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Greater variability in environmental stress favours trees that prioritise storage of carbohydrate reserves over growth: a modelling analysis

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Abstract

Trees use reserves of non-structural carbohydrates (NSC) to help them survive and recover from stress periods. However, accumulation of reserves is at the expense of growth, resulting in a growth-storage trade-off. Tree species may pursue different storage strategies to optimise fitness in environments with differing degrees of stress, but it is not clear which storage strategies provide a competitive advantage in which environments.

We use a forest gap model to explore competitive outcomes among idealised tree species with different combinations of two carbon storage-related traits: carbon utilisation rate (fast-slow spectrum) and switch time from growth to storage (risky-safe spectrum). We investigate the competitive success of alternative growth vs storage strategies in simplified environments which have a non-specific annual stress period. We vary stress intensity (the mean stress duration) and stress stochasticity (the variance of stress duration) to determine the effect of increased stress on composition outcomes.

Community composition shifted from growth-prioritising strategies to storage-prioritising strategies with increasing stress intensity and stochasticity. The major driver of this shift in community composition was increased mortality, due to depletion of carbon reserves, in species with growth-prioritising strategies.

Our results demonstrate that considering carbon storage strategies can provide new insights into tree survival and adaptation of tree communities to increasing stress caused by climate change.

1 Introduction

Climate change is increasing the duration, frequency and intensity of environmental stresses such as droughts and extreme temperatures, with significant consequences for vegetation globally. Trees, because of their long life-spans, may be especially susceptible to increasing stress (Bojórquez et al., 2019; Dai, 2013; Reichstein et al., 2013). There are now many reports of large-scale tree mortality events globally following extreme hot-droughts (Allen et al., 2015). During a hot-drought event, tree mortality can be caused by failure of the hydraulic system due to lack of water availability (Nolan et al., 2021). However, mortality can also be caused by the lack of available carbon, either to supply energy during stress, or to enable recovery post-stress. In some cases, mortality may not occur until months or years following the stress event (Dietze et al., 2014a; Trugman et al., 2018),

Carbon availability is thus a key determinant of survival during and after stress. Uptake of carbon via photosynthesis is limited during stress periods (Muller et al., 2011), meaning that plants depend on the availability of carbon reserves to supply their energy requirements. Post-stress, carbon uptake may remain limited because of stress-induced damage to photosynthetic structures (Carnicer et al., 2011; Schwalm et al., 2017). Recovery requires investment into new structures, and it can take several months to several years for metabolic activity and growth rates to return to pre-stress levels (Huang et al., 2018; MacAllister et al., 2019; Ruehr et al., 2019). Thus, storing carbon in the form of non-structural carbohydrates (NSC) is essential for plants to survive and recover from stress periods when carbon assimilation is limited (Adams, Germino, et al., 2013; Tixier et al., 2019; Wiley, 2020).

To predict the responses of trees to climate extremes using process-based models, it is therefore important to incorporate a representation of NSC dynamics. However, efforts to model plant carbon storage are hampered by the limited theoretical understanding behind the mechanisms enabling plant survival (Hartmann et al., 2020; Sala et al., 2010). As a result, modelling of NSC dynamics has often used a simple accounting mechanism in which excess carbon that is not used for functions such as growth, maintenance or reproduction is stored for future use. This ‘passive storage’ approach can be contrasted with an ‘active storage’ approach, which is based on the idea that plants have adapted to optimise their long-term survival in uncertain environments by storing carbon (Wiley and Helliker, 2012). There is a long-term trade-off between storage of carbon vs use of carbon for growth and reproduction, meaning that patterns of carbon allocation and storage during stress might be optimised to maximise plant fitness.

Several dynamic optimisation models have been developed that consider this idea, simulating perennial plants that maximise their reproductive output over several years punctuated by stress periods. Such models have found that the optimal growth schedule typically follows a three-phase pattern within a single year: a period of growth (at maximum growth-rate), followed by storage or reproductive output (growth fully ceased), and finally the stress period (Iwasa and Cohen, 1989; Kozłowski and Uchmanski, 1987; Kozłowski and Wiegert, 1987; Pugliese and Kozlowski, 1990). Similarly, Stefaniak et al. (2024) investigated the optimal allocation of carbon to growth vs storage over time before and during a stress period and found the optimal allocation schedule to switch from growth to storage in advance of the stress period in almost all cases. However, the timing of the switch varied depending on the optimisation goal assumed. If it was assumed that plants maximise total storage, the switch time is earlier than if it was assumed that plants maximise total biomass. This variation reflects a key challenge of optimisation approaches: defining what is an appropriate proxy for plant fitness (Franklin et al., 2012).

An appropriate optimisation goal is difficult to define for the trade-off between growth and storage of carbon because it ultimately depends on the long-term outcome of competition. In order to outcompete its neighbours, and gain more resources by growing taller, a plant may adopt a strategy of faster growth, but this may come at the cost of lower carbon stores and higher vulnerability to mortality (Atkinson et al., 2014; Myers and Kitajima, 2007). Some studies find that larger trees are more susceptible to stress mortality due to increased hydraulic and metabolic demand (Rose et al., 2009; Rowland et al., 2015; Trugman et al., 2018). However, higher growth rates may also increase the speed of recovery (Myers and Kitajima, 2007) and support larger resource uptake rates which in turn can lead to larger carbon stores. Thus, it is not immediately obvious which strategy is best fitted to a given environment, making it difficult to propose an optimisation goal.

Another type of model, gap models, offer an opportunity to explore the relative success of different growth vs storage strategies and how this success varies with environment. Gap models simulate interspecific population dynamics within a stochastic patch of forest (Bugmann, 2001). Individual trees are modelled explicitly, with competition for resources, particularly light, limiting growth and survival of smaller individuals. Gap model simulations can capture a significant breadth of plant behaviour and relevant feedback mechanisms, while community dynamics become an emergent property which can be further examined. Crucially, gap models focus on long-term, rather than short-term, community dynamics allowing for the examination of success in differently aged ecosystems and of a species in a given environmental regime (Morin et al., 2021; Norby et al., 2001). More recently, trait-, size-, and patch-structured models (TSPMs) have expanded the functionality of gap models to focus on trait dynamics (Falster et al., 2011). TSPMs specifically aim to examine the response and sensitivity of community composition to variation in individual-level functional traits, rather than aiming to reproduce observations of real forests. The TSPM modelling framework developed by Falster et al. (2011) has been made available as a modifiable code based (plant, Falster et al., 2016) making both the traditional gap model and TSPM functionality more accessible.

Here, we expand on the existing *plant* model introduced by Falster et al. (2016), and use the extended model to examine the growth-storage trade-off under competition and environmental stochasticity. Use of a gap model allows the exploration of the impact of competition on the growth-storage trade-off and avoids the need to specify a particular proxy to represent fitness. The goal of this work is to understand long-term fitness of different growth/storage allocation strategies in different environments. In order to describe the spectrum of growth / storage allocation strategies, we specifically examine two key parameters: 1) the switch time, between growing and storing, which emerged from the optimisation models (Stefaniak et al., 2024); and 2) the rate of carbon utilisation (from storage compartment) in growth as a reflection of the plant growth rate (Eller et al., 2018). By considering four combinations of these two traits (i.e., (i) fast-risky, (ii) fast-safe, (iii) slow-risky, and (iv) slow-safe), this work investigates a complex growth-storage trade-off spectrum. Environmental stress is characterised as a stress period that occurs each year during which photosynthesis is zero. Stress intensity is represented by the average duration of this stress period, and stochasticity is represented by the variability of that duration. Using this model, we investigate the following research questions:

A. How does the stochasticity and intensity of stress affect the success of different strategies, and how does it change community dominance?
B. If species dominance is altered, what are the primary drivers of this change?

2 Methodology

2.1 Model

The gap model was implemented in the *plant* software package (Falster et al., 2016), developed to simulate the size-structured dynamics of plants competing for light in a patch. Importantly, *plant* allows users to run alternative models within the same framework. The default model (here denoted FF16) includes individual-based competition for light, with growth and mortality affected by traits and size, via effects on photosynthesis, respiration, turnover and resource allocation.

To implement the carbon storage allocation scheme, we created a new model version (here denoted plantNSC) that expands on the default FF16 model by adding a stored carbon pool to the carbon allocation model. The implementation includes accumulation and utilisation of NSCs for individuals, with subsequent effects on growth and mortality rates. Below we describe key elements introduced in the plantNSC model version. A full list of functions implemented in the model can be found in Table A1.

The storage utilisation scheme assumes that incoming carbon first enters the storage pool before being utilised for growth and reproduction (Fig. 1). This representation is commonly used in optimal allocation models (Chiariello and Roughgarden, 1984; Iwasa and Cohen, 1989; Iwasa and Levin, 1995; Stefaniak et al., 2024) and in some mechanistic models (e.g., Jones et al., 2020; Mahmud et al., 2018). Models differ, however, in how they represent the use of stored carbon. Here, we use an active storage utilisation scheme which is controlled by two traits: the switch time from growth to storage, t_s, and the storage utilisation parameter, α_s.

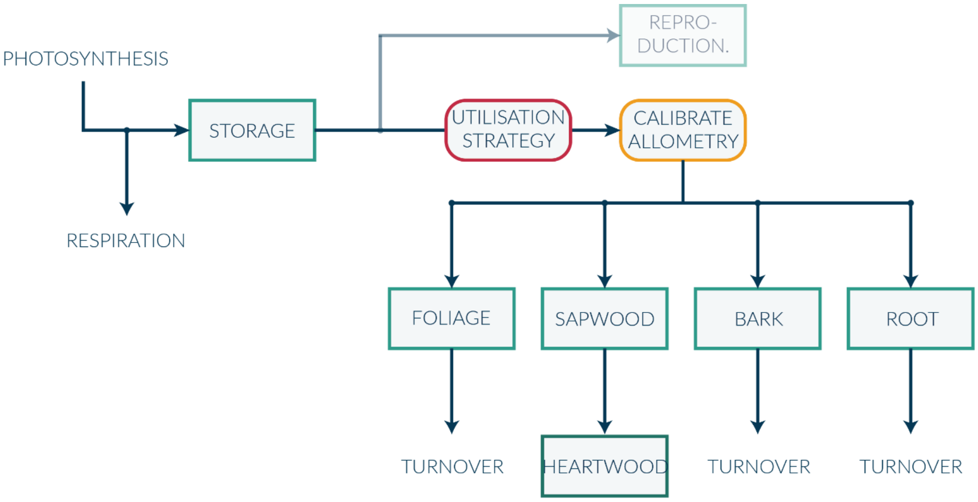

Figure 1 The carbon allocation scheme used in the model. Net carbon uptake (NCU; Photosynthesis - Respiration) first enters the storage pool before being utilised for growth of functional components and reproduction. The input to storage can be either positive or negative, depending on whether respiration exceeds photosynthesis. The amount of carbon utilised for growth is controlled by the utilisation strategy (red box) which is defined by the two trait parameters (the switch time from growth to storage, t_s, and the storage utilisation parameter, α_s). The allocation of growth among foliage, sapwood, bark, and root is controlled by allometric relationships with height and leaf area. Loss to turnover is kept at constant rates throughout the years. Litter carbon from foliage, bark, and root is lost from the plant, while the carbon from sapwood turnover is converted to heartwood. Reproduction is included in the model at a nominal amount kept for realism of carbon costs but not function. Reproduction only occurs when the utilisation of carbon is positive.

The rate of NSC utilisation U defines the plant's utilisation strategy (Fig. 1, red box) and is given by:

$$U = \begin{cases} \alpha_s M_{st} & if \quad t < t_s \\ 0 & if \quad t \geq t_s \end{cases}, \tag{1}$$

where t is the time of year, t_s is the switch time parameter, α_s is the storage utilisation rate parameter and M_{st} is the size of the storage pool. Note that Eq. 1 allows for the plant to continue growing in some cases despite being stressed, if t_s is later than the onset of stress that year. To aid computation, Eq. 1 is implemented as a logistic step function to remove discontinuity.

Two parameters govern the allocation strategy: (1) switch time, t_s, and (2) storage utilisation rate, α_s. The switch time parameter, t_s, represents the time-point at which it is optimal to switch from growing to storing in optimisation models (Engen and Saether, 1994; Iwasa and Cohen, 1989; Stefaniak et al., 2024; Wenk and Falster, 2015). Here, t_s is a fixed time of the year, independent of the stress onset. The storage utilisation rate parameter on the other hand, governs the rate at which storage is converted into tissue. Together, these two parameters form a growth-storage trade-off. Later switch time and higher storage utilisation rate confer larger growth but higher respiration costs and lower available storage which may lead to higher mortality during stress (Fig. 1). Conversely, an earlier switch time and lower storage utilisation rate allow for larger storage pools which may increase survival during stress but at a cost of decreased growth and higher likelihood of shading by taller plants.

Following the FF16 strategy, the carbon allocation and allometry scheme is based on the Pipe Model Theory (Shinozaki et al., 1964). The scheme assumes a relationship between height growth and leaf area and in turn between leaf area and the size of the tree needed to support the desired leaf area. The introduction of stress causes a loss of the allometric balance between components because U is zero during storage periods and the size of a component i can decrease. To address this issue, the change in size of component i was made dependent on a calibration factor c_i:

$$\frac{\mathrm{d}M_i}{\mathrm{d}A_l} = c_i(H, A_l, M_i)\frac{\mathrm{d}M_i{}'}{\mathrm{d}A_l}\ , \tag{2}$$

where $\frac{\mathrm{d}M_i{}'}{\mathrm{d}A_l}$ is the original allometric function from Falster et al. and the calibration factor is given by:

$$c_i(H, A_l, M_i) = \frac{2}{1+\exp\left(-c_k(M_i'(H,A_l)-M_i)\right)}. \tag{3}$$

Here, c_k is the calibration rate parameter, $M_i{}'(H, A_l)$ is the allometrically correct pool size for a plant of height H and leaf area A_l and M_i is the actual pool size. If the calibration is correct the growth rate stays constant ($c_i = 1$); if it is too small for the current size of the plant the growth to that part is prioritised to aid with recovery (up to double the usual speed of growth), and if the component is too big, growth is slowed down for the benefit of other components. c_k controls the speed of the prioritisation with a higher value leading to a larger increase in priority and faster calibration, and a low value leading to slow calibration and longer periods of adjustment. Height allometry is adjusted in the same way as pool biomass.

The per capita instantaneous mortality rate of a plant has three parts that are summed to determine the total mortality rate: (1) a constant, independent mortality rate (d_I) which represents the random chance of death due to events unaccounted for in the model (retained from original model); (2) productivity-dependent mortality (d_P) which represents the effect of light stress (adjusted to account for environmental stress); and (3) storage-dependent mortality (d_S) which represents the effect of low NSC reserves (newly introduced). Mortality rate is thus:

$$d(x, H, M_{st}, E_a, E_s, t) \ = \ d_I \ + \ d_P(x, H, E_a, E_s, t) \ + \ d_S(x, M_{st}), \tag{4}$$

The productivity-dependent mortality declines with carbon budget:

$$d_P(x, H, E_a, E_s, t) = E_s(t)\alpha_{dP1}\exp\left(-\alpha_{dP2}X\right) \tag{5}$$

where $X = B/A_l$, that is the net carbon uptake per unit leaf area. When the plants are stressed ($E_s(t) = 0$) photosynthesis goes to zero and B becomes negative. To avoid all plants dying during this period, the productivity-dependent mortality is multiplied by the stress factor E_s. α_{dP1} and α_{dP2} control the mortality function and can be adjusted for individual strategies.

The storage-dependent mortality follows the same structure, with the mortality rate decreasing as the storage concentration increases:

$$d_S(x, H, M_{st}) = \alpha_{dS1} \exp\left(-\alpha_{dS2} X\right) \tag{6}$$

where $X = M_{st}/M_a$ is the storage concentration in live biomass. Parameters α_{dS1} and α_{dS2} control the shape of the mortality function and can be adjusted for individual strategies. Within a given time step, Δt, the probability an individual tree dies is then given by:

$$p_D(t) = 1 - \exp(-\Delta t\, d\,(x, H, M_{st}, E_a, E_s, t)) \tag{7}$$

Survival through germination is also dependent on the productivity of the new plant (Falster et al. 2016). The process has been adjusted to account for stress with germination halting throughout the stress period and introducing an initial storage pool. New plants arrive at the patch with height H_0, correct allometry scaling of the strategy for live biomass ($M_{a0}(H_0)$) and a storage pool of size M_{st0},

$$M_{st0} = \beta_s\, M_{a0}(H_0) \tag{8}$$

where β_s is the initial storage concentration for a new plant.

2.2 Environment

Each year, the environment is characterised by a period of no stress followed by a period of stress. We simulated incoming light based on the solar regime experienced in Sydney, Australia: Falster et al. 2011), with the time of the switch between no-stress and stress each year derived from a normal distribution. Outside of the annual stress period, the only factor affecting individual tree photosynthesis is light competition, which is based on the tree's height. The model assumes a uniform horizontal leaf area distribution with all the leaves at height *z* equally shaded (Bugmann, 2001), but leaf area is distributed vertically. Because patches are kept small to allow for computational performance, this scheme is deemed adequate for the model. For bigger patches, however, a crown projection area implementation that includes spatially heterogeneous interaction would be more appropriate (Lexer and Hönninger, 2001). When the plant is stressed by the environment, photosynthesis, germination and productivity-driven mortality are all halted, and respiration is reduced.

2.3 Parameter Estimation

Allometric growth parameters were derived principally for *Eucalyptus grandis* using additional data from the related species *Eucalyptus nitens*, *Eucalyptus pilularis*, *Eucalyptus saligna* and *Eucalyptus urophylla*. Data were obtained from the BAAD database (Falster et al., 2015) and allometric relationships were calculated using linear regression with the statistical modelling software R. The database was further used to validate chosen parameters in short (< 20 years) single-plant simulations to ensure allometry was maintained. Where data were not available in the BAAD data base, additional data were extracted from literature where possible, or default FF16 model parameters were used. Simulations established optimal parameters for parameters without simple physiological counterparts. Table A2 provides full details of parameter values and origin.

2.3.1 Parameter Estimation for Competing Strategies

We chose two contrasting values for the two focus parameters, which in combination gave four competing strategies. The values were chosen using a sensitivity analysis for each parameter across a range of plant heights and storage concentrations (full details available in Supplementary Information A: Parameter Estimation).

Sensitivity analysis simulations were run for a single plant, for one year with no light-limitation and with stress duration of 91.25 and 54.75 days (corresponding to the average t_{crit} values of 0.85 y and 0.75 y used in model simulations). Any simulations where the storage became negative were excluded from the simulation. From these simulations, two values for each parameter were chosen for a total of four contrasting allocation strategies. The strategies were named as follows: the “Risky - Safe” spectrum represents the switch time, t_s, varying from high to low; and the “Fast – Slow” spectrum represents the storage utilisation rate, α_s varying from high to low. The four strategies are therefore:

- *Fast-Risky* ($t_s = 0.5$ y, $\alpha_s = 0.3$ kg C kg^{-1}C d^{-1})
- *Fast-Safe* ($t_s = 0.25$ y, $\alpha_s = 0.3$ kg C kg^{-1}C d^{-1})
- *Slow-Risky* ($t_s = 0.5$ y, $\alpha_s = 0.1$ kg C kg^{-1}C d^{-1}) and
- *Slow-Safe* ($t_s = 0.25$ y, $\alpha_s = 0.1$ kg C kg^{-1}C d^{-1}).

Following the initial one-year sensitivity analysis, the model was run for individual trees for one year to further explore the effect of different strategies.

The four strategies affecting the Growth-Storage trade-offs are illustrated in Fig. 2.

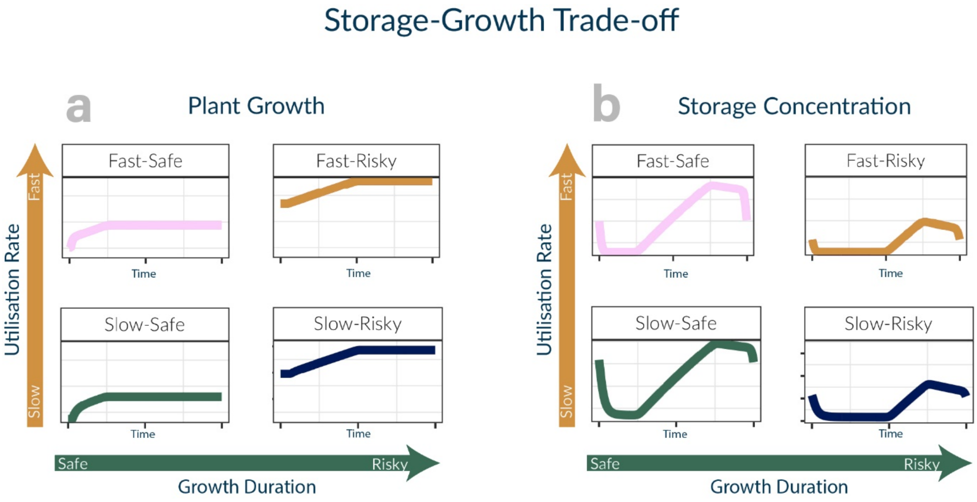

Figure 2 Storage-Growth Trade-offs as represented by the four strategies. Graphs illustrate the rough shape of (a) height growth and (b) storage concentration over the course of a year. The largest differences in growth are determined by the switch time t_s, with shorter growth (smaller t_s values) representing a storage-prioritising plant and longer growth (larger t_s values) representing a growth-prioritising plant. The largest difference in storage concentration is determined by the storage utilisation rates α_s with slower rates being on the storage priority end of the spectrum and faster rates on the growth priority end.

2.4 Simulations

The model was run repeatedly for 100 years with all four strategies present to investigate outcome of competition. An adaptive time-step was used with a range of 10^{-6} to 10^{-1} y. The environment treatments varied between stress intensity and stress stochasticity.

The environmental stress was varied for each run as follows. A total of 8 environmental treatments were chosen, with two average stress intensities crossed with four levels of stochasticity from no stochasticity to high stochasticity. For each environment treatment, five random stress sequences were generated from the probability distribution defining that treatment (only one for the treatments with no stress stochasticity). The model was run four times for each of the stress sequences to account for model stochasticity associated with germination and mortality (from hereon, referred to as stress-sequence repetitions). Additionally, a control simulation was run with no stress ($t_{crit} = 1$), no stochasticity and no storage-related mortality. A summary of these simulations is given in Table 1.

Table 1 Summary of Environmental Treatments. Mean stress is the average stress duration in a given year (days), SD stress indicates the standard deviation of the stress duration, num stress is number of stress-treatment repetitions, num seq is number of stress-sequence repetition (see text), num tot is the total number of repetitions for that treatment.

Name	Mean Stress	SD Stress	Num Stress	Num Seq	Num Tot	Notes
Control	0	0	1	4	4	No storage-related mortality
Low Stress-No Stochasticity	54.75	0	1	4	4	-
Medium Stress-No Stochasticity	91.25	0	1	4	4	-
Low Stress-Low Stochasticity	54.75	15	5	4	20	-
Medium Stress-Low Stochasticity	91.25	15	5	4	20	-
Low Stress-Medium Stochasticity	54.75	30	5	4	20	-
Medium Stress-Medium Stochasticity	91.25	30	5	4	20	-
Low Stress-High Stochasticity	54.75	60	5	4	20	-
Medium Stress-High Stochasticity	91.25	60	5	4	20	-

The size of the patch was set to be 100 m^2 following Bugmann (2001).

An initial simulation (for a high stochasticity environment) was run for 400 years to find the optimal number of years after which the outcome of competition is clear (although due to the stochastic nature of the stress and simulations themselves, no equilibrium or steady-state can be fully observed).

Each environmental treatment had all 4 allocation strategies present, with each strategy given an equal seed rain (0.5 seeds m^{-2} yr^{-1}) which was calculated from the FF16 deterministic model with the parameters used in the simulation. The simulations were run on a high performance, high memory server cluster with an average simulation duration of 3 days. The high intensity of the simulation is attributed to the number of trees in each patch that need to be tracked including deceased plants which are kept track of in the algorithm.

2.4.1 Analysis of Simulation Results

All data transformation and analysis were performed using the R statistical programming software (R Core Team, 2018) and the package *tidyverse* (Wickham et al., 2019). Each simulation was pre-processed to remove trees with a diameter smaller than 5 cm. This was done due to the large number of small trees which established but did not survive past one year of simulation. Time series outputs were averaged using a rolling average for observation and a time-series of 20 y < t < 100 y was examined for indicators of relationships between strategy successional status.

To analyse final outcomes, basal area values in the last 10 years of the simulation (90 y < t < 100 y) were averaged for each run. Treatment means and standard deviations were then calculated. To analyse the effect of environmental stress on the final yield, a linear regression, accounting for individual strategies and treatment, was performed. To assist with interpretation of those results, an omega squared, ω^2, value was used to calculate the effect size based on the comparison between proportions of variance of predicting variables (LeCroy and Krysik, 2007) which was interpreted using measures described in (Field, 2013). Both operations were done using the R package *effectsize* (Ben-Shachar et al., 2020). The *scico* R package was used to for creating colour palettes for the figures (Crameri, 2023).

3 Results

One example run was selected from the Low-stress, Medium-stochasticity treatment to illustrate forest development in the model. In this run, the Slow strategy trees show a much higher success compared to the Fast strategy trees. The dominance of the Slow strategy is visible in the height (Fig. 3) and *productivity* (Fig. S5) of the individual plants and in the *number* of individual plants (Fig. S6) and although the Slow-Safe and Slow-Risky strategies maintain a relatively similar average height, the Slow-Safe strategy is most successful in terms of Net Carbon Uptake (Fig. S5), being responsible for up to three quarters of NCU across the patch. Contributing to the dominance of the Slow strategies is the mortality under shading of Fast strategies which have lower minimum storage concentrations (Fig. S7).

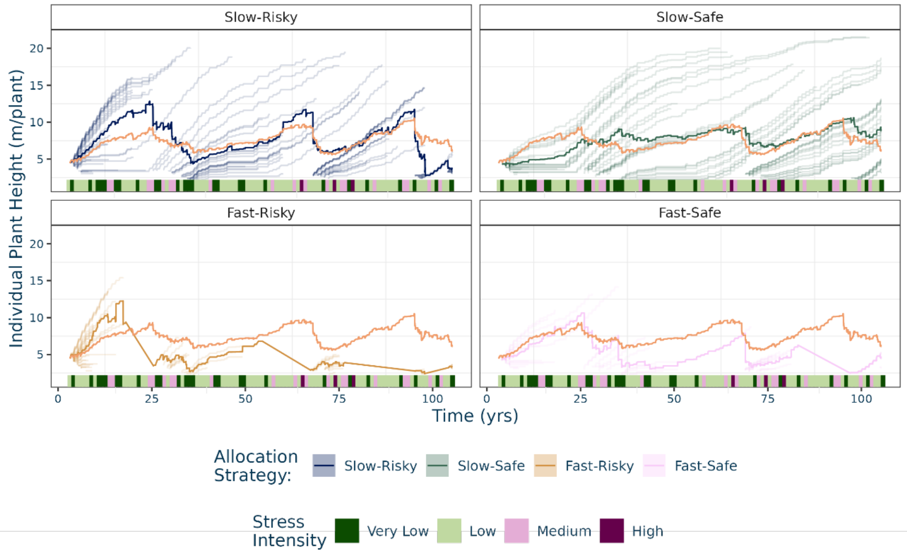

Figure 3 Height distribution of individuals over 100 years on a 100 m2 patch. Each panel shows one allocation strategy in the population ((a) slow-risky, (b): slow-safe, (c): fast-risky and (d): fast-safe). Pale lines show individual trees; darker lines of each colour show the average for all individuals of that strategy; dark blue line shows average height for the entire population. The rug on each figure shows the duration of the stress in a given year (green for very low stress intensity <30d, blue for low (30 to 75d), yellow for medium (75 to 105d) and red for high (105 to 150d)). Periods of no height increase in an individual can be explained by an allometric mismatch after the period of stress. During the recovery period, growth is prioritised in the plant components that are most imbalanced until allometric relationships are regained.

3.1 Effect of stress on final basal area

We found that only two of the four strategies can co-exist in any given environment. In the control simulation, where there is no stress and no mortality associated with low carbohydrate storage, the Fast-Risky and Slow-Risky strategies outcompeted both Safe strategies, as a result of the longer growing period of the Risky strategies (Fig.

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3). Once stress is introduced, only the Slow approaches are viable, indicating there is an advantage to lowering the rate of storage utilisation, α_S.

The Fast-Safe strategy fails in all environments. Under the no-stress scenario, the benefit of the faster utilisation rate is outweighed by the earlier switch time (shorter growth duration), and the strategy is outcompeted by Risky strategies. When stress is introduced, the faster utilisation rate creates a higher mortality risk early in the season. The plants are outcompeted by both the Slow-Risky strategy plants, which can grow faster and shade them, and the Slow-Safe strategy which has a larger buffer against stress.

Introducing stress and storage-related mortality into the simulations reduces final basal area by between 30% and 50% (Fig. 4). These reductions are larger than the respective 15% and 25% reduction in photosynthetic days and is close to twice the reduction in the size of a single individual due to stress (Fig. S3) suggesting introducing stress and competitive interaction must play a role beyond loss of photosynthetic uptake due to reduction in number of photosynthetic days.

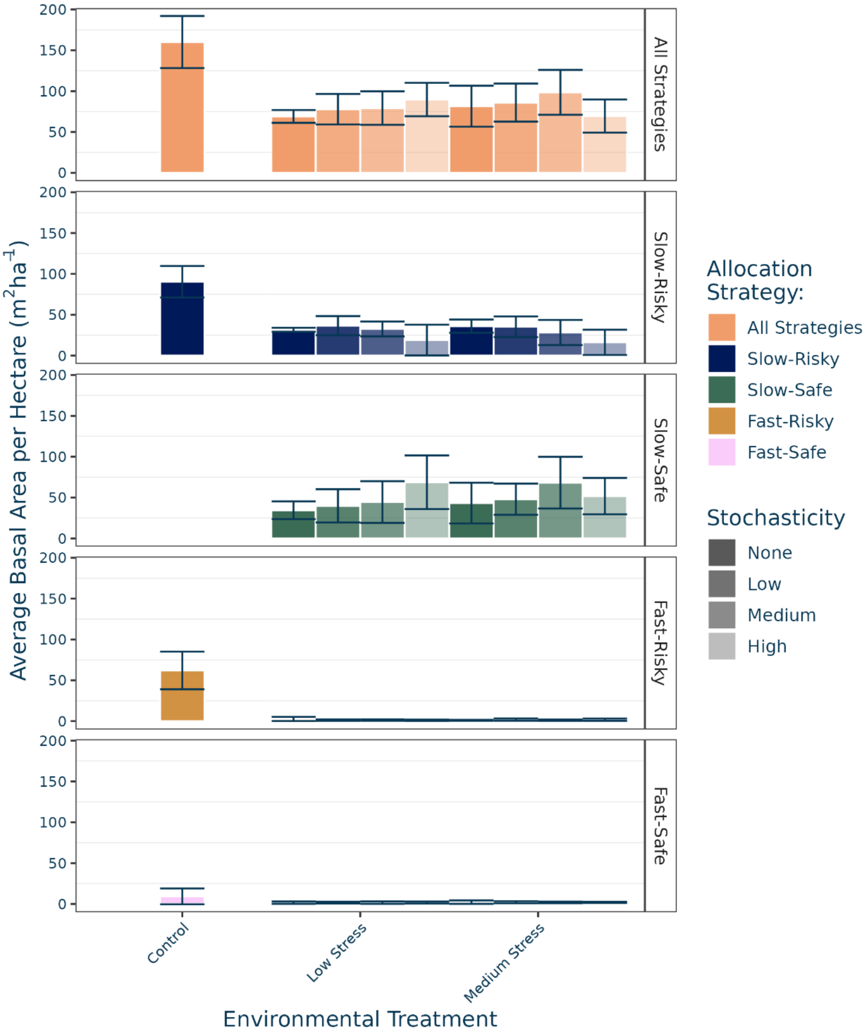


Figure 4 Final yield as determined by the basal area averaged first across each time point in years 90-100 of data and then by environmental repetition (N = 4 in control treatments with no stochasticity and N = 20 in treatments with stochasticity > 0). Error bars represent the standard deviation across environmental repetitions. Rows represent strategies, with the first row combining all strategies across the plot. Shading represents the stochasticity of the environment with the darkest colours representing environments with no stochasticity and lightest colours showing environments with the highest stochasticity.

3.2 Environment treatment effect on final basal area

Table 2 shows that stress stochasticity affects the competitive dominance. As stochasticity increases, there is a decreasing basal area of the Slow-Risky strategy ("large effect" in Table 2) and an increasing basal area of the Slow-Safe strategy ("medium effect"). Plants using the Fast strategy are uncompetitive and exhibit no or a small change in basal area.

In contrast, the average stress duration does not have a consistent effect on competitive outcome (Table 3). The basal area of the Slow-Safe strategy is increased with increasing stress duration ("small effect" for all levels of stochasticity and low stochasticity and "medium effect" for medium stochasticity in Table 3) but this trend is reversed when plants are subjected to high stochasticity. Under medium stress and high stochasticity, there can be years with extreme environmental stress that can significantly inhibit all strategies. There is a small decrease in basal area of Slow-Risky plants with increasing stress, with mostly a "very small" effect. However, this decrease may be enough for the Slow-Safe strategy to become more successful, thereby increasing its overall basal area. The effect may also be affected by the response at high stochasticity when both Slow-Risky and Slow-Safe decrease in basal area which is likely caused by increased mortality due to an increased number of high and very high stress years.

Table 2 Results of statistical analysis of relationship between final basal area and stochasticity. Model fitted is $\log(BA) \sim a\, stress_{sd}$+ log(intercept), where BA is the final basal area (m2/ha) for each strategy and $stress_{sd}$ is stress stochasticity (as explained by the standard deviation around the mean of onset of stress). Each model was run for a subset of mean stress duration (either low stress or medium stress) and for the combined data. Significance of each model parameter is given in brackets ('*': p <= 0.001, '**': p <= 0.01; '*' p <= 0.0; '.': p <= 0.1; '-' p > 0.1). Additionally, an ω^2 value was calculated to measure the effect size and an interpretation of the value is given based on interpretation guidelines from Field (2013).**

Strategy	**Stress Dur Mean**	**Parameter Value**		ω^2	**Field 2013**
		log(intercept)	a (yr^{-1})		
Slow-Risky	All Means	3.88 (***)	-0.03 (***)	0.25	large
	Low Stress	3.94 (***)	-0.03 (***)	0.30	large
	Medium Stress	3.82 (***)	-0.03 (***)	0.22	large
Slow-Safe	All Means	3.57 (***)	0.01 (**)	0.05	small
	Low Stress	3.82 (***)	0.00 (-)	-0.01	very small
	Medium Stress	3.33 (***)	0.01 (***)	0.12	medium
Fast-Risky	All Means	0.14 (-)	0.00 (-)	0.00	very small
	Low Stress	0.01 (-)	0.00 (.)	-0.01	very small
	Medium Stress	0.30 (.)	-0.01 (**)	0.06	small
Fast-Safe	All Means	0.31 (***)	0.00 (-)	0.00	very small
	Low Stress	0.45 (***)	0.00 (-)	-0.01	very small
	Medium Stress	0.16 (-)	0.00 (-)	-0.02	very small

Table 3 Results of statistical analysis of relationship between final basal area and stochasticity. Model fitted is $\log(BA) \sim a\, stress_{ave}$+ log(intercept), where BA is the final basal area (m2/ha) for each strategy and $stress_{ave}$ is stress stochasticity (as explained by the mean of onset of stress). Each model was run for a subset of stochasticities (from no stochasticity to high stochasticity) and for all stochasticities combined. Significance of each model parameter is given in brackets as explained by the p-value ('*': p <= 0.001, '**': p <= 0.01; '*' p <= 0.0; '.': p <= 0.1; '-' p > 0.1). Additionally, an omega-squared value was calculated to measure the effect size, and an interpretation of the value is given based on interpretation guidelines from Field 2013.**

Strategy	**Stress Stochasticity**	**Parameter Value**		ω^2	**Field 2013**
		Log (intercept)	a(yr^{-1})		
Slow-Risky	All Stochasticity	1.33 (-)	-2.14 (***)	0.00	very small
	No	4.43 (***)	1.15 (-)	-0.01	very small
	Low	3.15 (***)	-0.47 (-)	-0.02	very small
	Medium	-0.49 (-)	-4.63 (-)	0.04	small
	High	0.71 (-)	-1.96 (-)	-0.02	very small
Slow-Safe	All Stochasticity	5.12 (***)	1.64 (-)	0.01	small
	No	3.72 (-)	0.26 (-)	-0.14	very small

	Low	5.83 (***)	2.72 (-)	0.03	small
	Medium	7.74 (***)	4.85(**)	0.12	medium
	High	2.07 (-)	-2.38 (-)	0.03	small
Fast-Risky	All Stochasticity	1.38 (-)	1.68 (-)	0.00	very small
	No	-5.94 (-)	-7.79 (-)	0.11	medium
	Low	2.51 (-)	2.95 (-)	0.00	very small
	Medium	-1.99 (-)	-2.42 (-)	0.00	very small
	High	4.94 (**)	6.25 (*)	0.10	medium
Fast-Safe	All Stochasticity	2.70 (**)	2.93 (*)	0.03	small
	No	2.90 (-)	3.14 (-)	-0.10	very small
	Low	2.87 (-)	3.13 (-)	0.01	very small
	Medium	2.24 (-)	2.45 (-)	-0.01	very small
	High	2.96 (*)	3.12 (-)	0.03	small

3.3 Stress and Mortality

The stress and shade contributions to mortality were further examined by looking at mortality during stress periods and under canopy shading across all simulated environments which include stress. During the stress period, productivity-dependent mortality is switched off, and trees only die because of storage-dependent mortality. The proportion of individual deaths during stress for each strategy is calculated as the number of plants of the strategy which die in each stress period, divided by the total number of plants of that strategy which were alive during that period. The proportion of deaths during stress increases with the duration of the stress in a logistic relationship (Fig. 5A, Fig. S8). In Risky strategies, 50% of plant mortality occurs when stress is 165 days (Fast-Risky) and 172 days (Slow-Risky), while in the Safe strategies these numbers are 266 days (Fast-Safe) and 299 days (Slow-Safe; Fig. S9).

Outside of the stress period, productivity-dependent mortality can occur in addition to storage-dependent mortality. The proportion of deaths in the population is shown as a function of canopy openness (the percent of light reaching the top of the plant, with 0 being total darkness and 1 being full light) in Fig. 5B (also Fig. S9). Trees are grouped by canopy openness and the proportion of trees in each canopy openness group that die that year is calculated. The proportion of deaths has an exponential decay relationship with canopy openness (Fig. 5B). The higher the light level, the lower the proportion of deaths, with differences driven by the rate of carbon utilisation (Fast-Slow) spectrum. Slow strategy plants tolerate shade better than Fast strategy plants (showing a faster decline of mortality with increased light).

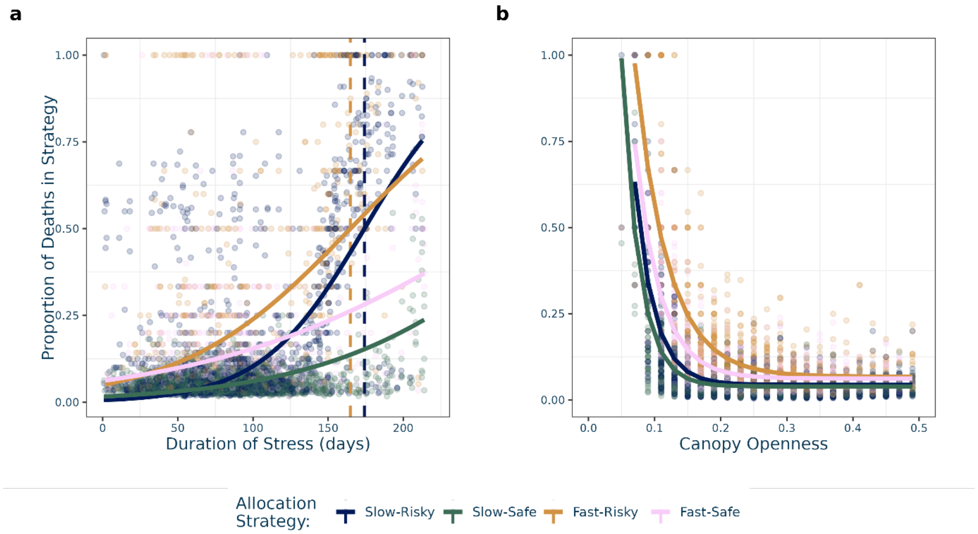


Figure 5 Annual proportion of population of each strategy dying in all simulations A) as a function of stress duration and B) light environment. In A) a logistic equation is fitted to the data and the point of 50% death for each strategy is indicated by the vertical dashed line (not shown for the Slow-Safe and Fast-Safe strategies for which this point is beyond the data observed). In B) the light environment is represented by canopy openness, calculated as the proportion of incident light available at the plant height. Deaths with canopy openness = 1 (no shading) were removed, and an exponential decay function was fitted to each set of data.

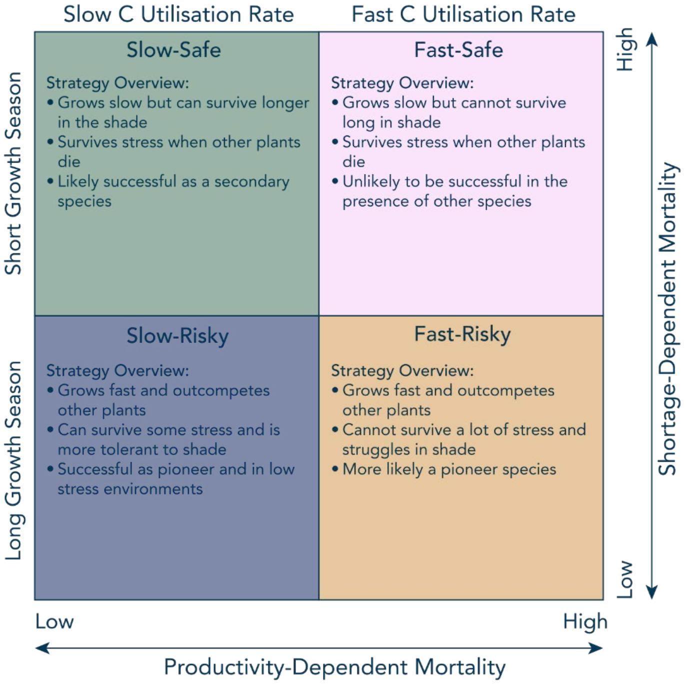
4 Discussion

In this study we used a gap model to examine the effects of introducing a carbon storage strategy to a vegetation community model. We explore the long-term outcomes of competition among different plant carbon storage utilisation strategies and how they are affected by environmental stochasticity. Specifically, we investigated trade-offs between different growth-storage strategies by varying two parameters: the speed of carbon utilisation (Slow-Fast utilisation spectrum) and length of the growth period determined by the growth-storage switch point (Safe-Risky spectrum, short to long growth period).

The primary factor determining the outcome of competition was differential mortality rates; such that (i) a long growth period (Risky strategy) reduced the chance of survival during a stress period, and (ii) a fast carbon utilisation rate (Fast strategy) reduced the size of the carbon storage pool, thereby reducing the shade-tolerance of an individual tree. In general, the Slow-Risky strategy may reflect a shade-tolerant and slow-growing, secondary succession species, while the Fast-Risky strategy may reflect a fast-growing shade-intolerant species. It is important to note, however, that all other plant traits were held constant in our simulations, so the differences among strategies reflect differences in carbon allocation only. It is likely that other physiological or morphological traits would amplify the differences among species.

When seasonal stress was absent from the model, the successful strategies were the two Risky strategies, with shade-driven productivity-based mortality being the primary cause of mortality. In more stressful environments, the Slow-Safe strategy allowed trees to survive, while the Fast-Risky strategy drops out because it exposes trees to stress-induced mortality. In contrast, trees in the Fast-Safe strategy were not successful in any of the simulations: they were not successful in early succession, when they were outcompeted by longer growing and therefore taller individuals, nor in secondary succession because they were not shade tolerant. A summary of the four strategies and their differences is shown in Fig. 6.

When stress was introduced, the successful strategies were the two Slow strategies. Trees in the Slow-Safe strategy could survive extended periods of time in shade with limited photosynthesis, likely due to higher carbon storage minima offsetting the low photosynthetic gain. Once taller trees died due to annual seasonal stress, trees in the Slow-Safe strategy could grow to the top of the canopy. On the other hand, the Slow-Risky trees were more susceptible during the seasonal stress due to lower carbon stores but could grow rapidly and outcompete other plants for light. As with the Slow-Safe strategy, Slow-Risky trees also had a high carbon storage minimum, which facilitated the survival of small saplings in the shade. The failure of the Fast-Risky strategy was strongly associated with stress-related mortality exacerbated by the inability of trees to survive in shade. The Fast-Safe strategy also failed, predominantly due to the lack of shade-tolerance in trees, which led to mortality before a canopy gap became available.



Slow-Safe

Strategy Overview:
- Grows slow but can survive longer in the shade
- Survives stress when other plants die
- Likely successful as a secondary species

Fast-Safe

Strategy Overview:
- Grows slow but cannot survive long in shade
- Survives stress when other plants die
- Unlikely to be successful in the presence of other species

Slow-Risky

Strategy Overview:
- Grows fast and outcompetes other plants
- Can survive some stress and is more tolerant to shade
- Successful as pioneer and in low stress environments

Fast-Risky

Strategy Overview:
- Grows fast and outcompetes other plants
- Cannot survive a lot of stress and struggles in shade
- More likely a pioneer species

Figure 6 Summary of model outcomes by plant strategy. Storage-dependent mortality differentiates between strategies on the Safe-Risky spectrum, with Safe strategies being more tolerant of stress conditions. Productivity-dependent mortality differentiates between strategies on the Slow-Fast spectrum of carbon utilisation, with Slow strategies being more tolerant of shaded conditions.

4.1 Effect of environmental stress

In addition to its effect on community composition, stress led to a significant decrease in carbon sequestration, as determined by the total basal area of the plants (Fig. 3). Moreover, stress affected the outcome of competition among strategies (between Slow-Risky and Slow-Safe), with stochasticity (defined as more variance around an average stress duration) having a more pronounced effect than the mean stress duration. Increasing stochasticity of the stress led to an increase in the number of Slow-Safe strategy trees and a decrease in Slow-Risky trees.

Rather than average intensity, the presence of extreme events drawn from the stress duration distribution affected the decline of trees in the Slow-Risky strategy in the high stochasticity environments.

Our modelling results are consistent with observations that dominant species exhibit storage-mediated adaptation to variance in stressful conditions. Trees in strongly seasonal and non-seasonal tropical forests show similar, species-driven NSC concentrations during the wet season, but trees in seasonally dry forests show differences in NSC composition by transitioning to higher soluble sugar content during the dry season when storage mobilisation is important (Signori-Müller et al., 2021). The shift in intra-annual NSC-dynamics along the observed seasonality gradient may suggest a shift between growth-prioritisation and storage-prioritisation to survive stress during the dry season.

Our results are also consistent with observed strategy shifts within species when growing in different environments. Trait plasticity allows populations of a species to adopt different strategies in different environments. There is evidence for shifts from growth-prioritising strategies to storage-prioritising strategies within species across environmental stress gradients, including rainfall (Bachofen et al., 2018; Hao et al., 2021) and elevation gradients (Wang et al., 2018). In the model developed here, water relations are not included but shifts in storage along stress gradients may be comparable to the shift from Risky plants to Slow-Safe plants in the model with rising stress duration.

As carbon storage strategy may be adapted to local conditions (e.g., Blumstein and Hopkins, 2021), the increased variability of local weather conditions and more extreme disturbances associated with climate change (IPCC, 2021) may contribute to significant shifts in community composition. Traits conferring drought- and heat-resistance have been increasingly emerging as contributors to plant survival in ecosystems worldwide. Shifts in community composition have been observed in tropical ecosystems towards increased representation of drought-resistance trees (Feeley et al., 2011) and shifts in plant trait representation towards decreased specific leaf area and increased wood density, which are indicative of increased hydraulic resistance (Swenson et al., 2020). Long-term vegetation shifts towards more drought-resistant individuals have also been observed after severe droughts in south-western USA (Mueller et al., 2005). However, changes in species composition may not occur if there is a plastic change over time in the strategy of an individual. Trait plasticity, although not considered in the study, may be an important factor shaping tree mortality in response to increasingly intense and varied environmental stress (Gallagher et al., 2019; Lanuza et al., 2020; Lecina-Diaz et al., 2021) and further has been shown to affect the range size of congeneric tree species (Chacón-Madrigal et al., 2018) in response to environmental cues (Hofhansl et al., 2021).

4.2 Improving Modelling of Carbon Storage and Survival of Stress

Improving the representation of carbon storage in models should be considered a priority (Merganičová et al., 2019). Beyond improving model realism, the representation of carbon storage in models is important for two reasons; (i) capturing accurate mortality mechanisms (McDowell et al., 2022) and (ii) removing the direct coupling between photosynthesis and growth (Keane et al., 2001). Without carbon storage, models assume that all growth is supported by carbon gain within the same timestep, a dynamic which is unrealistic on sub-annual time steps (Fatichi et al., 2014, 2019; Piper, 2020). Although the number of models implementing carbon storage is increasing, there are still no consistent guidelines for modelling carbon storage (Dietze et al., 2014b). While some studies have looked at sensitivity of single carbon storage parameters (Fisher et al., 2010; Jones et al., 2020) or the effects of model structure (Jones et al., 2020; Richardson et al., 2013; Trumbore et al., 2015), further examination of the sensitivity of more complex allocation strategies is warranted.

Specifically, we suggest including rate of carbon utilisation and a duration of growth in species which grow in seasonal environments. The rate of carbon utilisation strongly affects tree shade tolerance by providing additional carbon source as supported by model simulations (Kobe, 1997) and experimental studies (Atkinson et al., 2014; Myers and Kitajima, 2007; Rose et al., 2009). Similarly, the switch time parameter affects survival during seasonal stress. Experimental studies have shown decreases in growth along an environmental stress gradient (Wang et al., 2018) and as an acclimatory response of tree seedlings to past stress (Vander Mijnsbrugge et al., 2019), thereby supporting the role of decreased growth duration in mitigating stress periods. While mechanisms of tree mortality under stress are often complex, involving a number of contributing factors, including susceptibility to hydraulic damage, herbivory or pathogens, these model predictions support the theory that stored carbon plays an important role in buffering the damage caused by stress (McDowell et al., 2008).

Another important direction for future work would be to explore the implications of allowing other plant traits, such as leaf economic traits or hydraulic traits, to vary in concert with the two carbon storage traits considered here. It is possible that relationships between traits might emerge as a result of the competition simulated in the gap model. Although some studies find no clear relationships between storage patterns and other plant traits (e.g. (Signori-Müller et al., 2021)) including phenological traits captures intra-annual NSC dynamics in three Mediterranean crop species (Tixier et al., 2020).

Finally, storage dynamics may change throughout the lifetime of an individual. For example, the storage utilisation rate has been found to vary with plant age in a model-data-assimilation study (Mahmud et al., 2018). Diurnal NSC concentrations within a plant also have been shown to change between seedlings and mature plants within the same study (Baber et al., 2014) and differences between carbon allocation strategies were found in trees of different heights (Sala and Hoch, 2009; Woodruff and Meinzer, 2011). It would be valuable in future work to relax assumptions about the static nature of plant traits to examine a wider range of strategies.

5 Conclusions

Using a gap model, our study provided an evaluation of the effect of environmental stress and stochasticity on the performance and survival of trees with different carbon storage strategies. The representation of carbon storage strategy defined by two traits, storage utilisation rate and duration of growth, allowed a nuanced response to different types of stress to be captured, and highlighted the role of carbon storage in determining tree survival. The results obtained in this study showed a community shift towards storage-prioritising strategies, as seen in the shift from Slow-Risky to Slow-Safe plants, when challenged with increased stochasticity and stress intensity. Shifts in the modelled community assembly of trees, in response to increased environmental stochasticity and intensity, supports previous observations of shifts in plant community composition towards more stress-resilient plant strategies. Our study shows that including storage and storage-prioritising strategies in modelling is important to advance our capacity to capture tree survival and adaptation to climate change.

Code and data availability:

Simulation outputs, model and data analysis are freely available.
Pre-processed simulation results can be found at:
https://doi.org/10.5281/zenodo.17552724
Model can be found at:
https://github.com/foxeswithdata/plant
Data analysis can be found at: https://github.com/foxeswithdata/storage_plant_simulation_analysis/tree/main

Author contributions:

EZS, BEM and DTT designed the study, EZS developed the model and performed simulations and analysis, DSF assisted with model development, EZS wrote the manuscript with contributions from BEM, DSF and DTT. All authors edited and approved the final manuscript.

Competing Interests:

The authors declare no conflicts of interest.

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References

Adams, H. D., Germino, M. J., Breshears, D. D., Barron-Gafford, G. A., Guardiola-Claramonte, M., Zou, C. B., and Huxman, T. E.: Nonstructural leaf carbohydrate dynamics of Pinus edulis during drought-induced tree mortality reveal role for carbon metabolism in mortality mechanism, New Phytol., 197, 1142–1151, https://doi.org/10.1111/nph.12102, 2013.

Allen, C. D., Breshears, D. D., and McDowell, N. G.: On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene, Ecosphere, 6, art129, https://doi.org/10.1890/ES15-00203.1, 2015.

Atkinson, R. R. L., Burrell, M. M., Rose, K. E., Osborne, C. P., and Rees, M.: The dynamics of recovery and growth: how defoliation affects stored resources, Proc. R. Soc. B Biol. Sci., 281, 20133355, https://doi.org/10.1098/rspb.2013.3355, 2014.

Baber, O., Slot, M., Celis, G., and Kitajima, K.: Diel patterns of leaf carbohydrate concentrations differ between seedlings and mature trees of two sympatric oak species, Botany, 92, 535–540, https://doi.org/10.1139/cjb-2014-0032, 2014.

Bachofen, C., Moser, B., Hoch, G., Ghazoul, J., and Wohlgemuth, T.: No carbon "bet hedging" in pine seedlings under prolonged summer drought and elevated CO2, J. Ecol., 106, 31–46, https://doi.org/10.1111/1365-2745.12822, 2018.

Ben-Shachar, M. S., Lüdecke, D., and Makowski, D.: {e}ffectsize: Estimation of Effect Size Indices and Standardized Parameters, J. Open Source Softw., 5, 2815, https://doi.org/10.21105/joss.02815, 2020.

Blumstein, M. and Hopkins, R.: Adaptive variation and plasticity in non-structural carbohydrate storage in a temperate tree species, Plant Cell Environ., 44, 2494–2505, https://doi.org/10.1111/pce.13959, 2021.

Bojórquez, A., Álvarez-Yépiz, J. C., Búrquez, A., and Martínez-Yrízar, A.: Understanding and predicting frost-induced tropical tree mortality patterns, Glob. Change Biol., 25, 3817–3828, https://doi.org/10.1111/gcb.14775, 2019.

Bugmann, H.: A Review of Forest Gap Models, Clim. Change, 51, 259–305, 2001.

Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sanchez, G., and Penuelas, J.: Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought, Proc. Natl. Acad. Sci., 108, 1474–1478, https://doi.org/10.1073/pnas.1010070108, 2011.

Chacón-Madrigal, E., Wanek, W., Hietz, P., and Dullinger, S.: Traits indicating a conservative resource strategy are weakly related to narrow range size in a group of neotropical trees, Perspect. Plant Ecol. Evol. Syst., 32, 30–37, https://doi.org/10.1016/j.ppees.2018.01.003, 2018.

Chiariello, N. and Roughgarden, J.: Storage Allocation in Seasonal Races of an Annual Plant: Optimal Versus Actual Allocation, Ecology, 65, 1290–1301, https://doi.org/10.2307/1938334, 1984.

Crameri, F.: Scientific colour maps, , https://doi.org/10.5281/zenodo.8409685, 2023.

Dai, A.: Increasing drought under global warming in observations and models, Nat. Clim. Change, 3, 52–58, https://doi.org/10.1038/nclimate1633, 2013.

Dietze, M. C., Matthes, J. H., and Arnone, J.: A general ecophysiological framework for modelling the impact of pests and pathogens on forest ecosystems., Ecol. Lett., 17, 1418–1426, https://doi.org/10.1111/ele.12345, 2014a.

Dietze, M. C., Sala, A., Carbone, M. S., Czimczik, C. I., Mantooth, J. A., Richardson, A. D., and Vargas, R.: Nonstructural Carbon in Woody Plants, Annu. Rev. Plant Biol., 65, 667–687, https://doi.org/10.1146/annurev-arplant-050213-040054, 2014b.

Eller, C. B., de V. Barros, F., R.L. Bittencourt, P., Rowland, L., Mencuccini, M., and S. Oliveira, R.: Xylem hydraulic safety and construction costs determine tropical tree growth: Tree growth vs hydraulic safety trade-off, Plant Cell Environ., 41, 548–562, https://doi.org/10.1111/pce.13106, 2018.

Engen, S. and Saether, B.-E.: Optimal allocation of resources to growth and reproduction, Theor. Popul. Biol., 46, 232–248, 1994.

Falster, D. S., Brännström, Å., Dieckmann, U., and Westoby, M.: Influence of four major plant traits on average height, leaf-area cover, net primary productivity, and biomass density in single-species forests: a theoretical investigation: Influence of functional traits on emergent vegetation properties, J. Ecol., 99, 148–164, https://doi.org/10.1111/j.1365-2745.2010.01735.x, 2011.

Falster, D. S., Duursma, R. A., Ishihara, M. I., Barneche, D. R., FitzJohn, R. G., Vårhammar, A., Aiba, M., Ando, M., Anten, N., Aspinwall, M. J., Baltzer, J. L., Baraloto, C., Battaglia, M., Battles, J. J., Bond-Lamberty, B., van Breugel, M., Camac, J., Claveau, Y., Coll, L., Dannoura, M., Delagrange, S., Domec, J.-C., Fatemi, F., Feng, W., Gargaglione, V., Goto, Y., Hagihara, A., Hall, J. S., Hamilton, S., Harja, D., Hiura, T., Holdaway, R., Hutley, L. S., Ichie, T., Jokela, E. J., Kantola, A., Kelly, J. W. G., Kenzo, T., King, D., Kloeppel, B. D., Kohyama, T., Komiyama, A., Laclau, J.-P., Lusk, C. H., Maguire, D. A., le Maire, G., Mäkelä, A., Markesteijn, L., Marshall, J., McCulloh, K., Miyata, I., Mokany, K., Mori, S., Myster, R. W., Nagano, M., Naidu, S. L., Nouvellon, Y., O'Grady, A. P., O'Hara, K. L., Ohtsuka, T., Osada, N., Osunkoya, O. O., Peri, P. L., Petritan, A. M., Poorter, L., Portsmuth, A., Potvin, C., Ransijn, J., Reid, D., Ribeiro, S. C., Roberts, S. D., Rodríguez, R., Saldaña-Acosta, A., Santa-Regina, I., Sasa, K., Selaya, N. G., Sillett, S. C., Sterck, F., Takagi, K., Tange, T., Tanouchi, H., Tissue, D., Umehara, T., Utsugi, H., Vadeboncoeur, M. A., Valladares, F., Vanninen, P., Wang, J. R., Wenk, E., Williams, R., de Aquino Ximenes, F., Yamaba, A., Yamada, T., Yamakura, T., Yanai, R. D., and York, R. A.: BAAD: a Biomass And Allometry Database for woody plants: *Ecological Archives* E096-128, Ecology, 96, 1445–1445, https://doi.org/10.1890/14-1889.1, 2015.

Falster, D. S., FitzJohn, R. G., Brännström, Å., Dieckmann, U., and Westoby, M.: plant: A package for modelling forest trait ecology and evolution, Methods Ecol. Evol., 7, 136–146, https://doi.org/10.1111/2041-210X.12525, 2016.

Fatichi, S., Leuzinger, S., and Körner, C.: Moving beyond photosynthesis: from carbon source to sink-driven vegetation modeling, New Phytol., 201, 1086–1095, https://doi.org/10.1111/nph.12614, 2014.

Fatichi, S., Pappas, C., Zscheischler, J., and Leuzinger, S.: Modelling carbon sources and sinks in terrestrial vegetation, New Phytol., 221, 652–668, https://doi.org/10.1111/nph.15451, 2019.

Feeley, K. J., Davies, S. J., Perez, R., Hubbell, S. P., and Foster, R. B.: Directional changes in the species composition of a tropical forest, Ecology, 92, 871–882, https://doi.org/10.1890/10-0724.1, 2011.

Field, A.: Discovering statistics using IBM SPSS STATISTICS, 4th ed., SAGE, https://doi.org/10.5860/choice.43-3433, 2013.

Fisher, R., McDowell, N., Purves, D., Moorcroft, P., Sitch, S., Cox, P., Huntingford, C., Meir, P., and Ian Woodward, F.: Assessing uncertainties in a second-generation dynamic vegetation model caused by ecological scale limitations, New Phytol., 187, 666–681, https://doi.org/10.1111/j.1469-8137.2010.03340.x, 2010.

Franklin, O., Johansson, J., Dewar, R. C., Dieckmann, U., McMurtrie, R. E., Brannstrom, A., and Dybzinski, R.: Modeling carbon allocation in trees: a search for principles, Tree Physiol., 32, 648–666, https://doi.org/10.1093/treephys/tpr138, 2012.

Gallagher, R. V., Allen, S., and Wright, I. J.: Safety margins and adaptive capacity of vegetation to climate change, Sci. Rep., 9, 8241, https://doi.org/10.1038/s41598-019-44483-x, 2019.

Hao, B., Hartmann, H., Li, Y., Liu, H., Shi, F., Yu, K., Li, X., Li, Z., Wang, P., Allen, C. D., and Wu, X.: Precipitation Gradient Drives Divergent Relationship between Non-Structural Carbohydrates and Water Availability in Pinus tabulaeformis of Northern China, Forests, 12, 133, https://doi.org/10.3390/f12020133, 2021.

Hartmann, H., Bahn, M., Carbone, M., and Richardson, A. D.: Plant carbon allocation in a changing world – challenges and progress: introduction to a Virtual Issue on carbon allocation: Introduction to a virtual issue on carbon allocation, New Phytol., 227, 981–988, https://doi.org/10.1111/nph.16757, 2020.

Hofhansl, F., Chacón-Madrigal, E., Brännström, Å., Dieckmann, U., and Franklin, O.: Mechanisms driving plant functional trait variation in a tropical forest, Ecol. Evol., 11, 3856–3870, https://doi.org/10.1002/ece3.7256, 2021.

Huang, M., Wang, X., Keenan, T. F., and Piao, S.: Drought timing influences the legacy of tree growth recovery, Glob. Change Biol., 24, 3546–3559, https://doi.org/10.1111/gcb.14294, 2018.

IPCC: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, edited by: Masson-Delmotte, V., Zhai, P., Pirani, A., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M. I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J. B. R., Maycock, T. K., Waterfield, T., Yelekçi, O., Yu, R., and Zhou, B., Cambridge University Press, 2021.

Iwasa, Y. and Cohen, D.: Optimal Growth Schedule of a Perennial Plant, Am. Nat., 133, 480–505, 1989.

Iwasa, Y. and Levin, S. A.: The Timing of Life History Events, J. Theor. Biol., 172, 10, 1995.

Jones, S., Rowland, L., Cox, P., Hemming, D., Wiltshire, A., Williams, K., Parazoo, N. C., Liu, J., da Costa, A. C. L., Meir, P., Mencuccini, M., and Harper, A. B.: The impact of a simple representation of non-structural carbohydrates on the simulated response of tropical forests to drought, Biogeosciences, 17, 3589–3612, https://doi.org/10.5194/bg-17-3589-2020, 2020.

Keane, R. E., Austin, M., Field, C., Huth, A., Lexer, M. J., Peters, D., Solomon, A., and Wyckoff, P.: Tree mortality in gap models: Application to climate change, Clim. Change, 51, 509–540, https://doi.org/10.1023/A:1012539409854, 2001.

Kobe, R. K.: Carbohydrate Allocation to Storage as a Basis of Interspecific Variation in Sapling Survivorship and Growth, Oikos, 80, 226, https://doi.org/10.2307/3546590, 1997.

Kozłowski, J. and Uchmanski, J.: Optimal individual growth and reproduction in perennial species with indeterminate growth, Evol. Ecol., 1, 214–230, https://doi.org/10.1007/BF02067552, 1987.

Kozłowski, J. and Wiegert, R. G.: Optimal age and size at maturity in annuals and perennials with determinate growth, Evol. Ecol., 1, 231–244, https://doi.org/10.1007/BF02067553, 1987.

Lanuza, O. R., Espelta, J. M., Peñuelas, J., and Peguero, G.: Assessing intraspecific trait variability during seedling establishment to improve restoration of tropical dry forests, Ecosphere, 11, https://doi.org/10.1002/ecs2.3052, 2020.

Lecina-Diaz, J., Martínez-Vilalta, J., Alvarez, A., Banqué, M., Birkmann, J., Feldmeyer, D., Vayreda, J., and Retana, J.: Characterizing forest vulnerability and risk to climate-change hazards, Front. Ecol. Environ., 19, 126–133, https://doi.org/10.1002/fee.2278, 2021.

LeCroy, C. W. and Krysik, J.: Understanding and interpreting effect size measures, Soc. Work Res., 31, 243–248, https://doi.org/10.1093/swr/31.4.243, 2007.

Lexer, M. J. and Hönninger, K.: A modified 3D-patch model for spatially explicit simulation of vegetation composition in heterogeneous landscapes, For. Ecol. Manag., 144, 43–65, 2001.

MacAllister, S., Mencuccini, M., Sommer, U., Engel, J., Hudson, A., Salmon, Y., and Dexter, K. G.: Drought-induced mortality in Scots pine: opening the metabolic black box, Tree Physiol., 39, 1358–1370, https://doi.org/10.1093/treephys/tpz049, 2019.

Mahmud, K., Medlyn, B. E., Duursma, R. A., Campany, C., and De Kauwe, M. G.: Inferring the effects of sink strength on plant carbon balance processes from experimental measurements, Biogeosciences, 15, 4003–4018, https://doi.org/10.5194/bg-15-4003-2018, 2018.

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., and Yepez, E. A.: Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought?, New Phytol., 178, 719–739, https://doi.org/10.1111/j.1469-8137.2008.02436.x, 2008.

McDowell, N. G., Sapes, G., Pivovaroff, A., Adams, H. D., Allen, C. D., Anderegg, W. R. L., Arend, M., Breshears, D. D., Brodribb, T., Choat, B., Cochard, H., De Cáceres, M., De Kauwe, M. G., Grossiord, C., Hammond, W. M., Hartmann, H., Hoch, G., Kahmen, A., Klein, T., Mackay, D. S., Mantova, M., Martínez-Vilalta, J., Medlyn, B. E., Mencuccini, M., Nardini, A., Oliveira, R. S., Sala, A., Tissue, D. T., Torres-Ruiz, J. M., Trowbridge, A. M., Trugman, A. T., Wiley, E., and Xu, C.: Mechanisms of woody-plant mortality under rising drought, CO2 and vapour pressure deficit, Nat. Rev. Earth Environ., 3, 294–308, https://doi.org/10.1038/s43017-022-00272-1, 2022.

Merganičová, K., Merganič, J., Lehtonen, A., Vacchiano, G., Sever, M. Z. O., Augustynczik, A. L. D., Grote, R., Kyselová, I., Mäkelä, A., Yousefpour, R., Krejza, J., Collalti, A., and Reyer, C. P. O.: Forest carbon allocation modelling under climate change, Tree Physiol., 39, 1937–1960, https://doi.org/10.1093/treephys/tpz105, 2019.

Morin, X., Bugmann, H., de Coligny, F., Martin-StPaul, N., Cailleret, M., Limousin, J.-M., Ourcival, J.-M., Prevosto, B., Simioni, G., Toigo, M., Vennetier, M., Catteau, E., and Guillemot, J.: Beyond forest succession: A gap model to study ecosystem functioning and tree community composition under climate change, Funct. Ecol., 35, 955–975, https://doi.org/10.1111/1365-2435.13760, 2021.

Mueller, R. C., Scudder, C. M., Porter, M. E., Talbot Trotter, R., Gehring, C. A., and Whitham, T. G.: Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts: Drought-induced differential tree mortality, J. Ecol., 93, 1085–1093, https://doi.org/10.1111/j.1365-2745.2005.01042.x, 2005.

Muller, B., Pantin, F., Génard, M., Turc, O., Freixes, S., Piques, M., and Gibon, Y.: Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs, J. Exp. Bot., 62, 1715–1729, https://doi.org/10.1093/jxb/erq438, 2011.

Myers, J. A. and Kitajima, K.: Carbohydrate storage enhances seedling shade and stress tolerance in a neotropical forest, J. Ecol., 95, 383–395, https://doi.org/10.1111/j.1365-2745.2006.01207.x, 2007.

Nolan, R. H., Gauthey, A., Losso, A., Medlyn, B. E., Smith, R., Chhajed, S. S., Fuller, K., Song, M., Li, X., Beaumont, L. J., Boer, M. M., Wright, I. J., and Choat, B.: Hydraulic failure and tree size linked with canopy die-back in eucalypt forest during extreme drought, New Phytol., 230, 1354–1365, https://doi.org/10.1111/nph.17298, 2021.

Norby, R. J., Ogle, K., Curtis, P. S., Badeck, F.-W., Huth, A., Hurtt, G. C., Kohyama, T., and Peñuelas, J.: Aboveground growth and competition in forest gap models: An analysis for studies of climatic change, Clim. Change, 51, 33, https://doi.org/10.1023/A:1012510619424, 2001.

Piper, F. I.: Decoupling between growth rate and storage remobilization in broadleaf temperate tree species, Funct. Ecol., 34, 1180–1192, https://doi.org/10.1111/1365-2435.13552, 2020.

Pugliese, A. and Kozlowski, J.: Optimal patterns of growth and reproduction for perennial plants with persisting or not persisting vegetative parts, Evol. Ecol., 4, 75–89, https://doi.org/10.1007/BF02270717, 1990.

R Core Team: R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria, 2018.

Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M. D., Seneviratne, S. I., Zscheischler, J., Beer, C., Buchmann, N., Frank, D. C., Papale, D., Rammig, A., Smith, P., Thonicke, K., van der Velde, M., Vicca, S., Walz, A., and Wattenbach, M.: Climate extremes and the carbon cycle, Nature, 500, 287–295, https://doi.org/10.1038/nature12350, 2013.

Richardson, A. D., Carbone, M. S., Keenan, T. F., Czimczik, C. I., Hollinger, D. Y., Murakami, P., Schaberg, P. G., and Xu, X.: Seasonal dynamics and age of stemwood nonstructural carbohydrates in temperate forest trees, New Phytol., 197, 850–861, https://doi.org/10.1111/nph.12042, 2013.

Rose, K. E., Atkinson, R. L., Turnbull, L. A., and Rees, M.: The costs and benefits of fast living, Ecol. Lett., 12, 1379–1384, https://doi.org/10.1111/j.1461-0248.2009.01394.x, 2009.

Rowland, L., da Costa, A. C. L., Galbraith, D. R., Oliveira, R. S., Binks, O. J., Oliveira, A. A. R., Pullen, A. M., Doughty, C. E., Metcalfe, D. B., Vasconcelos, S. S., Ferreira, L. V., Malhi, Y., Grace, J., Mencuccini, M., and Meir, P.: Death from drought in tropical forests is triggered by hydraulics not carbon starvation, Nature, 528, 119–122, https://doi.org/10.1038/nature15539, 2015.

Ruehr, N. K., Grote, R., Mayr, S., and Arneth, A.: Beyond the extreme: recovery of carbon and water relations in woody plants following heat and drought stress, Tree Physiol., 39, 1285–1299, https://doi.org/10.1093/treephys/tpz032, 2019.

Sala, A. and Hoch, G.: Height-related growth declines in ponderosa pine are not due to carbon limitation, Plant Cell Environ., 32, 22–30, https://doi.org/10.1111/j.1365-3040.2008.01896.x, 2009.

Sala, A., Piper, F., and Hoch, G.: Physiological mechanisms of drought-induced tree mortality are far from being resolved, New Phytol., 186, 274–281, https://doi.org/10.1111/j.1469-8137.2009.03167.x, 2010.

Schwalm, C. R., Anderegg, W. R. L., Michalak, A. M., Fisher, J. B., Biondi, F., Koch, G., Litvak, M., Ogle, K., Shaw, J. D., Wolf, A., Huntzinger, D. N., Schaefer, K., Cook, R., Wei, Y., Fang, Y., Hayes, D., Huang, M., Jain, A., and Tian, H.: Global patterns of drought recovery, Nature, 548, 202–205, https://doi.org/10.1038/nature23021, 2017.

Shinozaki, K., Yoda, K., Hozumi, K., and Kira, T.: A quantitative analysis of plant form-the pipe model theory: I. Basic analyses, Jpn. J. Ecol., 14, 97–105, 1964.

Signori-Müller, C., Oliveira, R. S., Barros, F. de V., Tavares, J. V., Gilpin, M., Diniz, F. C., Zevallos, M. J. M., Yupayccana, C. A. S., Acosta, M., Bacca, J., Chino, R. S. C., Cuellar, G. M. A., Cumapa, E. R. M., Martinez, F., Mullisaca, F. M. P., Nina, A., Sanchez, J. M. B., da Silva, L. F., Tello, L., Tintaya, J. S., Ugarteche, M. T. M., Baker, T. R., Bittencourt, P. R. L., Borma, L. S., Brum, M., Castro, W., Coronado, E. N. H., Cosio, E. G., Feldpausch, T. R., Fonseca, L. d'Agosto M., Gloor, E., Llampazo, G. F., Malhi, Y., Mendoza, A. M., Moscoso, V. C., Araujo-Murakami, A., Phillips, O. L., Salinas, N., Silveira, M., Talbot, J., Vasquez, R., Mencuccini, M., and Galbraith, D.: Non-structural carbohydrates mediate seasonal water stress across Amazon forests, Nat. Commun., 12, 2310, https://doi.org/10.1038/s41467-021-22378-8, 2021.

Stefaniak, E. Z., Tissue, D. T., Dewar, R. C., and Medlyn, B. E.: Optimal carbon storage during drought, Tree Physiol., 44, 34–45, https://doi.org/10.1093/treephys/tpae032, 2024.

Swenson, N. G., Hulshof, C. M., Katabuchi, M., and Enquist, B. J.: Long-term shifts in the functional composition and diversity of a tropical dry forest: a 30-yr study, Ecol. Monogr., 90, https://doi.org/10.1002/ecm.1408, 2020.

Tixier, A., Gambetta, G. A., Godfrey, J., Orozco, J., and Zwieniecki, M. A.: Non-structural Carbohydrates in Dormant Woody Perennials; The Tale of Winter Survival and Spring Arrival, Front. For. Glob. Change, 2, 18, https://doi.org/10.3389/ffgc.2019.00018, 2019.

Tixier, A., Guzmán-Delgado, P., Sperling, O., Amico Roxas, A., Laca, E., and Zwieniecki, M. A.: Comparison of phenological traits, growth patterns, and seasonal dynamics of non-structural carbohydrate in Mediterranean tree crop species, Sci. Rep., 10, 347, https://doi.org/10.1038/s41598-019-57016-3, 2020.

Trugman, A. T., Detto, M., Bartlett, M. K., Medvigy, D., Anderegg, W. R. L., Schwalm, C., Schaffer, B., and Pacala, S. W.: Tree carbon allocation explains forest drought-kill and recovery patterns, Ecol. Lett., 21, 1552–1560, https://doi.org/10.1111/ele.13136, 2018.

Trumbore, S., Czimczik, C. I., Sierra, C. A., Muhr, J., and Xu, X.: Non-structural carbon dynamics and allocation relate to growth rate and leaf habit in California oaks, Tree Physiol., 35, 1206–1222, https://doi.org/10.1093/treephys/tpv097, 2015.

Vander Mijnsbrugge, K., Turcsan, A., Moreels, S., Van Goethem, M., Meeus, S., and Van der Aa, B.: Does Drought Stress on Seedlings Have Longer Term Effects on Sapling Phenology, Reshooting, Growth and Plant Architecture in Quercus robur, Q. petraea and Their Morphological Intermediates?, Forests, 10, 1012, https://doi.org/10.3390/f10111012, 2019.

Wang, A.-Y., Han, S.-J., Zhang, J.-H., Wang, M., Yin, X.-H., Fang, L.-D., Yang, D., and Hao, G.-Y.: The interaction between nonstructural carbohydrate reserves and xylem hydraulics in Korean pine trees across an altitudinal gradient, Tree Physiol., 38, 1792–1804, https://doi.org/10.1093/treephys/tpy119, 2018.

Wenk, E. H. and Falster, D. S.: Quantifying and understanding reproductive allocation schedules in plants, Ecol. Evol., 5, 5521–5538, https://doi.org/10.1002/ece3.1802, 2015.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., and Yutani, H.: Welcome to the Tidyverse, J. Open Source Softw., 4, 1686, https://doi.org/10.21105/joss.01686, 2019.

Wiley, E.: Do Carbon Reserves Increase Tree Survival during Stress and Following Disturbance?, Curr. For. Rep., 6, 14–25, https://doi.org/10.1007/s40725-019-00106-2, 2020.

Wiley, E. and Helliker, B.: A re-evaluation of carbon storage in trees lends greater support for carbon limitation to growth, New Phytol., 195, 285–289, https://doi.org/10.1111/j.1469-8137.2012.04180.x, 2012.

Woodruff, D. R. and Meinzer, F. C.: Water stress, shoot growth and storage of non-structural carbohydrates along a tree height gradient in a tall conifer: Growth, water stress and carbohydrate storage, Plant Cell Environ., 34, 1920–1930, https://doi.org/10.1111/j.1365-3040.2011.02388.x, 2011.

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