

Decreased water limitation under elevated CO₂ amplifies potential for forest carbon sinks

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Increasing atmospheric CO₂ concentrations and changing rainfall regimes are creating novel environments for plant communities around the world. The resulting changes in plant productivity and allocation among tissues will have significant impacts on forest carbon storage and the global carbon cycle, yet these effects may depend on mechanisms not included in global models. Here we focus on the role of individual-level competition for water and light in forest carbon allocation and storage across rainfall regimes. We find that the complexity of plant responses to rainfall regimes in experiments can be explained by individual-based competition for water and light within a continuously varying soil moisture environment. Further, we find that elevated CO₂ leads to large amplifications of carbon storage when it alleviates competition for water by incentivizing competitive plants to divert carbon from short-lived fine roots to long-lived woody biomass. Overall, we find that plant dependence on rainfall regimes and plant responses to added CO₂ are complex, but understandable. The insights developed here will serve as an important foundation as we work to predict the responses of plants to the full, multidimensional reality of climate change, which involves not only changes in rainfall and CO₂ but also changes in temperature, nutrient availability, and disturbance rates, among others.

rainfall | forest dynamics | plant allocation | carbon storage | evolutionarily stable strategy

The fate of the terrestrial carbon sink hinges on the role of limitation by other resources (1, 2). If additional atmospheric CO₂ causes forests to run up against limitation by other resources, it is possible that a forest carbon sink caused by CO₂ fertilization could diminish or reverse. The fate of this service by plants, currently estimated to mitigate 30% of anthropogenic emissions per year (3), is one of the most uncertain components of global climate predictions (4). Despite this importance, however, the role of resource limitation in carbon sinks is poorly understood and poorly incorporated into global models (1, 2, 5, 6).

Here we investigate the effect of water limitation of photosynthesis on forest carbon storage and sinks. With additional CO₂ in the atmosphere, more CO₂ diffuses into leaves, whereas approximately the same amount of water escapes. This increase in water use efficiency at the leaf level has been well documented in experiments (7, 8) and observed in biomes around the world (9, 10). However, fossil CO₂ is not the only factor altering water relations in plant communities. Rising temperatures (11), changing rainfall regimes (12), and nitrogen deposition (13) can also have effects on plant water balance. A complete understanding of forest carbon storage and carbon sinks thus requires understanding a truly complex system.

To build the mechanistic models we need to predict forest carbon storage in novel circumstances, we favor bringing together model components whose behavior we can understand and test with controlled experiments. Here we focus on water-limited photosynthesis and increasing atmospheric CO₂ concentration in isolation from other global change factors.

The influence of average annual rainfall on plant productivity and dominant vegetation type has long been recognized (14–16),

but rainfall manipulation experiments demonstrate that plant responses to rainfall can also depend significantly on the timing of rainfall distribution (17, 18). Recent theoretical work also highlights the complexity of plant dependence on water. Incentives to individuals in competition for water as a shared resource can have significant and sometimes counter intuitive influences on plant allocation strategies (19–22). If water is limiting, competition belowground drives each plant to invest in fine roots at a level that maximizes its own competitive ability, but that can decrease the growth rates of all individuals when every plant adopts the same strategy: a “competitive overinvestment.” Farrior et al. (22) found that competitive overinvestment in fine roots trades off with competitive overinvestment in structural biomass (wood) used by the plants in height-structured competition for light. A tradeoff between short-lived fine roots and long-lived woody biomass has a large effect on carbon storage (23).

Results from a model/experiment comparison show that a theoretical understanding of competitive overinvestments can explain otherwise counter intuitive responses of real plant communities to resource additions (24). This study shows the key to understanding fine-root responses to water and nitrogen additions is that the plants are effectively sequentially limited by water and nitrogen. Because of the variability of precipitation, the belowground resource that limits photosynthesis repeatedly shifts from water to nitrogen and back. The competitive dominant allocation strategy for fine roots and woody biomass turns out to be a weighted average of the purely water-limited strategy and the purely nitrogen-limited strategy. Sequential limitation allows us to

Significance

With increasing atmospheric CO₂ and a changing climate come changes in both plant water use efficiency and rainfall regimes. The effects of these changes on forests, including feedbacks to the carbon cycle, are complex. Through a theoretical analysis combining CO₂, soil moisture dynamics, and individual-based competition in forests, we find that (i) carbon storage has a complex and significant dependence on rainfall amount and timing and (ii) the main effect of increasing CO₂ in water-limited forests is a decrease in the amount of time trees spend in water limitation. This main effect is predicted to reduce competitive overinvestment in fine roots, drive competitive trees to increase investment in woody biomass, and greatly increase forest carbon storage in live biomass.

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Data deposition: The code used to find these numerical solutions and produce the figures of the paper has been deposited at <https://github.com/cfarrior/EcoHydroAllocation/tree/V1>.

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build understanding of forests commonly limited by both water and nitrogen by separately studying the special cases of pure water limitation (studied here) and pure nitrogen limitation.

For water-limited plants, two parameters are critical to the competitive dominant allocation strategy: (i) the productivity of the periods in water limitation and (ii) the proportion of time plants spend in water limitation (Fig. 1). Productivity during water limitation is met by a tragedy of the commons: shared access to water makes the competitive dominant strategy one where all of the productivity during water limitation is spent on fine roots. This competitive overinvestment in fine roots increases with the productivity of plants during the period of water limitation (22). In contrast, the most competitive strategy invests productivity from periods without water limitation in structures that enhance competitive ability for light: leaf layers that can capture enough sunlight to pay for their own costs (or more) and woody biomass. The mapping from rainfall regimes of real forests to these two abstract quantities (productivity and proportion of time in water limitation), however, is not obvious and is complicated by the fact that the quantities also depend on the allocation strategies of plants in the community. For example, plants with many leaf layers will have high maximum photosynthetic rates and spend more time in water limitation than plants with fewer leaf layers.

Moreover, the effect of elevated CO_2 on these quantities is both counterintuitive and complex, and yet is the key to predicting the size of the carbon sink cause by elevated CO_2 . First, elevated CO_2 enhances productivity during water limitation (enhanced water-use efficiency), but this enhanced productivity is only met by a more intense tragedy of the commons. For a competitive dominant plant, all of the additional carbon gained from elevated CO_2 is spent on short-lived fine roots, providing little carbon sink and representing a down-regulation of the additional carbon storage that would have occurred with constant proportional allocation. Second, elevated CO_2 also decreases the proportion of time plants spend in water limitation. All of the carbon that would have been fixed under water limitation at lower CO_2 but is now fixed under water saturation at higher CO_2 (imagine the increase in blue from shifting s^* down in Fig. 1) is now allocated to leaves and wood, generating a strong carbon sink and representing an up-regulation of the additional carbon storage that would have occurred with constant proportional allocation. To predict the relative importance of these opposite

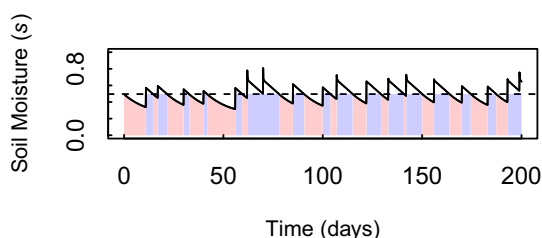


Fig. 1. A soil moisture trace for a closed-canopy forest filled with canopy plants that are water-limited below soil moisture, s^* (dashed line). Rainfall arrives as a Poisson marked process, increasing soil moisture (peaks) that is then diminished by plant transpiration and other losses. Competitive plants invest the productivity of water-limited periods (represented by red shading) into fine roots, whereas they invest the productivity of periods when water is not limiting (represented by blue shading, productivity independent of s) into leaves and wood. Allocation to wood is the dominant driver of carbon storage because of its greater longevity. The soil moisture threshold of water limitation (s^* , dotted line) proximally determines the relative durations of the water-unlimited (blue) and water-limited (red) periods and thus the allocation to wood. However, the threshold s^* is itself a function of leaf-level water use efficiency (and thus atmospheric CO_2), plant hydraulic conductance, leaf and fine-root allocation, and soil texture (Eq. 2).

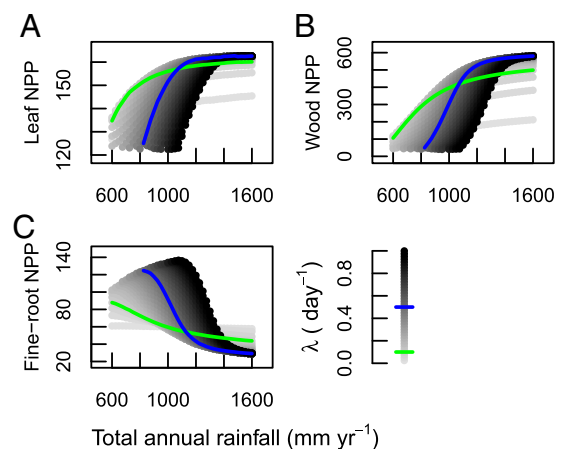


Fig. 2. Predicted allocation of (A) leaf, (B) structural (wood), and (C) fine-root NPP per-unit crown area for canopy trees, where each point corresponds to a different rainfall regime. Within each value of total annual rainfall, the storm frequency (λ , day^{-1}) increases with shading intensity. Green and blue lines mark the range of commonly observed values of λ : 0.1 (green) to 0.5 (blue).

effects, we need a model of continuously varying soil moisture including the contributions of stochastic rainfall events and their interaction with allocation strategy.

Here we combine the strengths of the Farris et al. (22) model of individual tree competition for water and light in a forest stand with the Rodriguez-Iturbe et al. (25–27) model of soil moisture dynamics based on stochastic rainfall regimes. Strategically, we continue to use simplified representations of tree physiology and the environment to develop a model from which we can derive mechanistic insights and testable results. This model will provide a valuable baseline for understanding of the role of water-limited photosynthesis on carbon allocation strategies and forest carbon sinks both in observations and global model predictions.

Methods

Here we present the basic components of the model needed to understand our results. A more detailed description of motivation and all equations can be found in *SI Appendix 1*. The model was designed to have an intermediate level of mechanistic detail. To focus on understanding interactions of forest carbon storage, rainfall regimes, and carbon fertilization, we strategically kept the model simplified in other respects. As such, we assume all forests are saturated by all resources except for water and light, and many other physiological details are ignored here.

Soil Moisture. At any moment in time, soil moisture, s , is the result of several inputs and losses. Inputs include water delivered to the soil in rainfall events, whereas losses include interception, evaporation, runoff, plant transpiration, and leakage. Because this paper focuses on variation in transpiration and rainfall, we describe only these in detail. Rain arrives in discrete events modeled at the daily timescale. The arrival of rain events (i.e., occurrence of days with rain) is approximated as a Poisson marked process, where the time between rainfall events is exponentially distributed with an average waiting time of λ^{-1} days. The amount of rain that falls during an event is drawn from an exponential probability density function, characterized by α : the average amount of rainfall (millimeters) in an event (e.g., a rainy day). For convenience of interpretation, we describe rainfall regimes by total annual rainfall (R) and storm frequency [λ ; where $\alpha = R/(\lambda \times 365)$].

The rate of plant transpiration [$T(s)$, mm/m^2 per day] is a function of both soil moisture and plant traits. The lowest soil moisture at which plants operate is s_w . If s is greater than s_w and lower than a critical soil moisture value, s_c^* , plants are water limited and take up water in proportion to its availability [$T_{\max}(s - s_w)/(s_c^* - s_w)$]. When soil moisture is high enough to saturate plant demand ($s > s_c^*$), transpiration is independent of soil moisture and runs at a maximum rate (T_{\max}).

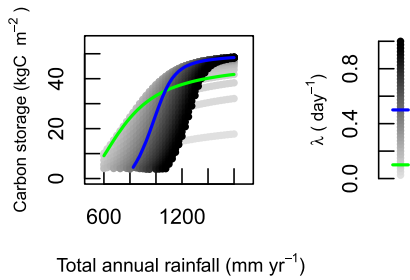


Fig. 3. Steady-state carbon storage in live biomass of a forest dominated by individuals with ESS carbon allocation (Fig. 2). Within each value of total annual rainfall, the storm frequency (λ , day^{-1}) increases with shading intensity. Green and blue lines mark the range of commonly observed values of λ : 0.1 (green) to 0.5 (blue).

Individual-Based Competition for Light and Water. Individual trees are exactly the same except for their yearly allocation to leaves, fine-roots, and structural biomass per-unit crown area. As an individual allocates to structural biomass, it grows in trunk diameter, height, and crown area allometrically.

The water-unlimited photosynthetic rate per-unit crown area of an individual (i , $A_{L,i}$) is dependent on the number of leaf layers (l_i) and light level at the top of the crown (L_i ; *SI Appendix 1*). It is assumed that tree crowns are flat topped with no overlap among individual crowns. However, self-shading within the plant decreases the photosynthetic rate of lower leaf layers. Roots, with area r_i , take up water in proportion to the amount of water available in the soil ($s - s_w$). If this is less than the water needed to meet the water-unlimited photosynthetic rate of the leaves ($s_i^* - s_w = A_{L,i}/(r_i K_p \omega)$), the plants operate photosynthesis in proportion to their water uptake

$$A_i = t \left[\int_{s_w}^{s_i^*} \omega K_p (s - s_w) p(s) ds + \int_{s_i^*}^1 p(s) A_{L,i} ds \right], \quad [1]$$

where t is the length of the growing season, $p(s)$ is the probability density of s during the growing season, K_p is the plant hydraulic conductance from the soil through the fine roots to the leaves, and ω is the exchange rate of carbon assimilated per unit water transpired at the site of the stomata (i.e., the water use efficiency). It is assumed that ω does not vary among leaves in the forest, and K_p does not vary among trees.

The total carbon assimilated per year (A_i) is used for respiration, growth, and replacement of leaves and fine roots, reproduction, and growth of structural biomass. We assume that investment in reproduction per-unit crown area is zero for understory trees and constant for canopy trees. Then, given l_i , r_i , L_i , and the distribution $p(s)$, allocation to structural biomass (dS/dt) and thus diameter growth rate can be calculated (*SI Appendix 1*).

To find the light level available to each individual, L_i , we use the perfect plasticity approximation (PPA), an analytically tractable forest dynamics model that accurately approximates the dynamics of a fully spatial forest simulator (28, 29). In its simplest form, the PPA is the approximation that there is a single size (i.e., diameter D^*), above which tree crowns are in full sun (L_0) and below which trees are shaded by a single layer of canopy trees. This result follows from the assumption that individual trees are good at foraging horizontally for light. In a forest at equilibrium size structure, it follows that there are only two distinct levels of resource availability that trees experience throughout their lives: an understory level and a canopy level [see ref. 22 for a demonstration that competitive trees have only two levels of allocation: one for canopy trees (described by l_c , r_c) and one for understory trees (l_u and r_u)].

Trees also have a probability of mortality that is independent of size but that is higher in the understory (μ_u) than in the canopy (μ_c). Thus mortality is effectively a function of light level and size. For simplicity, however, we assume this mortality rate is independent of water availability. Thus, our model only incorporates the role of water in limiting carbon assimilation but does not include its influence on mortality.

Soil moisture [$p(s)$], as described above, is a function of transpiration rates of all trees in the forest stand. The maximum rate of transpiration for the stand is then the sum of the water-unlimited rates of transpiration for canopy and understory trees. Because understory trees cover much less ground area and also have far less photosynthesis than canopy trees, the transpiration of canopy trees is a good approximation of stand-level transpiration. Likewise, the soil moisture at which the forest is water limited (s^*)

can be approximated by that of canopy trees. Then, for a forest composed of individuals with canopy allocation strategy l_c and r_c :

$$T_{\max} \approx \frac{A_L(L_0, l_c)}{\omega} \quad \text{and} \quad s^* \approx \frac{A_L(L_0, l_c)}{\omega K_p r_c} + s_w. \quad [2]$$

Evolutionarily Stable Strategy Analysis and CO₂ Fertilization. To predict competitive dominant tree allocation strategies in different environments, we find the strategy (if one exists) that would win in competition with any other strategy. The competitive dominant (if one exists) is formally the evolutionarily stable strategy, the allocation strategy that when in monoculture cannot be invaded by any other (ESS) (30) (*SI Appendix 1 and 5*).

Carbon stored in live biomass is the sum of the carbon in leaves, fine roots, and structural biomass (wood) of all trees in the forest. We calculate this when the net primary productivity, density, and size structure of a forest containing only the competitive dominant strategy is in dynamic equilibrium (once mortality balances growth and reproduction).

To investigate potential feedbacks between enhanced atmospheric CO₂ and forest carbon storage, we impose a one-time permanent increase in the atmospheric CO₂ concentration by modifying leaf-level photosynthetic rates, specifically by increasing leaf-level water use efficiency (ω) and two photosynthetic efficiency parameters (α_f and V). Parameters are multiplied by an enhancement factor of 1.57, 1.12, and 1.44, respectively, following experimental results (*SI Appendix 1*). We find the new ESS allocation strategies and carbon storage at the point when the forest reaches a new dynamic equilibrium. The difference in the carbon storage under elevated and baseline CO₂ is the total carbon sink or source (if negative) to the atmosphere. To parse the mechanisms of changing carbon storage, we also increased either leaf-level water-use efficiency alone or the photosynthetic efficiency parameters alone.

Parameter Estimation. Parameter values used in numerical estimates can be found in *SI Appendix 2*. Parameter values generally are estimated for temperate deciduous forests. Because some of the parameter values are inevitably uncertain, site-specific, or both, the numerical predictions must be taken cautiously. Figures are produced for all rainfall regimes that produce closed-canopy forests on the dry end and approach saturating responses to rainfall on the wet end. The code used to find these numerical solutions and produce the figures of the paper is available for download so that readers may easily produce predictions for alternate parameter values of their choosing (code is written in R) (31).

Results

The competitive-dominant (ESS) tree carbon allocation pattern depends on both total annual rainfall and its temporal distribution (Fig. 2). Increasing total annual rainfall, on average, increases

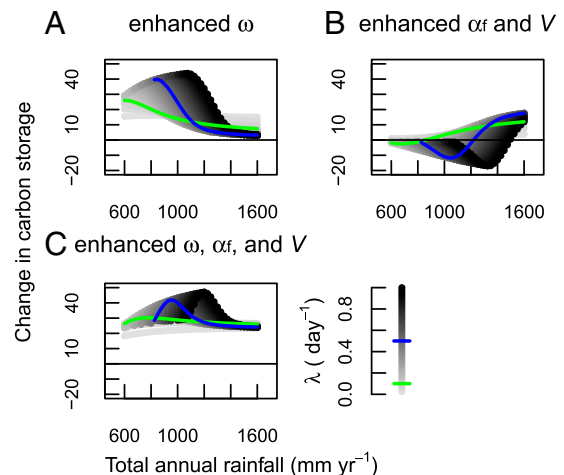


Fig. 4. Changes in forest carbon storage (kgC/m^2) in live biomass due to a one-time permanent percent increase in intrinsic water-use efficiency (57% increase in ω) (A), photosynthetic efficiency (12% increase in α_f and 44% increase in V) (B), and both (C). Storm frequency (λ , day^{-1}) increases with shading intensity. Green and blue lines mark the range of commonly observed values of λ : 0.1 (green) to 0.5 (blue).

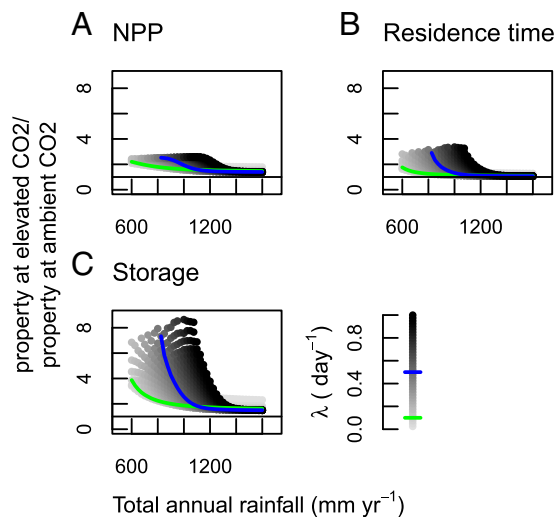


Fig. 5. Relative stand-level responses following CO₂ fertilization (enhanced ω , α_f , and V) across rainfall regimes: (A) stand-level NPP, (B) average residence time of carbon in the forest, and (C) carbon storage of the forest. Storm frequency (λ , day⁻¹) increases with shading intensity. Green and blue lines mark the range of commonly observed values of λ : 0.1 (green) to 0.5 (blue).

annual allocation by the most competitive strategy to leaves (leaf NPP in the figure) and structural biomass (wood NPP) and decreases annual allocation to fine roots (fine-root NPP). The effect of the temporal distribution of rainfall (λ) depends on the total rainfall itself. At low rainfall, increasing λ on average increases fine-root NPP and decreases wood and foliage NPP. However, at high total rainfall, increasing λ , on average, decreases fine roots and increases wood and foliage NPP. For a detailed analysis of the responses of competitive allocation patterns to rainfall regimes, see *SI Appendix 3*. Note the effects of λ are not small: they are on the order of the effects of changing total annual rainfall itself.

The effect of the rainfall regime on carbon storage is similar to the effects on wood NPP: increasing with total annual rainfall and the influence of storm frequency (λ) dependent on total annual rainfall (Fig. 3).

The effects of rainfall regime on the carbon sink following a one-time permanent increase in leaf-level physiological parameters (elevated CO₂) are complex. Enhanced leaf-level water-use efficiency (ω) without increases in the photosynthetic efficiency parameters produces strong carbon sinks in forests with rainfall less than 1,100 mm/y (Fig. 4A). This effect is responsible for the large sinks predicted under elevated CO₂ and relatively low total annual rainfall (elevated ω , α_f , and V ; Fig. 4C). Carbon storage is predicted to increase by a factor of 8 in some cases (Fig. 5C).

If photosynthetic efficiency (α_f and V) increases without enhanced water-use efficiency, the conditions for plant water limitation become less stringent, which increases the time in water limitation (because it increases the numerator in Eq. 2). The increase in time in water limitation causes the most competitive allocation strategy to divert carbon from long-lived structural biomass to short-lived fine roots, creating a carbon source at low and intermediate total annual rainfall levels (Fig. 4B). However, the effect of increased α_f and V are weaker than the effects of increased ω , and therefore CO₂ fertilization produces a carbon sink in all rainfall regimes examined (Figs. 4C and 5). The largest carbon sinks occur at intermediate total annual rainfall levels where that rain is delivered most evenly in time (high λ). In what follows, we will discuss only results for perturbation of all three leaf-level parameters (ω , α_f , and V) in concert.

Changes in carbon storage can be broken down into changes in productivity and changes in the residence time of carbon in the forest. In this model, both NPP and carbon residence time increase with CO₂ fertilization (Fig. 5A and B). Together, these effects multiply to create the large relative increases in carbon storage found in sites with low total annual rainfall (< 1,100 mm/y; Fig. 5C).

The imposed CO₂ fertilization produces photosynthetic rate enhancements with a maximum range of 1.12 (as for α_f) to 1.57 (as for ω), yet some forests' NPP responds by factors much greater than 1.57 (Fig. 5A). Part of the amplification is caused by increases in allocation to leaves relative to fine roots, which increases productivity (Fig. 5A). The rest is caused by increased allocation to wood relative to fine roots (Fig. 5B), because wood's average residence time is more than 30 times longer than that of fine roots (62.5 vs. 2 y). Again, the carbon storage is the product of NPP and average residence time (Fig. 5C).

From the model with simplified rainfall (22), we know that an important mediator of the changes in allocation of trees is the proportion of the growing season trees spend without water limitation (q ; see Fig. 1 and *SI Appendix 3* for discussion). Competition for water drives high investment in fine roots, but that investment is proportional to $(1 - q)$, which is the proportion of the growing season during which they are competing for water. Thus, changes in q caused by CO₂ fertilization and its

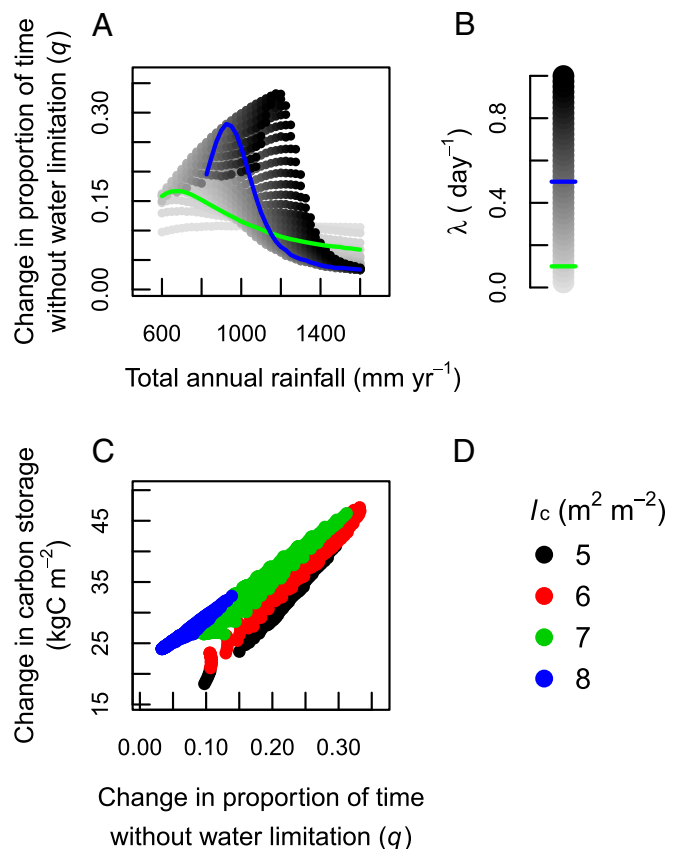


Fig. 6. (A) Change in proportion of time trees spend without water limitation (q ; *SI Appendix, Table S3.1*) following CO₂ fertilization (enhanced ω , α_f , and V) across rainfall regimes. Storm frequency (λ , day⁻¹) increases with shading intensity (legend in B). Green and blue lines mark the range of commonly observed values of λ : 0.1 (green) and 0.5 (blue). (C) Change in carbon storage following CO₂ fertilization (enhanced ω , α_f , and V) vs. the change in q . The canopy tree leaf area index for each forest before fertilization (rounded to the nearest integer) is color coded (legend in D).

feedbacks with competitive allocation patterns can have large influences on allocation of NPP and carbon storage. In this model, changes in q explain 86% of the variation in the size of carbon sinks (linear regression, $n = 1,612$; $df = 1,610$; $R^2 = 0.856$; Fig. 6). The rest is accounted for by differences in the leaf area index, which increases the photosynthetic rate gained by the change in q .

Discussion

Our results imply that the dominant plant allocation strategy, carbon storage, and carbon sinks from CO₂ fertilization all have a complex dependence on rainfall regime. If the frequency of storms is constant, increasing total annual rainfall (i.e., increasing the sizes of storms) increases allocation to wood and thus carbon storage. The impact of changing frequency of storms for a given amount of total annual rainfall depends on the amount of total rainfall. At the low end of rainfall, decreasing the frequency of storms (and increasing rainfall per storm) makes carbon storage higher, whereas at the high end of rainfall, it makes carbon storage lower. Overall, decreasing the frequency of storms decreases the sensitivity of carbon storage to rainfall. Likewise, the size of a carbon sink caused by elevated CO₂ is almost independent of rainfall when storms are infrequent. If storms are frequent, however, the largest carbon sinks occur at intermediate levels of rainfall. Strikingly, the size of carbon sinks relative to carbon storage at ambient CO₂ is many times higher than the enhancement of productivity at the level of a leaf. Subsequent changes in plant allocation strategy have a large influence on carbon sinks and their dependence on rainfall regime.

Why is the predicted carbon sink amplified so much at intermediate-to-low annual rainfall and high storm frequency? Amplification across rainfall regimes occurs because increased leaf-level productivity makes more leaf layers worthwhile (they produce more carbon than they cost). Competitive plants then increase allocation to leaves, which further increases plant NPP (Fig. 5A). With greater NPP, allocation to wood increases and thus carbon residence time increases (Fig. 5B). In addition, at intermediate-to-low annual rainfall, there are big changes in the fraction of NPP gained while plants are not water limited (q ; Fig. 6). We know from previous work (22) and confirm in *SI Appendix 4*, Fig. S4.2 that competitive overinvestment in fine roots consumes a large fraction of productivity in low- q (often water limited) environments, where large increases in q are possible. Thus, the large amplification of the CO₂ fertilization is made possible by the large competitive overinvestments in fine roots at ambient CO₂, which are shifted in the most competitive strategy under elevated CO₂ toward productive and long-lived tissues.

This qualitative pattern of shifting from fine roots to leaves and wood with greater water availability is consistent with models of optimal tree allocation patterns in isolation (without the influence of competition). However, not all of parameter space follows this tradeoff. In fact, certain changes in rainfall regime lead to increased investment in fine roots with no change in absolute allocation to leaves or wood. This pattern is a signature of competitive overinvestment: investment that maximizes a strategy's competitive ability but that decreases its own growth rate when that strategy is in monoculture (22) (*SI Appendix 4*). Such competitive overinvestment is a common feature of game theoretic models of belowground competition by plants (19, 20, 22, 32–35), and evidence of overinvestment has been found in experiments (19, 24, 36).

With a model of simplified rainfall, Farrior et al. (22) concluded that enhanced water-use efficiency caused by CO₂ fertilization during water-limited periods would cause increased investment in fine roots at the expense of wood, which would down-regulate the carbon sink. The rainfall model in Farrior et al. (22) was too simple to determine whether this effect is larger or smaller than the opposite predicted (decreased fine root allocation and an amplified sink) because elevated CO₂ increases the length of the period of water saturation (q). By modeling soil moisture as a continuous variable dependent on rainfall regime and with feedbacks from plant strategies, we find that the enhanced water use efficiency during periods of water limitation is overwhelmed by the more numerically important decrease in time trees spend in water limitation, which shifts allocation away from fine roots and toward wood (Fig. 6A).

Despite the differences in the absolute and relative size of carbon sinks across rainfall regimes, our model predicts that, with no change in rainfall regime, under elevated CO₂, all forests will provide substantial carbon sinks. The predictions do not provide an explanation for the idiosyncratic growth responses to elevated CO₂ in experimental (8) and observational (9) studies of forests. As concluded in Penuelas et al. (9), this is an indication that there are likely other significant environmental changes occurring at the same time. Changes in rainfall regimes themselves, nitrogen limitation, phosphorous limitation, and biophysical feedbacks are also likely important.

However, our model predictions can explain the complex responses of controlled field experiments to temporal manipulation of rainfall. Responses of aboveground net primary productivity (ANPP) to experimental repackaging of ambient rainfall into fewer, larger rainfall events depend on site productivity (37). At a less productive experimental site, ANPP increased in response to such an experimental repackaging (38), whereas at a more productive site, ANPP decreased in response to the manipulation (39). These contrasting responses align with our model predictions for allocation to leaves with decreasing λ at low and high total annual rainfall, respectively. Although these experiments are on nonwoody species, we previously adapted the structure of this model to grassland species and saw that qualitative predictions for absolute allocation to leaves and fine roots per-unit area do not differ between grassland and forest models (24).

With this paper, we generate a baseline understanding of what can be expected from changing rainfall regimes and increasing CO₂ in isolation from other global change factors. We are now working to include these mechanisms and feedbacks into models that include nitrogen limitation and biophysical feedbacks to predict the importance of these competitive allocation strategies for forests globally. With an understanding of the range of complexity that occurs in response to water limited photosynthesis, we are better positioned to understand the roles of other global change factors, including drought mortality.

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