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Article type : Research Article

Handling Editor: Julieta Rosell

Improving predictions of tropical tree survival and growth by incorporating measurements of whole leaf allocation

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Abstract

1. Individual-level demographic outcomes should be predictable upon the basis of traits. However, linking traits to tree performance has proven challenging likely due to a failure to consider physiological traits (i.e., hard-traits) and the failure to integrate organ-level and whole plant-level trait information.

2. Here, we modeled the survival rate and relative growth rate of trees while considering crown allocation, hard-traits, and local-scale biotic interactions, and compared these models to more traditional trait-based models of tree performance.

3. We found that an integrative trait, total tree-level photosynthetic mass (estimated by multiplying specific leaf area and crown area) results in superior models of tree survival and growth. These models had a lower AIC than those including the effect of initial tree size or any other combination of the traits considered. Survival rates were positively related to higher values of crown area and photosynthetic mass, while relative growth rates were negatively related to the photosynthetic mass. Relative growth rates were negatively related to a neighbourhood crowding index. Furthermore, none of the hard-traits used in this study provided an improvement in tree performance models.

4. *Synthesis*. Overall, our results highlight that models of tree performance can be greatly improved by including crown area information to generate a better understanding of plant responses to their environment. Additionally, the role of the hard-traits in improving models of tree performance is likely dependent upon the level of stress (e.g. drought stress), micro-environmental conditions, or short-term climatic variations that a particular forest experiences.

Key Words: Community Ecology, Demographic Rate, Forest Ecology, Functional Trait, Trait Integration

Introduction

Variation in individual performance (i.e., survival and growth) determines the structure and dynamics of natural populations and communities. Differential performance is largely determined by the interaction between the individual phenotype and the abiotic and biotic environment (Arnold,1983; McGill, Enquist, Weiher & Westoby 2006). Ecologists have linked commonly-measured morphological and physiological traits, known as functional traits, to demographic rates, to facilitate predictive models of populations and communities into the future.

There is a core suite of functional traits widely measured in plant ecology. These include specific leaf area (SLA), maximum height, wood density and seed mass. These traits are often referred to as "soft-traits" due to their relative ease of measurement across many individuals and species and because they are, typically, indirectly related to a physiological rate or life-history tradeoff of interest (Westoby, 1998; Hodgson, Wilson, Hunt, Grime, & Thompson, 1999). These soft-traits are those most commonly used in tree demographic models (Poorter *et al*. 2008; Wright *et al.* 2010). Maximum height (Westoby, 1998; Bazzaz, Ackerly & Reekie, 2000; Westoby, Falster, Moles, Vesk & Wright, 2002; Poorter, Bongers, Sterck & Wöll, 2005), wood density (Enquist, West, Charnov & Brown, 1999; Chave *et al.* 2009), and seed mass (Rees, 1996; Westoby, 1998) typically explain the greatest amount of variance in tree performance in tropical forests when compared to leaf traits like SLA (Poorter *et al.* 2008; Wright *et al.* 2010). However, forest ecologists have had variable success in linking these core commonly-measured suite of functional traits to tree growth and mortality rates (Poorter *et al*. 2008; Wright et al. 2010; Paine *et al*. 2015; Yang, Cao & Swenson, 2018; Worthy & Swenson, 2019; Iida & Swenson, 2020).

There are multiple ways in which trait-based models of tree survival and growth may be improved (Yang, Cao & Swenson, 2018). These include, (i) measuring traits on individuals instead of using species mean values, (ii) considering less easily-measured traits, (iii) integrating leaf-level trait data into the context of whole biomass allocation, and (iv) accounting for biotic interactions. The first of these possibilities has been shown to be important in studies that have measured individual-level trait data on thousands of individuals from tens to hundreds of co-occurring sub-tropical and tropical tree species (e.g., Liu *et al*. 2016; Umaña, Zhang, Cao, Lin & Swenson, 2017). However, this approach may prove impractical in many cases. Therefore, here, we focus on the remaining three issues: considering less easily-measured traits (i.e. hard-traits) more closely aligned with plant physiological rates, the integration of leaf-level trait data into the context of whole biomass allocation, and accounting for local-scale biotic interactions.

One way forward for trait-based predictions of tree demographic performance is to measure additional traits, linked to physiological processes, beyond the core suite of

commonly-measured soft functional traits. Soft-traits may be strongly correlated with traits that are more difficult to measure (e.g., photosynthetic rates), making them the most pragmatic approach for predicting tree population and community structure and dynamics (e.g., Diaz *et al*. 2004). However, soft-traits may be weakly correlated or not correlated at all with important physiological rates and tradeoffs. Thus, tree survival and growth may be best predicted by less commonly-measured traits. Such traits often referred to as "hard-traits", are often difficult to measure, but are more closely linked to physiological processes of interest (Hodgson, Wilson, Hunt, Gime, & Thompson, 1999; Lavorel & Garnier, 2002; Swenson *et al.* 2017; Yang, Cao & Swenson, 2018). For example, traits directly related to water use efficiency, such as leaf carbon stable isotope composition (Farquhar, O'Leary & Berry, 1982; Dawson, Mambelli, Plamboeck, Templer & Tu, 2002) and leaf vein length per unit area (Sack & Frole, 2006; Brodribb, Feild & Jordan, 2007; Sack & Scoffoni, 2013, but see Gleason *et al*. 2016), should be strongly associated with individual tree performance under hydraulic stress or drought events by significantly affecting photosynthetic capacity and leaf hydraulic conductance (Angert, Huxman, Barron-Gafford, Gerst & Venable, 2007; Correia *et al.* 2008; Gebrekirstos, van Noordwijk, Neufeldt & Mitlöhner, 2011; Sack *et al.* 2013; Iida *et al.* 2016). Thus, it is crucial to determine the importance of these traits in tropical forests, in which drought events are expected to increase (Chadwick, Good, Martin & Rowell, 2016). These hard-trait data can be used in tree performance models and then competed against models that include only soft-trait data.

A second potential way forward is placing organ-level trait data into a whole plant allocation context. Previous work has demonstrated that tree architectural traits such as crown width (Iida *et al.* 2014b) or estimates of the amount of leaf area deployed for light interception (e.g., Falster, Brännström, Dieckmann, & Westoby, 2011) are valuable for understanding the functional strategies of plants and/or their performance. The most obvious and important starting place for accomplishing this goal is an integration of the most commonly measured leaf traits, SLA (i.e., the inverse of leaf mass per area [LMA]), and whole crown biomass leaf area allocation (i.e., an estimation of leaf area ratio). SLA reflects a fundamental tradeoff relating resource capture, leaf investment and leaf lifespan at the scale of a leaf (Reich, Walters & Ellsworth, 1997). However, individuals and

153 species vary widely in their relative allocation to whole crowns and this variation makes
154 it unlikely that SLA alone will serve as a robust predictor of tree demographic rates
155 (Yang, Cao & Swenson, 2018). Individual-level and inter-specific variation in crown
156 biomass allocation or whole plant leaf mass divided by whole plant mass have been
157 identified as critical predictors of plant growth or relative growth rate, respectively
158 (Garnier, 1991; Enquist *et al*. 2007). Despite this, a placement of leaf traits into a crown
159 context is not frequently done in the current trait-based tree growth modeling literature,
160 which likely greatly reduces our ability to predict plant performance (Yang, Cao &
161 Swenson, 2018; Yang *et al*. 2020). Thus, variables representing allocation to leaves
162 should also be considered in models of tree survival and growth and these models should
163 be compared to models lacking this information.
164 Lastly, the role of local-scale biotic interactions (e.g., competition) need to be
165 considered to understand the survival and growth responses resulting from the
166 interactions between focal trees and their neighbours. Plant performance is expected to be
167 affected by local population densities via positive or negative interactions (Pacala &
168 Silander, 1985; Chesson 2000; Uriarte *et al*. 2010). Neighbourhood models that consider
169 the density, size and distance of neighbouring trees have been increasingly used in trait-
170 based studies to determine the role of neighbourhood competition in tree community
171 structure and dynamics (e.g., Uriarte *et al*. 2010; Canham, LePage, & Coates, 2004;
172 Uriarte, Canham, Thompson, & Zimmerman, 2004; Zambrano *et al*. 2019).
173 Here, we compare models of tropical tree survival and growth that incorporate
174 traits linked to tree water use (i.e. leaf carbon isotope composition (leaf δC^{13}), leaf
175 hydraulic capacity and photosynthetic rates (i.e. leaf vein length per unit area), a measure
176 of crown area multiplied by LMA to estimate tree-level allocation to photosynthetic mass
177 (M_p), and neighbourhood crowding. In this work, we ask the following questions.
178 1) How correlated are soft-traits with hard-traits? We predict a strong positive
179 correlation between leaf traits associated with hydraulic and photosynthetic capacity
180 (e.g., Brodribb *et al*. 2007) (i.e., vein length per unit area and LMA), and between leaf
181 traits related to water use efficiency such as leaf carbon isotopic composition with
182 phosphorus concentration (Brück *et al.* 2000), and wood density (Santiago *et al.* 2004).
183 Answering this question is critical because if these two types of traits are significantly

correlated, it would indicate that hard-traits may not be as valuable to measure and will likely not dramatically improve tree survival and growth models. 2) Does the use of an estimate of total tree-level photosynthetic mass (M_p) improve model fits of tree survival and growth as compared to models that do not include this information? We predict that the inclusion of M_p will improve model fit as it relates to crown resource allocation of the whole tree-level that ultimately affects survival and growth rates. 3) Do models of tree survival and growth that include traits related to water use and photosynthetic capacity (i.e., hard-traits) outperform models that include commonly measured soft-traits? We expect that including hard-traits will improve tree performance models as these traits are closely linked to physiological responses such as photosynthetic capacity and leaf hydraulic conductance. 4) Does including the effects of neighbourhood crowding improve the models of tree survival and growth? We predict strong neighbourhood crowding effects on tree survival and growth, due to either competition for similar resources or shared enemies reducing individual performance.

Methods

Luquillo forest dynamics plot

This study was conducted in the Luquillo Forest Dynamics Plot, a 16-ha long-term forest plot located in northeast Puerto Rico (18° 20' N, 65° 49' W; LTFP). The plot, divided into 400 20x20m quadrats, has been censused every five years since 1990, where all free-standing woody stems ≥ 1 cm in diameter at breast height (*dbh*) were identified and measured (Zimmerman, 2010). The plot is located in a subtropical wet forest type with *Dacryodes excelsa* (Burseraceae) and the palm *Prestoea acuminata* (Arecaceae) as the most dominant species. The mean annual rainfall is 3500mm/yr and mean monthly temperatures range between 21-25ºC. The plot experienced severe hurricane damage in 1989, 1998 and 2017 due to hurricanes Hugo, Georges and Maria. The censuses used in this study included only those most distant from hurricane disturbance (2005 and 2011) and previous work has shown that the forest largely recovered from Hugo and Georges prior to the 2005 census (Swenson *et al.* 2012)

Functional trait measurement

We used soft-trait data for 111 woody plant species that were previously collected (Swenson *et al.* 2012; Umana *et al.* 2015; Swenson & Umana, 2015). These traits were collected from 5 to 10 adult trees per species and included: leaf phosphorus (P; percentage P of dry mass), leaf carbon (C; percentage C of dry mass) and leaf nitrogen (N; percentage N of dry mass) concentration; wood specific gravity (referred to as wood density WD); leaf area (LA; cm^2); specific leaf area (SLA; $cm^2\ g^{-1}$); maximum tree height (H_{max}; m); and seed dry mass (SM; g). In addition to these traits, we also measured two hard-traits related to plant hydraulics. The first was vein length per unit area (VLA; $mm\ mm^{-2}$) measured following the protocol described in Iida *et al*. (2016). Briefly, two leaves from the outer crown per species were cut into 1x1cm squares, cleared with NaOH, stained with safranin, mounted on slides and imaged at 20x magnification. Next, the length of non-primary veins in the image was quantified by tracing the veins in ImageJ. A VLA value for 60 of the species was generated by averaging values from 3-5 individuals per species. Detailed physiological studies have shown that VLA is strongly positively correlated with photosynthetic capacity (Brodribb *et al*. 2007). We also quantified leaf carbon stable isotope ratios (leaf δC^{13}; ‰) using leaves collected between January and March 2008 (i.e. midway between censuses and during the driest part of the year). The isotope analyses were conducted using mass spectrometry at the Cornell University Stable Isotope Laboratory using leaves from 1-3 adult trees per species. Carbon stable isotope levels are indicative of water use efficiency (Farquhar, O'Leary & Berry, 1982; Dawson, Mambelli, Plamboeck, Templer & Tu, 2002) and, therefore, may indicate plant performance during periods of limited water.

Trait correlations

Trait values were first log-transformed to approximate normality if their distributions from the raw data were not approximately normal. Correlations between the hard-traits and soft-traits were examined using Pearson's correlation coefficient. In addition, we applied a principal component analysis (PCA) to all traits from the same 60 species from which all trait data were available to determine trait relationships and the contribution of each trait to the principal components.

Total tree-level photosynthetic mass

Total tree-level photosynthetic mass (M_p) was calculated for each individual from 17 of the 30 most common species in the plot. These 17 species account for ~56% of the individuals (excluding palm species) and 13% of the species in the plot in the 2005 census. We established species-specific crown allometries from field measurements (Table S1). Specifically, we measured the stem diameter and the crown radius in two cardinal directions for 5 to 25 individuals (with dbh ranging from = 0.5cm to 56.3cm) per species to produce species-specific allometries (Eq. 1, Table S1, Figure S1; r^2=0.66-0.97). The species-specific M_p was obtained implementing equations (1), (2) and (3) that describe the crown area allometry in terms of individual tree crown radius as follows (Hunt 1978; Poorter 1989; Niklas & Enquist, 2001; Yang, Cao & Swenson, 2018):

$$\log(radius) = slope * \log(dbh) + intercept \quad Eq.\ (1)$$

$$CA = \pi * radius^2 \quad Eq.\ (2)$$

$$M_p = LMA * CA \quad Eq.\ (3)$$

where *intercept* and *slope* are species-specific estimates from the $\log_{10}$-$\log_{10}$ allometric regressions, and leaf mass per area (*LMA*) = 1/ SLA, which is related to leaf lifespan and photosynthetic rates (Reich *et al.* 1997). We estimated the M_p across all individuals (*i*) of each species based upon their dbh_i values and crown area (CA_i). It is important to note that this approach simplifies the estimate of M_p by making the unrealistic, but a most simple, assumption that all individuals and species have an identical leaf area index.

Neighbourhood crowding index

We examined the effects of neighbours by calculating a total Neighbour Crowding Index (NCI). The negative influence of a neighbour was calculated as follows:

$$\mathrm{NCI_i} = \sum_{\mathrm{j}} \frac{dbh_j^2}{d_{ij}^2} \quad Eq.\ (4)$$

The index varies as a function of the squared *dbh* of the neighbour (*j*) and an inverse function of the squared distance (*d*) of the focal tree (*i*) to the neighbour (*j*) (Canham, LePage & Coates, 2004; Uriarte, Canham, Thompson & Zimmerman, 2004). The effect was calculated within a 20-m radius around the focal tree (*i*) and summed over all neighbours. Previous studies have shown that the effects of the neighbours can be detected within a radius smaller than 20m (Hubbell 2001; Uriarte, Canham, Thompson & Zimmerman, 2004; Uriarte *et al*. 2010), and that, in this forest, the effects of NCI are consistent across different radii (5m-30m) (Zambrano *et al*. 2020). We used all 128 species in the 2005 census as neighbours (*j*) and estimated NCI for all individuals (*i*) of the 17 species for the demographic models.

Modeling tree demographic rates: including total photosynthetic mass

We used census data for the same 17 non-palm species for which we had species-specific allometries including all individuals with *dbh* values greater than or equal to one. We included 17,007 individuals for the survival models and 10,538 individuals for the growth models (see Table S4 for individuals per species). We measured tree survival by determining the presence of the individual in the next census. In addition, we calculated tree relative growth rate (RGR, cm y^{-1}) as follows:

$$RGR = (lndbh_{t+\Delta t} - lndbh_t)/\Delta t \quad Eq.\ (5)$$

where dbh_t is measured at a successive time steps t (Δt, measured in years). A value of 1 was added to the observed data before log-transforming. Additionally, negative values obtained (n = 1056), possibly due to stem shrinkage, measurement error, or breakage, were discarded before the log-transformation. Tree survival was fitted using a binomial function while tree growth was modeled using a Gaussian function. For both survival and growth, we used generalized linear mixed effect models (*lmer* and *glmer* functions from the lme4 package in R, Bates *et al.* 2015) as follows:

$$Y_{isk} = \alpha_S + \beta_S\, Variable + \tau_S + \tau_k \quad Eq.\ (6)$$

where Y_{iSk} represents survival (1: alive or 0: dead) or log-transformed RGR values for each individual tree *i* of species *S*, $Variable$ represents any of the following (see Model selection and assessment): dbh_{0_i} (the initial dbh in 2005), M_{p_i} (the tree-level total photosynthetic mass), CA_i (crown area) of each individual *i*, or LMA_S (leaf mass per area) of species S. τ_S and τ_k are random effects of differences in species *S* and quadrat *k*, respectively. α_S is species-specific intercept and β_S are species-specific coefficients representing the effect of the parameters. Parameters were z-score standardized (subtracting the mean and dividing by the standard deviation) prior to analyses.

Model selection and assessment

First, we examined whether including M_p or any of its components, LMA_S and CA_i, instead of dbh_i increased the quality of the tree survival and growth models by fitting one model for each variable with a similar structure (intercept and the random effects) (Eq.6; Table 2). We used three different methods to select the best model: (i) the Akaike's information criterion (AIC), (ii) Akaike weights (w_i) and (iii) Cross-Validation/loss function (C-V loss). For AIC, we used a delta-AIC threshold of 2 units (AIC differences relative to the smallest AIC value: $AIC_i - AIC_{min}$). For Akaike weights, we compared the likelihood (weight of evidence) of each model to the best model by computing their Akaike's weights (Burnham & Anderson, 2002). Lastly, for the C-V loss method we calculated the test error (loss) associated to each model (i.e., goodness of fit) by performing a 10-fold cross-validation. This approach provides a direct estimate of the test error and makes fewer assumptions about the true underlying model (James, Witten, Hastie & Tibshirani, 2013). We chose the "best model" or "best models" as the one/ones with low AIC, high Akaike weight, and low C-V loss scores. To calculate the C-V loss, the data was randomly divided into 10-folds of approximately equal size. Nine of the folds were used to train the models and the one remaining fold to test the models (James, Witten, Hastie & Tibshirani, 2013). This process was repeated ten times in which a different group was treated as the test set. For the ten folds, we calculated the averaged loss for each model (the error associated with fitting each of the models on the data). We implemented two loss functions to assess the goodness of fit of a model (i.e. model quality) by estimating its prediction error on new (i.e. test) data (Hastie, Tibshirani &

Friedman, 2009). For tree survival models only, we used a log-loss function (cross-entropy cost function from the package MLmetrics in R, Yan 2016) that accounts for uncertainty in the predictions. For tree growth, we calculated the Huber loss that uses a quadratic loss function for small residuals or a linear loss function when residuals exceed the minimum value of the 90th quantile (package qrmix in R, Resa, Emir & Cabrera, 2017). Thus, this function avoids the effects of large outliers that make the quadratic loss less robust (Hastie, Tibshirani & Friedman, 2009). When comparing models using the loss function values, the smallest value indicates the model with higher performance when predicting unseen data. In other words, this value indicates which model can be expected to perform better on other sets of data (James, Witten, Hastie & Tibshirani, 2013).

Modeling tree demographic rates: including soft- and hard-traits

Following the selection of the best predictor (M_p, *LMA*, *CA*, or *dbh*) of survival and growth using Eq. 6 (Table 2), we fit all different model combinations that included the selected predictors, both soft- and hard-traits, and the neighbour crowding index. The models were fit controlling for multicollinearity among traits (excluding trait combinations with Pearson's correlation coefficient $|r| \geq 0.60$) using the function *pdredge* from the package MuMIn in R (Bartoń 2018), setting:

$$Y_i = \alpha_S + \beta_{1S}\, Variable + \beta_{2S}\, soft_S + \beta_{3S}\, hard_S + \beta_{4S}\, NCI_i + \tau_S + \tau_k \quad Eq.\ (7)$$

where *Variable* represents the selected parameter (*Mp*, *CA*, *dbh*, or *LMA*), $soft_S$ and $hard_S$ represent all the soft- and hard-traits used at the species level *S*, and NCI_i represents a neighbourhood crowding index at the individual level *i*. The τ_S and τ_k parameters are random effects for species *S* and quadrat *k*, respectively. The α_S is a species-specific intercept, β_{1S}-β_{4S} are species-specific coefficients representing the effect of the parameters. The data were z-score standardized (subtracting the mean and dividing by the standard deviation). We performed model selection following the same methodology described above in the Model selection and assessment section.

Model averaging

When multiple models were indiscernible (AIC_i - AIC_{min} ≤2) due to similar Akaike weights and C-V losses, we carried out multi-model inference to increase precision and reduce bias (Burnham & Anderson, 2002). This methodology first selects a model set from which model averaging is performed including model selection uncertainty from the set of models. We compared the standardized coefficients to determine the relative importance of the variables in the averaged model. Predicted versus observed values were plotted to test the fit of the model. All the analyses were carried out with the R software version 3.5.1 (R Development Core Team 2008).

Results

Correlations between soft- and hard-traits

We found positive correlations between leaf δC^{13} and leaf phosphorus concentration (r = 0.27, P=0.004, n = 105; Figure 1a), between leaf δC^{13} and wood density (r=-0.20, P=0.03, n=105; Figure 1b),and between VLA and leaf carbon concentration (r = 0.45, P<0.001, n = 60; Figure 1c). No significant correlations were found between the other traits studied (Table S2). In the PCA, the first three principal components (PCs) accounted for 60.2% of the total variance. PC1 accounted for 27.8% of the total variance and was possibly related to resource capture. At the negative end of this axis, we found species with high leaf phosphorus and nitrogen concentrations, and low wood density, while the positive end had species with low values of leaf phosphorus and nitrogen concentrations, and high wood density. The PC2 accounted for 18.4% of the total variance and was possibly related to maximum height, with large-statured, low specific leaf area and large seeded species found at positive values of this axis, while at negative values of this axis we found small-statured species with high specific leaf area and small seeds. The PC3 accounted for 13.9% of the total variance and was possibly related to water use, with species showing low values of vein length area, and leaf carbon concentration, and high values of leaf δC^{13} at high values of this axis, while at negative values of this axis species display high values of leaf vein length area and leaf carbon concentration, and low values of leaf δC^{13} (Table S3 & Figure S2).

Demographic models

For tree survival the models that included M_p or *CA*, instead of *LMA* or *dbh*, showed a slight improvement in the model quality (Table 2). Therefore, we fit all the different combinations of tree survival models, controlling for multicollinearity among traits, (models with M_p: 588; models with *CA*: 588) that included M_p, neighbourhood crowding, and soft- and hard-traits (Table S5), and models that included *CA*, neighbourhood crowding, and soft- and hard-traits (Table S6). We selected the models that had a $\Delta AIC \leq 2$ (Table 3), but since multiple models had indiscernible AIC values, and the Akaike weights provided no strong evidence for a single superior model, we performed model averaging (see results in Table 4). The averaged model that included total photosynthetic mass (M_p) as a predictor showed that survival increases with total photosynthetic mass, but the other traits were not significantly related to survival (Figure 2a & Table 4). The averaged model that included crown area (*CA*) as a predictor showed, in order of importance, *CA*, carbon concentration, maximum height, and leaf phosphorus concentration as significant predictors of tree survival, with survival increasing with *CA* and maximum height, and decreasing with leaf carbon and phosphorus concentrations (Figure 2b & Table 4). Leaf nitrogen concentration, seed mass, vein length per unit area, neighbourhood crowding, leaf δC^{13}, leaf area, and wood density showed low support and no statistical significance. In addition, the observed versus predicted plots (Figure S3) showed no difference between the survival averaged models with *Mp* and *CA* suggesting that both models perform equally well.

For tree growth, the model that included M_p instead of its components (*LMA*, *CA*, or *dbh*) showed an improvement in the model quality as evidenced by a reduction in both AIC and the C-V loss (Table 2). The inclusion of soft- and hard-traits and the neighbourhood crowding information in growth models resulted in two models with indiscernible AICs that included M_p, wood density, and neighbourhood crowding as strong predictors of tree growth (Table 5). The averaged growth model showed that tree growth decreases with high values of M_p, wood density, and neighbourhood crowding (Figure 3 & Figure S4, Table 6). Similar to survival models, none of the tree growth models with indiscernible AIC or $|r| < 0.6$ for tree relative growth rate included leaf δC^{13} or vein length area as independent variables at a significance level of 0.05.

Discussion

Modeling individual-level performance including trait information is a key goal in ecology (e.g., Poorter *et al*. 2008; Iida *et al*. 2014a; Paine *et al*. 2015; Iida *et al*. 2016). It has been suggested that tree survival and growth models may be improved by integrating leaf-level traits with whole plant allocation to leaf area, through the measurement of less commonly-measured traits more directly linked to physiological rates, and the inclusion of local-scale biotic interactions (Yang, Cao & Swenson, 2018). Here, we have shown that growth models that integrate leaf-level traits (i.e., 1/SLA) with whole tree crown allocation were superior to models that did not include crown information. Similarly, survival models that integrate leaf-level traits with whole tree crown allocation or total crown area were superior to models that did not include them. Surprisingly, less commonly-measured traits (hard-traits), such as leaf δC^{13} and leaf vein length per area, were not better predictors of tree survival and growth compared to traits widely measured in plant ecology. In addition, neighbourhood crowding showed a strong effect on tree growth, but not tree survival. In the following, we discuss our key results in more detail.

How are soft-traits with hard-traits correalated?

Plant ecologists often utilize easily-measured functional traits in their research to estimate key tradeoffs relating to organismal form and function. These traits are referred to as soft-traits, which are contrasted with hard-traits that are potentially more directly tied to physiological rates and performance, but less easily measured. Thus, trait-based analyses of plant performance may be strengthened by the measurement of hard-traits, but this may largely hinge on the degree of correlation between soft- and hard-traits. Our results showed little to no correlation between the hard-traits measured (leaf δC^{13}, vein length per area (VLA)) and commonly-measured soft-traits (wood density, maximum tree height, seed mass, leaf nitrogen concentration, leaf phosphorus concentration, leaf carbon concentration, leaf area and specific leaf area (SLA)) (Table S2). The only exceptions were correlations found between leaf δC^{13} with leaf phosphorus concentration, and with wood density, and VLA with leaf carbon concentration (Figure 1, Table S2). A positive relationship between leaf δC^{13} and leaf phosphorus concentration has been previously

461 described in other tropical forests (e.g., Baraloto *et al.* 2010). High values of soil
462 phosphorus, which directly determine leaf phosphorus concentration (Wright *et al.* 2004),
463 have been shown to increase plant water use efficiency (e.g., glasshouse experiment by
464 Brück *et al.* 2000; Tibetan plateau by Song *et al.* 2010; and Canadian prairies by Kröbel
465 *et al.* 2012), which corresponds with less negative values of leaf δC^{13}. Contrary to our
466 expectations, the weak negative relationship between leaf δC^{13} and wood density could
467 be explained by a decoupling of stem and leaf hydraulic traits in this forest (but see
468 Santiago *et al.* 2004 for scaling of these traits). A positive correlation between VLA and
469 leaf carbon concentration, highlighting the role of VLA with respect to within-leaf
470 support investment and not only its relation with hydraulics, has been reported previously
471 (Niinemets *et al*. 2007). Leaf veins are composed of xylem and phloem cells (Sack &
472 Scoffoni 2013), which contain mainly lignin, cellulose, and other structural
473 carbohydrates. Thus, an increase in the number of veins per unit area should be
474 associated with an increase in the amount of lignin in the leaf, which coincides with the
475 concentrations of total carbon (Poorter & Villar, 1997).
476 The negligible correlations between hard-traits with soft-traits in our study
477 suggest that the soft-traits measured here are insufficient proxies of VLA and leaf δC^{13}.
478 Nevertheless, it is possible that the strength of the correlations shown here, and the
479 importance of these hard-traits for modeling plant performance would be different if we
480 included ontogenetic differences (Grime *et al.* 1997; Poorter *et al.* 2008; Wright *et al.*
481 2010), considered another set of species (Sack *et al.* 2013), or focused on a period time
482 after intense drought events given the association of these hard-traits with tree
483 performance under hydraulic stress.
484
485 *Total tree-level photosynthetic mass and crown area as better predictors of tree*
486 *performance*
487 Studies that have only considered leaf-level traits such as SLA (e.g., Wright *et al.* 2010;
488 Paine *et al.* 2015) on large organisms (e.g., trees) likely have a reduced capacity to
489 predict demographic rates due to individual- and species-level variation in overall crown
490 allocation and architecture. Instead, total photosynthetic mass (M_p), as others have
491 proposed (e.g., Hunt, 1978; Poorter, 1989; Garnier, 1991; Enquist *et al.* 2007; Yang, Cao

& Swenson, 2018) should be a stronger predictor of plant survival and growth than SLA. By estimating M_p via measurements of crown area integrated with *LMA* (i.e 1/SLA), we generated stronger models of tree demographic rates than those including initial *dbh* (Table 2).

The fact that survival models including crown area and models including total photosynthetic mass performed similarly suggests that omitting *LMA* and measuring crown area alone would be sufficient to improve the predictions of tree survival in this forest (Table 3 & Figure S3). This result highlights the importance of individual-level measurements (i.e., crown area, leaf area index) for improving predictions of tree performance (Poorter *et al.* 2008; Wright *et al.* 2010; Yang, Cao & Swenson, 2018; Yang *et al.* 2020; Iida & Swenson, 2020). It is also important to note the negative effect of M_p on growth. This result could be driven by big trees, expected to have big canopies, growing slower, or by variations in individual crown depths not included in this study.

We note that our estimates of M_p are still crude in that they do not consider overall crown volume and measurements of the leaf area index, but they do provide a marked improvement of the traditional paradigm of relating leaf-level traits to demographic rates without context relating to crown allocation. It is, potentially, also important to note that the impact of M_p (reduced AIC, included in all the best models, and high variable importance/significance) in our models was large relative to that gained by adding or removing soft- and hard-traits (see below, Table 2, Table 3 & Table 5). Thus, future work should start from a foundation of crown measurements in models of tree demographic rates.

Hard-traits did not improve model predictions of tree survival and growth

Contrary to our expectations, soft-traits were better predictors of tree performance than hard-traits related to water use. These soft-traits have been found to be related to tree survival and growth in other tropical forests (e.g. Enquist, West, Charnov & Brown, 1999; Poorter *et al.,* (2008); Chave *et al.* 2009; Wright *et al.,* (2010)). In a study of five neotropical forests, Poorter *et al.,* (2008) found that wood density was the best predictor of relative growth rates while survival rates increased with maximum height. Using the

forest plot used in this study, Uriarte *et al*. (2010) found that models in which the effects of neighbourhood interactions were scaled to trait values such as wood density provided stronger predictions of tree performance. Similarly, Zambrano *et al.* (2020) found that maximum height and leaf phosphorus concentration influenced the strength (positively and negatively, respectively) of neighbourhood interactions on survival rates.

Several explanations can be attributed to the limited model improvement when adding hard-traits. One potential, but unlikely, reason is that water-related traits are not an important predictor of performance. These traits are expected to be strongly associated with individual performance under hydraulic stress or drought events, but they might not be critical for tree performance during periods lacking intense dry events (such as the period evaluated in this study: 2005-2011). Rather, these water-related traits may be more important in the context of future drought events or in other forests experiencing strong droughts (Chadwick, Good, Martin & Rowell, 2016; Santiago *et al*. 2018). A second possibility is that these traits must be considered in light of more contextual information regarding regional-to-local scale abiotic gradients (Zambrano, Marchand, & Swenson, 2017; Yang, Cao & Swenson, 2018). A third possibility that we consider to be the most probable is that these hydraulic traits can be sensitive to micro-environmental conditions or short-term climatic variations and they may need to be measured at those scales (Correia *et al.* 2008; Seibt, Rajabi, Griffiths & Berry, 2008; Baraloto *et al.* 2010; Paine *et al.* 2015). Thus, links between leaf δC^{13} values and growth may be detected at a finer temporal scale than we could assay in this study. Lastly, it could be possible that the link between these hard-traits (VLA and leaf δC^{13}) and tree performance is directly influenced by changes in plant allocation resulting from differences in ontogeny and tree size (Gibert, Gray, Westoby, Wright, & Falster, 2016; Falster, Brännström, Dieckmann, & Westoby, 2011; Iida *et al.* 2014a, 2016; Falster, Duursma, & FitzJohn, 2018). For example, plant traits such as LMA are known to change as the plant grows (Wright *et al*. 2010) due to changes in specific-size plant requirements to allocate biomass or increments on construction costs (Gibert, Gray, Westoby, Wright, & Falster, 2016; Iida & Swenson, 2020). Therefore, tree survival and growth models need be further refined to consider changes associated with plant ontogenetic stage or size (Falster, Duursma, & FitzJohn, 2018) in order to detect significant patterns.

Finally, including information regarding neighbour crowding only improved the quality of our tree growth models (Table 5). Increased neighbourhood crowding reduced tree growth, which was consistent with previous work in this forest (Uriarte, Canham, Thompson & Zimmerman, 2004; Uriarte *et al*. 2010; Zambrano *et al*. 2019; Zambrano *et al*. 2020). Although the previously described negative impact of crowding on tree survival (e.g., Weiner 1990; Hubbell *et al*. 2001), neighbourhood crowding was not a strong predictor of survival in this study. Specifically, survival models including neighbourhood crowding had indiscernible AIC values compared to other models (Table 3), but in the averaged survival models, the effect of neighbourhood crowding was relatively small suggesting that removing it from the models does not impact the predictions. This may be due to species responding differentially to neighbourhoods by having variable effective radii (Uriarte, Canham, Thompson & Zimmerman, 2004; Zambrano *et al*. 2020), or because the neighbourhood crowding index did not include species-specific functional trait values (Uriarte *et al*. 2010).

Conclusions

Studies linking traits to tree performance usually fail to include physiological traits and whole plant allocation information. In this study we considered the importance of hard-traits, crown allocation, an integration of organ-level traits and crown allocation, and biotic interactions to determine whether models of tropical tree performance could be improved in comparison to models that only use easily-measured soft-traits. Given that the leaf δC^{13} and VLA traits failed to improve the models and did not strongly correlate with the leaf and stem traits, we suggest that soft-traits used in this study might not be useful as proxies of leaf δC^{13} and VLA in this forest, and that these hard-traits might not be useful without contextual information regarding water availability (i.e., drought events) and/or finer scale sampling.

Lastly, the inclusion of a whole crown allocation data or crown area improved our predictions of tree performance. This result underscores the importance of integrating organ-level trait data with whole plant allocation data when modeling the performance of tropical trees and how they interact with the abiotic and biotic environment. Thus, future studies should strive to incorporate individual-level crown data and continue to seek out

additional less commonly-measured traits and biotic interactions that will improve tree survival and growth models.

Acknowledgements

This work was funded by a Smithsonian ForestGeo grant and US NSF funding to NGS (DEB-1545761 and DEB-1802812). We would like to thank the comments from two anonymous reviewers and the editors that greatly improved this manuscript. The authors thank Krittika Petprakob for comments that improved the manuscript, and Boris Ngouajio for tracing the leaf images. Repeat censusing of the Luquillo Forest Dynamics Plot lead by J.K. Zimmerman, N. Brokaw, M. Uriarte and J. Thompson, has been made possible by these awards to the plot and Luquillo LTER (BSR-9015961, DEB-0516066, BSR-88111902, DEB-9411973, DEB- 008538, DEB-0218039, and DEB-0620910) and the hundreds of field workers that have collected the data.

Authors' contributions

V.E.R. and N.G.S. generated the research idea; N.G.S., Y.I. and M.N.U. organized and conducted trait data collection; V.E.R. and J.Z. analyzed the data; and V.E.R. and N.G.S. wrote the paper with comments from all other authors.

Data Accessibility Statement

All forest plot data are available on the Luquillo LTER data website: https://doi.org/10.6073/pasta/6061298660b4ceb806ba49805a950646. Soft-trait data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.j2r53/1 (Swenson & Umaña, 2015). Allometric relationships are provided in the supplemental material. Hard-trait data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.4mw6m908c (Swenson, Iida & Rubio, 2020). Code for this study is available on https://doi.org/10.5281/zenodo.4273902.

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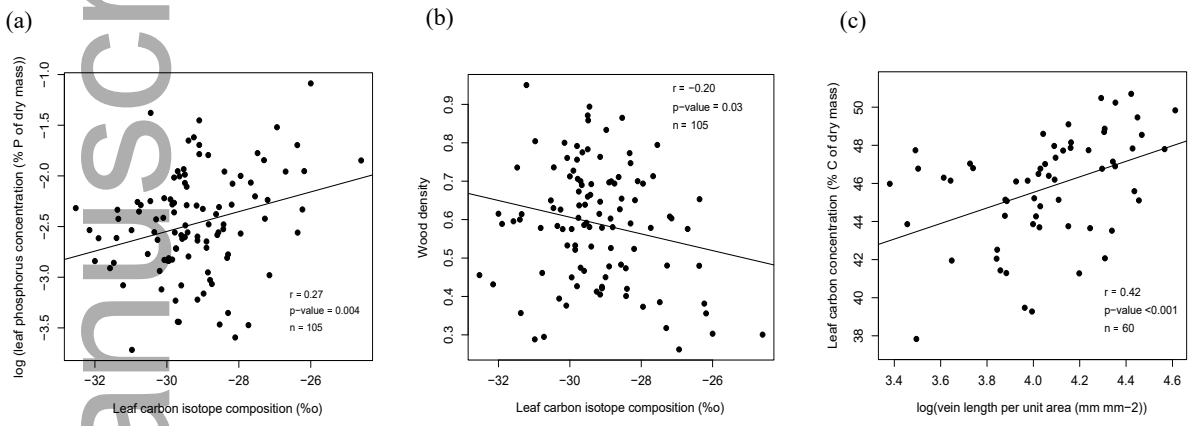
955

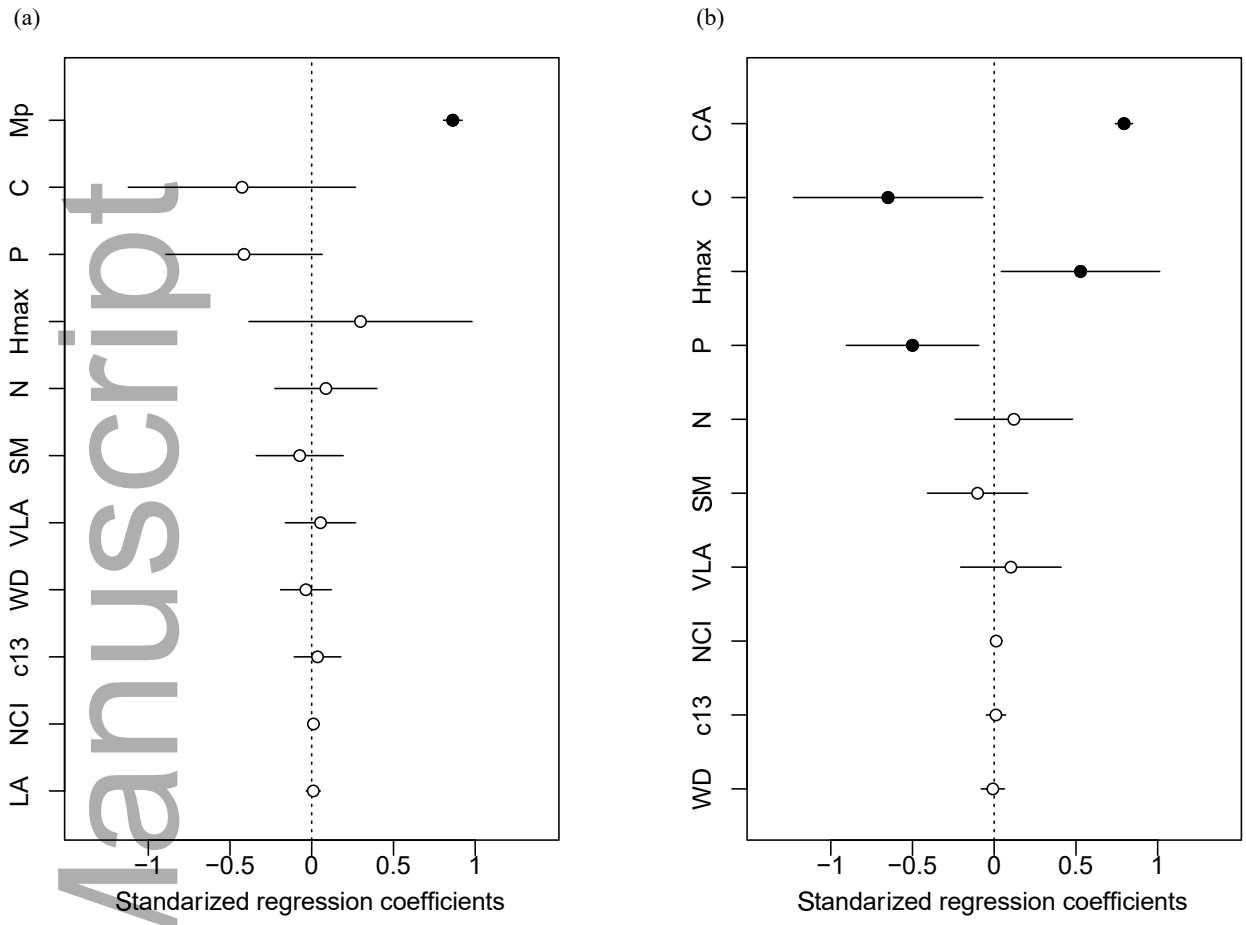
956 **FIGURES**



957

958 **Figure 1.** (a) Correlation between leaf carbon isotope composition and leaf phosphorus
959 concentration. (b) Correlation between leaf carbon isotope composition and wood
960 density. (c) Correlation between vein length per unit area (VLA) and leaf carbon
961 concentration. The Pearson correlation coefficient (r), sample size (n), and p-value are
962 shown for each graph.

963



964

965 **Figure 2.** Standardized regression coefficients for the averaged survival models. Two
966 averaged models were applied: (a) a model including photosynthetic mass (M_p) and traits;
967 and (b) a model including photosynthetic crown area (CA) and traits. Refer to Table 1 for
968 abbreviations. Variables are displayed in order of importance. Lines represent 95%
969 confidence intervals, while circles represent the model estimated value. Open circles are
970 non-significant effect, and filled black circles represent a significant parameter at alpha =
971 0.05. Refer to Table 4 for details.

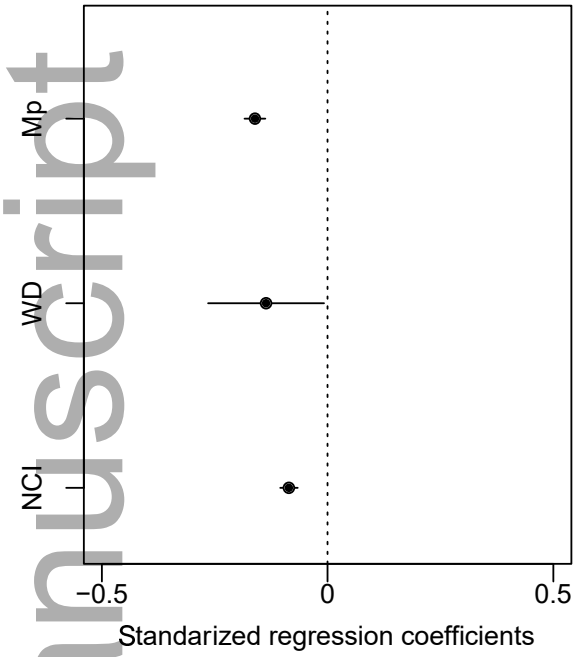


Figure 3. (a) Model standardized regression coefficient for the averaged growth model. Variables are displayed in order of importance. Refer to Table 1 for abbreviations. Lines represent 95% confidence intervals, while the circles represent the model estimated value. Filled black circles represent a significant effect. Standardization was performed by log-transforming and scaling (z-scoring, subtracting the mean and dividing by the standard deviation) the variables. Refer to Table 6 for details.

TABLES

Table 1. Soft- and hard-traits considered as potential predictors of tree survival and growth rates.

Soft-traits		
Commonly measured but weakly correlated or not correlated at all with important physiological rates	Leaf phosphorus concentration	P (%P)
	Leaf carbon concentration	C (%C)
	Leaf nitrogen concentration	N (%N)
	Wood density	WD
	Leaf area	LA (cm^2)
	Specific leaf area	SLA ($cm^2\ g^{-1}$)
	Maximum tree height	H (m)
	Seed dry mass	SM (g)
Hard-traits		
Difficult to measure but closely linked to physiological processes of interest	Stable leaf carbon isotope composition	δC^{13} (‰)
	Vein length per unit area	VLA ($mm\ mm^{-2}$)

988
989
990 **Table 2.** Survival (S) and growth (RGR) models. The table shows the models compared
991 to determine whether including total photosynthetic mass estimates (M_p) outperformed
992 models that included the components of M_p by themselves. Also included were an
993 intercept (ßo), crown area (*CA*), initial diameter at breast height (*dbh*), and leaf mass per
994 area (*LMA*). Variables that are significant in a model are bolded. Moreover, Akaike' s
995 value (AIC), ΔAIC (AIC_i - AIC_{min}), Akaike weights (w_i), and Cross-Validation loss (C-V
996 loss) are shown for each model. Lower Cross-Validation loss (C-V loss) values are
997 underlined showing the model with best goodness of fit and higher probability of being
998 the best model.
999

Model	AIC	ΔAIC	wi	C-V loss
S ~ ßo + *Mp*	16049.8	0	0.495	<u>0.453323</u>
S ~ ßo + *CA*	16058.6	0	0.498	<u>0.453323</u>
S ~ ßo + *dbh*	16049.8	8.8	0.006	0.453670
S ~ ßo + *LMA*	17063.6	1013.77	<0.001	0.485296
RGR ~ ßo + *Mp*	28388.4	0	0.615	<u>0.281690</u>

RGR ~ ßo + *CA*	28389.4	1	0.381	0.281712
RGR ~ ßo + *dbh*	28398.5	10.1	0.004	0.281812
RGR ~ ßo + *LMA*	28548.7	160.3	<0.001	0.282589

1000

1001

1002 **Table 3.** Survival (S) models that include total photosynthetic mass (M_p) or crown area
1003 (*CA*). The table shows the set of models for survival with ΔAIC ≤2 that include the
1004 intercept (ßo), and soft- and hard-traits (refer to Table 1 for abbreviations). Moreover,
1005 Akaike' s value (AIC), ΔAIC (AIC_i - AIC_{min}), Akaike weights (w_i), and Cross-Validation
1006 loss (C-V loss) are shown for each model.

Model	AIC	ΔAIC	w*i*	C-V loss
S ~ ßo + Mp + C + Hmax + P	16047.6	0	0.095	0.453325
S ~ ßo + Mp + C + Hmax + P + N + SM + VLA	16047.7	0.1	0.089	0.453337
S ~ ßo + Mp + C + Hmax + P + NCI	16048.1	0.4	0.076	0.453288
S ~ ßo + Mp + C + Hmax + N + P + SM + NCI + VLA	16048.2	0.5	0.073	0.453301
S ~ ßo + Mp + P	16048.4	0.8	0.065	0.453317
S ~ ßo + Mp + C + P	16048.5	0.9	0.061	0.453324
S ~ ßo + Mp + C + Hmax + P + c13	16048.7	1.0	0.056	0.453331
S ~ ßo + Mp + P + NCI	16048.8	1.2	0.053	0.453281
S ~ ßo + Mp + C + Hmax + N + P + SM + VLA + c13	16048.9	1.3	0.051	0.453344
S ~ ßo + Mp + C + P + NCI	16048.9	1.3	0.049	0.453287
S ~ ßo + Mp + Hmax + P	16049.0	1.3	0.048	0.453314
S ~ ßo + Mp + C + P +wsg	16049.1	1.4	0.046	0.453325
S ~ ßo + Mp + C + Hmax + P + NCI + c13	16049.1	1.5	0.045	0.453294
S ~ ßo + Mp + C + Hmax + P + wsg	16049.2	1.6	0.042	0.453327
S ~ ßo + Mp + Hmax + P + NCI	16049.4	1.8	0.039	0.453277
S ~ ßo + Mp + P + LA	16049.4	1.8	0.039	0.453311
S ~ ßo + Mp + C + P + NCI + wsg	16049.5	1.9	0.037	0.453289
S ~ ßo + Mp + C + c13	16049.6	2	0.035	0.453336
S ~ ßo + CA + C + Hmax + P	16045.0	0	0.268	0.453334
S ~ ßo + CA + C + Hmax + P + NCI	16045.4	0.4	0.217	0.453298
S ~ ßo + CA + C + Hmax + P + N + SM + VLA	16046.0	1.0	0.163	0.453347
S ~ ßo + CA + C + Hmax + N + P + SM + NCI + VLA	16046.4	1	0.134	0.453311
S ~ ßo + CA + C + Hmax + P + c13	16046.7	1.7	0.115	0.453336
S ~ ßo + CA + C + Hmax + P + wsg	16046.9	1.9	0.104	0.453335

Table 4. Average survival (S) models that include total photosynthetic mass (Mp) or crown area (CA), and soft- and hard-traits (refer to Table 1 for abbreviations). Variables are displayed in order of importance. Also included are the unconditional (model selection uncertainty not conditional in any particular model from the set) sampling standard error ($\widehat{SE}$), unconditional confidence intervals (Lower CI and Upper CI), and absolute Wald values are shown for each variable.

Variable	Estimate	$\widehat{SE}$	Lower CI	Upper CI	|Wald Z|
S ~ ßo + Mp + C + Hmax + P + N + SM + VLA + NCI + c13 + WD + LA					
Mp	0.863	0.029	0.806	0.919	29.8
C	-0.427	0.355	-1.122	0.269	1.20
H	0.298	0.348	-0.384	0.980	0.86
P	-0.415	0.244	-0.894	0.064	1.70
N	0.086	0.159	-0.225	0.398	0.54
SM	-0.073	0.136	-0.339	0.192	0.54
VLA	0.053	0.109	-0.160	0.267	0.49
NCI	0.010	0.017	-0.023	0.043	0.61
c13	0.035	0.073	-0.108	0.178	0.48
WD	-0.036	0.079	-0.191	0.119	0.45
LA	0.010	0.022	-0.034	0.053	0.43
S ~ ßo + CA + C + Hmax + P + N + SM + VLA + NCI + c13 + WD					
CA	0.794	0.027	0.742	0.846	29.8
C	-0.649	0.296	-1.229	-0.070	2.20
H	0.528	0.247	0.043	1.013	2.13
P	-0.500	0.206	-0.904	-0.096	2.42
N	0.120	0.183	-0.239	0.479	0.66
SM	-0.102	0.156	-0.408	0.204	0.65
VLA	0.102	0.157	-0.205	0.409	0.65
NCI	0.012	0.018	-0.023	0.047	0.69
c13	0.010	0.030	-0.049	0.070	0.34

WD	-0.009	0.036	-0.080	0.063	0.24

Table 5. Growth (RGR) models. The table shows the set of models with indiscernible ΔAIC ≤2 that include intercept (ßo) and traits (refer to Table 1 for abbreviations). Moreover, Akaike value (AIC), ΔAIC (AIC_i - AIC_{min}), Akaike weights (w_i), and Cross-Validation loss (C-V loss) are shown for each model.

Model	AIC	ΔAIC	wi	C-V loss
RGR ~ ßo + Mp + WD + NCI	28321.7	0	0.67	0.281006
RGR ~ ßo + Mp + NCI	28323.1	1.4	0.33	0.281043

Table 6. Average growth (RGR) models that include total photosynthetic mass (Mp) and soft- and hard-traits (refer to Table 1 for abbreviations). Variables are displayed in order of importance. Also included are the unconditional (model selection uncertainty not conditional in any particular model from the set) sampling standard error ($\widehat{SE}$), unconditional confidence intervals (Lower CI and Upper CI), and absolute Wald values are shown for each variable.

Variable	Estimate	$\widehat{SE}$	Lower CI	Upper CI	|Wald Z|
		RGR ~ ßo + Mp + WD + NCI			
Mp	-0.161	0.012	-0.184	-0.138	13.71
WD	-0.136	0.065	-0.265	-0.008	2.08
NCI	-0.086	0.010	-0.105	-0.066	8.72