Review The Impacts of Droughts in Tropical Forests

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Tropical forests exchange more carbon dioxide (CO₂) with the atmosphere than any other vegetation type and, thus, form a crucial component of the global carbon cycle. However, the impacts of anthropogenic climate change on drought occurrence and intensity could weaken the tropical forest carbon sink, with resulting feedback to future climates. We urgently need a better understanding of the mechanisms and processes involved to predict future responses of tropical forest carbon sequestration to climate change. Recent progress has been made in the study of drought responses at the molecular, cellular, organ, individual, species, community, and landscape levels. Although understanding of the mechanisms is incomplete, the models used to predict drought impacts could be significantly improved by incorporating existing knowledge.

Droughts in Tropical Forests

Tropical forests cover 10% of the surface of the Earth, but account for 25% of the terrestrial carbon pool and one-third of **net primary production (NPP**; see Glossary); thus, they form a crucial component of the global carbon cycle [1,2]. There has been widespread concern that climate change impacts, particularly an increase in the frequency, duration, and/or intensity of droughts, could weaken the current tropical forest **carbon sink**, with resulting feedback to future climates [3,4]. In 2010, a drought in Amazonia turned the forest from a net sink to a net source [3]. Moreover, tropical forests support around half of all terrestrial plant and animal species, including 96% of tree species [5], with the highest diversities in areas with the most reliable rainfall [6]; thus, droughts could also threaten biodiversity.

Most tropical forests experience annual dry periods, but this review deals only with droughts, defined as periods of 'abnormally dry weather long enough to cause a serious hydrological imbalance' [7]. Tropical droughts are often associated with multi-year climatic cycles and, therefore, interannual variation makes long-term trends hard to detect [8]. However, many model forecasts suggest that drought frequency and intensity in some tropical forest areas will increase over the remainder of this century [4,9]. The uncertainty partly reflects the varied ways in which droughts are defined, including indices that identify precipitation and runoff deficits, as well as those that represent the balance between precipitation and potential evapotranspiration (PET) [10]. The last of these is most relevant to ecological impacts and it is these indices that show the most consistent increase in the risk of extreme droughts in the tropics in model projections, because of the impact of robust predictions for warming on PET [1,11]. Even if droughts remain the same in terms of rainfall, increased temperature will make them more stressful for plants. Moreover, forest fragmentation dramatically increases dry-season desiccation of forest canopies [12] and deforestation leads to hotter and drier regional climates, because reduced evapotranspiration outweighs the cooling effect of the increase in **albedo** [13].

Trends

Forecasts from climate models suggest an increased risk of droughts in tropical forests over the next few decades, potentially threatening the large existing carbon sink.

Natural droughts and rainfall exclusion experiments result in decreased tree growth and increased mortality, with large trees most affected in both cases.

Mechanisms at the tree level are still incompletely understood. Hydraulic failure seems to be robustly associated with tree death, but other failure modes, including carbon starvation and phoem failure, may also be significant.

The drought tolerance of economic trees has been increased by experiment transfers of genes from model plants, suggesting that at least some components of the molecular mechanisms are universal. Some elements of drought responses at the cellular and molecular level have been identified in model plants, but we are still a long way from a full mechanistic understanding.

Drought responses at the community level and above include changes in species composition and, where humans are present, interactions between droughts, forest fragmentation, and fire.

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Domination of tropical forests by large, long-lived trees means that experiments are difficult and observations must extend over multiple decades. Therefore, predictions for the future rely on

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models [14,15]. Drought responses are already incorporated into the vegetation component of the **earth system models** used to predict climate change, but these are not based on the latest information, differ widely in their predictions, and do not match observations from experimental droughts [4,15–17]. We urgently need a better understanding of the mechanisms and processes involved in drought-associated mortality and growth reductions to improve the models and predict future responses of tropical forest carbon sequestration to climate change.

Observed Impacts of Droughts

Mortality of tropical trees has been widely observed in both natural droughts [18,19] and **throughfall** exclusion experiments (Box 1) [20]. Some mortality lags one or more years after a drought [21–23]. Vulnerability varies among species, sizes, ages, growth rates, and locations, with tree vigor the best predictor of individual mortality [24]. At most sites, large, long-lived trees are at the greatest risk [21,25]. These contribute disproportionately to both biomass and productivity in tropical forests [26,27] and, therefore, this mortality has a large impact on carbon emissions and storage. They also have keystone ecological roles, providing substrates for epiphytes, cavities for hole-nesting species, and favorable microclimates for understorey plants [25]. Vulnerability appears to be greatest for trees in aseasonal rainforests, where dry periods occur only at multiannual intervals [21,22], and least in forests that experience severe annual water stress [28]. Within forests, trees from wetter microhabitats are more vulnerable [22], while shade-tolerant species, with a more conservative resource-use strategy, are less so [29]. When a drought is not severe or prolonged enough to cause mortality, small branches and leaves may be shed in the upper canopy [30] and satellite microwave observations suggest that canopy damage persists for several years [31,32].

Droughts also cause declines in diameter growth rates in tropical forests, with large trees again most affected [19,25]. It cannot be determined from diameter measurements alone whether this reflects declines in photosynthesis and, thus, **gross primary production** (**GPP**), or changes in carbon allocation within trees, but data from both atmospheric measurements and permanent forest plots indicate large declines in CO_2 uptake by tropical forests in drought years [3,23]. During the Amazonian drought of 2010, photosynthesis and, thus, GPP were reduced, but trees maintained total NPP [23]. The authors speculated that trees used carbohydrate reserves to maintain constant growth and respiration during the initial stages of the drought, and subsequently maintained NPP by reducing autotropic respiration unrelated to growth [23]. The decrease in respiration continued after the drought had ended, potentially allowing replenishment of carbohydrate stores.

Box 1. Throughfall Exclusion Experiments

Throughfall exclusion experiments (TFE) allow ecologists to simulate the impact of reduced rainfall on individual plants, community dynamics, and carbon budgets [20,86]. Typically, 30–70% of **throughfall** is diverted with plastic sheets and gutters, with leaf litter that falls on the sheets transferred to the soil below to maintain nutrient cycling. These experiments differ from natural droughts in that they dry the soil, but do not dry the air. Moreover, not only is the vapor pressure deficit (VPD) increased in natural droughts, but solar radiation usually also increases as a result of reduced cloud cover. By contrast, TFEs allow droughts to be created wherever and whenever convenient, and also allow the creation of more extreme conditions than currently occur naturally. There have so far been eight TFE studies in natural tropical forests, but only three were on large plots (1600–10 000 m²), two in Amazonia lasting 6–13 years and one in Sulawesi lasting 2 years. The largest plot studies are expensive and, therefore, unreplicated, but smaller plots cannot be used for large trees because of the horizontal extent of their roots systems.

The impacts of TFEs on tropical forests are generally similar to those of natural droughts, but develop more slowly [20,86]. Tree mortality is surprisingly resistant to 50% rainfall exclusion for up to 2 years, but then rises rapidly after a threshold is reached at the point where soil moisture falls below 50% of that which is extractable by the vegetation [86]. It would be interesting to know whether a similar threshold applies during natural droughts or if the additional stress from increased VPD and solar radiation kills trees before this value is reached. The longest-running experiment (more than 12 years) found further evidence of resilience in the surviving trees, with photosynthetic capacity maintained, despite an increase in leaf respiration, which suggests increased repair and support costs [20].

Glossary

Aquaporins: cell membrane proteins that act as water channels. Albedo: the proportion of solar radiation reflected by a surface. Carbon sink: a natural system that removes more CO₂ from the atmosphere than it releases and, thus, slows anthropogenic climate change.

Earth system models: models used to predict future climates that couple the physical, chemical, and biological aspects of the earth system. Embolisms: air bubbles in xylem

vessels that lead to blockage of water conduction.

Gross primary production (GPP): the rate of fixation of carbon by photosynthesis.

Hydraulic segmentation: the hypothesis that hydraulic conductance in shorter-lived, expendable organs, such as leaves and fine roots, is decoupled from that in longer-lived, more expensive organs, such as stems, with the vulnerability of leaves and fine roots acting as a safety valve for the stems.

Late-embryogenesis abundant

(LEA) proteins: small proteins that accumulate in response to water deficits and protect other proteins and membranes from desiccation or osmotic stress.

Net primary production (NPP):

GPP minus plant respiration (i.e., the net carbon gain by the plant community).

Throughfall: rainfall that is not intercepted by the forest canopy.

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In the longer term, there is evidence that an increased frequency of severe droughts and/or a long-term drying trend has led to increases in drought-tolerant dry forest species and declines in drought-sensitive wet forest tree species in West Africa [33] and Central America [34]. An increase in liana abundance in Neotropical forests has also been tentatively attributed to greater intensity of seasonal droughts [35]. However, in drier areas, any gradual changes in species composition are being overwhelmed by interactions among droughts, forest fragmentation, and fires spreading from cleared areas, leading to rapid forest degradation [4,28,36,37]. Trees in the drier, more-open forest types survive low-intensity surface fires that kill trees in wetter forests (Figure 1), but can be killed when fuel loads and, thus, fire intensities are increased by disturbance [36]. Droughts and fires have additive effects on mortality, with fires killing mostly the smaller subcanopy trees that are more tolerant of droughts [38]; thus, fire greatly increase carbon emissions in drought years [1,3]. In the 2010 drought year, fire emissions in Amazonia accounted for more of the change in carbon balance than reduced growth [3]. By contrast, aerosols from fires may increase forest productivity by increasing diffuse radiation, offsetting some of the drought-related decline [39].

Mechanisms at the Tree Level

The greater vulnerability of the largest trees suggests that the fundamental problem is the need to transport water from drying soil to the exposed leaves, which may be 50 m or more above (Figure 2). Roots deep enough to access groundwater allow trees to avoid drought altogether or delay its impact [40]. Rainforest trees concentrate their roots in the upper soil layers to maximize nutrient uptake, but deeper water is also used and can maintain high leaf water potentials during dry periods [41]. Indeed, maximum root depths appear to have been considerably



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Figure 1. Fire in Dry Tropical Forest in Northern Thailand. Although lightning-started fires can occur naturally during droughts, most fires in tropical forests today are lit by humans, either deliberately, or spread accidentally into the forest from adjacent cultivated areas. Trees in the drier, more-open forest types survive low-intensity surface fires, such as this one, which would kill trees in wetter forests, where fires do not occur naturally. Reproduced from Wikimedia Commons.

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Figure 2. Vertical Profile of a Tropical Forest during a Drought. The largest trees are most vulnerable to the direct impacts of droughts, including reduced growth and mortality, because of their exposed canopies and tall trunks, while understorey trees are usually less vulnerable. However, small, thin-barked trees are more vulnerable to ground fires; thus, the impacts of droughts and fires are additive.

underestimated, and increase with dry-season length [42]. Subsurface water storage is sufficient to maintain canopy photosynthesis during the dry season above an annual rainfall of *ca*. 2000 mm [43], but the extent of carry-over between years is unknown [44]. Water stored retrievably in stems, roots, and leaves can also buffer fluctuations in water supply on a daily to seasonal basis [45,46], but it is not clear how useful this is in abnormally prolonged dry periods.

On the demand side, deciduousness is a frequent adaptation to seasonal water stress in tropical trees, and an increase in leaf shedding is a common response to drought [38,44,47,48]. Drought deciduousness is more common in emergent and canopy trees than in the subcanopy and understorey, highlighting the biophysical challenges of maintaining a water supply to the canopy during droughts [25]. Dropped leaves must be replaced when the drought ends, incurring a construction cost and delaying recovery of function, while evergreen trees can adjust to droughts by closing stomata and, thus, reducing water loss. However, stomatal closure also reduces photosynthesis, potentially starving the tree if carbohydrate reserves are used up. It also reduces cooling of leaves and stems, by evaporation and mass transfer, respectively, which may lead to lethal high temperatures in hot, dry weather [49]. Moreover, even drought-adapted species continue to lose water after stomatal closure, although at a lower rate [46,50].

By contrast, if the stomata remain open, more negative xylem potentials provide greater force to drive water transport from the soil, but increase the risk of **embolism**, which reduces water transport by reducing connectivity. Tall trees are at greater risk because both gravity and the path-length resistance increase tension in the water column, while more exposed crowns increase evaporative demand [25] (Figure 2). Accumulating solutes that lower water potentials can maintain both water uptake and cell turgor [51,52], but it is unclear how this benefits the

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growth and survival of trees, since leaf function during severe droughts is likely to be limited by access to available soil moisture and the maintenance of hydraulic conductivity [51]. Moreover, in severe droughts, trees may use **hydraulic segmentation** to maintain the function of expensive stems and branches, while sacrificing cheaper and more vulnerable fine roots and leaves [53]. If all else fails, trees can survive severe droughts by sprouting new shoots after the death of the trunk or major branches [54].

Actual mechanisms behind drought-related tree mortality are still incompletely understood, making accurate modeling impossible (Figure 3). Most evidence points to hydraulic failure as the proximal culprit [20,54], although carbon starvation has also been suggested [55]. Hydraulic vulnerability is inherently difficult to measure and recent studies with new observational techniques cast doubt on earlier conclusions regarding the frequency and reversibility of xylem embolisms [56]. Current evidence suggests that embolisms occur only under extreme drought stress and that refilling of conduits in stems is possible only in some species and only after the drought is over [56–58]. Recovery from sublethal drought damage normally seems to involve the production of new xylem elements [56]. In angiosperms, irreversible drought damage occurs when around 88% of vessels in the stems are embolized [54], and all trees appear to operate



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Figure 3. Suggested Mechanisms Linking Droughts with Reduced Growth and Increased Tree Mortality in Tropical Forests. Solid arrows are supported by more evidence than open arrows. Rainfall reductions and/or temperature increases reduce soil moisture and increase the atmospheric vapor pressure deficit. Rainfall reductions are often also associated with cloudless skies that increase solar radiation intensity. Together, these cause plant water deficits, which can further reduce soil moisture by increasing water uptake. Plants experience more negative xylem water potentials and respond by leaf fall and/or stomatal closure. After this point, the mechanisms become less clear. Hydraulic failure as a result of xylem embolisms appears to the major proximate cause of mortality, but the roles of carbon starvation and other possible failure modes are unclear. Where humans are present in the surrounding landscape, fires also contribute to tree mortality, while a role for pests and pathogens is likely but not yet supported by direct evidence from the tropics.



with a similarly narrow safety margin between the lowest water potentials experienced under field conditions and the level leading to hydraulic failure [53].

Carbon starvation, as a result of trees trying to protect hydraulic function, could be an alternative or additional trigger for mortality during droughts. The strongest evidence comes from experiments with seedlings [55], but the role of nonstructural carbohydrates (NSC) in adult trees is unclear, because of their multiple stores and functions. How much is too little? NSC appears to have an important role in plants under stress, both as a reservoir for growth and respiration when stomata are closed, and in maintaining turgor and phloem transport [59]. However, photosynthetic capacity was maintained and NSC stores not depleted after 13 years of experimental drought in the Brazilian Amazon [20]. Other suggested mortality triggers include phloem failure by turgor collapse or viscosity build-up [60], although the problems of field observations on phloem have so far precluded any test of this.

One key issue is the direct impact of drought on tree growth [61–63]. Plant growth needs both enough turgor pressure to expand the new cells and enough carbon to supply the solutes, structural materials, and energy needed. Water stress inhibits growth long before photosynthesis, probably through turgor loss, suggesting that growth controls total plant photosynthesis more often than the other way round [64]. A direct hydraulic limitation on growth is also consistent with the strong correlation between water availability and forest canopy height at the global scale [11]. If this is correct, droughts impact trees by reducing growth (the carbon sink) and the resulting accumulation of unused assimilates in leaves then reduces photosynthesis. By contrast, current vegetation models are source driven, with drought influencing growth via stomatal closure and reduced photosynthesis [62]. Evolution tends to match sources and sinks; thus, source-driven models may give the right results for wrong reasons, but robust predictions for novel future conditions require that the mechanistic basis of models is correct.

Whatever the ultimate causes of reduced growth and increased mortality, observations and experiments show a diversity of drought responses within a community, and physiological measurements suggest this reflects an equal diversity of drought avoidance and tolerance strategies among co-occurring species. Estimates of leaf water potential at wilting (turgor loss point; a key measure of leaf tolerance to drought stress) ranged from -1.4 to -3.2 MPa in Amazonian trees, suggesting a potential for very different responses to drought within a single community [65]. It is often assumed that there is a trade-off between the ability of the xylem to resist the formation and spread of embolisms and its ability to efficiently transport water: the safety-efficiency trade-off. However, although it seems to be impossible for plants to achieve both high safety and high efficiency, the relevant traits otherwise appear to vary more or less independently, suggesting that this trade-off is not a major contributor to the diversity of drought responses [50]. Leaf and stem traits have received most attention in comparative studies, but rooting depth, leaf phenology, stem water storage, and other drought-related traits also vary widely between species and may have similar impacts on vulnerability [28].

Drought-related trait values are not necessarily fixed within an individual. Although acclimation to drought has been little studied in trees, it is likely to be particularly important because of their long lifespans. Also, droughts develop slowly in comparison with other extreme events, giving time for physiological adjustments. There is evidence for widespread but moderate plasticity in the leaf water potential at wilting, driven by osmotic adjustment [52], and trees could also reduce water needs during droughts by increasing leaf photosynthetic capacity [66]. During multiyear droughts, whole-tree structural changes are possible, including changes in leaf area and root growth [20], and the production of new xylem that is less vulnerable to drought conditions [67].



Recent successes with increasing drought tolerance in commercial tree species by transferring genes from model plants [68,69] suggest that a better understanding of drought responses at the cellular and molecular level might help to predict responses at the tree level. However, although some components of the drought sensing and signaling networks have been identified in model trees, we are still a long way from a full mechanistic understanding [70]. The accumulation of **late-embryogenesis-abundant (LEA)** proteins under water deficits may be involved in protein and membrane stabilization, while **aquaporins** and other classes of water-transport protein are involved in maintaining water balance [70]. Epigenetic changes may also contribute to the ability of plants, particularly long-lived ones, to acclimate to changing environments.

Indirect impacts of droughts favor different tree traits. Mortality from drought-associated fires is best predicted by tree size and bark thickness, with smaller, thin-barked trees most vulnerable [71]. Outside the tropics, there is evidence that pest and/or pathogen attacks increase tree mortality during droughts [72]. This has not been documented in tropical forests, but evidence that trees prioritize growth during droughts, when photosynthesis is reduced, and, therefore, decrease investment in tissue maintenance and defence, suggests that increased vulnerability to pests and pathogens partly explains the increased postdrought mortality [23].

Predicting Future Responses at the Community and Landscape Level

Individual trees die, but this reduces the forest carbon sink only if there is a net loss of carbon at the community and landscape level. Predicting responses of multispecies communities is difficult, since forests are not simply the sum of the component trees and theoretically optimal drought-response strategies at the individual level may not work when trees are competing for the same limited pool of soil moisture [66]. Moreover, at larger spatial scales, both tree diversity and microsite variability are expected to buffer the community-level impacts of droughts to some extent [73]. In general, it appears that short-term droughts cause selective tree mortality, while a long-term drying trend leads to changes in species composition, favoring drought-tolerant species [33,74]. The nature of the response will depend on drought severity in comparison with the long-term conditions that determined the current species composition.

Initially, changes in species composition will involve selection within the local species pool, with drought-tolerant species increasing and drought-sensitive ones declining, but in the longer term, plant migration will increase the size of the pool from which species are selected [75]. Some nontropical tree species also show substantial within-species variation in drought tolerance [68], which could allow adaptation at the population level without migration. Long-term changes in the species and functional composition of the forest could either mitigate or exacerbate impacts on the carbon cycle, depending on the effect on carbon sequestration [33]. In landscapes with humans, interactions between drought and fires, exacerbated by logging and other disturbances, will also lead to changes in species composition, favoring fire-tolerant tree species and/or grass invasion in areas with a long dry season [36,76]. This could lead to the rapid conversion of forest to savanna in areas where the climate is suitable for either [77].

Anthropogenic increases in atmospheric CO_2 concentrations could have a substantial direct effect on drought impacts in tropical forests, but until results are available from free-air CO_2 enrichment (FACE) experiments [78], the magnitude of this effect will continue to be controversial. Theory, tree-ring data, and chamber-based studies of tropical tree seedlings suggest that elevated CO_2 levels substantially increase water-use efficiency, thus reducing water stress [2,4,15]. Modeling studies suggest that this would significantly mitigates the negative impacts of increases in drought frequency and intensity [15], but these predictions cannot yet be tested. Atmospheric CO_2 concentrations are already high compared with when most existing tropical forest species evolved and so our 'baseline' may already incorporate substantial impacts.

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The increasing deposition of nitrogen and phosphorus from agriculture, industry, biomass burning, and long-distance dust transport may also influence the drought tolerance of tropical forest trees [15]. Fertilization experiments have shown mixed results, but suggest that increased nutrient availability leads to higher hydraulic conductivity, increased resistance to cavitation, and decreased stomatal conductance, but more negative water potentials as a result of increased leaf area [79]. These observations need to be tested for generality and the mechanisms are currently unclear.

Minimizing the Impacts of Droughts

The most urgent need is for early detection of developing droughts, followed by continuous monitoring of their impacts as they develop. A variety of passive and active satellite sensors, including ones that measure optical reflectance, microwave backscatter, thermal signals, gravitational fields, near-surface relative humidity, and atmospheric CO_2 concentrations, can be used to detect droughts and monitor impacts [80,81]. The challenge is to integrate these sources of information in near real-time (hours) and to extrapolate them back (decades) from progressively sparser data for calibration against ground observations. Once a drought has started, the priority is preventing the spread of land-management fires into adjacent forests [1,36,37]. Although most attempts to do this have been unsuccessful, enough has been learned to suggest that a combination of satellite detection with on-the-ground enforcement and firefighting, plus adequate penalties for starting fires during droughts, should work [82].

On a longer timescale, better management of logging could reduce dry fuel loads and fire risk, while ending deforestation or, where this is impossible, retaining large, contiguous forest blocks rather than scattered fragments, would help reduce both fires and edge-related drying of the forest. All major tropical forest countries made commitments to reducing deforestation for the 2015 United Nations Climate Change Conference (COP21)ⁱ, so this is not an unattainable goal.

Improving Predictions

Current vegetation models deal poorly with extreme events and fail to reproduce the biomass loss from drought-induced tree mortality in these forests, making predictions of future climate change impacts on carbon cycling unreliable [15]. Although our understanding of the mechanisms is incomplete, the models could be significantly improved by incorporating current knowledge. Future models will need to integrate processes across multiple scales, from the molecular to global, and to be validated against observations and experiments [80]. Very large trees contribute disproportionately to carbon storage and fluxes in tropical forests [26,27] and this function is concentrated in remarkably few species (1.5% of the total in the Amazon and Central Africa), suggesting that a research focus on these could simplify the next generation of models. However, less common tree species cannot be ignored, since these are more likely to have unusual combinations of functional traits and, thus, provide a degree of insurance against environmental changes in the longer term [83].

Concluding Remarks

If protected from clearance, logging, and fires, uptake by tropical forests could offset a significant proportion of the emissions from fossil fuels during the transition to a low-carbon future [84,85]. However, this carbon pool is vulnerable to droughts and drought-associated fires, as shown by the large interannual variability in the carbon balance of the Amazon region in recent decades [3]. Current evidence suggests that tree mortality is triggered by hydraulic failure, which is consistent with measurements showing that tropical forest trees operate within very narrow hydraulic safety margins. Failure ultimately results from embolism formation in the xylem and, thus, loss of conductance, but this in turn reflects a whole-tree imbalance between uptake and loss of water. The challenge now is to understand the mechanistic links between drought stress and hydraulic

Outstanding Questions

What fraction of NSC in trees can be mobilized under stress and what, if any, is its role in drought sensitivity?

How much plasticity and heritable genetic variation is there for droughtrelated traits in tropical forests trees?

How can we overcome the challenges of monitoring root functioning during droughts under field conditions?

How widely are the molecular responses to drought shared among flowering plants, from model herbs to tropical forest trees?

Will rising atmospheric CO_2 concentrations reduce the impacts of future droughts on tropical forests?

How will increasing inputs of nutrients, particularly nitrogen, affect the vulnerability of tropical forest trees to droughts?

Can real-time satellite monitoring help reduce the current synergy between droughts, forest fragmentation, and fire?

How can we manage tropical forests to enhance their resilience to drought?

failure, and then to incorporate this understanding into improved models. These models can then be combined with remote-sensing data to detect, monitor, and assess developing droughts, and to predict the consequences of future climate change in tropical forest regions. These predictions, in turn, can be used to identify and prioritize local actions to reduce exacerbating factors, including logging, forest fragmentation, and poor fire management.

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ⁱ http://unfccc.int/focus/indc_portal/items/8766.php

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