Optimal set of leaf and whole-tree elements for predicting forest functioning

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Abstract. The role played by environmental factors in the functioning of forest ecosystems is relatively well known. However, the potential of the elemental composition of trees (i.e., elementomes) as a predictor of forest functioning remains elusive. We assessed the predictive power of elemental composition from different perspectives: testing whether whole-plant element stocks or concentrations explain forest production and productivity (i.e., production per unit of standing biomass) better than leaf elements or environmental factors; identifying the optimal set (combination and quantity) of elements that best predicts forest functioning. To do so, we used a forest inventory of 2000 plots in the northeast of the Iberian Peninsula, containing in-site information about the elementomes (C, Ca, K, Mg, N, Na, P, and S) of leaves, branches, stems and barks, in addition to annual biomass production per organ. We found that models using leaf element stocks as predictors achieve the highest explained variation in forest production. The optimal dimensionality was achieved by combining the foliar stocks of C, Ca, K, Mg, N, P, and interactions (C×N, C×P, and N×P). Forest biomass productivity was best predicted by forest age. Hence, our results indicate that leaf element stocks are better predictors of forest biomass production than element concentrations or stocks of the whole trees, suggesting that analyzing leaves alone is a good enough approach to study ecosystem functioning.

1 Introduction

Environmental conditions influence the assembly of tree communities, thus forming different forest types across distinct environmental gradients (Chu et al., 2019; Sardans et al., 2016). Such gradients encompass specific niches (e.g., climatic conditions) that drive functional adaptations of the species (e.g., morphology or physiology traits) (Lavorel et al., 2007; Wang et al., 2022). As the backbone of functional adaptations to such niches, the concentration of elements (e.g., C, N, and P, amongst others) in organisms is a key factor driving ecosystem structure and functioning (Fernández-Martínez, 2022; Peñuelas et al., 2019). Element concentrations in tree biomass vary along environmental gradients, species, and forest age, which are key drivers of forest functioning (Santiago et al., 2004; Sardans and Peñuelas, 2014). Therefore, investigating the combination and concentration of distinct elements is vital to better understanding forest functioning.

31   The multi-dimensional concentration of elements of an organism has been defined as the elementome (Peñuelas et
32   al., 2019). Assessing the elementomes of different species allows for a better understanding of how they withstand
33   contrasting environmental conditions, since their ecological strategies rely on different element concentrations and functional
34   traits (Peñuelas et al., 2019; Fernández-Martínez, 2022; Reich and Oleksyn, 2004). Further, considering that elementomes
35   differ across species and populations in response to environmental gradients, forest ecosystems distributed over climatic
36   gradients are expected to vary in both their species composition and elementomes (Sardans et al., 2021; Vallicrosa et al.,
37   2022).

38   Most studies analyzing ecosystem functioning found significant correlations with leaf elementomes (Fernández-
39   Martínez et al., 2020; Šímová et al., 2019; Yan et al., 2023). However, whole organism elementomes should be more
40   strongly correlated with ecosystem functioning (e.g., forest production in biomass) since they encompass information about
41   several functional traits other than those related to leaves (Schreeg et al., 2014; Xing et al., 2022; Zhang et al., 2018a). For
42   example, positive relationships between N and P concentrations in different plant organs (e.g., stems, branches, and leaves)
43   are essential for tree growth and productivity (Ding et al., 2022). Thus, to consider the concentrations of whole-organism
44   elementomes, one should calculate them by weighing the elementomes of different organs by their relative biomass
45   (Fernández-Martínez, 2022). However, to date, no study has assessed and compared the performance of leaf versus whole
46   organism elementomes in predicting ecosystem functioning.

47   Considering the elementome concentration and element stocks at the whole plant and at the leaf level may
48   contribute to enhancing the understanding of ecosystem processes (Luo et al., 2020; Rocha et al., 2011). For instance, tree
49   elementomes' concentration significantly impacts ecosystem productivity (Bitomský et al., 2023; Elser et al., 2010). Forest
50   biomass productivity is affected by the variation of elementomes in different stand ages, e.g., limited N and P content in
51   older stands (Zhang et al., 2018a; Zhang et al., 2022). Different stand ages also shape the tree element stocks (i.e., elements
52   stored within the biomass) in tree organs (Hoover and Smith, 2023; Rodríguez-Soalleiro et al., 2018). Nevertheless, the
53   predictive performance of elementomes compared to element stocks in explaining ecosystem functioning remains scarcely
54   understood. Furthermore, it remains unexplored whether elementomes and element stocks predict forest functioning better
55   than environmental factors (e.g., climate) and stand age.

56   Finally, the optimal elemental set (OES) — the minimum set (number and combination) of elements — for
57   achieving the best prediction of organism and ecosystem functioning remains elusive. Most studies investigating
58   elementomes in forested ecosystems only focused on C, N, P, and K (Sardans et al., 2017; Schreeg et al., 2014; Vallicrosa et
59   al., 2022; Xing et al., 2022; Zhang et al., 2018b), while fewer ones have also included other important elements for the
60   functioning of organisms and ecosystems, like Ca, S, and Mg (Sardans et al., 2016; Sardans et al., 2021, 2015) (Bai et al.,
61   2019; Huang et al., 2019). Acquiring knowledge on forest ODs can improve predictions of forest ecosystem functioning by
62   increasing our mechanistic knowledge of how organisms and ecosystems work.

63   In this study, we used a database including forest element composition and biomass growth in the northeast of the
64   Iberian Peninsula. This region is a suitable model for investigating topics related to OES (optimal elemental set) since it is

composed of an environmental gradient reflected in distinct forest formations. We aimed to answer four questions: Are the whole-plant elements (elementomes and stocks) better predictors of forest functioning (production and productivity) than only leaf elements? Do element stocks better explain forest functioning than elementomes? What is the OES that best predicts forest functioning? Do element stocks and elementomes (leaf and whole plant) explain better forest functioning than environmental factors and stand age? We departed from three central hypotheses: H1: whole-plant elements (elementomes and stocks) are better predictors of forest functioning (biomass production and productivity) than only leaf elements; H2: element stocks better explain functioning than elementomes, as the former incorporates the effect of age in forest functioning; H3: OES effects in forest biomass production and productivity models are greater in models using whole organisms than leaf elementomes.

2 Material and Methods

2.1 Study Area

This study was conducted across the northeast of the Iberian Peninsula (ca. 31,900 km^2), bounded in the north by the Pyrenees and in the east by the Mediterranean Sea. We chose this region due to its heterogeneous climatic conditions associated with large ranges in altitude (i.e., 0 to > 3000 m) and distance from the sea, which together result in wide variations in mean annual temperature (from 1 °C to 28 °C) and precipitation (annual mean from 350 to >1500 mm) (Martín Vide et al., 2008). The Mediterranean climate is mostly characterized by mild winters, dry and warm summers, and a high degree of interannual variability in precipitation. These pronounced climatic gradients allow for the establishment of three predominant forest types: Mediterranean evergreen angiosperm forests (dominated by *Quercus ilex* trees), Mediterranean gymnosperms (stands of *Pinus halepensis*, *Pinus nigra*, *Pinus pinea*, *Pinus sylvestris*, *Pinus uncinata*, and often with *Quercus petraea* and *Q. ilex* among them), and wet temperate deciduous angiosperms (with *Fagus sylvatica*, *Quercus faginea*, *Quercus robur*, *Q. petraea*, *Abies alba*, and *P. sylvestris* dominating at altitudes from 800 to 1500 m and *P. uncinata* from 1600 to 2400 m) (García et al., 2004; Bolòs i Capdevila, 1991).

2.2 Forest Inventory and Elemental Data

We used the Ecological and Forest Inventory of Catalonia (IEFC) database (Gracia et al., 2004) (http://www.creaf.uab.es/iefc). This database includes tree diameters, basal area, biomass, and annual forest production of leaves, branches, barks, and stems, as well as the corresponding elemental composition of these organs. The forest sites from which we compiled the data represent sampling plots (10 m radius) distributed throughout Catalonia. The sampling was conducted at a density of one plot per square kilometer (sq km) of natural or managed forest (Gracia et al., 2004). For plots having more than five tree species, only the five most abundant ones (DBH > 5 cm) were recorded, and a tree core sample

99 was used to calculate the stand age and annual tree growth over the last five years (Vilà et al., 2003). The estimation of

100 branch and leaf biomass was based on normalized dimensional analysis (Duvigneaud, 1971; Wittaker and Woodwell, 1969).

101 The concentrations of the elements, i.e., elementomes (N, C, P, K, S, Mg, and Ca), of the individuals of each species were

102 measured for samples of wood, bark, branches, and leaves by drying and grinding them to obtain homogeneous samples

103 (Vayreda et al., 2016). Then, from an anhydrous subsample (oven-dried at 75 ºC) and of known weight, the concentration of

104 nutrients was determined. The concentrations of C and N were determined by gas combustion chromatography in a C.E.

105 elemental analyzer INSTRUMENTS (Wigan, UK), while the concentrations of P, S, Mg, Ca, and K were determined by

106 Inductively Coupled Plasma (ICP) in a Jobin Yvon JI-38 spectrophotometer (Edison, USES) (Vayreda et al., 2016). A

107 complete description of the methods employed in this forest inventory (e.g., sampling procedures, allometric equations, data

108 processing, etc.) can be found in Gracia et al. (2004).

109 From the IEFC dataset, we extracted the data regarding forest stand ages, biomass of tree individual organs, forest

110 biomass production, and concentration of N, C, P, K, S, Mg, and Ca available for 2227 tree individuals (with a diameter at

111 breast height (DBH) > 5 cm) from 48 species located in 2000 plots. The stand age is expressed in years and was obtained

112 from the growth rings of tree wood cores in each plot (Gracia et al., 2004). In each plot, a core was taken from a tree that

113 represented the center of the size class (diametric class), which was defined from 5 to 5 cm DBH (e.g., 5–10 cm; 15-20 cm;

114 20–25 cm, etc.). Finally, it was calculated as the weighted average of the stand age based on the number of trees per DBH

115 class. The elementomes of the trees were obtained for each organ: leaves, branches, barks, and stems (except for roots, which

116 are missing in the inventory). To access the procedures, parameters, and allometric equations used to calculate the biomass

117 of each organ, please see the methodological details of the IEFC described in Gracia et al. (2004). In our analyses, we used

118 forest biomass production calculated considering the following equation: $P = (Bt^2 – Bt^1)/5$, where Bt^2 is the current biomass

119 (t ha^{-1}: tons per hectare) per area and Bt^1 is the biomass 5 years before (Vayreda et al., 2005; Vilà et al., 2003). Thus, forest

120 production responds to the net increase in biomass in the ecosystem per year (t ha^{-1} y^{-1}). Further, to obtain forest productivity

121 (production per unit of standing biomass, y^{-1}), we summed the biomass of tree organs (leaves, branches, bark, and stem

122 wood) to get the whole aboveground tree biomass. Then, we divided forest production by the whole tree biomass.

123 For our analyses (see section Statistical Analyses), we used values of concentration (g/100 g) and stocks of N, C, P,

124 K, S, Mg, and Ca for only leaves and the whole organism. The whole-organism elementome was calculated as the weighted

125 average of the elemental concentration (g 100 g^{-1}) of the different plant organs. The stocks (t ha^{-1}) of the elements per organ

126 were calculated as the biomass of the organ multiplied by the concentration of the element. Finally, we summed the stocks of

127 each element from the different organs to obtain the whole plant stock.

128

129 **2.3 Climatic Data**

130 For each forest plot, we acquired data on the 19 bioclimatic variables provided by the WorldClim database version

131 2 at a very high spatial resolution (approximately 1 km^2) (Fick and Hijmans, 2017). From the 19 variables, we selected only

132 the ones with coefficients of correlation < 0.70 (Dormann et al., 2013) to avoid biasing the statistical models (see the section

133 Statistical Analysis) due to multicollinearity. Our final set of climatic variables was composed of temperature seasonality,

134 mean temperature of the wettest quarter (three months), precipitation of the wettest month, precipitation of the driest quarter,

135 precipitation of the warmest quarter, and precipitation of the coldest quarter.

136

2.4 Statistical Analysis

138

139   To test our hypothesis on the highest performance of elementomes and element stocks of the whole tree for

140 predicting forest functioning (biomass production and productivity) compared to leaves or to environmental variables

141 (climate) and stand age, we first constructed gaussian GAMMs (generalized additive mixed models) using the R package

142 "mgcv" (Wood, 2017). For predicting forest biomass production, we used five different models characterized by the

143 following sets of predictors: i) elementomes of the whole plant; ii) element stocks of the whole plant; iii–iv) the same as

144 items i and ii but for the leaves; and v) the environment (climate) and stand age. To predict forest productivity, we used three

145 different models with the following sets of predictors: i) elementomes of the leaves; ii) of the whole plant; and iii) the

146 environment and stand age. The predictors representing elementomes and element stocks were N, C, P, K, S, Mg, Ca, and

147 the interactions C×P, C×N, and N×P. For forest productivity, stocks were not included as predictors to avoid statistical

148 redundancy since the productivity calculation involves the sum of organ biomass and stocks also use organ biomass (details

149 in the Forest Inventory and Elemental Data section).

150   To adequately fit the GAMMs and eliminate spatial autocorrelation effects on the residuals, we included the

151 coordinates (longitude and latitude) of the forest plots as fixed smoothed terms with Duchon splines (Duchon, 1977; Wood,

152 2003), while also adding species as random effects. This approach guaranteed that the degrees of freedom of the splines

153 (Edf) were correctly fitted according to the required number of knots (k) for the GAMMs to reach residual independence. To

154 verify whether potential spatial effects were sufficiently eliminated, the residuals extracted from the GAMMs were modeled

155 in spatial variograms using the function "fit.variogram" of the R package "gstat" (Pebesma, 2004). We found no significant

156 remaining spatial effect on the residuals of the models. Further, to achieve the normality of the residuals, we transformed the

157 target forest production into its natural logarithm in all models. For the proper fit and convergence of the models regarding

158 forest biomass productivity, we normalized (mean divided by the standard deviation) all elementomes using the built-in

159 "scale" R function.

160   To find the optimal elemental set (OES) of the elementome for predicting forest production and productivity and to

161 discern whether leaf or whole plant elementomes work better for this purpose, we performed a model selection procedure

162 based on the Akaike information criterion (AIC) (Burnham and Anderson, 2002). Such procedure consisted of including the

163 global GAMMs (with the same eight models above described: five for production and three for productivity) in the function

164 "dredge" of the "MuMIn" package (Bartoń, 2023) in R programming environment version 4.3.3 (R Development Team

165 Core, 2024). The use of the minimum AIC selection procedure allowed us to extract the best combinations (subsets) of

166 predictors from our global models to predict forest functioning. We applied the same selection procedure to models with the

167   environment and age as predictors. In all selections, we considered the subsets with the lowest AIC values as the best
168   models.

169   We also considered all subsets of selected models with delta (ΔAIC) < 4 as equally robust and statistically reliable,
170   thus allowing us to retain relevant and valuable information beyond single-best models (Burnham et al., 2011). From these
171   subsets (ΔAIC < 4), we extracted information on the performance of the models (R-squared) and the number of variables
172   they selected. Then, we assessed the predictive performance (R-squared: R2) by accessing the models' outputs in two ways:
173   by the subset models according to the number of selected predictors and by the overall performance only of the single best
174   models. This two-way performance ranking allowed us to compare the performance of only the single best models (lowest
175   AICs) with sets of models equally reliable (ΔAIC < 4).

176   Finally, to obtain a reliable overview of which were the most important variables for explaining forest functioning,
177   we performed model averaging for models with ΔAIC < 4 using the function "model.avg" of the "MuMIn" package (Bartoń,
178   2023) in R 4.3.3. We used the argument "beta=TRUE" to standardize the coefficients, allowing for a comparison of the
179   relative importance of each predictor variable in the average models. Model averaging computes an average model output
180   from the estimates of a set of models and weights their relative importance by their AIC (Burnham and Anderson, 2002).
181   Therefore, this approach allowed us to obtain information on the importance of predictor variables extracted from the best
182   model subsets (i.e., ΔAIC < 4).

183   The complete routine with the codes used to execute the models described and presented in this study can be
184   accessed in Diniz (2024).

185

186   **3 Results**

187

188   By assessing the predictive performance of the best single models (lowest AIC; Table A1, Appendix A), we
189   answered the questions regarding the performance of the whole plant (elementomes and stocks) *vs*. leaves and of the
190   elementomes *vs*. stocks for explaining forest functioning. Our results indicated that leaves (rather than whole plants) and
191   stocks (rather than elementomes) are the best predictors of forest functioning. We found that the best model of forest
192   biomass production using leaf element stocks as predictors explained 58% of the variance and had nine variables: C, Ca, K,
193   Mg, N, P, C×N, C×P, and N×P (Fig. 1a). Conversely, the best model, including as predictors the whole-plant element stocks
194   (Fig. 1a), explained a lower portion (28%) of the variance of forest biomass production and had three predictors (C, N, and
195   C×N). Regarding the best models of forest production, including elementomes as predictors, we found that leaf elementomes
196   also explained more variance (22%) than whole plant elementomes (13%) Fig. 1a. The best leaf elementome model
197   included six variables (C, Ca, N, P, C×P, and N×P), and the best whole plant elementome model included only one (Ca).
198   Similarly, leaf elementomes were the best predictors of forest biomass productivity (Fig. 1b; 28% of variance explained),
199   and the best model included three variables (Ca, K, and N). The best whole plant elementome included only K and explained
200   a lower variance (15%) of biomass productivity.

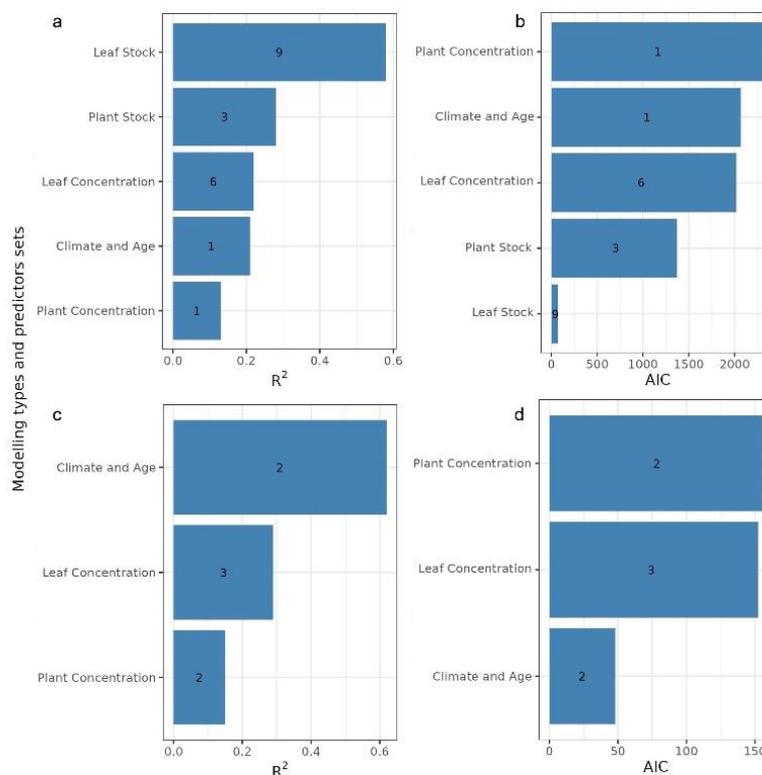
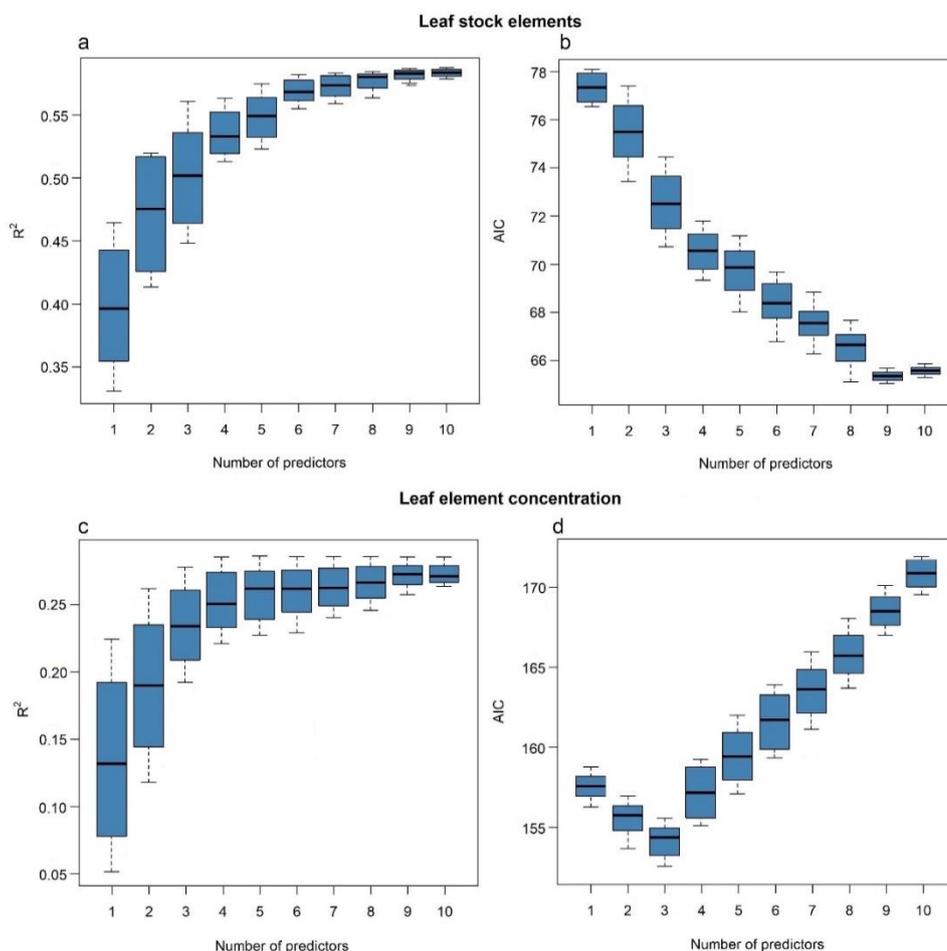



Figure 1: R² and AIC of the best models for explaining forest biomass production (a, b) and productivity (c, d), considering as predictors the stocks and the concentration of elements only for the leaves and for the whole plant, and climate and forest age. Numbers within the bars show the number of variables selected. Plant concentration = whole-plant elementomes.

Our subsets of models equally robust (ΔAIC< 4) showed that the optimal elemental set (OES) for predicting forest biomass production from leaf element stocks (Fig. 2a) was nine variables (C, Ca, K, Mg, N, P, C×N, C×P, and N×P). This model subset explained an average of 58% of the variance in forest biomass production. The subset of models using whole-plant element stocks exhibited the second-best predictive performance for forest biomass production (R2 = 0.29; Fig. A1, Appendix A). Differently, the subset of models using climatic variables and whole plant elementomes as predictors displayed the lowest prediction of forest biomass production (Fig. A1). The variance of forest productivity was moderately explained (28%) by models selecting three variables (Ca, K, and N) of leaf elementomes (Fig. 1c, d) and poorly explained (15%) by models with whole-plant elementomes (Fig. A2, Appendix A). Forest productivity was best explained (R2 = 0.68) with the subset of models that included two variables (temperature seasonality and stand age) (Fig. A2).

We also found that climate and stand age (Fig. A1, Appendix A) explained 21% of the variance in forest biomass production, while leaf element stocks explained 58% (Fig. 1a and 2a). On the other hand, the best subset of models that had

218 forest age and temperature seasonality as predictors displayed the best performance and explained 62% of the variance in

219 forest biomass productivity (Fig. A2, Appendix A).

220

221 **Figure 2: Forest biomass production (a, b) and productivity (c, d) predicted by leaf element stocks (a, b) and leaf**

222 **element concentration (c, d). Results demonstrated by the performance (AIC and R^2) of the most robust subsets of**

223 **models (ΔAIC < 4).**

224

225   The average models are based on different subsets of variables (i.e., leaves vs. whole plant elementomes and stocks,

226 and elementomes vs. stocks; Table A2, Appendix A) and demonstrated that P, Ca, and N — from both models based

227 exclusively on leaf element stock and models only with leaf elementomes — are the most important predictors for explaining

228 spatial variability in forest production (Fig. 3 a, c; Fig. A3, Appendix A). Conversely, the whole plant elementomes and

229 element stocks of the P exerted a low and non-significant influence on forest biomass production (Fig. 3 b, d). N stocks

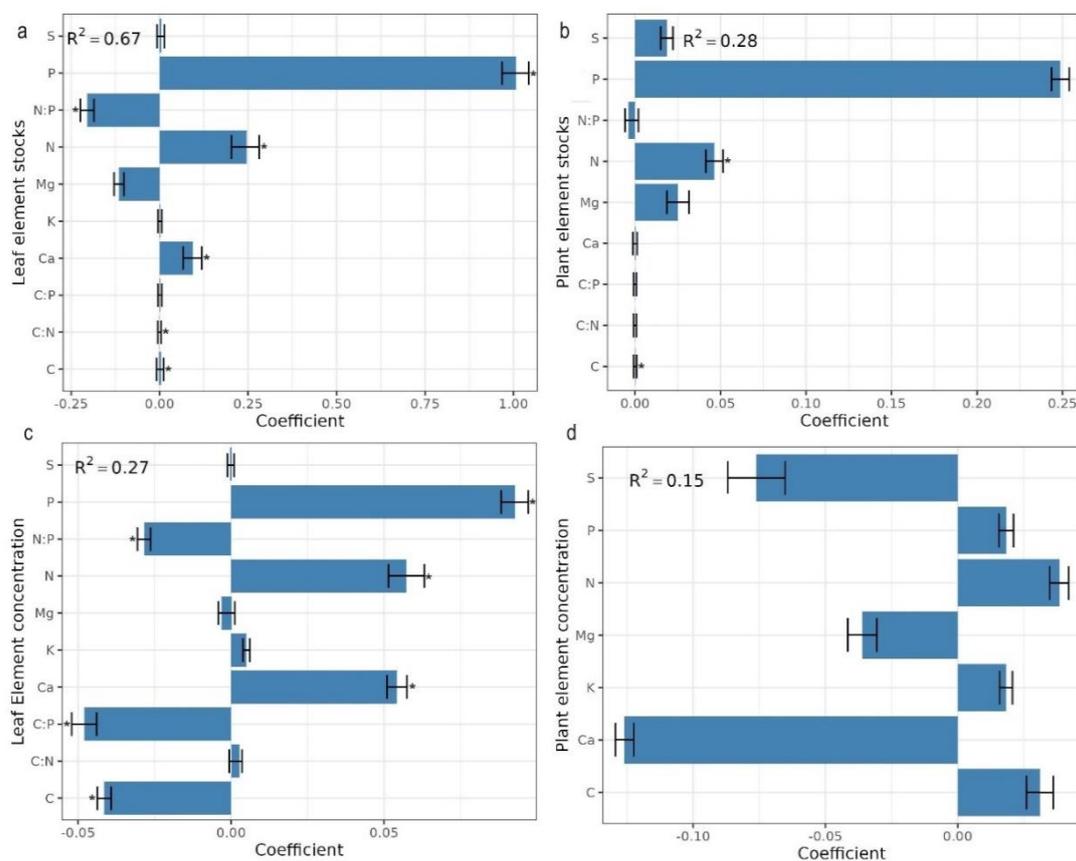
230 (leaves and whole plant) and N leaf concentration were positively correlated to forest biomass production (Figures 3 a, b,

231 and c, respectively; Fig. S3). On the other hand, in leaves, the interactions N×P (Fig. 3a) and C×P (Fig. 3c) and the

232 concentration of C (Fig. 3 c) exerted a significant and negative effect on biomass production. The negative interaction of

233 N×P indicated that the higher the value of P, the lower the effect of N on biomass production. Similarly, the negative

234 interaction of C×P implied that higher values of P reduce the effect of C on biomass production. The average models using

235 leaf and whole-elementome predictors were unable to predict forest biomass productivity (Fig. 4).

236

237 **Figure 3: Standardized coefficients from the model averaging (ΔAIC< 4) for the prediction and explanation of forest**

238 **biomass production, considering as predictors the stocks (a, b) and the concentration (c, d) of elements only for the**

239 **leaves (a, c) and for the whole plant (b, d). R^2 is the average of R-squared derived from all models with ΔAIC < 4.**

240 **Plant element concentration = Whole plant element concentration. * Indicates significant coefficient.**

241

242   Climatic variables also displayed significant effects on forest biomass production. Temperature seasonality and

243 precipitation in the coldest quarter were negatively correlated with biomass production (Fig. 5a). Conversely, precipitation in

244 the driest quarter correlated positively with biomass production (Fig. 5a). However, forest biomass productivity was not

245 influenced by climate but decreased significantly with stand age (Fig. 5b).

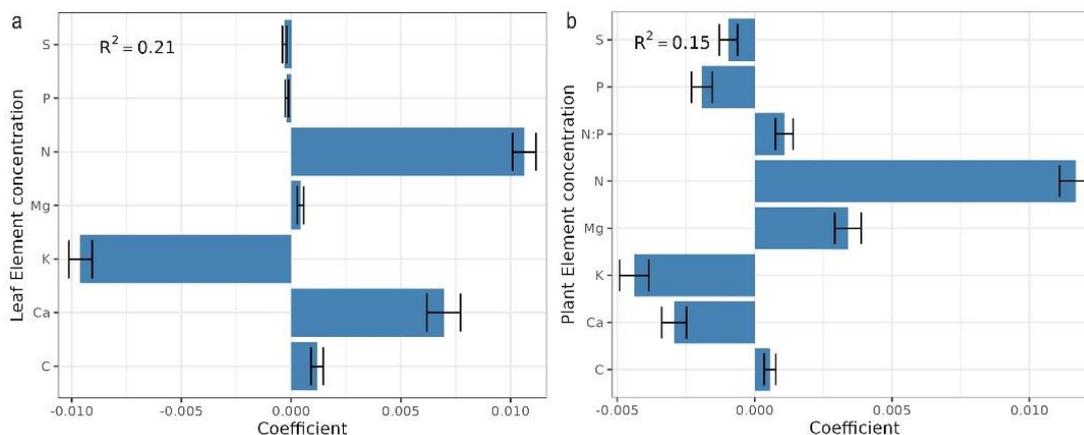



Figure 4: Standardized coefficients from the model averaging (ΔAIC < 4) for the prediction of forest biomass productivity, considering as predictors the concentration of elements only for the leaves (a) and for the whole plant (b). R² is the average of R squared derived from all models with ΔAIC < 4. Plant element concentration = Whole plant element concentration. * Indicates significant coefficient.

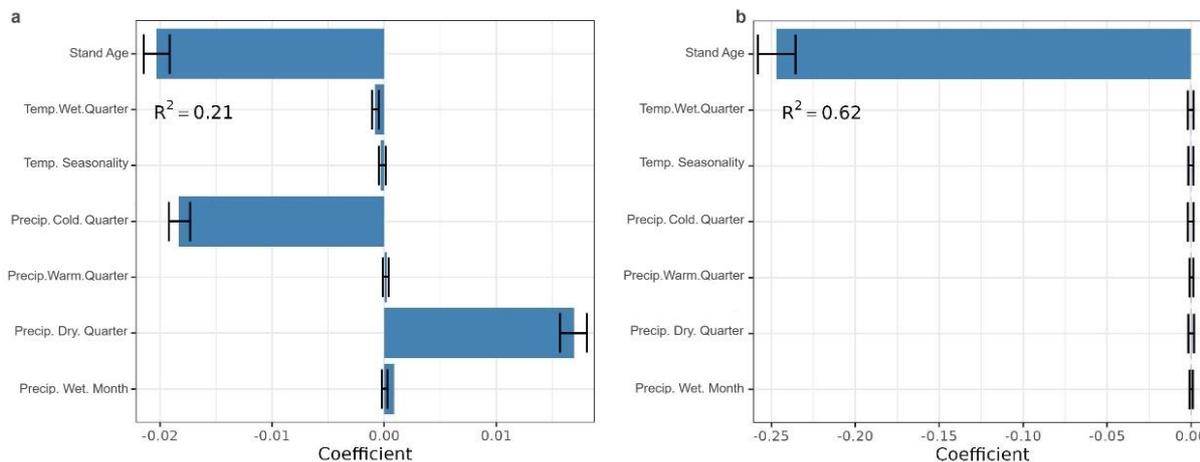



Figure 5: Standardized coefficients from the model averaging (ΔAIC < 4) for the prediction of forest biomass production (a) and productivity (b), considering as predictors climate variables and stand age. Temp. Wet. Quarter: Mean temperature of the wettest quarter; Temp. Seasonality: Temperature Seasonality; Precip. Cold. Quarter: Precipitation of Coldest Quarter; Precip. Warm. Quarter: Precipitation of Warmest Quarter; Precip. Dry. Quarter: Precipitation of Driest Quarter; Precip. Wet. Month: Precipitation of Wettest Month. R² was averaged from all models with ΔAIC < 4. * Indicates significant coefficient.

4 Discussion

We refuted the hypothesis that using whole plant elementomes and element stocks predicts forest biomass production better than leaf elementomes and element stocks alone. Models including nine leaf element stocks (C, Ca, K, Mg, N, P, C×N, C×P, and N×P) displayed the highest performance in predicting forest biomass production. On the other hand, stand age was the best predictor of forest biomass productivity. Altogether, these findings suggest that forest production can be best predicted by foliar element stocks and biomass productivity by stand age. Further, our average models indicate that changes in forest biomass production are mostly explained by concentrations and stocks of Ca, P, and N.

Our finding that leaf element stocks are the main predictors of forest biomass production was unexpected. Since the whole plant considers different parts of the plant (e.g., stems, branches, bark) that require different nutrient concentrations to exert distinct functions (e.g., uptake, transport, storage), it could be expected that using concentrations and stocks of elements of the whole plant would have higher predictive performance (Zhang et al., 2018; Delpiano et al., 2020; Sardans et al., 2023) than only using elements of leaves. However, even though the leaves do not encompass the whole functional space of a tree, they represent the essential photosynthetic part of a plant and are capable of rapid nutrient cycling and responsiveness to environmental conditions (Foster & Bhatti, 2020). For instance, N and P, the most important elements limiting plant growth, are more readily available in leaves for use in metabolic (e.g., growth) and ecosystem processes (e.g., biomass production) than in other organs (Liu et al., 2019; Roth-Nebelsick & Krause, 2023; Töpfer, 2021). Thus, the practical implication of our results for further studies is that foliar element stocks may hold sufficient information to derive robust predictions of forest functioning.

Foliar nutrient stocks are crucial for enhancing plant fitness by enhancing photosynthesis and thus biomass production (Gilliham et al., 2011; Taiz et al., 2014; Beechey-Gradwell et al., 2020). Sufficient reserves of macronutrients such as K, Ca, and Mg in specific leaf cell types are also vital for plant growth (Gilliham et al., 2011). The positive effect of the combination of stored elements on growth is indicated by our best model for biomass production, which had as predictors the foliar stocks of C, Ca, K, Mg, N, P, C×N, C×P, and N×P. Further, our average models also indicated the leaf stocks of Ca, P, and N as the most important predictors of forest biomass production.

The superior performance of leaf element stocks, compared to whole-plant element stocks and concentrations, also might be due to suitable environmental conditions resulting in increased foliar biomass (Rodríguez-Soalleiro et al., 2018b; Urbina et al., 2011). In suitable climatic conditions (e.g., high precipitation), plant growth might be positively affected by high concentrations of foliar N and P (Kerkhoff et al., 2005; P. Reich and Oleksyn, 2004; Sardans and Peñuelas, 2014). We found a positive effect of precipitation in the driest quarter, N and P, on forest biomass production. Since the summer in most of the territory addressed in this study coincides with temperatures and marked water stress (Martín Vide et al., 2008), plants may invest in a strategy of retaining larger foliar nutrient reserves to cope with drought (Waring, 1987.; Gessler et al., 2017). Therefore, our observed increased precipitation concomitantly with high temperature seasonality might favor foliar nutrient storage and consequently biomass production (Fernández-Martínez et al., 2017; Lie et al., 2018; Roa-Fuentes et al., 2012).

295   The highest predictive performance was achieved by using foliar stocks including C, Ca, K, N, Mg, and P as
296   predictors, which is congruent with the known high influence of the uptake and redistribution of these elements in forest
297   biomass production (Bond, 2010; Whittaker et al., 1979). Such an optimal set of elements is influenced by the effects of
298   climate and stand age on their uptake, redistribution, and storage (Woodwell et al., 1975; Augusto et al., 2008; Rodríguez-
299   Soalleiro et al., 2018; Dynarski et al., 2023; Li et al., 2021). Thus, the driving role of climate in the optimal elemental set is
300   expected to influence forest functioning ultimately. Indeed, we found that climate (precipitation in the driest quarter and
301   temperature seasonality) correlated positively and significantly with biomass production. These findings suggest climate as
302   the main factor that influenced the optimal combination of foliar stocks of C, Ca, K, Mg, N, P, C×N, C×P, and N×P in
303   predicting biomass production (X. Wang et al., 2022; Yang et al., 2019; Q. Zhang et al., 2021).

304   Among the elements in the abovementioned optimal combination for predicting forest biomass production, N and P
305   stand out. We found that higher leaf stocks of N and P were related to higher biomass production. Plant growth is highly
306   influenced by the proportions of N and P, and particularly by the ratios N:P (Ågren, 2008; Gusewell, 2004; Sardans et al.,
307   2011; Willby et al., 2021). The plant N:P ratio reflects the balance between uptake and loss of N and P (Gusewell, 2004).
308   Our negative interaction with N×P indicates that the higher the leaf stocks of P, the lower the effect of N leaf stocks on
309   biomass production. Such a higher importance of P compared to N for biomass production might be due to the typically
310   higher foliar resorption of P than of N (Vergutz et al., 2012; Mulder et al., 2013).

311   The highest importance attributed to P for explaining forest biomass production is probably an outcome of its
312   continuous storage in the forest biomass (Sardans and Peñuelas, 2015; Y. Wang et al., 2022). Thus, the observed prominent
313   role of P might be representing a long-term adaptative strategy of trees to store it in biomass and slow its loss from
314   ecosystems (Sardans and Peñuelas, 2015). Sardans and Peñuelas (2015) using data from the Catalan Forest Inventory, found
315   that trees with high woody biomass (branches plus stems) hold a higher P content than N and a higher P:N ratio with forest
316   ageing.

317   Aside from N and P, Ca also displayed a positive effect on forest biomass production and productivity, which is
318   congruent with the importance of this element for photosynthesis, nutrient absorption, and plant growth (Hirschi, 2004;
319   Ågren, 2008; Hochmal et al., 2015). However, the average models indicated that the concentration of elements (e.g., Ca and
320   N in leaves and whole- plants) and climate were not significantly influential on biomass productivity. Rather, we observed a
321   significant negative relationship between stand age and forest biomass productivity, probably explained by the increase of
322   forest biomass and the decrease of forest nutrient availability with age (Fernández-Martínez et al., 2014; Goulden et al.,
323   2011).

324   Finally, the smaller importance of C compared to other elements in our average models might also partially explain
325   the decrease in forest biomass productivity. Productivity reduction might be caused by the predominance of leaf and fine-
326   root turnovers in carbon allocations compared to other plant parts (Yu et al., 2017). The availability of foliar nutrients,
327   particularly P, strongly affects photosynthetic carbon gain in forests, contributing to variations in biomass productivity

328 (Mercado et al., 2011). Consequently, the production of living biomass in other parts (i.e., stems and barks) reduces, and
329 overall productivity tends to decrease (Jonsson et al., 2020; Ryan et al., 1997; Schoonmaker et al., 2016; Yu et al., 2017).

330   In this study, we bring new insights into the effects of the optimal elemental sets, compared to climate and stand
331 age, on both forest biomass production and productivity. As practical implications for future research, our results indicate
332 that using only data on leaf elements, especially stocks, allows us to achieve robust predictions of variations in forest
333 biomass. Such information contributes to decision-making by researchers and forest managers about the types of data
334 (elements of the whole plant or just leaves) they should prioritize collecting when assessing forest growth.

335

336 **5 Conclusions**

337

338   We found that elemental concentrations and stocks of leaves predict forest biomass production and productivity
339 better than those of the whole plant. Leaf stocks explained the highest amount of variance in forest biomass production, thus
340 suggesting that element stocks are better predictors than element concentrations. The optimal elemental set for predicting
341 forest biomass production can be achieved using leaf elemental stocks of C, Ca, K, Mg, N, P, C×N, C×P, and N×P as
342 predictors. Among these elements, N and P stocks and concentrations were the most positively correlated with biomass
343 production. Conversely, the concentration of elements and climate did not significantly influence forest biomass
344 productivity, which was mainly driven by stand age. Altogether, our results indicate that focusing on the use of leaf
345 elements, especially stocks, as predictors is sufficient for predicting forest biomass variation.

346

347 **Code and Data Availability**

348

349   The data used in this study are maintained by the CREAF institute and are available upon request. Complete
350 information about the data and instructions for requesting its use can be accessed at the link: http://www.creaf.uab.es/iefc/.
351 Codes used to produce the models are provided by Diniz (2024).

352

353 **Author Contribution**

354

355   Écio Souza Diniz: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Visualization,
356 Writing - original draft, Writing - review & editing. Eladio Rodríguez-Penedo: Data Processing, Formal analysis, Writing –
357 review. Roger Grau-Andrés: Methodology, Validation, Writing - review. Jordi Vayreda: Data curation, Writing - review.
358 Marcos Fernández-Martínez: Methodology, Validation, Supervision, Visualization, Project administration, Writing – review,
359 Funding Acquisition.

360

361

362 **Competing Interests**

363

364 The authors declare that they have no conflict of interest.

365

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Appendix A: Model Performance

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Table A1: Performance of the best models (lowest AIC) showed in Figure 1 and the numbers (N) of predictors they selected for predicting forest production and productivity. Response = dependent variable. Leaf Conc. and Plant Conc. are leaf element concentration and whole plant element concentration, respectively. Clim. Age are climatic variables and stand age. Temp. Season = Temperature Seasonality; Temp. Wet. Quart. = Mean Temperature of Wettest Quarter; Prec. Dr. Quart. = Precipitation of Driest Quarter; Prec. Cold.Quart. = Precipitation of Coldest Quarter; Age = Stand age.

Response	Predictors	N	R2	AIC	Selected variables
Production	Leaf Stock	9	0.58	64.7	C, Ca, K, Mg, N, P, C×N, C×P, and N×P
Production	Plant Stock	3	0.28	1369.2	C, N, and C×N
Production	Leaf Conc.	6	0.22	2019.4	C, Ca, N, P, C×P, and N×P
Production	Plant Conc.	1	0.13	2326.2	Ca
Production	Clim. Age	1	0.21	2066.1	Temp. Season., Temp. Wet. Quart., Prec. Dr. Quart., Prec. Cold.Quart.
Productivity	Leaf Conc.	3	0.28	152.2	Ca, K, and N
Productivity	Plant Conc.	2	0.15	155.5	K
Productivity	Clim. Age	2	0.62	48.1	Temp. Season., Age

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Table A2: Total number (Total N) of models' subsets produced by the selection with "dredge" using different predictors' set for predicting forest production and productivity. N (ΔAIC<4) is the number of models equally robust under ΔAIC < 4 and used to calculate the average models.

Target	Predictors	Total N	N (ΔAIC<4)
Production	Leaf Stock	575	10
Production	Plant Stock	575	10
Production	Leaf Concentration	852	10
Production	Plant Concentration	852	8
Production	Climate and Age	511	7
Productivity	Leaf Concentration	850	7
Productivity	Plant Concentration	850	8
Productivity	Climate and Age	511	7

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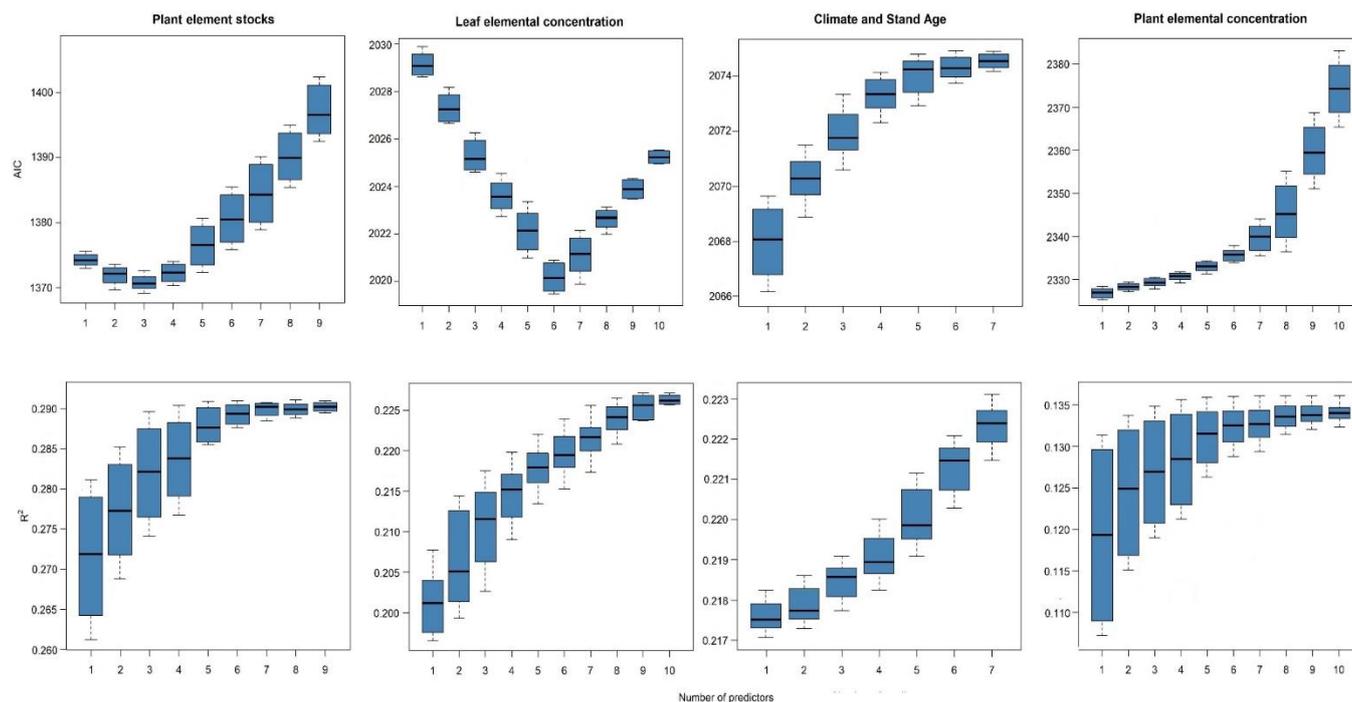
Figure A1: Performance (AIC and R2) of the most robust models (ΔAIC < 4) in predicting forest production according to the number of selected predictors. The models' performance demonstrated by their AIC and R2: Plant stocks (a, e); Leaf elemental concentration (b, f); climate and stand age (c, g); Whole-plant elemental concentration (d, h).

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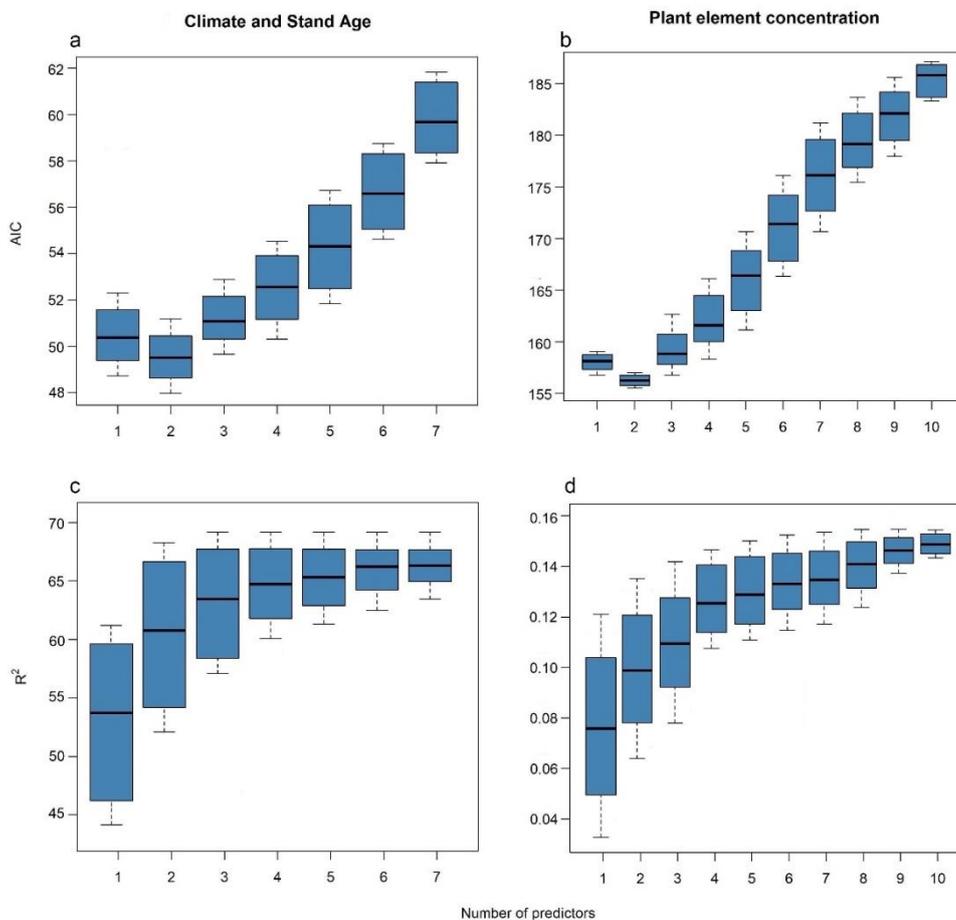
Figure A2: Performance of the most robust models (ΔAIC < 4) in predicting forest productivity according to the number of selected predictors. The models' performance demonstrated by their AIC and R-squared: climate and stand age (a, c); Whole-plant elemental concentration (b, d).
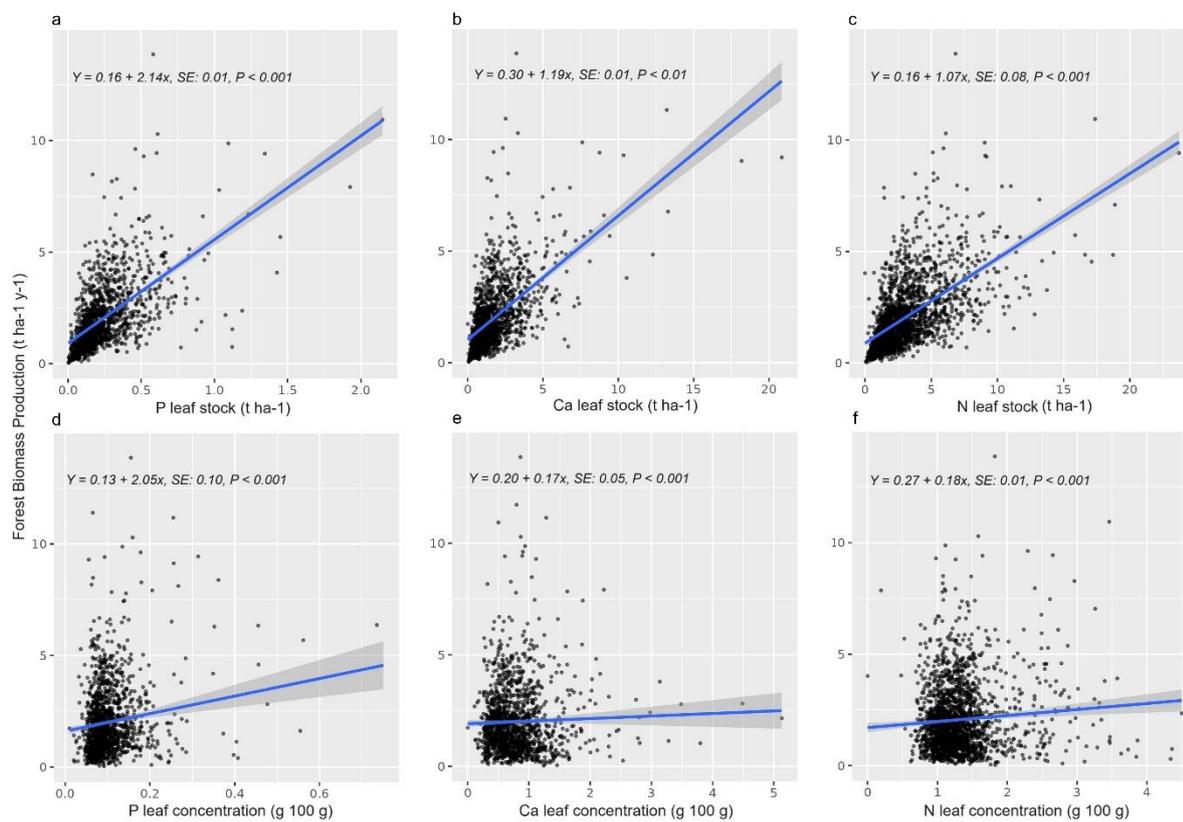
Figure A3: Partial residuals plots showing the estimated effects of the elemental concentrations and stocks of Ca, P, and N on forest biomass production. *SE*: **Standard error.**