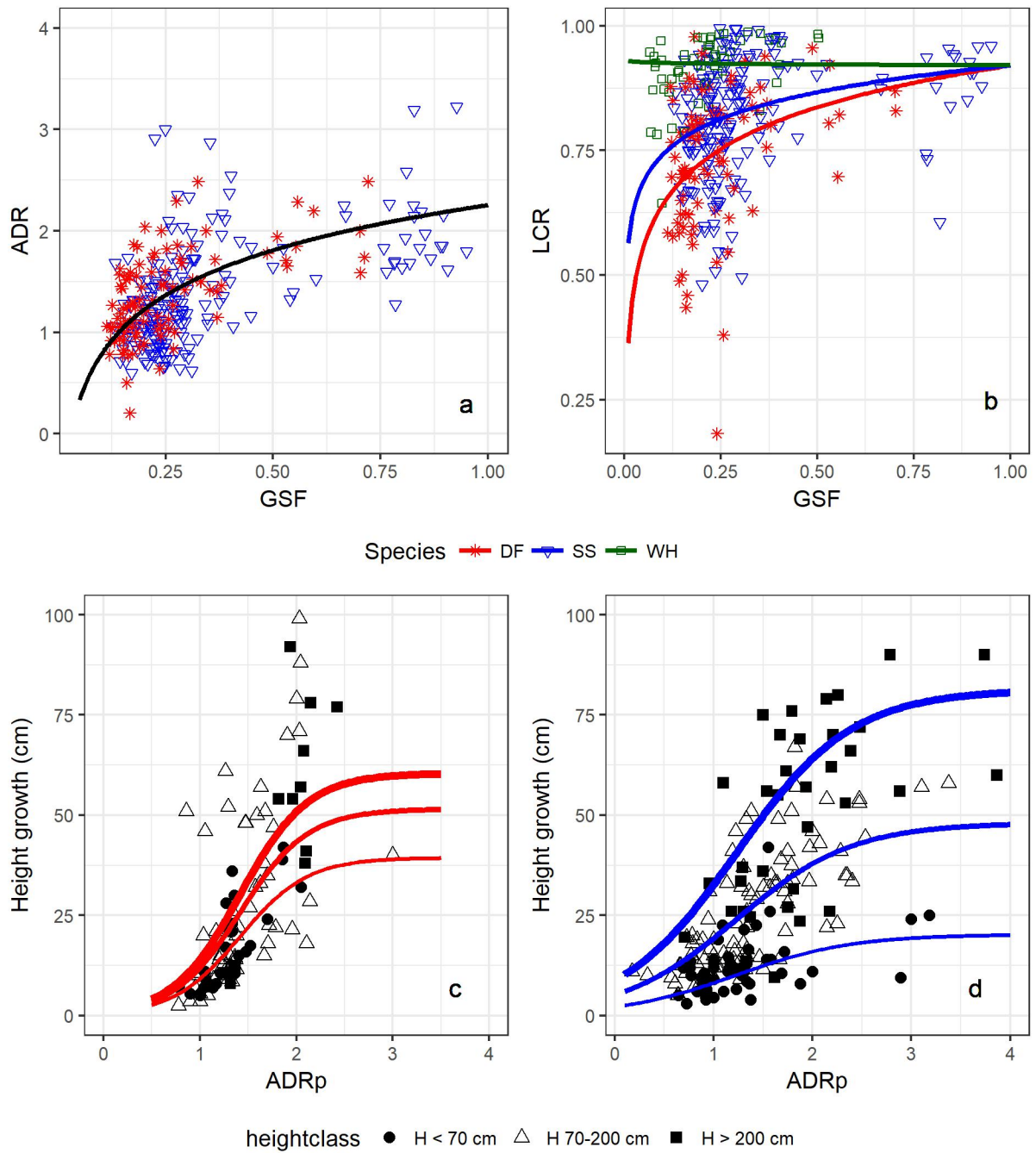


Figure 6. Simulated (lines) and observed (points) for: graph a, Apical Dominance Ratio (ADR) as function of light availability (GSF, Global Site Factor), the continuous black line is for both Douglas fir (DF) and Sitka spruce (SS); graph b: Live Crown Ratio (LCR) as function of light availability (GSF, Global Site Factor) and species (WH, western hemlock); graphs c and d, respectively Douglas fir and Sitka spruce height growth as function of Apical Dominance Ratio of the previous year (ADRp) and tree size: from top to bottom in both graphs, the lines are for trees respectively having height equal to the 95% quantile of the population considered, to the mean, and to the 5% quantile.

Table 1. Details of study areas and tree measured. Values of light (GSF, Global Site Facto) and size are given as minimum-mean-maximum. Height, height before the last growth season, DRC, diameter at 10 cm above root collar; n, the sample size. Larch, *Larix spp.*; Spruce, *Picea abies* and *Picea sitchensis*, Douglas fir, *Pseudotsuga menziesii*, Scots pine, *Pinus sylvestris*; mixed broadleaves, *Acer spp.*, *Fagus sylvatica* and *Quercus spp.*

Forest	Coordinates (WGS84)	Canopy species	Light (GSF)	Sitka spruce				Western hemlock				Douglas fir	
				Height (cm)	n	DRC (mm)	n	Height (cm)	n	DRC (mm)	n	Height (cm)	n
Aberfoyle (Scotland)	56° 13' N 4° 21' W	Larch, spruce	0.13-0.25-0.39	25-151-410	31	2-14-25	19	-	-	-	-	-	-
Clocaenog (Wales)	53° 04' N 3° 24' W	Spruce, Larch	0.12-0.41-0.95	21-184-607	89	1-12-30	34	27-108-407	20	2-9-27	18	61-116-230	18
Coed-Y-Brenin (Wales)	52° 48' N 3° 53' W	Douglas fir, mixed broadleaves	0.13-0.18-0.25	-	-	-	-	112-137-188	4	17-21-26	4	31-137-322	18
Gwydyr (Wales)	53° 05' N 3° 48' W	Douglas fir, mixed broadleaves, Scots pine	0.07-0.18-0.38	45-124-200	16	-	-	83-138-190	10	-	-	41-76-133	11
Kielder (England)	55° 13' N 2° 27' W	Spruce	0.16-0.24-0.38	15-87-241	49	3-10-27	33	75-175-271	6	5-13-24	6	-	-
Lakes district (England)	54° 30' N 3° 09' W	Douglas fir	0.12-0.24-0.83	34-133-243	18	3-15-31	5	79-175-271	5	12-14-16	3	29-130-301	25
Mortimer (England)	52° 21' N 2° 45' W	Mixed broadleaves, Douglas fir	0.07-0.15-0.34	-	-	-	-	91-191-376	10	11-23-45	9	34-170-286	13
Wykeham (England)	54° 16' N 0° 33' W	Larch, Scots pine, spruce	0.11-0.28-0.53	16-113-320	30	2-12-33	26	33-157-422	11	2-13-35	11	41-113-272	16
Total			0.07-0.40-0.95	15-140-607	187	2-12-33	117	27-145-422	66	2-12-45	51	29-125-322	101

Table 2. Best growth model for each case, showing the family of the equation. SS, Sitka spruce; DF, Douglas fir; WH, western hemlock; H, height; DRC, diameter above root collar. Empty cell: the coefficient was excluded in the best model. NA: the coefficient does not appear in the equation used. Then, *r* is the Pearson correlations coefficient between simulations and observations; RMSE, the Root-Mean-Square-Error (in cm for height and mm for diameter); MAE, the Mean Absolute Error (in cm for height and mm for diameter); MAPE, the MAE relative to the observations.

Model	Coefficient										r	RMSE	MAE	MAPE
	A	K	A2	K2	C	S	Pa	Pk	Ps	Pc				
SS/HEIGHT (n=187) - Logistic														
Value	5.624	0.340	-	-0.043	NA	0.117	0.430	0.101	-	NA	0.88	9.5	7.1	37.6%
p-value	0.003	0.003	-	0.014	NA	0.000	0.000	0.106	-	NA				
SS/DRC (n=117) - Logistic														
Value	2.406	0.369	-0.369	-	NA	0.118	0.581	-	-	NA	0.94	0.9	0.6	39.0%
p-value	<0.001	<0.001	<0.001	-	NA	<0.001	<0.001	-	-	NA				
WH/HEIGHT (n=66) - Michaelis-Menten														
Value	170.9	7.033	-	-	NA	NA	-	0.476	NA	NA	0.79	11.6	8.8	27.0%
p-value	0.005	0.048	-	-	NA	NA	-	<0.001	NA	NA				
WH/DRC (n=51) - Michaelis-Menten														
Value	1.936	0.308	-0.161	-	NA	NA	0.666	-	NA	NA	0.76	1.5	1.1	32.5%
p-value	0.003	0.055	0.070	-	NA	NA	<0.001	-	NA	NA				
DF/HEIGHT (n=101) - Asymptotic-with-offset														
Value	10.809	1.219	-	-	0.083	NA	0.390	-	NA	-	0.84	12.5	9.6	61.6%
p-value	0.061	0.010	-	-	<0.001	NA	<0.001	-	NA	-				

Table 3. Details for the models describing (a) apical dominance ratio (ADR) as function of light (GSF, Global Site Factor); (b) Live Crown Ratio (LCR) as function of light and species; (c) and (d), the height growth respectively of Douglas fir and Sitka spruce as function of ADR of the previous year (ADR_p). It is indicated whether the model is based on a Generalized Linear Mixed Model (GLMM) or on the non-linear Logistic equation. Hp, is the height of the tree in the previous year, SS is Sitka spruce, WH is western hemlock.

(a) ADR = f(light) (n=284) - GLMM				
Coefficient	Intercept	log(GSF)		
Value	2.254	0.641		
p-value	<0.001	<0.001		
(b) LCR = f(light) (n=331) - GLMM				
Coefficient	Intercept	log(GSF)	log(GSF):SS	log(GSF):WH
Value	0.921	0.121	-0.043	-0.123
p-value	<0.001	<0.001	<0.001	<0.001
(c) DF/Height = f(ADR_p) (n=98) - Logistic				
Coefficient	A	K	S	Pa
Value	18.202	1.416	0.349	0.217
p-value	0.102	<0.001	<0.001	0.035
(d) SS/Height = f(ADR_p) (n=180) - Logistic				
Coefficient	A	K	S	Pa
Value	4.033	1.232	0.582	0.501
p-value	<0.001	<0.001	<0.001	<0.001

SUPPLEMENTARY INFORMATION

We show here: Equation S 1, how to obtain the input value for half-maximum-growth in case of the Asymptotic-with-offset equation from the parameter lcr , considering the compensation point C ; Table S.1, the summary of the biological effects of the various coefficients for the non-linear functions; Table S.2, the full list of Akaike Information Criteria (AIC) values for each model tested; Figure S.1, the schematics of the tree measurements; Figure S.2, the 95% prediction intervals for each model. For the latter, the 95% prediction intervals for each model were calculated for each model by i) resampling 1,000 times the coefficients according to a multivariate distribution using the same variance-covariance of the calibrated model (using the package *MASS* from R Statistical Software); ii) calculating the predictions using all the new combinations of coefficients; iii) identify the 97.5% and 2.5% quantiles of those predicted values as upper and lower boundaries.

$$\text{Equation S 1: } Input = \log(2) / \exp(lcr) + C$$

Table S.1. Summary of the biological effects of the various coefficients used in the non-linear functions

Asym	All equations	A	Value of maximum growth (in cm or mm).
		A2	Effect of competition on the maximum growth: if 0, it is null; if negative, it decreases the maximum growth.
		Pa	Effect of tree size on the maximum growth: null at 0, then increases the maximum growth with a stronger effect as this parameter increases.
xmid/lcr	All equations	K	Correlated to the growth rate to reach the maximum growth: for $xmid$, the higher the value, the slower the rate; for lcr , the opposite. Also, different scale for the different equations.
		K2	Effect of competition on the growth rate: if 0, it is null; if negative, it decreases the growth rate, both in $xmid$ and $rate$.
		Pk	Effect of tree size on the growth rate: null at 0, then increases the growth rate with a stronger effect as this parameter increases, both in $xmid$ and lcr .
scale	Logistic	S	Positively correlated to the steepness of the sigmoid curve.
		Ps	Effect of tree size on the steepness of the sigmoid curve: null at 0, then increases the steepness with a stronger effect as this parameter increases.
cp	Asymptotic-with-offset	C	Light level (GSF) equivalent to null growth (compensation point).
		Pc	Effect of tree size on the compensation point: null at 0, then decreases the compensation point with a stronger effect going towards 1 and above.

Table S.2. Akaike Information Criteria (AIC) for all models from each equation and combination species/growth. *SS* is Sitka spruce, *DF* is Douglas fir, *WH* is western hemlock, *H* is Height, *DRC* is diameter above root collar. Under Size and

Competition, it is indicated which main parameters of the equation were influenced by respectively tree size and intra-regeneration competition. An empty cell means that a model could not be successfully calibrated. For each combination species/growth: bold, all the models considered in the group of best candidates (difference in AIC less than 2 points from the model with lowest AIC, models with no biological validity discarded); bold, italicized and in red, the best model selected for each combination growth/species

Equation	Size	Competition	SS/H	SS/DRC	WH/H	WH/DRC	DF/H
Logistic	None	None	1509	-	-	-	830
Logistic	None	A	1512	-	-	-	831
Logistic	None	K	-	-	-	-	-
Logistic	A	None	1357	315	-	173	794
Logistic	A	A	1345	283	-	171	795
Logistic	A	K	1345	284	-	171	796
Logistic	K	None	1406	333	-	-	813
Logistic	K	A	1398	304	-	-	808
Logistic	K	K	1386	305	-	-	809
Logistic	S	None	1401	-	-	-	821
Logistic	S	A	1393	339	-	-	-
Logistic	S	K	1392	339	-	-	-
Logistic	A-K	None	1354	315	-	-	795
Logistic	A-K	A	1345	284	-	173	796
Logistic	A-K	K	1340	286	517	170	806
Logistic	A-S	None	1357	347	-	176	794
Logistic	A-S	A	-	285	-	173	795
Logistic	A-S	K	1347	-	-	-	796
Logistic	K-S	None	1359	315	-	-	798
Logistic	K-S	A	-	292	-	172	-
Logistic	K-S	K	-	295	-	173	-
Logistic	A-K-S	None	1349	313	-	-	795
Logistic	A-K-S	A	1344	286	-	169	796
Logistic	A-K-S	K	1339	289	-	174	797
Michaelis-Menten	None	None	1516	-	541	233	-
Michaelis-Menten	None	A	1518	-	-	-	-
Michaelis-Menten	None	K	1517	628	-	225	-
Michaelis-Menten	A	None	1370	-	521	178	-
Michaelis-Menten	A	A	1359	-	607	171	-
Michaelis-Menten	A	K	<i>1358</i>	-	-	172	-
Michaelis-Menten	K	None	1365	617	519	177	1014
Michaelis-Menten	K	A	1359	629	518	-	1011
Michaelis-Menten	K	K	1356	652	-	173	-
Michaelis-Menten	A-K	None	1366	-	-	179	-
Michaelis-Menten	A-K	A	-	-	-	-	-
Michaelis-Menten	A-K	K	-	-	-	-	-
Asymptotic-with-offset	None	None	-	-	-	-	-
Asymptotic-with-offset	None	A	-	-	-	-	-
Asymptotic-with-offset	None	K	-	-	-	-	-

Asymptotic-with-offset	A	None	1365	-	-	-	790
Asymptotic-with-offset	A	A	1353	313	-	-	801
Asymptotic-with-offset	A	K	1353	-	-	-	-
Asymptotic-with-offset	K	None	1377	-	-	-	793
Asymptotic-with-offset	K	A	1371	-	524	-	795
Asymptotic-with-offset	K	K	-	335	-	-	-
Asymptotic-with-offset	C	None	-	-	-	-	-
Asymptotic-with-offset	C	A	-	-	-	-	-
Asymptotic-with-offset	C	K	-	-	-	-	-
Asymptotic-with-offset	A-K	None	1353	-	-	-	-
Asymptotic-with-offset	A-K	A	-	-	-	-	801
Asymptotic-with-offset	A-K	K	1347	-	-	-	-
Asymptotic-with-offset	A-C	None	1365	-	-	-	800
Asymptotic-with-offset	A-C	A	1355	-	-	-	802
Asymptotic-with-offset	A-C	K	1353	-	-	-	-
Asymptotic-with-offset	K-C	None	1368	369	-	-	-
Asymptotic-with-offset	K-C	A	-	-	-	-	-
Asymptotic-with-offset	K-C	K	-	-	-	-	-
Asymptotic-with-offset	A-K-C	None	1354	-	-	-	-
Asymptotic-with-offset	A-K-C	A	-	-	-	-	-
Asymptotic-with-offset	A-K-C	K	-	-	-	-	-

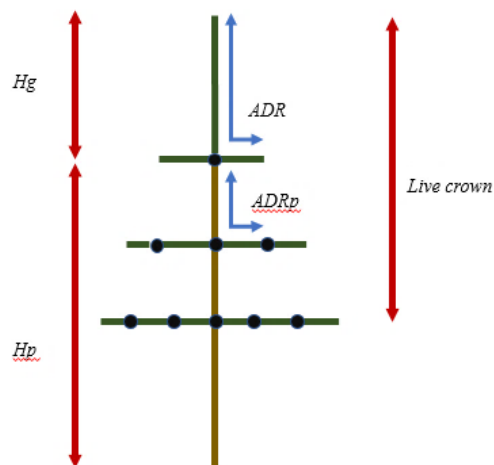


Figure S.1. Schematics of tree height and crown measurements. H_g , height growth; H_p , tree height before the growth; ADR and ADR_p , the apical dominance ratio respectively of the current vegetative season and of the previous one (the arrows showing the corresponding leader and lateral shoots).

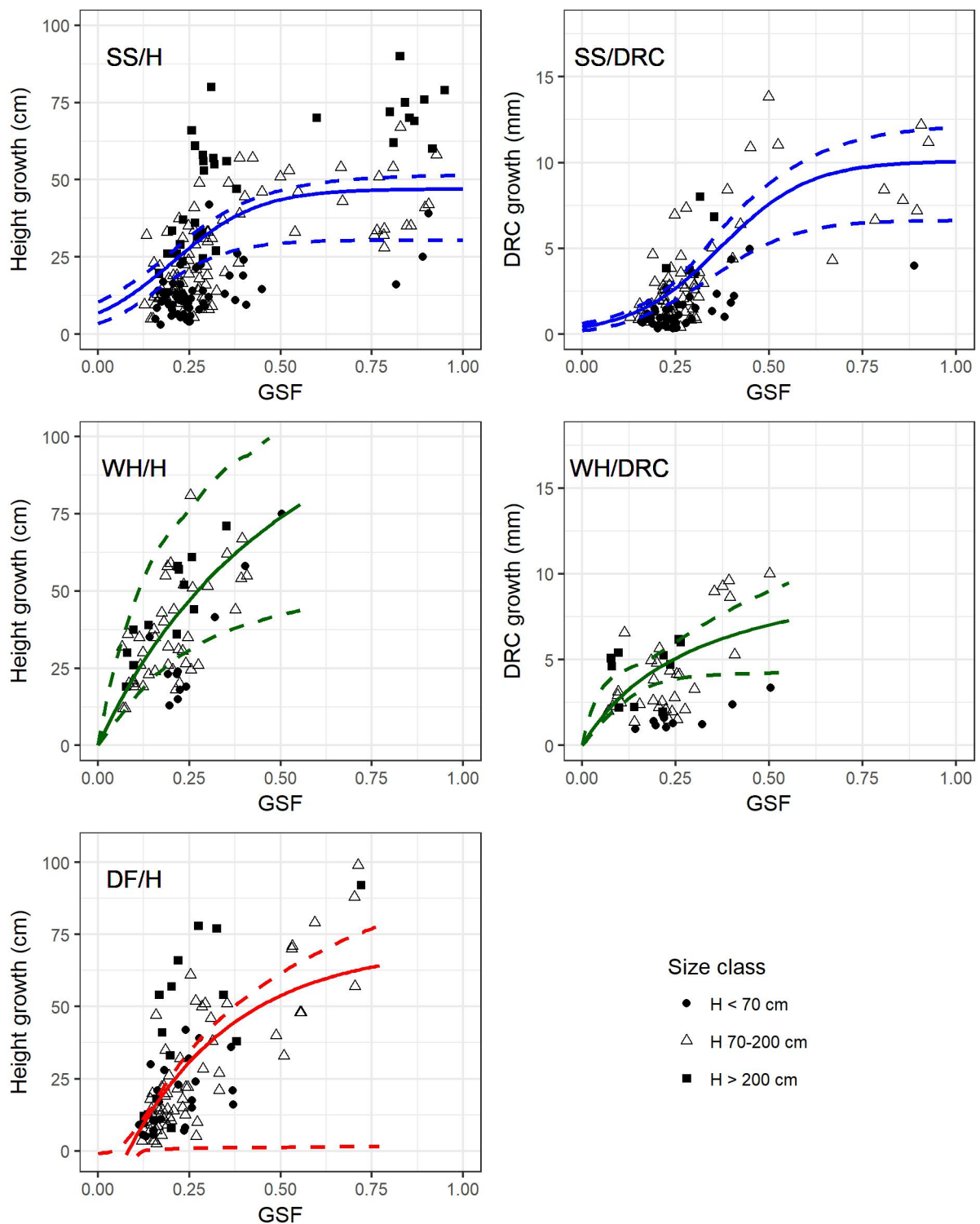


Figure S.2. Simulated growth patterns (continuous line) of each growth model as function of light (GSF, Global Site Factor), for a tree of average height or diameter, and in absence of competition, plotted with the observations (points). SS is Sitka spruce; DF, Douglas fir; WH, western hemlock; H, Height; DRC, Diameter above Root Collar; DBH, Diameter at Breast Height. The dashed lines are the upper and lower boundaries defining a 95% prediction Interval.