

Supplementary Information

Table S1 List of functions used in the model. References included where equation is used in the article or where it was used in the original paper plant model including equation number from the plant model description in Falster et al supplementary information 1 (S1) and supplementary information 2 (S2).

Variable	Function	Document Reference
Carbon Exchange		
Average Photosynthesis per leaf area	$\bar{p}(x, H, E_a, E_s(t)) = E_s(t) \int_0^H p(x, E_a(z)) q(z, H) dz$	Falster S2 (2)
Photosynthesis at height z	$p(x, E_a(z)) = \frac{\alpha_{p1}}{E_a(z) + \alpha_{p2}}$	Falster S2 (1)
Respiration of component i	$\frac{dR}{dt} = \left(r_{min} + \frac{E_s(t)}{2} \right) \sum_{i=l,b,s,r} M_i r_i$	Modified from Falster S2 (3)
Carbon Allocation		
Change in live biomass	$\frac{dM_a}{dt} = U = \begin{cases} t_y < t_s \Rightarrow a_s M_{st} \\ t_y \geq t_s \Rightarrow 0 \end{cases}$	Equation 1
Height Growth	$\frac{dH}{dt} = \frac{dH}{dA_l} \times \frac{dA_l}{dM_a} \times \frac{dM_a}{dt}$	Modified from Falster S2 (4)
Cost of deploying leaf area	$\frac{dA_l}{dM_a} = \left(\frac{dM_l}{dA_l} + \frac{dM_r}{dA_l} + \frac{dM_s}{dA_l} + \frac{dM_b}{dA_l} \right)^{-1}$	Falster S2 (5)
Change in component i	$\frac{dM_i}{dt} = \frac{dM_i}{dA_l} \times \frac{dA_l}{dM_a} \times \frac{dM_a}{dt} - k_i M_i$	Modified from Falster S2 (3) and (4)
Allometry adjusted component change with leaf area	$\frac{dM_i}{dA_l} = c_i(H, A_l, M_i) \frac{dM_i'}{dA_l}$	Equation 2
Allometric calibration of component i	$c_i(H, A_l, M_i) = \frac{2}{1 + \exp(-c_k(M_i'(H, A_l) - M_i))}$	Equation 3
Change in leaf mass with leaf area	$\frac{dM_l}{dA_l} = \Phi$	Falster S2 Table 2
Change in sapwood mass with leaf area	$\frac{dM_s}{dA_l} = \rho \theta \eta_c \left(H + A_l \frac{dH}{dA_l} \right)$	Falster S2 Table 2
Change in bark mass with leaf area	$\frac{dM_b}{dA_l} = \alpha_{b1} \rho \theta \eta_c \left(H + A_l \frac{dH}{dA_l} \right)$	Falster S2 Table 2
Change in root mass with leaf area	$\frac{dM_r}{dA_l} = \alpha_{r1}$	Falster S2 Table 2
Change in height with leaf area	$\frac{dH}{dA_l} = \alpha_{l1} \alpha_{l2} (A_l)^{\alpha_{l2}-1}$	Falster S2 Table 2
Change in sapwood area with leaf area	$\frac{dA_s}{dA_l} = \theta$	Falster S2 Table 2

Change in bark area with leaf area $\frac{dA_b}{dA_l} = \alpha_{b1}\theta$ Falster S2 Table 2

Reproduction

Reproduction Allocation $\frac{dF}{dt} = \frac{\alpha_{f1}}{1 + \exp\left(\alpha_{f2}\left(1 - \frac{H}{H_{mat}}\right)\right)} M_{st}$ Falster S1 (6)

Seed Production $f(x, H, E_a, E_s) = \frac{dF}{\omega + \alpha_{f3}}$ Falster S1 (10)

Leaf Area Distribution

Cumulative fraction of plant's leaves above z $Q(z, H) = \left(1 - \left(\frac{z}{H}\right)^\eta\right)^2$ Falster S2 (12)

Leaf area at height z of plant of height H $q(z, H) = 2\frac{\eta}{H}\left(1 - \left(\frac{z}{H}\right)^\eta\right)\left(\frac{z}{H}\right)^{\eta-1}$ Falster S2 (13)

Storage Allocation

Change in storage pool $\frac{dM_{st}}{dt} = \frac{dB}{dt} - \frac{dM_a}{dt} - \frac{dF}{dt}$ Introduced

Net Mass Production $\frac{dB}{dt} = \alpha_{bio}\alpha_y\left(A_l\bar{p} - \frac{dR}{dt}\right)$ Modified from Falster S2 (3)

Diameter Growth

Growth in basal area $\frac{dA_{st}}{dt} = \frac{dA_b}{dt} + \frac{dA_s}{dt} + \frac{dA_h}{dt}$ Falster S2 (7)

Diameter growth $\frac{dD}{dt} = (\pi A_{st})^{-0.5} \frac{dA_{st}}{dt}$ Falster S2 (8)

Mortality

Mortality Rate $d(x, H, M_{st}, E_a, E_s, t)$ Equation 4
 $= d_l + d_p(x, H, E_a, E_s, t)$
 $+ d_s(x, M_{st})$

Productivity-dependent mortality rate $d_p(x, H, E_a, E_s, t) = E_s(t)\alpha_{dp1} \exp\left(-\alpha_{dp2} \frac{dB}{dA_l}\right)$ Equation 5

Storage-dependent mortality rate $d_s(x, H, M_{st}) = \alpha_{ds1} \exp\left(-\alpha_{ds2} \frac{M_{st}}{M_a}\right)$ Equation 6

Probability of Mortality $p_D(t) = 1 - \exp(-d(x, H, M_{st}, E_a, E_s, t))$ Equation 7

Germination

Probability of plant survival through germination $S_G(x', H_0, E_{a0}) = \frac{1}{1 + \left(\alpha_{d0} \frac{A_l}{dB}\right)^2}$ Falster S1 (21)

Size of initial storage pool $M_{st0} = \beta_s M_{a0}(H_0)$ Equation 8

Environment

Environmental stress

$$E_s(t_y) = \begin{cases} t_y < t_{crit} & \Rightarrow 1 \\ t_y \geq t_{crit} & \Rightarrow 0 \end{cases}$$

Introduced

Table S2 Parameters used in the model. Source indicates what data were used in the parameter derivation. “Simulations” indicates model testing on individual plants throughout model development and FF16 refers to the parent strategy described in (Falster et al., 2016). All other sources are citations to papers. Where a source is missing, a further explanation is included in the main text.

Description	Symbol	Unit	Value	Source
<i>Plant Storage</i>				
Switch time	t_s	y	<i>varies</i>	-
Rate of storage conversion to biomass (storage utilisation rate)	α_s	kg kg ⁻¹ y ⁻¹	<i>varies</i>	-
Initial storage concentration following germination	β_{s1}	kg kg ⁻¹	0.1	(Martínez-Vilalta et al., 2016)
Coefficient of the rate of transition between growth and no-growth periods	β_{s2}	y ⁻¹	120	Simulations
<i>Plant Construction</i>				
Crown-shape parameter	h		5	Simulations
Leaf mass per area	f	kg m ⁻²	0.1242302	(Falster et al., 2015)
Wood density	r	kg m ⁻³	505	(Falster et al., 2015)
Sapwood mass per unit leaf area	q	kg m ⁻²	0.00015089	(Falster et al., 2015)
Parameter for relationship of height of plant with leaf area	α_{l1}	m	-0.56936	(Drake et al., 2019; Falster et al., 2015)
Exponent of relationship between height and leaf area	α_{l2}		1.48185	(Drake et al., 2019; Falster et al., 2015)
Root mass per unit leaf area	α_{r1}	kg m ⁻²	0.027691	(Falster et al., 2015)
Ratio of bark cross-sectional area to sapwood area	α_{b1}	m ² m ⁻²	0.3768273	(Falster et al., 2015)
<i>Production</i>				
Leaf photosynthesis per area	α_{p1}	mol m ⁻² y ⁻¹	82.34303	Simulations
Saturation of leaf photosynthesis per area	α_{p2}	-	0.1072532	Simulations
Canopy openness at the top of the canopy	$E_a(z = \text{top})$	-	1	FF16
Yield = fraction of carbon fixed converted into mass	α_y	g g ⁻¹	0.7	FF16
Biomass per mol carbon	α_{bio}	kg mol ⁻¹	0.0245	FF16

Leaf respiration per mass	r_l	$\text{mol y}^{-1}\text{kg}^{-1}$	175.8027	FF16 (hyper-parameterisation)
Fine-root respiration per mass	r_r	$\text{mol y}^{-1}\text{kg}^{-1}$	217	FF16
Sapwood respiration per mass	r_s	$\text{mol y}^{-1}\text{kg}^{-1}$	2.412504	(Medlyn et al., 2005)
Bark respiration per mass	r_b	$\text{mol y}^{-1}\text{kg}^{-1}$	4.825008	(Medlyn et al., 2005)
Portion of respiration maintained through stress	r_{min}	mol mol^{-1}	0.5	Simulations
Turnover rate for leaves	k_l	y^{-1}	1.012133	FF16
Turnover rate for sapwood	k_s	y^{-1}	0.06	(Jeffreys, 1999)
Turnover rate for bark	k_b	y^{-1}	0.06	(Jeffreys, 1999)
Turnover rate for fine roots	k_r	y^{-1}	1	FF16
<i>Fecundity</i>				
Seed mass (mass allocated to single offspring)	Ω	kg C	0.1	Simulations
Height at maturation	H_{mat}	m	30	Simulations
Maximum allocation to reproduction	α_{f1}		0.05	Simulations
Parameter determining rate of change in dF/dt around H_{mat}	α_{f2}		50	FF16
Accessory cost per seed	α_{f3}	kg	0.000114	FF16
<i>Mortality</i>				
Survival probability during dispersal	S_D		0.25	FF16
Parameter influencing survival through germination	α_{D0}	$\text{kg y}^{-1}\text{m}^{-2}$	0.1	FF16
Intrinsic or growth-independent mortality	d_l	y^{-1}	0.01	FF16
Baseline rate for productivity-dependent mortality	α_{DP1}	y^{-1}	0.25	Simulations
Risk coefficient for dry-mass production per unit leaf area in productivity-dependent mortality	α_{DP2}	$\text{y kg}^{-1}\text{m}^{-2}$	20	Simulations

Baseline rate for storage-dependent mortality	α_{DS1}	y^{-1}	3	Simulations
Risk coefficient for storage concentration in storage-dependent mortality	α_{DS2}	$y m^{-2}$	300	Simulations

Parameter Estimation for α_s and t_s

Two parameters govern the allocation strategy: (1) switch time, t_s , and (2) storage utilisation rate, α_s . 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. 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.

We chose two contrasting values for the two 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. 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.

We varied t_s from 0 to 0.75 y to find the values such that the total live biomass or storage carbon pool was maximised at the end of the year (Fig. S1). The storage translocation parameter, α_s , was varied from 0.1 to 0.4 kgC kgC⁻¹ d⁻¹ and the relative growth rate of height and storage concentration were plotted for a range of parameter values and initial plant sizes (Fig. S2).

From these simulations, two values for each parameter were chosen for a total of four contrasting allocation strategies.

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

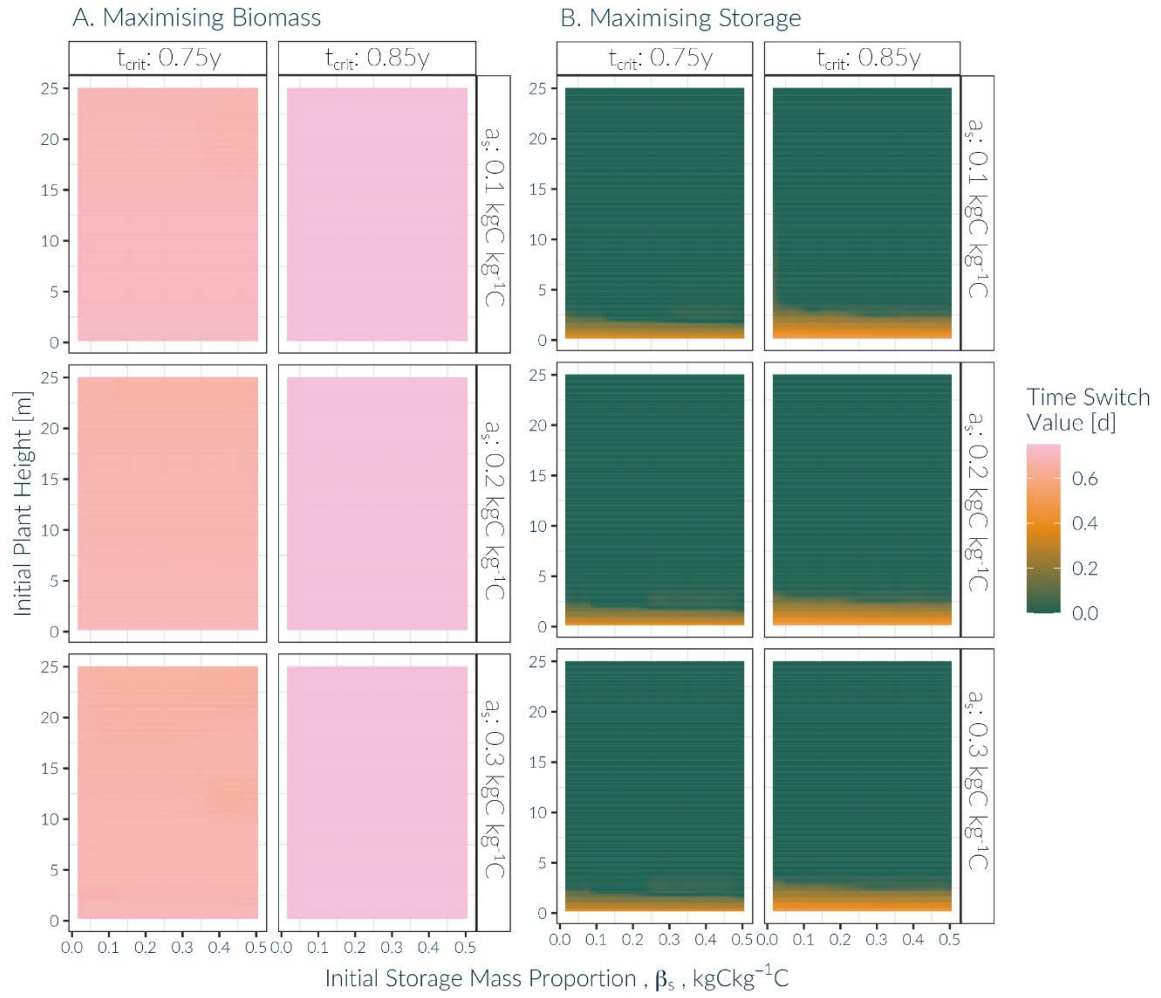


Figure S1 Sensitivity analysis of a simulated individual to the switch time parameter t_s for a range of initial plant heights (y-axis) and storage mass proportions (x-axis) and three values of α_s . The colours indicate the value of t_s that maximises the live mass of the plant at the end of the year (A) or the storage mass at the end of the year (B).

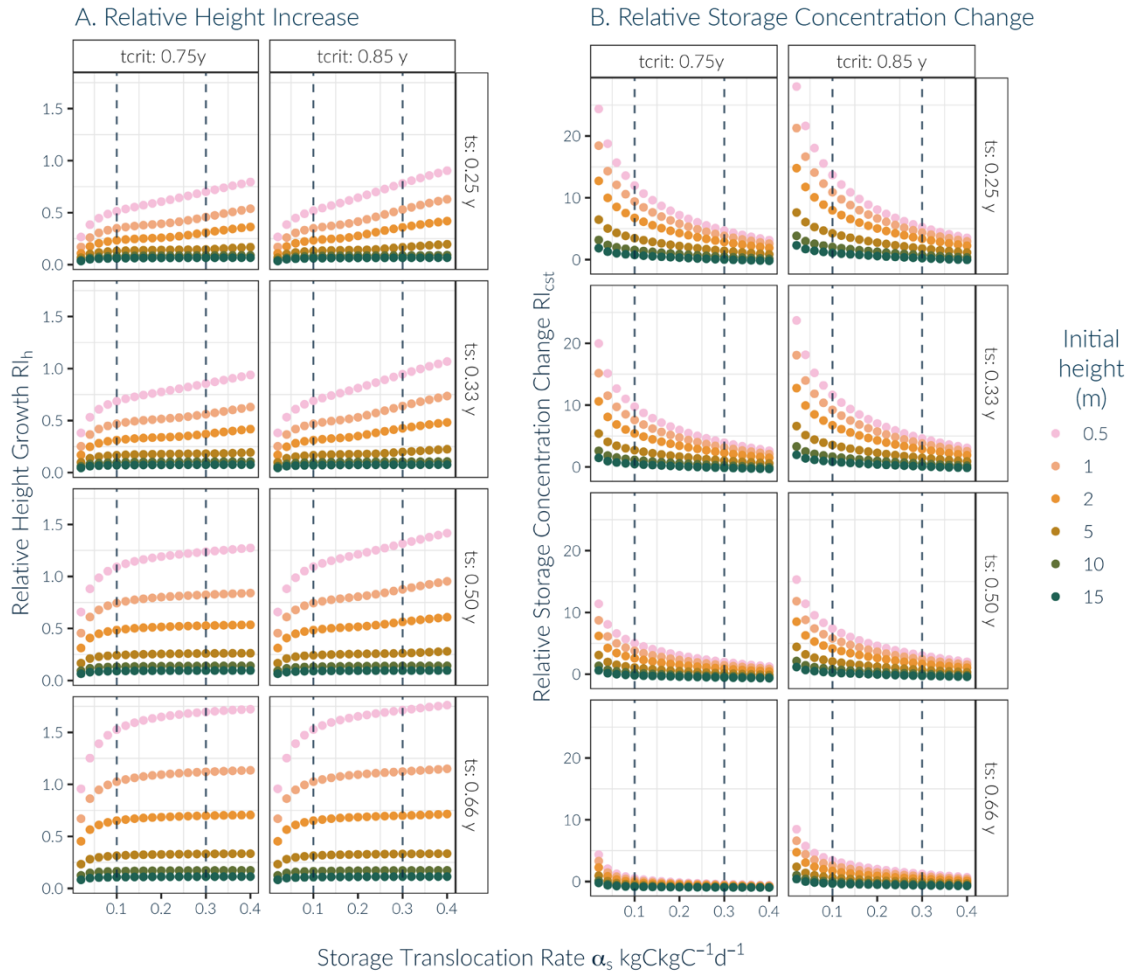


Figure S2 Sensitivity of growth of an individual plant for one year to the storage utilisation rate parameter (x-axis) for different environmental stress treatments (columns), time switch parameters (rows), and initial heights (colours). Dashed lines indicate the two values chosen as parameters. Panel A shows the relative increase in height and Panel B shows the relative change in carbon storage concentration.

To test the effect of these strategies on growth in the absence of competition, a single plant of each strategy was simulated for a 100-year period in an environment with no light competition and for the three average stress durations used in the model (Fig. S3): no stress, 54.75 days and 91.25 days. Both the strategy and the duration of stress affected the final size of an individual. The Risky-Safe spectrum has a much larger effect on the final plant size than the Fast-Slow spectrum. The reasons for these impacts can be seen by zooming in on one year (Fig. S4). The later switch time (longer growth duration) of Risky strategies contributes more to growth than the storage utilisation rate α_s (Fig. S4A). The significant difference in the plants of the Fast-Slow strategy spectrum comes during the recovery period when height growth is halted in favour of recovering allometric balance in the plant: the Fast strategy allows plants to recover their growth faster than those with the Slow strategy. The trade-off is that the Fast strategy also results in a smaller annual minimum of the NSC pool and, therefore, a higher potential for mortality during those periods (Fig. S4B).

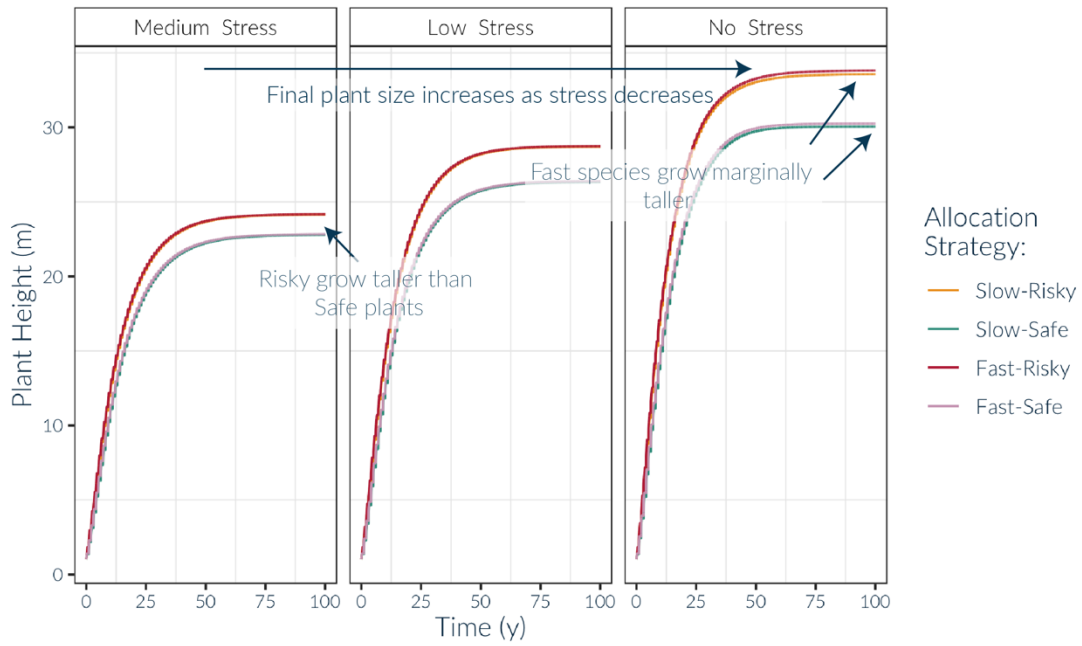


Figure S3 Trajectory of plant height for a single plant using each allocation trajectory and growing without competition under different deterministic stress regimes over a 100 year period. Each box represents a different stress regime: medium stress (left, 0.75 of the year is photosynthetically active), low stress (middle, 0.85 of the year is photosynthetically active) and no stress (right, plants can photosynthesise for the entire year). Each colour represents a different allocation strategy: slow-risky (yellow), slow-safe (green), fast-risky (red) and fast-safe (pink) with Risky strategies outcompeting the Safe ones and the Fast-Risky reaching the tallest heights and Slow-Safe being the shortest of the individuals. The trajectory of plant height is similar for all strategies with plants reaching a plateau after a period of relatively fast growth. This plateau increases with number of photosynthetically active years. Differences between the strategies also become more pronounced with a decrease in stress.

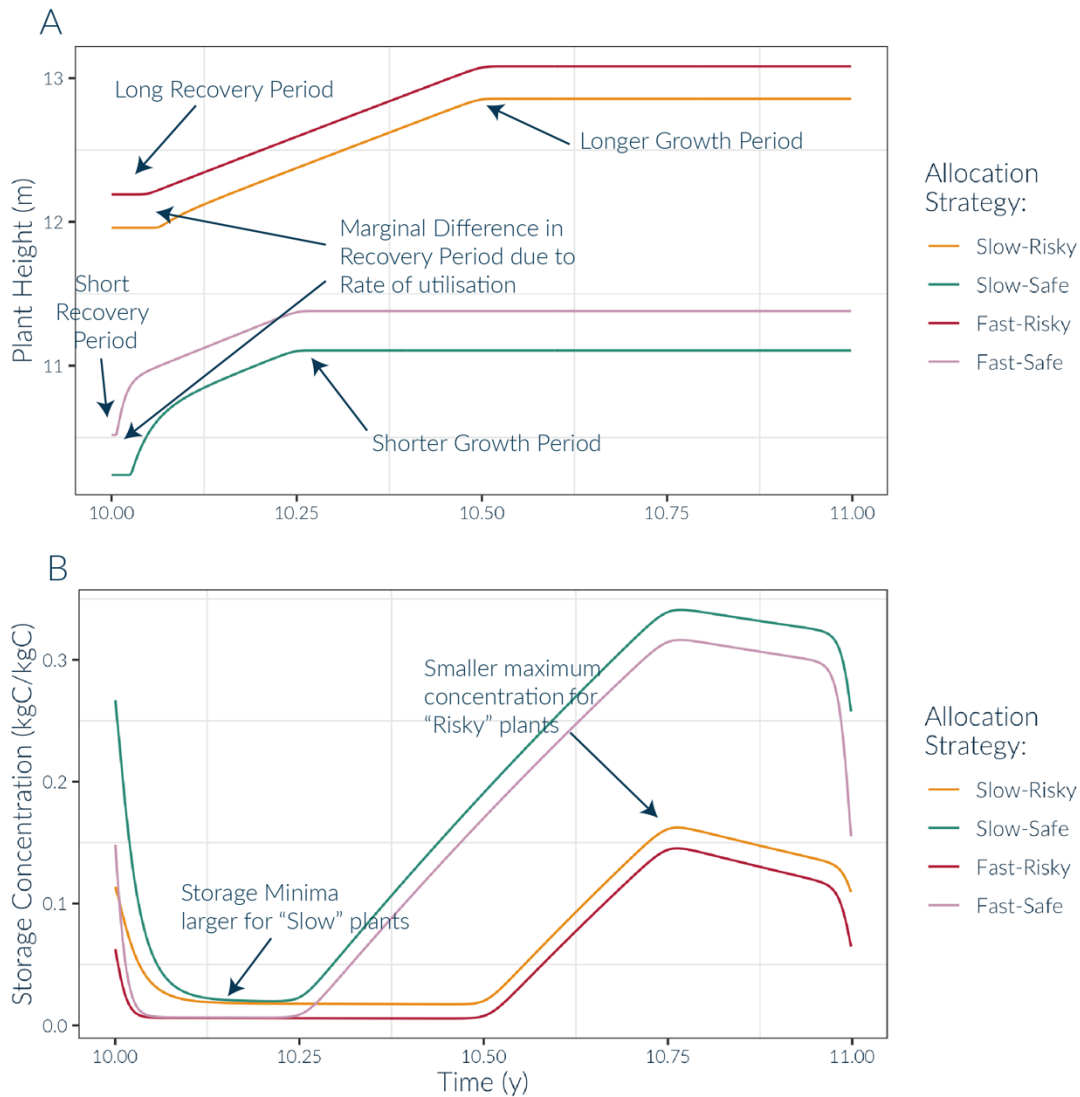


Figure S4 Illustration of variability in intra-annual height growth (A) and storage concentration (B) between strategies for a sample year. Strategies are represented by different colours: slow-risky (yellow), slow-safe (green), fast-risky (red) and fast-safe (pink). A: Initial lack of growth (the recovery period) is due to loss of allometric scaling over the previous stress season which leads to lack of vertical growth at the beginning of the year while missing pools are replenished. The Safe strategies have a shorter recovery period with a Fast translocation rate leading to marginally faster recovery period as opposed to Slow translocation rate strategies. The likely larger carbon pools of safe strategies lead to faster initial growth before achieving a constant rate, whereas Risky plants maintain a relatively stable growth rate for their entire height growth period. Most differences between strategies can be attributed to the difference between the switch time, that is to the Safe-Risky strategy spectrum. B: Due to a shorter growing period, Safe plants exhibit a larger concentration of carbon as opposed to Risky plants and therefore a larger maximum at the start of the stress period. The minimum of storage concentration is governed by the differences between translocation rates, α_s , rather than the switch time leading to a higher minimum of storage concentration for Slow strategies. The highest drawdown of carbon from storage can be attributed to growth rather than maintenance expenditure during the stress period.

References

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Supplementary Information B: Additional Figures



Figure S5 Total Net Carbon Uptake (NCU) summed across all individuals in a patch of a given strategy across a 100-year time scale on a 100m² patch. Light orange line shows the sum of NCU for the entire population regardless of strategy. Periods of no height increase in an individual can be explained by an allometric mismatch: since plants don't grow for a proportion of the year growth is prioritised in those components that are most imbalanced until balance can be regained.

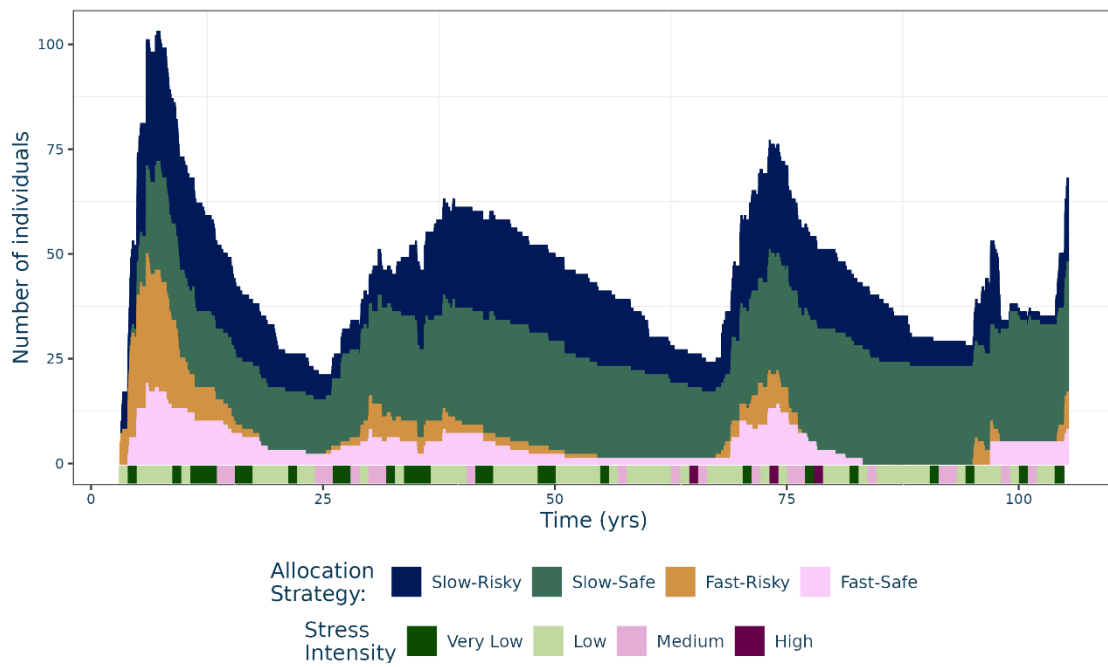


Figure S6 Number of individuals of each strategy living on the 100 m² patch over time. The rug shows the intensity of the stress in a given year as described by the length of the stress (green for very low stress intensity <30d, light green for low (30 to 75d), pink for medium (75 to 105d) and violet for high (105 to 150d)).

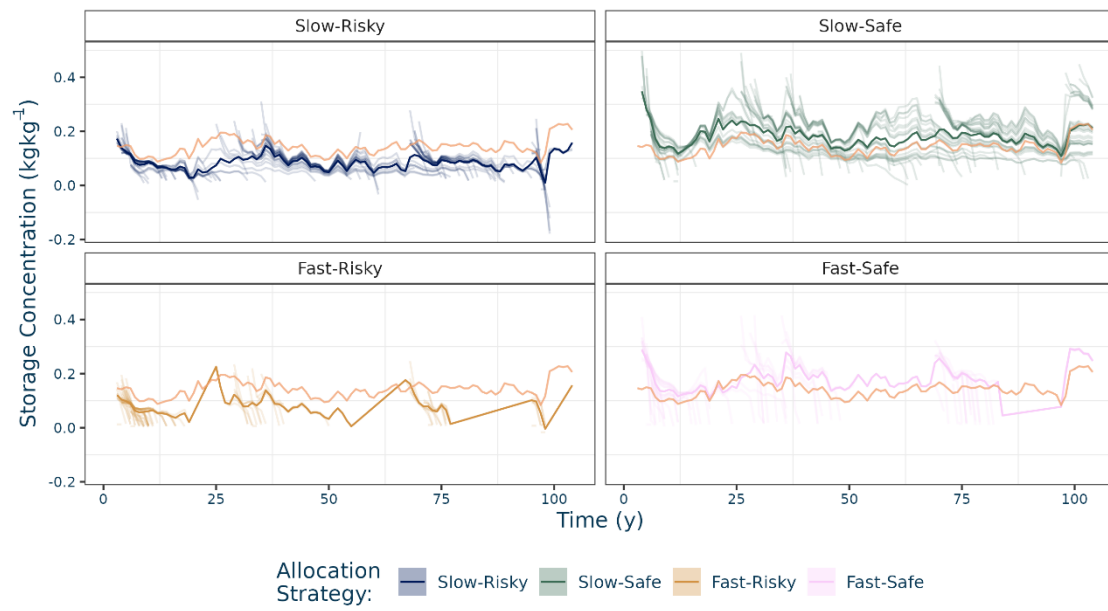


Figure S7 Stored carbon concentration in individual plants as a rolling 2-year average. Light orange line shows the average storage concentration for the entire population regardless of strategy.

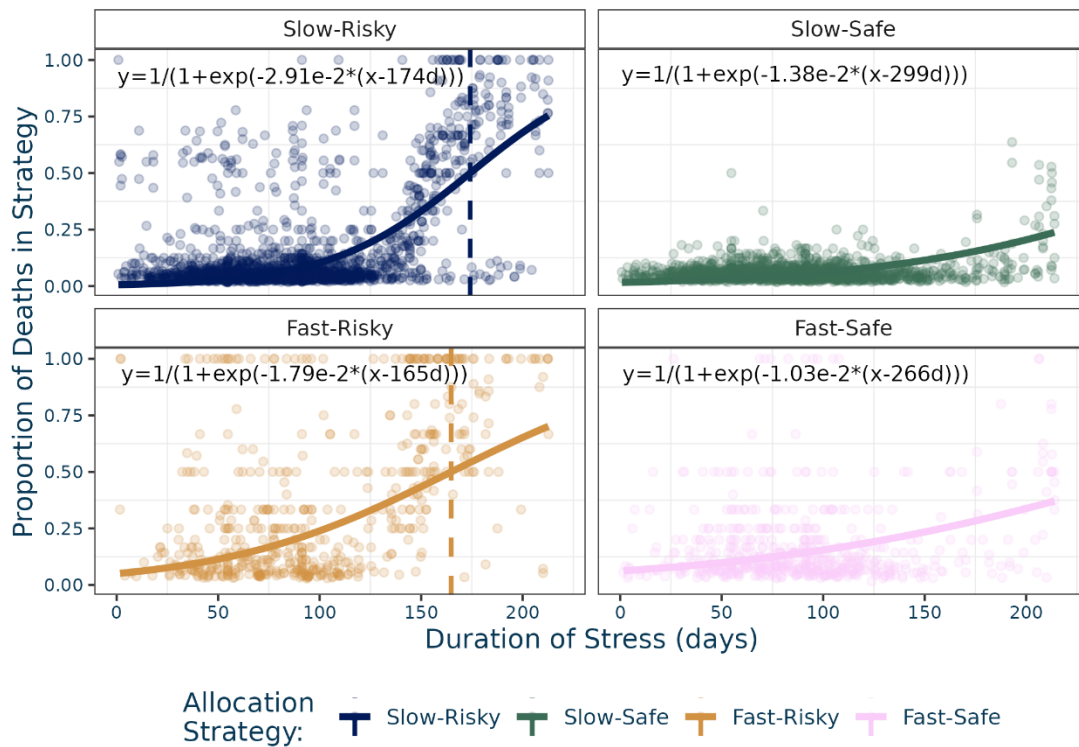


Figure S8 Proportion of population dying during a stress period (all simulations), as a function of stress duration. The proportion is calculated as the number of deaths of a given strategy divided by the total number of individuals of that strategy alive during the stress period, with each point signifying a single simulated year. Deaths outside of the stress period are not considered. A logistic equation is fitted to the data and the point of 50% death for each strategy is indicated by the vertical dashed line and indicated in the formula for that fitting (not shown for the Slow-Safe and Fast-Safe strategies for which this point is beyond the data observed).

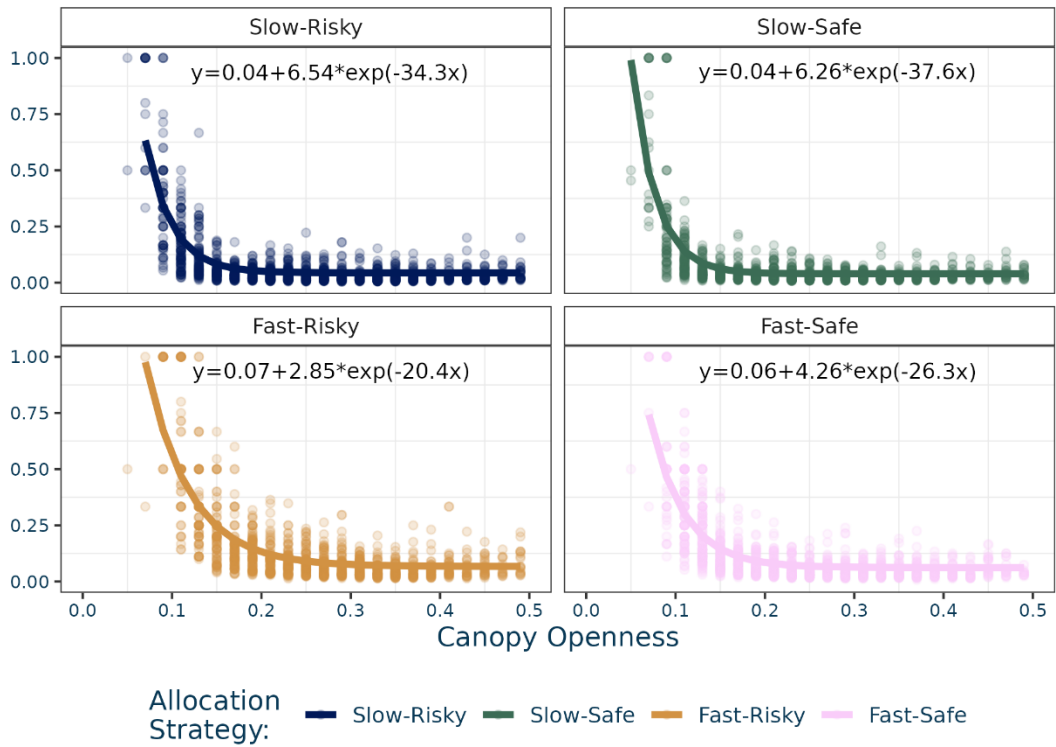


Figure S9 Relationship between population mortality and light competition for all simulations. The proportion of plant mortality is calculated as the number of deaths of plants of a given strategy which live in a given light environment divided by the total number of individuals of that strategy alive in that same light environment, with each point signifying a single simulated year. Deaths during the stress period are not included because productivity-driven mortality is assumed to be zero during stress. 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 were removed, and an exponential decay function was fitted to each set of data (solid line and equation in each panel).