

Drought-related mortality modifies mixing effects on light absorption and growth in mono-specific and mixed stands of Fagus sylvatica, Alnus glutinosa and Betula pendula.

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1	Drought-related mortality modifies mixing effects on light
2	absorption and growth in mono-specific and mixed stands of Fagus
3	sylvatica, Alnus glutinosa and Betula pendula
4	
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17	
 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 	Little is known about how drought-related mortality influences light absorption of surviving trees and consequent changes in tree species interactions. Here, we used the detailed tree-level light model (Maestra) in combination with measurements of tree dimensions, crown architectures and stand structures to examine experimental mixing effects of <i>Fagus</i> <i>sylvatica</i> , <i>Alnus glutinosa</i> and <i>Betula pendula</i> on light dynamics following a drought in Bangor, Wales. The experimental stands, planted in 2004, were composed of clusters with $1 - 3$ species in different combinations. Droughts occurred in 2011 and 2014 during the growing seasons, and trees were measured in 2014 and 2015. Species mixing resulted, on average, in higher tree growth, absorption of photosynthetically active radiation (APAR) and light use efficiency (LUE) compared to the mean of the monocultures. An exception was the monoculture of <i>Betula pendula</i> which was the most productive species, and had higher growth, APAR or LUE than some mixtures. Drought-related mortality reduced stand basal area across all plots by an average of 8.3% and tree density by 11%. This moderate change in structure did not result in significant increases in individual tree APAR, LUE, or growth. From a management perspective, mortality might need to
36 37	reduce stand density more strongly than it did in this study before light absorption or light-use efficiency are altered.

39 Introduction

40 The increasing frequency, duration, and intensity of droughts is impacting different types of forest 41 ecosystems in many regions of the world (IPCC, 2013). Tree mortality rates are increasing in many 42 forest types and climate zones as a consequence of, drought, water stress, and the subsequently increased activity of biotic agents (Allen et al., 2010, 2015). This mortality can strongly modify stand 43 44 structure and thus ecosystem functioning (Klos et al., 2009; Lindner et al., 2010; Anderegg et al., 45 2013; Bennett et al., 2015; Clark et al., 2016; Seidl et al., 2017). To assess potential options to increase 46 the resilience and adaptive capacity of forests in relation to climate change, it is important to know 47 how mortality-driven changes in structure influence ecosystem functions and services. Processes such 48 as light absorption, light-use efficiency, and subsequent growth of remaining trees will likely play a 49 central role in the ecosystem response to tree mortality.

50 Currently, establishing mixed-species forests is seen as one of the main strategies to 51 increase resistance, resilience, and adaptive capacity in relation to climatic change (Bauhus et al., 52 2017a; Messier et al., 2022), in addition, mixed species forests can be more productive than the mean 53 of the individual species monocultures (Zhang et al., 2012; Jactel et al., 2017; Feng et al., 2022). One 54 of the causes of the higher productivity of mixtures is light-related species interactions (Binkley et al., 55 1992; Forrester et al., 2012, 2018; Sapijanskas et al., 2014). Absorption of photosynthetically active radiation (APAR) and light use efficiency (LUE) in mixtures are influenced by canopy 56 57 stratification (Binkley et al., 1992; Forrester et al., 2012; le Maire et al., 2013), different crown shapes 58 and architectures (Bauhus et al., 2004; Sapijanskas et al., 2014; Forrester et al., 2018), interspecific 59 differences in physiology and phenology (Binkley et al., 1992; Augspurger and Bartlett, 2003; Lopez et 60 al., 2008; Forrester et al., 2012; Vitasse, 2013; Sapijanskas et al., 2014; Gressler et al., 2015), and stand 61 density (Will et al., 2005; Forrester et al., 2013, 2018; Sapijanskas et al., 2014; Dong et al., 2016).

62 Increases in canopy tree mortality rates may alter the interactions between species within mixtures. Mortality leads to open spaces in forest canopies, similar to thinning from above, and can also change 63 64 the vertical structure by removing species or trees that occupy specific positions within the canopy, 65 e.g. a thinning from below that removes overtopped and intermediate trees or subcanopy 66 species. Thinning usually leads to an increase in the productivity of the residual trees (Smith et al., 67 1997; Bauhus et al., 2017b) which may partly be caused by an increase in APAR or LUE of retained 68 individual trees. West and Osler (1995) found an increase in individual tree growth after thinning on 69 two sites of *Eucalyptus regnans*, which resulted from higher individual tree APAR. When there was no 70 understory, thinning also resulted in higher individual tree LUE. Increases in individual tree APAR and 71 LUE following thinning have also been reported in other studies (Forrester et al., 2013; Gspaltl et al., 72 2013). Tree loss by mortality, although a more gradual process than tree removal through thinning, 73 could have similar effects to thinning on APAR, LUE and growth.

74 Unlike thinning, the effect of natural mortality on APAR and LUE in mixed-species forests has received 75 very little attention. Therefore, the objective of this study was to examine how mortality in a 76 tree diversity experiment influenced tree and stand APAR and LUE. The experiment contained plots 77 with 1, 2 and 3 species-mixtures of *Fagus sylvatica, Alnus glutinosa* and *Betula pendula* in Bangor,

- Wales. All plots that were examined for this study included drought-induced tree mortality and weremeasured in the year that followed the drought.
- 80 We tested the following hypotheses:
- 1) Increases in APAR and LUE are both responsible for complementary effects on tree growth inmixtures compared with monocultures.
- 2) Intra-specific differences in crown architecture (in addition to inter-specific differences) contribute
 to increases in APAR and LUE in mixtures.
- 3) A reduction in stand density due to mortality results in an increase in individual tree growth, APARand LUE.
- 87

88 Methods

89 Site description & Experimental design

- 90 The investigations took place in some of the plots within the BangorDIVERSE experiment which is
- 91 part of TreeDivNet, a global network of tree diversity experiments. It was established with a total
- 92 area of 2.36 ha in March 2004 at the Henfaes Research Centre of Bangor University in Wales (UK)
- 93 (53° 14' 16.382"N, 4° 1' 0.922"W) at 13 18 m a.s.l near the coast (Ahmed *et al.*, 2016). Soils
- 94 are classified as Eutric Fluvic Cambisols (IUSS Working Group WRB., 2006) (Fluventic Dystrochrept,
- USDA system) and have fine loamy texture (Smith *et al.*, 2013).
- 96 The experiment has a hexagonal planting design where each species was planted with an inter-tree
- 97 spacing of 1 × 1 m (10 000 trees ha⁻¹). Each hexagonal plot originally contained 94 trees and a two-
- 98 row buffer strip with an additional 78 trees. In the plots that were examined in this study the species
- 99 pool containing Alnus glutinosa, Betula pendula and Fagus sylvatica was used to create a diversity
- 100 gradient comprising one-, two-, and three-species communities. This study was performed inll
- 101 species combinations (n=7) that occurred in oval or circular clusters of trees (Figure 1) and each of
- 102 the hexagonal plots was replicated five times, totalling 35 clusters. The two-row buffer strip
- 103 combined with the gradual change in species composition within each hexagon, from one cluster to
- 104 the next, is expected to minimise any potential edge effects between species combinations. During
- 105 data collection late in the summer of 2015, it was noticed that a considerable proportion of trees
- 106 had died since the inventory in 2014. Using the meteorologically data that were logged on-site, we
- 107 found that since the beginning of the experiment, we identified droughts occurring in 2011 and
- 108 2014, especially during the growing seasons when only half of the long-term average precipitation
- 109 occurred (Table 1). Prior to 2011 there had been negligible mortality within the plots.
- 110
- 111 *Quantification of the vertical structure and distribution of leaf area and leaf-area density*
- All tree diameters at 1.3 m (DBH) were measured in April 2014 and September 2015. To quantify the
- leaf area and leaf-area density distribution of each tree, we took detailed tree measurements for each
- of the three species on one individual in each species combination (cluster) and replicated it in each

plot in 2015. This procedure included measuring the following variables: diameter at 1.30 m, height, 115 live-crown length, crown area, as well as the diameters, heights, and cardinal directions (divided into 8 116 117 segments: N, NE, E, SE, S, SW, W, NW) of all branches on each of the sample trees. In addition, the 118 mean branch angle from the horizontal was estimated for each quarter of the live-crown length. A 119 sample branch was then taken from each quarter of these target trees to measure the mean leaf 120 angles from the horizontal, the branch length, leaf area, and leaf dry mass. For the latter, all leaves were removed from the sample branches, dried at 70°C, and weighed. Before drying, the leaf area of 121 122 a subsample was determined using the leaf area meter LI-3050C Transparent Belt Conveyor Accessory 123 (LI-COR Biosciences GmbH, Bad Homburg, Germany) to calculate the specific leaf area (m² kg⁴) for the 124 branch and thus the leaf area from the product of specific leaf area and leaf-dry weight of the branch. 125 In the next step, we used the branch measurements to develop allometric equations (as shown in 126 Equation 1) for each species to calculate all branch lengths within the crowns and the leaf area of all 127 target trees.

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d_b) + \beta_2 \ln(rh) + \beta_3 \left(\ln(d_b) * \ln(rh)\right) + \varepsilon$$
(1)

128

129 Where Y is branch length or branch leaf area, d_b is branch diameter, rh is relative height of the branch 130 within the live-crown length (base = 1, top = 0), and ε is a correction ratio used when back-131 transforming the In- transformed Y- variables. The correction ratio was calculated as the sum of the measured values divided by the sum of the (back-transformed) predicted values (Snowdon, 1991). All 132 133 allometry parameters are shown in the supporting information. The leaf area of a given branch was 134 assumed to be distributed evenly between the base of the branch, where it joined the tree stem, 135 and the height of the branch tips, which was calculated using the branch length and branch angle 136 measurements as described in Medhurst and Beadle (2001) and Forrester et al. (2013). In the last 137 step, the leaf area density (LAD, m² m³) was calculated by dividing the total crown into 10 layers. Each 138 layer contributed 10% of the live-crown length, and was assumed to have a volume of a semi-elliptical 139 cone for the top layer or a frustum of a semi-elliptical cone for the other nine layers (Equation 2). The 140 vertical distribution of LAD was fitted to a beta distribution (Equation 3, Wang et al., 1990) where the 141 LAD of a layer was a function of its relative height within the crown. The parameters of this 142 equation are required inputs to run the Maestra model (Grace et al., 1987; Wang and Jarvis, 1990; 143 Medlyn, 2004; Duurma and Medlyn, 2012), which was used to calculate individual tree APAR.

144

$$V = \frac{2}{3}\pi * h * r^{2} + \sum_{l=2}^{10} h * (d_{basal}^{2} + d_{top}^{2} + d_{basal} * d_{top}) * \frac{\pi}{12}$$
(2)

145

148

146 Where *V* is the total crown volume, *h* the height of the layer, *r* is the radius of the cone for the top 147 layer, d_{basal} is the crown diameter of the base of the frustrum and d_{top} the crown diameter of the top.

$$Y = a(x^b) * (1 - x)^{cc}$$
(3)

149 Where *a*, *b* and *cc* are fitted parameters, and *Y* is the leaf area density ($m^2 m^3$) at a relative height 150 of *x* within the canopy.

152 Field measurements and quantification of structure and growth at the tree and stand levels

- 153 In addition to the target trees mentioned above for which we measured individual tree leaf area (*la*),
- 154 crown diameter and vertical distribution of LAD, we also measured height and live-crown length for
- all trees within the plot, as well as DBH of all trees within the plot and the surrounding buffer trees. For
- all other trees, including buffer trees, the height, leaf area, crown diameter, and live crownlength were determined by predicting these variables as a function of DBH, separately for each

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(DBH) + \varepsilon$$

(4)

- 159 Where Y is height, leaf area, crown diameter, and live crown length, and ε is a correction ratio used 160 when back-transforming the ln- transformed Y- variables. The correction ratio was calculated as the 161 sum of the measured values divided by the sum of the (back-transformed) predicted values (Snowdon, 162 1991). Individual crown volumes (m³) were calculated for each tree from their crown diameter 163 and live-crown length by assuming semi-elliptical shapes (Equation 2).
- 164 Individual tree basal area increment (cm² year¹) was calculated by combining the DBH measurements 165 from 2015 with those of the previous inventory in 2014. We also recorded trees that had recently died 166 due to drought. This allowed us to use our allometric equations to calculate all variables for trees 167 that were alive in the previous inventory. We were therefore able to quantify the structure of the plots before and after the drought-related tree death. The Maestra model was then used to calculate the 168 169 individual tree APAR for two cases: a) following the mortality event (all trees that have died have no 170 leaves) and b) for the same structure as if no trees had died during the drought, assuming all trees still 171 have leaves.
- Stand variables calculated included the relative height, mean stand height (m), tree density (trees ha-173 ¹), leaf area index (m² m⁻²) basal area (m² ha⁻¹), basal area increment (m² ha⁻¹ year⁻¹), canopy depth (m), canopy-volume(m³ ha⁻¹) and canopy–leaf area density (m² m⁻³). The relative height of a given species was calculated as the mean height of the target species divided by the mean height of the total cluster. The canopy depth was calculated from the difference between the hight of the tallestestspan style="font-family:Calibri"> tree in a cluster and the height of the crown base of the tree with the lowest crown in that cluster.
- 179 To illustrate the change in stand structure caused by drought-related mortality, we examined 180 diameter distributions corrected for the species proportions (Supplementary Figures S1-S3; Figure 3). 181 That is, the number of trees in each diameter class was divided by the proportion of stand basal 182 area contributed by that species (not by the diameter class). The trend curves (Figure 3) were obtained using Friedman's SuperSmoother (Friedman, 1984b, 1984a) to smooth the (x,y) values. We 183 184 used the R function 'supsmu', from the 'stats' package and R 4.0.3 (R Core Team, 2020), which is a running lines smoother which chooses between three spans for the lines (Friedman, 1984b, 1984a). 185 186 The running lines smoothers are symmetric, with k/2 data points on each side of the predicted point, 187 and values of k as $0.5 \times n$, $0.2 \times n$ and $0.05 \times n$, where n is the number of data points. The best of the 188 three smoothers was chosen by cross-validation for each prediction. The best spans were then 189 smoothed using the running lines smoother and the final prediction chosen by linear interpolation.
- 190

191 *Climate data*

192 We obtained meteorological data from the ERA-Interim reanalysis daily dataset produced by the European Centre for Medium-Range Weather Forecasts (ECMWF) with a high spatial 193 194 resolution $(0.125^{\circ} \times 0.125^{\circ})$ (Dee et al., 2011). The climatic variables included monthly and daily mean 195 temperature, precipitation, solar radiation and thnumber of frost days. We extracted daily data 196 on surface solar radiation downwards (SSRD), from 2012 to 2017 and monthly climate data from 1979 197 to 2017. In addition, we obtained on-site meteorological data (based on hourly means) from 198 the Henfaes Research Centre of Bangor University for 2004 – 2014 to determine the precipitation 199 pattern for this period. The solar radiation was used as input to the Maestra model to calculate APAR 200 and LUE.

201

202 MAESTRA Light modelling to estimate APAR

203 Individual tree APAR was calculated using the MAESTRA model (Grace et al., 1987; Wang and Jarvis, 204 1990; Medlyn, 2004; Duursma and Medlyn, 2012). This 3D tree-level model calculates individual 205 trees' APAR based on their individual crown architecture (e.g. crown dimensions and leaf area and leaf 206 angle distributions), leaf optical properties (LAD and distribution, leaf transmittance and reflectance), 207 and the shading from neighbouring trees based on the positions of other trees within the plot (defined 208 by x and y coordinates, the slope and aspect of the site) and their crown architectures (e.g. Figure 2). 209 The growing season has been defined by the site-specific phenology of the leaf-bearing period of the 210 three species we studied. This was from Julian day 111 to Julian day 303. APAR was calculated for the 211 growing season (defined by the leaf-bearing period) and also for the whole year. The parameterization 212 data we used are provided in Supplementary Table S1.

213

214 Estimation of LUE and relative productivity (RP)

Tree level LUE (cm² GJ⁻¹) was calculated as the basal area increment of the individual tree (cm² year⁻¹) per APAR (GJ year⁻¹). Stand level LUE (m² GJ⁻¹) was calculated as the basal area increment of the whole

217 community (cluster) (m^2 ha-1 year-1) per APAR (GJ ha-1 year-1).

218 The relative productivity variable (Equations 5 and 6) quantifies whether mixing led to an increase 219 (RP>1) or decrease (RP<1) in a given variable compared to a monoculture at the stand level, per 220 species (Equation), or the whole plot community (Equation 5) (Williams and McCarthy, 2001; 221 Forrester and Pretzsch, 2015). The RP also accounts for the proportion of the species in the mixtures, 222 which was quantified in terms of leaf area index (LAI; m² m⁻²) or stand basal area, depending on the 223 response variable. For response variables tree density, basal area and basal area increment, we 224 quantified the species proportions in terms of stand basal area. All other proportions for the canopy 225 and light variables (canopy-depth, -volume, -proportion of canopy filled with tree crowns, -LAD, APAR 226 and LUE) were quantified in terms of LAI because it is considered more representative of the species 227 contributions to light dynamics, and species proportions by leaf area have been shown to provide 228 realistic estimates of species proportions on an area basis (Dirnberger and Sterba, 2014).

$$\operatorname{RP}_{\operatorname{community}} = \frac{p_{mix^{sp1, sp2, \dots}}}{::_{sp1}p_{mono^{sp1}} + ::_{sp2}p_{mono^{sp2}} + \dots}$$

(5)

$$RP_{species} = \frac{p_{mix^{sp1, (sp2...)}}}{::_{sp1}p_{mono^{sp1}}}$$
(6)

In Equation 5, is the productivity (or the performance of another response variable) of the
mixed species stand in relation to the productivity of their related monocultures (,)
and their proportional (,) amount on LAI or stand basal area depending on the stand variable
considered. Equation 6 is used to determine the relative productivity by species where is
the productivity of a given species (sp1) in a mixture with (sp2).

235

236 Statistical analysis

Differences between species mixing treatments or between species were examined using a Tukey test. All variables were visually assessed for normality. Regression models were fitted as hierarchical mixedeffects models using the R package nlme (Pinheiro *et al.*, 2020) and R 4.0.3 (R Core Team, 2020). To ensure that residuals were centred at zero and approximately normally distributed, the residual and normal quantile plots were assessed. For branch-level regressions, the random effect was tree nested within plot, and for tree-level regressions the random effect was the plot.

243

244 Results

245 Tree level effects of mixing, mortality, and stand structure

Across all clusters, the highest mortality rate occurred in *A. glutinosa* which resulted in a 21% reduction in basal area and a 32% reduction in tree density (Supplementary Table S2). The greatest reduction in *A. glutinosa* density occurred in the 3-species mixture and included trees from all diameter classes. In the monoculture and 2-species mixtures, mortality decreased from smaller to medium diameter classes (Supplementary Figure S2 (a-d)).

251 For A. glutinosa, DBH, height, live-crown length, and crown volume were larger in the mixture 252 with *B. pendula* than in monoculture (Table 2). When in combination with F. sylvatica, B. pendula crown parameters were not significantly larger, but DBH and leaf 253 254 area were higher compared to monocultures (Table 2). We found these differences in terms of the mixture before as well as after tree mortality, but we found no effect within the mixtures and 255 256 within the monoculture due to mortality. When A. glutinosa and B. pendula were mixed with the smaller F. sylvatica, the relative height increased accordingly for both species and decreased 257 258 for F. sylvatica. APAR was higher for the trees in 2-species mixtures without any B. pendula compared to the trees in monocultures or the 3-species mixture. This mixing effect only occurred for stands 259 260 containing *B. pendula* after the occurrence of mortality (Table 2) which, was the largest in 261 these clusters. Basal area growth and light use efficiency increased when growing with F. sylvatica (Table 2). 262

Drought-related mortality decreased the basal area of *B. pendula* by 3.1% and tree density by 9.9% (Supplementary Table S2). Only the smallest diameter classes were affected and almost all of them were in the monoculture and the 3-species mixture (Supplementary Figure S3 (a-d)). Nearly all examined tree variables, except LUE, increased for *B. pendula* when mixed with *F. sylvatica* (Table 2). In contrast, when *B. pendula* was combined with *A. glutinosa* or was in the 3-species mixture, there were no significant changes in its tree-level variables when compared to the monoculture. There wasno significant effect on these mixing results due to mortality within these clusters.

270 Unlike B. pendula, F. sylvatica showed a reduction in some variables in the 2-species combination 271 with B. pendula (Table 2). Since basal area growth remained the same, while a reduction in APAR 272 occurred, this led to a higher LUE compared to monocultures (Table 2). The relative height 273 of F. sylvatica was reduced by the presence of the two taller tree species in mixtures. Nevertheless, 274 with A. glutinosa as a neighbour, F. sylvatica was able to increase live-crown length, leaf area, crown 275 volume and also APAR (Table 2). In the 3-species mixture, in addition to the higher live-crown length, 276 crown volume, and APAR, F. sylvatica even achieved higher basal area growth as well as an increase 277 in LUE (Table 2). Mortality in *F. sylvatica* was negligible.

We did not detect any major shifts in species proportions due to mortality (Figure 3 e-l). However, there were small shifts in tree size distributions towards larger diameter classes for *B. pendula* and *A. glutinosa*, while for *F. sylvatica*, the smallest species, the mortality of the other two species caused a corresponding shift towards the smaller diameter classes (Figure 3 e-l).

Individual tree APAR was positively correlated with tree leaf area for all species (Supplementary Figure S4). For a given tree leaf area, APAR of *B. pendula* was significantly greater in 3-species mixtures and when combined with *F. sylvatica*, but significantly lower when mixed with *A. glutinosa* than in monocultures. *A. glutinosa* in a mixture with *F. sylvatica* and in 3-species mixture had a significantly greater APAR for a given leaf area compared to their monoculture. For *F. sylvatica* APAR remained the same as in all treatments (Supplementary Figure S4).

288

289 Stand level effects of mixing and mortality

290 Mortality within clusters reduced basal area by 8.3% and density by 11% (Supplementary Table S2). 291 As the smaller and medium diameter classes within the two larger species were mainly affected by 292 mortality, there was a decrease in the frequency of these diameters for the total stands of the 2- and 293 3-species mixtures (Figure 3 a-d). The visual inspection ofhe diameter class distribution was only 294 changed by mortality in the 3-species mixture, where we observed a shift toward the smaller diameter 295 classes (Figure 3 d).

296 The two-species mixture of *F. sylvatica* and *B. pendula* showed higher tree density, LAI, canopy depth, 297 canopy volume, and a higher proportion of filled canopy space when compared to the monoculture 298 of B. pendula (Supplementary Table S3, Figure 4 a, c). Compared to 299 the F. sylvatica monoculture canopy depth and canopy volume as well as basal area and basal area 300 growth were also higher in the mixture (Supplementary Table S3; Figure 4 a, d). Both species absorbed 301 more PAR in 2-species mixture than the respective monocultures 302 (Figure 4 e; Supplementary Table S3). The mixture of these species also achieved the highest overall 303 values in terms of canopy volume, LAI, basal area increment and APAR compared to all other clusters 304 (Figure 4 a, c-e).

The combination of *B. pendula* and *A. glutinosa* led to higher total means of LAI, canopy depth, canopy voume, basal area, and basal area increment as well as higher APAR when compared with the monoculture of A. *glutinosa* but not when compared with the *B. pendula* monoculture (Supplementary Table S3; Figure 4 a, c-e). The 2-species mixture of *F. sylvatica* and *A. glutinosa* resulted in higher tree density, LAI, canopy depth, canopy voume, proportion of filled canopy space, and APAR in comparison to the monoculture of *A. glutinosa*, and higher canopy depth, and basal area , but lower proportion of filled canopy space, than in the *F. sylvatica* monoculture (Supplementary Table S3, Figure 4 a, c, e). Both basal area increment and LUE were also higher in the mixture than in respective monocultures. Here, after the onset of mortality LUE for *A. glutinosa* became higher in the mixture than in the monoculture (Supplementary Table S3; Figure 4 f). No other mortality effects were significant.

316 The 3-species mixture showed higher tree density, LAI, canopy depth, canopy volume, proportion of 317 canopy space filled, and APAR when compared with A. glutinosa monocultures and lower tree 318 density and proportion of canopy space filled, but higher basal area and canopy depth, when 319 compared with F.&#a0;sylvatica monocultures before and after the drought-related mortality, except 320 APAR which was also higher in the 3-species mixture before mortality than 321 in F. sylvatica monocultures (Supplementary Table S3; Figure 4 b, c, e). There were no significant 322 differences between response variables in B. pendula between its monoculture and the 3-species 323 mixture, except for *canopy depth*. This pattern did not change with the following mortality.

324

325 Diversity level effects of mixing and mortality

326 On average, mortality reduced basal area across the three diversity levels by 16.2% across all 3-species 327 mixtures, 8.9% across all monocultures and 5.2% in the 2-species mixtures (Supplementary Table S2). 328 In terms of diversity level, 2-species mixtures benefited most compared to monocultures regarding 329 nearly all variables (Supplementary Table S4, Figure 5 a, c-f). The 3-species mixtures also 330 benefited compared to monocultures, except for tree density, basal area and LUE 331 (Supplementary Table S4; Figure 5 a, c-e). The canopy leaf area density was highest in monocultures 332 and significantly lower in the mixtures, which then did not differ further among the different mixtures. 333 Within a diversity level, mortality only led to a significant reduction in tree density in the 3-species 334 mixture (Supplementary Table S4). As a result of this mortality, the APAR of 3-species mixtures was 335 significantly lower than in 2-species mixtures, which was not the case before the mortality occurred (Figure 5 e). In contrast, mortality within the 3-species mixtures resulted in a slightly non-336 337 significant increased LUE, which was then not statistically different from the 2-species mixtures whereas this was the case before the mortality occurred. (Supplementary Table S4; 338 339 Figure 5 f).

340

341 Discussion

342

The basal area growth was lower, on average, in the monocultures (0.95 m² ha⁻¹ yr⁻¹) than in the 2species mixtures (2.1 m² ha⁻¹ yr⁻¹) and 3-species mixture (1.4 m² ha⁻¹ yr⁻¹). This was associated with higher APAR in the 2-species mixtures (18.3 GJ ha⁻¹ 10⁻³) and 3-species mixture (15.2 GJ ha⁻¹ 10⁻³) when compared to the monocultures (11.3 GJ ha⁻¹ 10⁻³). The stand LUE was also higher in the 2-species mixtures (109 m² GJ⁻¹ × 10⁶) and 3-species mixture (92 m² GJ⁻¹ × 10⁶) than in the monocultures (73 m² GJ⁻¹ × 10⁶). These findings are in accordance with <u>hypothesis 1</u> and with results from other studies which showed that higher growth in mixtures is often associated with increases in both APAR

and LUE (Binkley et al., 1992; Forrester et al., 2012; Forrester and Albrecht, 2014; Forrester, 2019). 350 351 Here, this result is predominantly attributable to tree species identity effects. For example B. 352 pendula was generally more productive and had higher APAR and LUE than the other species and 353 also maintained these advantages when growing in mixtures (Figure 4 D-F). Similarly, LAI was highest 354 in F. sylvatica monocultures and when this species was present in the mixtures, it increased LAI and 355 canopy volumes in these stands. As a result, the F. sylvatica-B. pendula mixture had the highest APAR 356 of any treatment, regardless of mortality effects (Figure 4 a, c, e). Species identity appear to have been 357 an important determinant of mixing effects on growth and APAR in most studies (e.g., le Maire et al., 358 2013; Forrester et al., 2019). This enhancement of APAR, and hence the growth of mixtures, was 359 probably at least partly caused by inter-specific differences in tree size (crowns, heights, crown 360 lengths), crown architecture (leaf angles), tree allometry and the effect these had on canopy attributes (e.g. varying leaf area density, canopy stratification, canopy volume). Inter-specific differences in 361 physiology, such as photosynthetic rates, LUE and the often observed synergistic effect of mixing fast-362 363 growing shade-intolerant species with initially slow-growing shade-tolerant species, may also have contributed to mixing effects on LUE, as was found in previous studies (Binkley et al., 1992; 364 365 Forrester et al., 2012; Baeten et al., 2019; Serrano-León et al., 2022).

Differences in growth or light absorption have also been linked to intra-specific differences in 366 367 physiology, mean tree sizes, crown architectures (e.g. leaf angles), and allometric relationships between stem size and crown characteristics (Sapijanskas et al., 2014; Dong et al., 2016; Forrester et 368 369 al., 2018; Serrano-León et al., 2022). In this study, there were only minor differences in allometric 370 relationships (e.g. Figure S4) and specific leaf area for a given species in the different species 371 combinations. Therefore, intra-specific variability may not have been as important in these stands. 372 There were also negligible shifts in the partitioning of light between size classes, such that competition 373 for light for all species was generally size-symmetric or slightly asymmetric as indicated by the linear 374 relationships between individual tree leaf area and APAR (Figure S4). While these findings contradict 375 our second hypothesis that intra-specific differences in crown architecture (in addition to inter-376 specific differences) contribute to increases in APAR and LUE in these mixtures, similar results have 377 been obtained in previous studies (e.g. Forrester, 2019; Plaga et al., "in review").

378 The drought-related mortality reduced stand basal area by only 8.5% and tree density by 11%. This 379 minor reduction in stand density had no significant influence on stand growth, APAR or LUE and no 380 influence on individual tree growth following the drought. This is consistent with many thinning 381 studies showing that minor changes in stand density (< 20% reduction in basal area) have little 382 influence on growth (Stoneman et al., 1996; Mäkinen and Isomäki, 2004; Will et al., 2005). Studies 383 that found such effects on growth and APAR were typically conducted at much higher thinning intensities, for example with a 65% reduction in tree density (Forrester, 2013) or a 74% reduction in 384 385 basal area (West and Osler, 1995; Gspaltl et al., 2013). This indicates that unless mortality removes 386 much larger proportions of stand density, it is unlikely to influence APAR.

Given the strong correlation between radiation, temperature and vapour pressure deficit under forest canopies, the minimal effects of mortality on APAR in this study may be associated with minimal effects on below canopy microclimates. Therefore, mortality or thinning events that remove small proportions of overstorey stand basal area may have a negligible influence on the ability of forests to function as an insulator for understorey communities (Davis et al. 2013; von Arx et al.
2012; Zellweger et al. 2020).

393 A small effect of mortality could only be observed for A. glutinosa, where mortality reduced their basal 394 area across all stands by 21% and even 63% in the 3-species stands (Supplementary Table S2) in which 395 all diameter classes of A. glutinosa were affected. This supports our assessment that APAR or LUE 396 will only change significantly when larger proportions of the stand density die . The reason for the 397 much higher drought-related mortality in A. glutinosa may be attributed to its preference for moist to 398 wet soil conditions (Houston Durrant et al., 2016; CABI, 2022). Although we observed a few small 399 changes in growth, APAR and LUE due to mortality, the gradient in mortality across the experiment 400 was too small to robustly test the third hypothesis, that a reduction in stand density due to mortality 401 results in an increase in individual tree growth, APAR and LUE. Changes in the structure after 402 drought could probably similarly influence APAR, but for this to happen, the effects of drought must 403 be much stronger than in this study.

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405 The results of this study should be interpreted with caution when extrapolating to other forests given 406 the young age of this experiment (10 years old), the high planting density of 10,000 plants per ha, and 407 the strong influence that site conditions (e.g. resource availability and climatic conditions) can have 408 on mixing effects. Crowns may be more responsive at this age than in older stands, and as trees age 409 there are changes in crown architecture and morphology (e.g. specific leaf area, leaf angle 410 distributions), and canopy structure that can influence APAR. Furthermore, drought can influence 411 mortality for several years following the end of a drought and our data collected only one year after 412 the drought may hence not yet capture all effects induced by the drought (Bigler et al., 2006, 2007; 413 Cailleret et al., 2017; Klockow et al., 2018; Powers et al., 2020; Trugman et al., 2021). 414 In our experiment, there was negligible mortality prior to 2011, and therefore, we assume that the 415 majority of mortality in this study was caused by drought. Trees that appeared to be dying in 2015 did 416 not recover, and we assumed there was negligible additional mortality after our measurements until 417 another severe drought in 2018, so it is likely that the major influence of the 201and 2015 drought on 418 APAR was quantified. Given that all plots were influenced by the drought, it is not possible to 419 distinguish the effect of changes in density on tree growth and LUE from those caused by water stress 420 during the drought.

The magnitudes of the mixing effects found in this study should not be extrapolated to other sites given that the relative sizes of mixing effects on growth can change with resource availability and climatic conditions (e.g. Forrester, 2014). These spatial dynamics of mixing effects could be examined by replicating mixtures along site gradients in resource availability and climatic conditions. They could also be predicted using process-based models that have been validated for their ability to predict mixing effects in forests, such as the 3-PG model (e.g. Forrester et al., 2017a).

The estimates of APAR obtained using the Maestra model in this study will be influenced by the model inputs for each individual tree. It was not possible to measure the leaf areas, vertical crown leaf area density distributions, or leaf angles for all trees and therefore allometric relationships were used. Allometric relationships between tree size and foliage mass or area for a given species can when it is growing in a mixture with other species (e.g. Laclau et al., 2008) and stand density (e.g. Monserud and Marshall, 1999; Forrester et al., 2017b). Similarly, mixing can influence the vertical distribution of leaf area within tree crowns (Garber and Maguire, 2005; Binkley, 1992).
Therefore trees from all treatments were sampled and used to derive the inputs for the Maestra
model. We assume that the APAR estimates used in this study are reliable because the mixing effects
on allometry and vertical crown leaf area density distributions were accounted for, and several studies
have found accurate comparisions between Maestra predictions of APAR and observed APAR or APAR
estimated using hemispherical photography (Charbonnier et al. 2013; le Maire et al. 2013; Forrester
et al. 2018, 2019).

- 440
- 441

442 Conclusion

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In conclusion, species mixing increased growth, APAR and LUE compared with the mean of the monocultures, with the exception of the most productive monoculture of *B. pendula*. The reduction in stand density caused by drought-related mortality was too small to notably influence APAR, LUE or growth. This is consistent with previous studies where greater reductions in density by thinning were required to significantly increase APR. With regards to forest management, minor reductions in stand density may be unlikely to cause significant effects on stand APAR, LUE, or growth.

450

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452

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465 **Conflict of interest statement**

466 None declared

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468 Data availability statement

469 The data underlying this article will be shared on reasonable request to the corresponding author.

- 470
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713 Table and Figure captions

Figure 1. Planting design of the mixing experiment hexagonal plots, which was replicated five times; A_x with green dot = A. glutinosa; B_x with blue dot = B. pendula; F_x with red dot = F. sylvatica; Ex_{xx} with black dots = buffer trees. The ovals with solid borderlines indicate mono-specific clusters, the ovals with dashed lines indicate clusters with two-species mixtures, and circles with dashed lines comprise tree clusters with the three-species mixture. The design minimises edge effects by placing similar cluster next to each other. Edge effects were not addressed in the analysis.

Figure 2: 3-D representation of one plot with all seven clusters without the buffer tree rows illustrating
 the canopy structure in terms of vertical stratification, canopy gaps and closure, horizontal
 overlapping and interlocking of the crowns. Trees with green crowns represent *F. sylvatica*, grey
 represents *B. pendula* and golden brown shows *A. glutinosa*.

- Figure 3 Size distributions illustrating the change in stand structure caused by drought-related mortality in *A. glutinosa – B. pendula* stands (a,e,i), *A. glutinosa-F. sylvatica* stands (b,f,j), *B. pendula-F. sylvatica* stands (c,g,k), and all 3 species (d,h,l). The size class is 1 cm. Trend curves were plotted by the use of Friedman's SuperSmoother (Friedman J.H., 1984b, 1984a) to smooth the (x,y) values. Note the different scales on the y-axes.
- 729 Figure 4 Means of canopy volume (a), canopy leaf area density (b), leaf area index (c), stand basal area 730 increment (d), annual absorption of photosynthetic active radiation APAR (e), and light use efficiency 731 (f) with and without recently died trees across all monocultures and mixtures. F. syl = F. sylvatica, B. 732 pen= B. pendula, A. glu = Alnus glutinosa in monoculture. B. pen F. syl, A. glu F. syl and A. glu F. syl = 733 species combination in two species mixture. A. qlu, B. pen, F. syl = three species mixture. Error bars 734 indicate the 95% confidence interval of LS mean. Means sharing a letter are not significantly different 735 (Tukey adjusted comparisons (p-value) with significance level alpha = 0.05; variables and 736 residuals were visually inspected for normality)
- 737

Figure 5. Means of canopy volume (a), canopy leaf area density (b), leaf area index (c), stand basal area increment (d), annual absorption of photosynthetic active radiation APAR (e), and light use efficiency (f) with and without recently died trees across all three diversity level. Error bars indicate the 95% confidence interval of LS mean. Means sharing a letter are not significantly different (Tukey adjusted comparisons (p-value) with significance level alpha = 0.05; variables and residuals were visually inspected for normality)

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Table 1: Mean annual precipitation, temperature and aridity index at the experiment. DOY are the
 Julian days 111 and 303 of the year that define the growing season. The aridity index is calculated from

751 the amount of precipitation (P) and temperature (T) as P/(T+10) (Martonne, 1926).

	All year			Growing season - (DOY=111-303)				
	1979- 2017	2011	2014	1979- 2017	2011	2014		
Precipitation (mm)	1013.1	471.8	621.2	567.4	270.8	270.4		
Mean temperature (°C)	9.4	11.4	11.9	12.65	14.0	14.5		
Aridity Index	52.2	22.1	28.4	25.1	11.5	11.1		

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755 **Table 2.** Mean tree variables in a planted tree diversity experiment for each species across all monocultures and mixtures in Bangor. Trees were planted in

756 2004 and measured in 2015. Black and grey/brown font indicates the means following mortality and the means recalculated assuming no drought-related

757 tree deaths, respectively. Values printed in bold and with different letters within a row indicate significant differences between mixing

treatments and mortality (P < 0.05) Compact letter display of all pairwise comparisions of least-squares means was generated using the R function 'cld'
 implemented in the multcomp package (Piepho, 2004). Significance of diversity treatments (div.level), mortality and their interaction are provided in the

760 three right columns.

Variable	Monoculture		2 species Mixture		2 species Mixture		3 species	s Mixture	p-value		
<i>F. sylvatica</i> (n=145 n=146)			+ A. glu	tinosa	+ B. pen	dula	+ A. glut + B. pend	inosa dula	div.level	mortality	interaction
Diameter (cm)	2.35 °	2.38 -	2.75 °	2.75 [.]	1.93 •	1.93 ^b	2.56 ^a	2.56 ^a	<0.0001	0.921	0.998
Height (m)	4.17 °	4.21 -	4.59 ^a	4.59 [•]	3.58 °	3.58 ^b	4.25 °	4.25 ^a	<0.0001	0.927	0.999
Crown diameter (m)	4.23 bc	4.26 ab	4.57 ^a	4.57 ^a	3.93 °	3.93 ·	4.37 ab	4.37 ^{ab}	<0.0001	0.941	1
Live-crown length (m)	2.89 °	2.91 ^a	3.70 ^b	3.70 ^b	2.61 °	2.61 *	3.49 °	3.49 ^b	<0.0001	0.956	1
Height to the live crown (m)	1.28 °	1.3 °	0.89	0.89 bc	0.97 •	0.97 ^b	0.76 °	0.76 °	<0.0001	0.926	0.999
Leaf area (m ²) **	4.80 °	4.94°	6.87 ^b	6.87 ^b	3.33 °	3.33 °	5.81 ab	5.81 ^{ab}	<0.0001	0.922	0.999
Crown volume (m ³) **	29.12 ac	29.67 ^a	43.87	43.87 ^b	22.33 °	22.33 °	36.93 •	36.93 •	<0.0001	0.946	1
Relative height	1 ª	1 -	0.81 ^b	0.83 •	0.56 °	0.56 ·	0.67 d	0.68 d	<0.0001	0.671	0.972
APAR (GJ tree -1 season -1) *	0.79ª	0.84 ^{ab}	1.21 bc	1.31 °	0.53 d	0.56 ad	1.16 bc	1.25 °	<0.0001	0.487	1
APAR (MJ per tree per day)*	2.16°	2.29 ••	3.30 ^{bc}	3.59 °	1.45 ^d	1.54 ad	3.19 bc	3.42 °	<0.0001	0.487	1
Basal area growth (cm ² year ¹) *	0.64 -	0.65ª	0.74 ab	0.74 ^{ab}	0.63 °	0.63 -	0.82	0.82	<0.0001	0.946	1
Light use efficiency (cm ² GJ ¹) *	0.69 °	0.69 -	0.73 abd	0.71 ab	0.84 ^{cd}	0.82 bcd	0.92 °	0.89 °	<0.0001	0.513	0.974
		1		-						11	
<i>B. pendula</i> (n=132 n=145)			+ A. glu	tinosa	+ F. sylve	atica	+ A. glut + F. sylvc	inosa atica	div.level	mortality	interaction
Diameter (cm)	5.46 °	5.89 -	5.91°	5.91 ^a	7.31 ^b	7.74 ⁵	5.87 °	6.03 ^a	0.0003	0.427	0.960
Height (m)	7.83 ^b	8.25 **	7.87⋼	7.87 •	8.89 ab	9.23 -	8.09	8.25 ^{ab}	0.019	0.399	0.952

Crown diameter (m) *	3.36 -	3.44 [°]	3.54∝	3.54 ₌	3.91 bc	4.03 ^b	3.54°	3.58 ∝	0.0006	0.461	0.972
Live crown length (m)	4.07 -	4.31 ab	4.48 ab	4.48 ^{ab}	5.15 .	5.40 °	4.49 ab	4.59 ₀₀	0.0045	0.488	0.976
Height to the live crown (m)	3.75°	3.92 ª	3.38°	3.38 ª	3.73ª	3.48 °	3.62°	3.67ª	0.159	0.563	0.978
Leaf area (m ²) **	4.58 °	5.14 ^a	5.28 ^{ac}	5.28 ∝	7.16 bc	7.85 ^b	5.23 -	5.48	0.0006	0.421	0.960
Crown volume (m ³) *	29.31 ^a	33.05 ^{ab}	34.75 **	34.75 ^₅	49.31 bc	56.15 °	34.75 ab	36.53 **	0.002	0.454	0.967
Relative height	1 °	1 ª	0.98 °	0.97 -	1.4 bc	1.44 ^b	1.27 °	1.32 ^{bc}	<0.0001	0.493	0.937
APAR (GJ per tree per season) *	1.95 °	2.47 ^a	2.15°	2.26 -	4.16 bc	4.98 ^b	2.5 °	2.93 ∝	0.0001	0.181	0.965
APAR (MJ per tree per day)*	5.34°	6.72 ^a	5.90°	6.14 ^a	11.41 ^{bc}	13.66 ^b	6.79°	8.04 ^{ac}	0.0001	0.181	0.965
Basal area growth (cm ² year ¹) *	2.53 °	2.77 ab	3.1 abc	3.1 abc	4.02 bc	4.57 ·	2.72 -	2.92 ab	0.009	0.489	0.982
Light use efficiency (cm ² GJ ⁻¹)	0.90 °	0.83 ª	0.97 °	0.93 ª	0.84 -	0.92 °	0.74 °	0.73 -	0.219	0.883	0.943
		1		1		_			I		
A. alutinosa (n=42 \mid n=68)	sa (n=42 n=68) + B. pendu.		ndula + F. sylva		ntica + B. pe + F. sy		+ B. pendula div.leve + F. sylvatica		mortality	interaction	
···· g							+ F. sylva	tica		/	
Diameter (cm)	5.21 ^b	5.55 ab	6.41 ae	6.86 de	7.72 cd	8.46 °	+ <i>F. sylva</i> 6.05 abe	tica 6.80 ^{acde}	<0.0001	0.091	0.947
Diameter (cm) Height (m)	5.21 ^b	5.55 ab 7.23 ab	6.41 ae 8.31 cd	6.86 de 8.89 c	7.72 cd 7.99 acd	8.46 c 8.19 acd	+ <i>F. sylva</i> 6.05 abe 7.48 abd	tica 6.80 acde 8.23 abcd	<0.0001 0.0005	0.091	0.947
Diameter (cm) Height (m) Crown diameter (m)	5.21 b 6.94 b 3.12 b	5.55 ab 7.23 ab 3.22 ab	6.41 ae 8.31 cd 3.28 ab	6.86 de 8.89 c 3.38 ab	7.72 cd 7.99 acd 3.54 a	8.46 c 8.19 acd 3.69 a	+ <i>F. sylva</i> 6.05 abe 7.48 abd 3.31 ab	tica 6.80 acde 8.23 abcd 3.51 ab	<pre><0.0001 0.0005 0.066</pre>	0.091 0.133 0.322	0.947 0.902 0.993
Diameter (cm) Height (m) Crown diameter (m) Live crown length (m)	5.21 b 6.94 b 3.12 b 3.19 c	5.55 ^{ab} 7.23 ^{ab} 3.22 ^{ab} 3.18 ^a	6.41 ae 8.31 cd 3.28 ab 4.38 bc	6.86 de 8.89 c 3.38 ab 4.69 b	7.72 cd 7.99 acd 3.54 a 3.56 ac	8.46 c 8.19 acd 3.69 a 3.60 abc	+ F. sylva 6.05 abe 7.48 abd 3.31 ab 3.60 ac	tica 6.80 acde 8.23 abcd 3.51 ab 3.72 abc	 <0.0001 0.0005 0.066 0.001 	0.091 0.133 0.322 0.727	0.947 0.902 0.993 0.9770
Diameter (cm) Height (m) Crown diameter (m) Live crown length (m) Height to the live crown (m)	5.21 b 6.94 b 3.12 b 3.19 c 3.81 c	5.55 ^{ab} 7.23 ^{ab} 3.22 ^{ab} 3.18 ^a 4.09 ^a	6.41 °° 8.31 °° 3.28 °° 4.38 °° 3.91 °	6.86 de 8.89 c 3.38 ab 4.69 b 4.18 a	7.72 cd 7.99 acd 3.54 a 3.56 ac 4.44 a	8.46 c 8.19 acd 3.69 a 3.60 abc 4.58 a	+ F. sylva 6.05 abe 7.48 abd 3.31 ab 3.60 ac 3.89 a	tica 6.80 acce 8.23 abcd 3.51 ab 3.72 abc 4.47 a	 <0.0001 0.0005 0.066 0.001 0.438 	0.091 0.133 0.322 0.727 0.276	0.947 0.902 0.993 0.9770 0.967
Diameter (cm) Height (m) Crown diameter (m) Live crown length (m) Height to the live crown (m) Leaf area (m ²)	5.21 ° 6.94 ° 3.12 ° 3.19 ° 3.81 ° 2.97 °	5.55 ** 7.23 ** 3.22 ** 3.18 * 4.09 * 3.16 **	6.41 °° 8.31 °° 3.28 °° 4.38 °° 3.91 ° 4 °°	6.86 de 8.89 c 3.38 ab 4.69 b 4.18 a 4.37 ac	7.72 cd 7.99 acd 3.54 a 3.56 ac 4.44 a 4.32 c	8.46 c 8.19 acd 3.69 a 3.60 abc 4.58 a 4.73 c	+ F. sylva 6.05 abe 7.48 abd 3.31 ab 3.60 ac 3.89 a 3.7 abc	tica 6.80 acde 8.23 abcd 3.51 ab 3.72 abc 4.47 a 4.26 abc 4.26 abc	 <0.0001 0.0005 0.066 0.001 0.438 0.002 	0.091 0.133 0.322 0.727 0.276 0.272	0.947 0.902 0.993 0.9770 0.967 0.979
Diameter (cm) Height (m) Crown diameter (m) Live crown length (m) Height to the live crown (m) Leaf area (m ²) Crown volume (m ³) *	 5.21 ° 6.94 ° 3.12 ° 3.19 ° 3.81 ° 2.97 ° 17.15 ° 	5.55 ab 7.23 ab 3.22 ab 3.18 a 4.09 a 3.16 ab 17.68 ab	 6.41 at 8.31 cd 3.28 ab 4.38 bc 3.91 a 4 abc 27.44 bc 	6.86 de 8.89 c 3.38 ab 4.69 b 4.18 a 4.37 ac 30.64 c	7.72 cd 7.99 acd 3.54 a 3.56 ac 4.44 a 4.32 c 24.1 abc	8.46 c 8.19 acd 3.69 a 3.60 abc 4.58 a 4.73 c 25.33 abc	+ F. sylva 6.05 abe 7.48 abd 3.31 ab 3.60 ac 3.89 a 3.7 abc 23.62 abc	tica 6.80 acde 8.23 abcd 3.51 ab 3.72 abc 4.47 a 4.26 abc 26.9 abc	 <0.0001 0.0005 0.066 0.001 0.438 0.002 0.009 	0.091 0.133 0.322 0.727 0.276 0.272 0.272	0.947 0.902 0.993 0.9770 0.967 0.979 0.999
Diameter (cm) Height (m) Crown diameter (m) Live crown length (m) Height to the live crown (m) Leaf area (m ²) Crown volume (m ³) * Relative height	 5.21 ° 6.94 ° 3.12 ° 3.19 ° 3.81 ° 2.97 ° 17.15 ° 1 ° 	5.55 ab 7.23 ab 3.22 ab 3.18 a 4.09 a 3.16 ab 17.68 ab 1 a	 6.41 at 8.31 cd 3.28 ab 4.38 bc 3.91 a 4 abc 27.44 bc 1.06 ac 	6.86 de 8.89 c 3.38 ab 4.69 b 4.18 a 4.37 ac 30.64 c 1.09 ac	7.72 cd 7.99 acd 3.54 a 3.56 ac 4.44 a 4.32 c 24.1 abc 1.36 b	8.46 c 8.19 acd 3.69 a 3.60 abc 4.58 a 4.73 c 25.33 abc 1.43 b	+ F. sylva 6.05 abe 7.48 abd 3.31 ab 3.60 ac 3.89 a 3.7 abc 23.62 abc 1.9 cd	tica 6.80 acde 8.23 abcd 3.51 ab 3.72 abc 4.47 a 4.26 abc 26.9 abc 1.32 bd	 <0.0001 0.0005 0.066 0.001 0.438 0.002 0.009 <0.0001 	0.091 0.133 0.322 0.727 0.276 0.272 0.569 0.179	0.947 0.902 0.993 0.9770 0.967 0.979 0.999 0.689
Diameter (cm) Height (m) Crown diameter (m) Live crown length (m) Height to the live crown (m) Leaf area (m ²) Crown volume (m ³) * Relative height APAR (GJ per tree per season)	 5.21 ° 6.94 ° 3.12 ° 3.81 ° 2.97 ° 17.15 ° 1.15 ° 	5.55 ab 7.23 ab 3.22 ab 3.18 a 4.09 a 3.16 ab 17.68 ab 1 a 1.41 ab	 6.41 a* 8.31 c* 3.28 ab 4.38 bc 3.91 a 4 abc 27.44 bc 1.06 ac 1.93 bc 	6.86 de 8.89 c 3.38 ab 4.69 b 4.18 a 4.37 ac 30.64 c 1.09 ac 2.40 c	7.72 cd 7.99 acd 3.54 a 3.56 ac 4.44 a 4.32 c 24.1 abc 1.36 b 2.42 c	 8.46 c 8.19 acd 3.69 a 3.60 abc 4.58 a 4.73 c 25.33 abc 1.43 b 2.76 c 	+ F. sylva 6.05 abe 7.48 abd 3.31 ab 3.60 ac 3.89 a 3.7 abc 23.62 abc 1.9 cd 1.89 bc	tica 6.80 acde 8.23 abcd 3.51 ab 3.72 abc 4.47 a 4.26 abc 26.9 abc 1.32 bd 2.14 abc	 <0.0001 0.0005 0.066 0.001 0.438 0.002 0.009 <0.0001 <0.0001 	0.091 0.133 0.322 0.727 0.276 0.272 0.569 0.179 0.134	0.947 0.902 0.993 0.9770 0.9770 0.979 0.999 0.689 0.986
Diameter (cm) Height (m) Crown diameter (m) Live crown length (m) Height to the live crown (m) Leaf area (m ²) Crown volume (m ³) * Relative height APAR (GJ per tree per season) APAR (MJ per tree per day)	 5.21 ° 5.21 ° 6.94 ° 3.12 ° 3.81 ° 3.81 ° 17.15 ° 1.15 ° 3.15 ° 	5.55 ^{ab} 7.23 ^{ab} 3.22 ^{ab} 3.18 ^a 4.09 ^a 3.16 ^{ab} 17.68 ^{ab} 1 ^a 1.41 ^{ab} 3.87 ^{ab}	 6.41 ** 8.31 ** 3.28 ** 4.38 ** 3.91 * 4 ** 27.44 ** 1.06 ** 1.93 ** 5.30 ** 	6.86 de 8.89 c 3.38 ab 4.69 b 4.18 a 4.37 ac 30.64 c 1.09 ac 2.40 c 6.57 c	7.72 cd 7.99 acd 3.54 a 3.56 ac 4.44 a 4.32 c 24.1 abc 1.36 b 2.42 c 6.61 c	 8.46 ° 8.19 acd 3.69 a 3.60 abc 4.58 a 4.73 ° 25.33 abc 1.43 b 2.76 ° 7.55 ° 	+ F. sylva 6.05 abe 7.48 abd 3.31 ab 3.60 ac 3.89 a 3.7 abc 23.62 abc 1.9 cd 1.89 bc 5.17 bc	tica 6.80 acce 8.23 abcd 3.51 ab 3.72 abc 4.47 a 4.26 abc 26.9 abc 1.32 bd 2.14 abc 5.86 abc	 <0.0001 <0.0005 0.066 0.001 0.001 0.438 0.002 0.009 <0.0001 <0.0001 <0.0001 	0.091 0.133 0.322 0.727 0.276 0.276 0.272 0.569 0.179 0.134	0.947 0.902 0.993 0.9770 0.9770 0.967 0.979 0.999 0.689 0.986

Light use efficiency (cm ² GJ ¹) **	0.58 °	0.58 ^a	0.69 ac	0.95 abc	1.95 bc	2.67 ^b	0.15°	0.24 -	0.0001	0.492	0.933
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761 APAR was predicted using the MAESTRA model.

^{*} Values were In-transformed before back transformed by Snowden-ratio (Snowdon, 1991).

^{**} Values were sqrt-transformed before back transformed by Snowden-ratio (Snowdon, 1991).

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[m]

Figure 1



Figure 2



Figure 3



Figure 4



Figure 5