

Review

Are Mixed Tropical Tree Plantations More Resistant to Drought than Monocultures?

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Academic Editor: Steven Jansen

Received: 25 March 2015 / Accepted: 3 June 2015 / Published: 5 June 2015

Abstract: Tropical tree plantations usually consist of a single exotic fast growing species, but recent research describes positive effects on ecosystem functions from mixed tropical tree plantations. In this review, we present the current knowledge of drought resistance of tropical mixed species plantations and summarize preliminary evidence from a tree biodiversity experiment in Panama. Converting mono-specific stands into mixed ones may improve stand stability and might reduce increasing abiotic and biotic disturbances due to climate change. However, little is known about the extent to which tropical tree species or tropical tree communities can resist increasing disturbances in the short term, e.g., water limitations due to increasing dry season intensity or length, or about their resilience after such disturbances and their capacity to adapt to changing conditions in the long term. Studies relating drought resistance and resilience to community diversity are missing. Further, we highlight the urgent need for a multifactorial manipulative throughfall reduction experiment in tropical environments. The outcome of such studies would greatly assist the forestry sector in tropical regions to maintain highly productive and ecologically sound forest plantations in a changing climate.

Keywords: drought stress; Neotropics; native tree species; biodiversity; plantation forestry

1. Tropical Plantation Forestry and Biodiversity

Tropical forests are a key component of the Earth system covering about 19.5 million km² of the terrestrial surface and containing 34% of the carbon stored in vegetation worldwide [1]. Tropical forests thus provide many ecological benefits, including provision of renewable raw materials and energy, maintenance of biodiversity, protection of soil and water resources, and regulation of Earth's climate system. Nevertheless, tropical forests are seriously threatened by deforestation due to the expansion of agriculture, pasture and urban lands, as well as increasing degradation by fire, air pollution and other disturbances due to climate change. Currently, about 50% of the original forest area has been lost in the tropics since the early 1980s [2,3]. Although deforestation rates have slowed globally, forest degradation through practices like selective logging and escaped fire continues to erode the remaining mature tropical forest area [4].

A major challenge of the forestry sector is to re-establish closed forest cover in deforested and degraded areas to mitigate effects associated with deforestation such as loss of biodiversity, soil degradation, erosion, flooding and salinization. The establishment of managed tree plantations on suitable tropical lands currently classified as degraded could satisfy the current and projected growing demand for industrial roundwood, while limiting the harvesting pressure on the remaining natural forests [5]. Furthermore, the overall global carbon sequestration could be substantially enhanced by reforestation in the tropics [6]. So far, most of the reforestation responsible for a gain in forested area in the tropics has been conducted in form of industrial monocultures involving a limited number of species. Most of these species originate from few genera (*i.e.*, *Pinus*, *Eucalyptus*, *Tectona*, *Gmelina* and *Acacia*) and are exotic to most of the areas where they are cultivated [7]. Such traditional mono-specific plantations have supplied a range of goods and services by providing a forest-like habitat connecting fragmented forests, filtration of waste water and temporally sequestering high amounts of carbon [5], but there is rising concern about their environmental sustainability as they make only minor contributions to the restoration of ecological functions and biodiversity compared to mixed-species plantations containing native tree species [8].

In the last two decades, new reforestation approaches in the tropics have emphasized the establishment of highly functional plantation forests with native species in mixed stands [8,9]. Recent studies suggest positive mixture effects on many ecosystem functions such as lower tree mortality, enhanced biomass productivity coupled with higher resource-use efficiency (including nutrients, water and light) by trees, higher decomposition rates and better nutrient retention [10–16]. In general, it is assumed that these responses of ecosystem processes are due to changes in species or functional-group diversity that might result from a combination of two different mechanisms [17]. The first mechanism is referred to as complementarity effect, encompassing niche differentiation or facilitation between species, leading to an improved resource partitioning and to an overall better performance of a tree community in relation to the performance of individual species growing in monoculture [17]. The second mechanism is referred to as sampling effect, where selective processes favor or penalize the performance of a single species or a group of species with specific traits and lead to the dominance of a species [17]. The combination of both mechanisms defines the overall net biodiversity effect or, in the case of productivity, over-/under-yielding [12].

The first studies in tropical forest systems conducted in native tree plantations in Costa Rica showed promising, although inconclusive, results. Mixed species plantations were almost as productive or equally productive as mono-specific plantations and in some cases even more productive [9,18–20]. A more recent study from a temperate area in Australia showed that individual trees in mixed stands reached higher tree heights, diameters, volume and aboveground biomass a few years after planting [21]. Results from studies in Panama suggest that higher productivity and thus carbon storage depended partly on the assemblage of certain species facilitating each other's performance, but complementarity of species generally increased with species numbers [13]. There are many more examples of such species facilitation leading to higher biomass productivity; they are usually based on the combination of certain species traits such as the combination of isohydric and anisohydric species [22]. Another example from Puerto Rico pointed out that mixed *Casuaria equisetifolia/Leucaena leucocephala* stands were more productive than single species stands [23]. This was mostly due to increased productivity of the nitrogen-fixing species in the mixed stands. The negative side of this higher productivity might be that it could be accompanied with higher water consumption making those plantations more susceptible to drought if water resources get depleted earlier or more extensively [14,22,24,25]. Nevertheless, in a study from Panama, trees planted in mixtures were able to maintain higher transpiration rates during the dry season [26] due to complementary soil water use between different species [27]. Trees growing in mixtures thus had a longer growing season and a higher biomass accumulation of those trees compared to trees growing in mono-specific stands. Further explanations for the observed over-yielding of mixed-species plots in the plantation in Panama were belowground niche differentiation [27,28] and enhanced light interception due to aboveground niche partitioning [29]. Overall, we can conclude that niche differentiation and complementarity due to functional diversity play a key role in the resilience of tropical trees to changing climatic conditions. However, most of the research in biodiversity experiments focused on ecological functioning in relation to overall productivity, and ecophysiological studies looking at the hydrological cycle are still scarce [22] although the topic has been receiving more attention over the last two to three years.

2. Climate Change Effects on Tropical Tree Plantations

Aggravating the already unfavorable social, economic, political and environmental circumstances of implementing reforestation programs in many tropical areas, the predicted climate changes in tropical regions will additionally complicate and compromise the success of future reforestation and tropical plantation forestry efforts. The projections from atmospheric models indicating reduced precipitation across large portions of the tropics and an increase in rainfall seasonality [30] may hamper their success. Changes in the spatial and temporal distribution of precipitation, especially a decrease in precipitation, and hence a long-term reduction in the amount of plant-available water will reduce aboveground biomass, tree productivity, and overall ecosystem photosynthesis and net carbon uptake in forests [31]. In the worst case, reduced water availability might make it impossible or too risky to cultivate certain tree species in tree plantations. Studies from natural tropical forests suggest that changes in precipitation patterns can cause increasing tree mortality, and over the long term, drought will result in changes in species composition and have positive ecosystem feedback [32–34]. Substituting existing species by other, more drought tolerant ones would be one option to adapt plantations

to a changing climate. New tree plantations could be established or already existing plantations could be replanted in the next rotation period with other species, preferably with native species, which may be better able to thrive with the changing environmental conditions [35]. Unfortunately, little information is known about which species would be suitable for the newly emerging climate scenario predictions. The suitability of a given species will largely depend on its resistance to a certain level of disturbance, or its resilience in recovering to e.g., the initial biomass levels following a disturbance [36]. Recent recommendations for innovative tree plantation designs, based on knowledge accumulated since the 19th century, suggest that besides the advantages in their productivity, diverse tree stands may be more resistant to disturbances [37]. Further, with the prospect of global climate change, converting mono-specific stands into mixed and diverse stands may increase stand stability and might reduce future carbon losses due to abiotic and biotic disturbances [38].

However, only little is known about the extent to which tropical tree species or tropical tree communities can resist increasing disturbances in the short term, e.g., water limitations due to increasing dry season intensity or length, or about their resilience after such disturbances and their capacity to adapt to changing conditions in the long term. Conclusions drawn from studies in one forest system may also not be transferred directly into another system as hydrological regimes are expected to depend largely on the forest structure [39]. Plantations, for example, differ from natural forests in their specific interception characteristics [40] and in their stand structure due to limited diameter range and homogenous planting designs [41]. To our knowledge, up to now, no manipulative and multifactorial study exists on the function of tropical tree species diversity in relation to water limitations and drought stress. However, results from grassland experiments point out that the positive relationship between plant diversity and drought resistance mainly depends on the pre-drought performance of a given species and not on diversity levels [42]. Nevertheless, the potential recovery (resilience) after drought was higher with increasing species diversity and independent from prior performance.

In this data synthesis, we present the current knowledge on different water-use strategies of tropical forest tree species and how those strategies affect the drought resistance of mixed tropical tree plantations. For this, we are summarizing evidence gained from a set of ecophysiological studies from a tree biodiversity experiment in Panama. In the end, we highlight that predictions and conclusions are limited in their explanatory power and that there is an urgent need for multifactorial manipulative throughfall reduction experiments in tropical environments. The outcomes of well-designed studies would help the forestry sector in tropical regions cope with a drastically changing climate and secure highly productive and more ecologically sound plantation forestry.

3. A Case Study from Panama

3.1. Seasonal Drought a Natural Phenomenon for Panama

The Republic of Panama is situated on the isthmus connecting the Northern and Southern American subcontinent. The country lies within the tropics mostly between the latitudes 7° and 10° north and the longitudes 77° and 83° west. The climate is thus characterized as a tropical moist climate with a distinct dry season. Most of the annual rainfall falls during the wet season, which is during an average year between May and December and lasts on average 131 days (Figure 1). The dry season starts in

mid-December and ends in April, although the beginning of the dry season may vary by three to four weeks and the end may vary by one or two weeks [43]. Especially the fast rewetting at the onset of the wet season in May can be very drastic as May is also on average the month with the highest rainfall. Despite the intra-annual changes in precipitation, Panama has additionally a steep rainfall gradient due to the continental divide with less than 1300 millimeters on the Pacific side and up to 4000 millimeters per year on the Caribbean side. Some typical forest tree species occur along the whole rainfall gradient and thus may exhibit a certain plasticity in drought resistance [44].

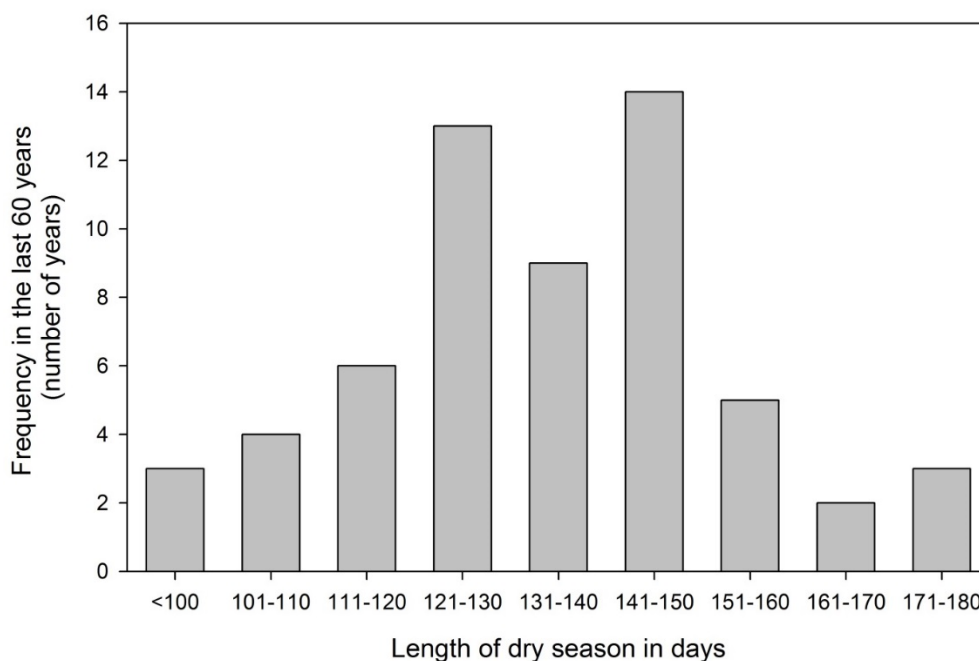


Figure 1. Frequency of dry season length in Panama since 1954. Average dry season length is 131 ± 19 days in an annual cycle (data from Paton [43]). Note: Dry seasons over 171 days in length are El Niño years in 1976, 1982 and 1998.

The potential natural vegetation in Panama is relatively diverse but the majority of the area was probably covered by a tropical moist lowland forest or a tropical moist transitional forest annually experiencing a distinct dry season [45]. The lowland forest in Panama is characterized by a wide range of tree species with differing leaf phenology and adaptations to deal with drought [46,47]. This ecosystem is one of the best studied tropical forests worldwide and has, with the research site at Barro Colorado Island (BCI), one of the oldest permanent forest inventory plots in the tropics. Consecutive and elevated tree mortality of mature trees after a prolonged natural drought has been studied and is well documented over two El Niño events in 1982 [48] and 1998 [49] (dry season length of the two El Niño years: 179 and 171 days, respectively [43]). Effects of drought on seedling mortality has been studied intensively along the above-mentioned rainfall gradient [44]. Seedling drought mortality may lead to a selective pressure to change forest composition rapidly and greater drought resistance in the future especially in a system with a fast species turnover in canopy trees of less than half a century [50]. The lowland forest in Panama with its large species pool consisting of dry season deciduous tree species and evergreen tree species has thus a relatively wide plasticity in coping with increasing drought intensity. Hence, this tree diversity and tree species composition play a very

important and crucial role on how the future forest will look like and how, for example, a widespread drought-induced tree die off would shape species range contraction [51]. However, natural forests are very complex and dynamic systems, and comparative studies of species gradients, the functionality of tree species and the role of biodiversity are therefore complicated to perform.

Tree biodiversity experiments have been shown to give more and better insights into the functionality of forest tree species [37]. Various tree biodiversity experiments have so far been established [39]; however, manipulative studies investigating the intensity of climatic change effects on tropical plant communities with varying plant diversity are still lacking. Further, ecophysiological studies on tree water use characteristics in relation to tree biodiversity are rare and results come mainly from temperate areas with no replicates of species stands in monoculture and/or replicates of the same species combination. This lack of ecophysiological studies in tree biodiversity experiments is probably due to the still relatively recent establishment of these tree biodiversity experiments and their limited tree size and canopy closure [22].

The Sardinilla Project in Panama, where the following summarized studies took place, is one of the oldest tree diversity experiments and part of a global network of tree diversity experiments in China, Malaysia, Finland, and Germany among others [37]. In Sardinilla, almost all components of biodiversity functioning have been previously studied, including intensive studies of tree water hydraulics and underlying processes [26,27,29,46]. Nevertheless, a manipulative precipitation experiment to evaluate the resistance, resilience and adaption capacity of mono-specific and multiple tree species stands to changing precipitation patterns has not been applied there yet and would, for example, provide a unique combination in the form of a throughfall reduction experiment. This would also give the opportunity to replicate scenarios or study multiple scenarios simultaneously, and possibly exclude or control the interference of co-varying factors. The expected behavior of monocultures and tree species mixtures under intensified drought scenarios can already be hypothesized by using the existing results on the tree hydraulics and is further discussed below.

3.2. The Experimental Site in Panama

The study site is located near the village of Sardinilla, Central Panama (9°19' N, 79°38' W), which is approximately 50 km north of Panama City. The elevation of the site is 70 m with a slightly undulating topography. Mean annual precipitation at nearby Buena Vista is 2350 mm, with only 25–50 mm of monthly rainfall during peak dry season (January–March), 120–130 mm of monthly rainfall during the two transition periods one in April and one December, and 250 mm of monthly rainfall during the rainy season (May to November) [46]. The mean annual temperature of the region is 26.2 °C. The soils are derived from Tertiary limestone and other sedimentary rocks resulting in a clayey Luvisol (pH 5.5; C 5%; N 0.4%) [52]. The original forest vegetation before clear cutting at the Sardinilla site was probably a tropical moist lowland forest, with similar species composition and forest structure to that on Barro Colorado National Monument [53], 40 km west of Sardinilla (9°09' N, 79°51' W). About the land use history of the site, it is known that the forest was clear-cut in 1952 and 1953 and small scale agriculture was established. A common practice in the area was to convert the agricultural fields after two years with crops (commonly used crops are corn, plantain and yucca) into pasture by seeding a high yielding C4 African grass, *Hyparrhenia rufa* [54].

In July 2001, the site was converted into an experimental tree plantation with the aim to investigate tree mixture effects (Sardinilla Project). On a total area of 9 ha, 24 different plots were established using altogether six tree species native to the natural tropical moist lowland forest (Table 1). The plantation was set up with plots of one, three and six tree species from three different ecological groups [55,56]. Two light demanding, early successional tree species (*Luehea seemannii* Triana & Planch and *Cordia alliodora* (Ruiz & Pavon) Oken), two light-intermediate tree species (*Anacardium excelsum* (Bert. & Balb. ex Kunth) Skeels and *Hura crepitans* L.) and two shade tolerant, late successional tree species (*Cedrela odorata* L. and *Tabebuia rosea* (Bertol.) DC.) were chosen for the establishment of the experimental plantation. The six tree species and three ecological groups were selected based on relative growth rates (RGR), measured on Barro Colorado Island (9.1% and 7.0%; 5.9% and 4.9%; 2.3% and 3.4%, respectively [55]). Under natural conditions on BCI, the tree species *Hura crepitans*, *Anacardium excelsum* and *Cedrela odorata* were classified as “brevi-deciduous”. *Cordia alliodora* and *Tabebuia rosea* were considered as “deciduous” and *Luehea seemannii* as “facultatively deciduous” [57]. Further, these species differ in their specific leaf area and intercept properties [58]. However, Meinzer *et al.* [57] also state that under the seasonally dry condition of the study region, leaf phenology seems to be a continuum with considerable overlap among categories. Interestingly, the classification into phenology groups was quite different for the different species compared to the observations from natural forests in the area [57]. Those differences might be due to methodological differences; e.g., the better access to the canopy for the observation of leaf cover in the tree plantation and the far higher number of replicates per species in the artificial system than in the highly diverse natural forest from Barro Colorado Island. The intense observation in the plantation further allows a more detailed classification of the species regarding to their leaf phenology. Despite this, the initially hypothesized differences in species functionality were proven manifold by various studies conducted at the site and were found to be true for a wide variety of ecosystem functions and processes [37]. For example, after a couple of years of growth, the initially hypothesized canopy stratification by trees with different growth rates became visible. Accordingly, the upper canopy was formed by the fast-growing light demanding species and the lower canopy by the late successional shade tolerant species [37]. Besides the ecological functioning of the tree species, *Anacardium excelsum* (wild cashew or espavé), *Cordia alliodora* (jennywood or bocote), *Cedrela odorata* (Spanish cedar or cedro) and *Tabebuia rosea* (roble) are valuable timber species with excellent wood properties. Many parts of *Hura crepitans* (sandbox tree, possumwood or jabillo) can be used for medical purposes and *Luehea seemannii* (this species was used by Erwin [59] for the estimation of the worldwide number of arthropod species) is commonly used as fire wood.

Table 1. Overview of the different types of diversity plots with the number of plots and explanation of species replication.

Mixture type	Number of plots	Replication of species
Monoculture	12	Each species replicated in two plots
3-species mixture	6	Three species, chosen randomly, for each successional group
6-species mixture	6	Adding three species, each from a different successional group, to the existing combination in a three species mixture

Each of the established plots ($n = 24$) has a size of 45 m by 45 m and tree saplings were planted with 3 m spacing between trees (225 trees per plot), which is the common planting design for industrial tree plantations in Central America [60]. Each of the plots is divided into four subplots 22.5 m by 22.5 m in size. Seeds were collected from forests within the Barro Colorado National Monument and germinated on-site at Sardinilla. Saplings of approximately 50 cm height were planted. The plantation is tended following standard forestry practices in Panama, the understory being cut three times a year. Survival of saplings was very high (>90%), however, *Cordia alliodora* did not establish in monoculture probably due to missing mycorrhiza in the bare pasture soil [60]. Therefore, this species was omitted in most of the investigations. Tree growth (tree height and diameter) was inventoried on an annual basis since 2001.

3.3. Results on Tree Water Hydraulics and Underlying Mechanisms of Tree Functionality

Between July 2007 and August 2008, a series of ecophysiological studies regarding the ecohydrology and the above- and below-ground niche separation and facilitation in the different monocultures and mixture plots were conducted (compare [26–29,46]). The ecohydrological studies included intensive assessment of annual tree transpiration rates in the different mixtures via sap flux measurements (for details see [26,46,61]) and the analysis of soil water uptake pattern with stable isotope (deuterium) measurements (for details see [27]). The effects of biodiversity on aboveground niche differentiations were modeled by combining the tight relationship between tree transpiration and seasonal changes in leaf phenology [29]. The results from those studies allow drawing some conclusions regarding the drought resistance of monocultures in comparison with mixed species plantations.

3.3.1. Different Traits in the Water Uptake Pattern of Species Lead to Diversity Effects

The results from Sardinilla suggest that the trees exploited a wide range of soil layers for water uptake. High annual rainfall seasonal changes in the depth of water uptake were observed. Those shifts support the idea that seasonal changes in water uptake are a common feature of tree species in moist tropical forests [27,57]. The five well established tree species in the plantation showed very distinct ways in which they acquainted soil water and could be classified in the three classes of shallow, intermediate and deep soil exploiters (Table 2) [27]. Those three classes explained, in addition, the three different types of phenology covered by the species [46]. The dry season deciduous species *Cedrela odorata* was also the species acquainting water only from very shallow soil layers. *Cedrela odorata* is hence a very good example for a typical drought avoiding species by leaf abscises as a strategy to minimize transpirational water loss during water limited periods [22]. *Luehea seemannii*,

Anacardium excelsum and *Hura crepitans* showed a distinct leaf senescence during the dry season and progressively lost their foliage to the end of the dry season [46]. These three species exploited medium deep soil layer, which probably were depleted at the end of the dry season and abscission was necessary to prevent cavitation. The third drought resistance strategy found at Sardinilla was the exploitation of deep soil layers by *Tabebuia rosea*. This species flushed even new leaves before the onset of the dry season and maintained fully foliated tree crowns until the beginning of the next wet season. Such behavior probably can be seen as a strategy to use the higher radiation availability for photosynthesis and take advantage of the lower leaf herbivore pressure during the dry season [46]. This theory supported the very pronounced seasonal shifts in the water uptake pattern in this species [27]. This species might play a critical role in the performance of the mixed species plots by hydraulic redistribution of soil water resources. The roots of *Tabebuia rosea* can extract water from deep moist soil layer and might release water into shallower drier soil, thereby facilitating other associated species in the mixed species plots by increasing water availability [62,63]. The facilitation might have led to the higher increment of basal area as plots containing *Tabebuia rosea* were the ones with the highest increment in basal area [56].

In addition to the evidence for interspecific differences in soil water uptake between trees growing in monocultures, there were significant differences in the water uptake when the tree species were assembled in mixtures [27]. This provided very strong evidence for complementary soil water uptake among co-occurring tree species in mixed tree stands. An important feature of the mixed species stands in regard to drought resistance is that differences in species traits such as the leaf phenology and water uptake pattern can reduce the competition for water resources during periods of water limitation [22,27]. Such complementarity in resource facilitation is often cited as one of the fundamental principles to explain the higher productivity of mixed stands compared with single species stands [64] and plays a key role in a possible higher drought resistance of mixed species plantations compared to monocultures.

Table 2. Overview of the classification of species following different behavior in the seasonal leaf phenology and soil water uptake pattern (after [27,46]).

Leaf phenology	Rooting depth	Water acquisition (soil depth)	Species
Dry season deciduous	shallow	0–30 cm	<i>Cedrela odorata</i>
Dry season leaf senescence	intermediate	30–60 cm	<i>Luehea seemannii</i> , <i>Anacardium excelsum</i> , <i>Hura crepitans</i>
Dry season green	deep	>60 cm	<i>Tabebuia rosea</i>

3.3.2. Mixed Species Stands Show Higher Dry Season Stand Transpiration Rates

The most striking result found in the Sardinilla experiment was, besides the commonly found convergence in tree water use and tree size of tropical trees [65], that stand transpiration increased linearly with tree species richness [26]. Tree diversity had positive effects on the community-level light capture resulting in enhanced tree growth [29], and mixed species stands were characterized by higher stand basal area. However, the most plausible explanation for higher water use was thus the increasing basal area in the monocultures and three-species mixtures, but the ratio of stand transpiration

to basal area was larger for the six-species mixtures [26]. Trees used a higher amount of water in the six species plots than in the monocultures and three species mixtures. This was explained by a slightly larger conductive sap wood area of trees growing in the six-species mixtures and by higher sap flux rates of trees in the six-species mixtures during certain times of the year. The variation in the conductive sap wood area is a commonly observed and faster growing trees have higher ratios of conductive sapwood area to stem area than slower growing trees [66]. The higher transpiration rates in the six species plots was attributed to higher canopy roughness and hence changes in the canopy boundary layer, facilitating transpiration during times of low vapor pressure deficit (wet season).

More important for the drought resistance of the mixtures is that differences in seasonal water use pattern could be classified analogously to the water uptake pattern. The drought avoiding, dry season deciduous species *Cedrela odorata* was characterized by only minimal water loss during the dry season [26]. There was a higher water use rate of the species during transition period in the mixed species plots, but all tree individuals were defoliated at the onset of the dry season regardless of the mixture (Figure 2). This suggests that leaf shedding of this species is not triggered by soil moisture as there were only minimal differences of soil moisture content between monocultures and mixtures during the transition period [26,27]. Hydraulic redistribution of other species might have facilitated delay leaf senescence, but not the actual time of leaf shedding. A similar effect is the mixture effect on tree species characterized by dry season leaf senescence. Those species have probably better access to soil water in the mixtures at the beginning of the dry season, but will increasingly become water limited leading finally to leaf abscission. The clearest advantage for a species growing in mixtures could be observed in *Tabebuia rosea* and its dry season transpiration rates (Figure 2). First of all showing a significant increase of transpiration rates during the dry season independent from the mixture type, it also showed some clear mixture effects on the transpiration rates. This was especially visible during the end of the dry season when this species could maintain very high transpiration rates in the mixture whereas the transpiration in the monocultures had already dropped due to soil water limitations.

The temporal separation of the advantages of growing in a mixture is interesting. The three different strategies in water uptake pattern and leaf phenology were favored from growing in the mixtures at different times, but all together resulting in an overyield in biomass and an enhanced water use in the diverse stands. However, net overyield did not increase linearly with species numbers and reached its maximum in plots containing three different tree species [56]. Those really well performing plots in three species mixtures contained species with very different water use strategies (*Cedrela odorata*, *Anacardium excelsum* or *Luehea seemannii* and *Tabebuia rosea*) [26,27]. This strong overyield in the three species mixture highlights the importance of the species assemblage and the effect of neighboring trees with different traits (Figure 3). Thus, there are some important parameters of biodiversity effects and especially the assemblage of tree species with varying traits is playing a key role. Positive effects of complementarity and niche facilitation on drought resistance of forests stands will only occur if species are sufficiently different enough in their water resource use strategies.

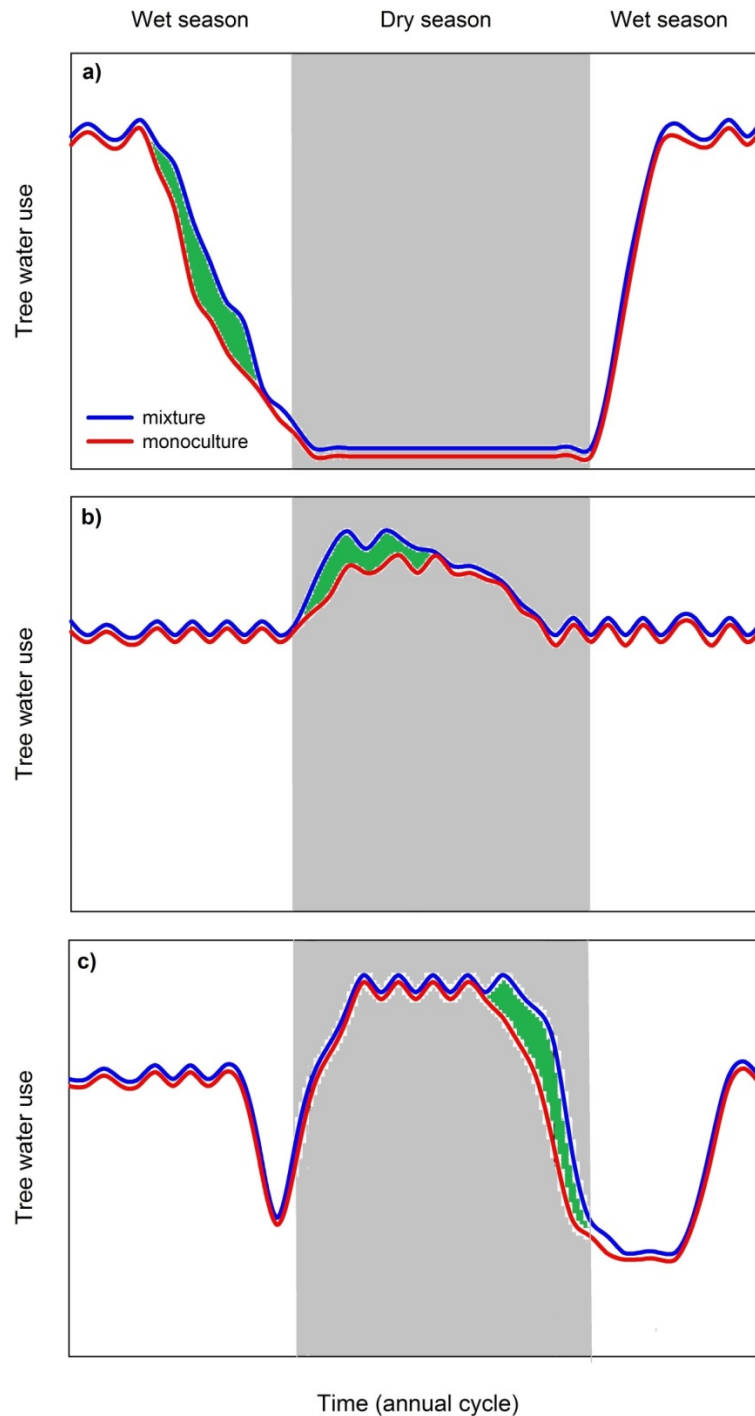


Figure 2. Schematic annual course of water use of three different tree species with different water use strategies and the differences between a given species growing in monoculture (red lines) or a mixed species plot (blue lines) compiled after Kunert *et al.* [26]. Green shaded area between the blue and red line represents the time lack between trees getting water limited growing in monoculture and trees growing in mixed stand. This time lack is probably due to complementarity in water use in the mixed species plots. **(a)** Annual course of a typical drought avoiding species (*Cedrela odorata*) with only minimal transpirational water loss during the dry season (grey shaded area); **(b)** dry season green species with leaf senescence (e.g., *Luehea seemannii*); and **(c)** *Tabebuia rosea* maintaining the canopy fully foliated during the dry season.

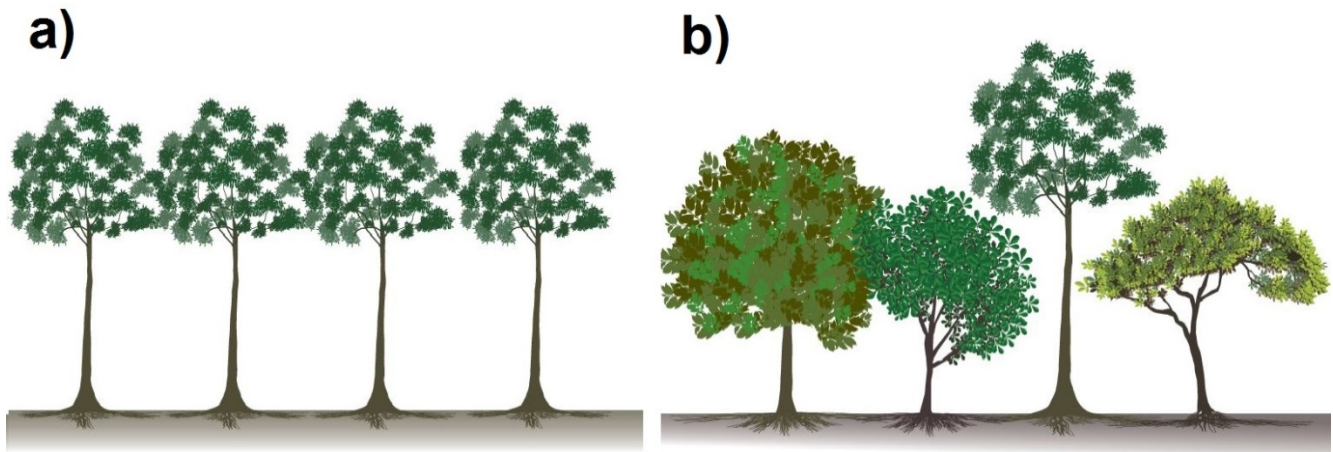


Figure 3. Schematic profile diagram of trees growing in (a) monoculture (*Cedrela odorata*) and (b) mixed species plots (from left to right, *Luehea seemannii*, *Anacardium excelsum*, *Cedrela odorata* and *Tabebuia rosea*). The trees are drawn accounting for their species specific natural canopy and root structure in scale of the height and rooting depth as measured in the plantation in Sardinilla, Panama. The better canopy stratification and root niche differentiation is visible in the mixed species stands (b) compared to the uniformity in monoculture (a).

3.3.3. Possible Limitations of Species Facilitation and Urgent Research Needs

The observed trait based niche facilitation of the different species will probably only function to some extent and might not apply during a prolonged drought with long-term water limitation. The alterations of the soil moisture regime during extended drought, the decomposition of soil organic matter and changes in nutrient release plus plant carbohydrate starvation will have long-term effects on the tree carbon cycling, and potentially on mortality [67]. The higher water use rates of the mixed species plots provide evidence for a higher and more complete exploitation of soil water in those plots. It can be assumed that due to the niche facilitation, the soil moisture is depleted more intensively at the end of the dry season [27]. This might also lead to higher water stress in the mixtures compared to monospecific stands and to a higher mortality of a certain less drought adapted species. Further, slow-growing plant species tend to be more resistant but less resilient than fast-growing species [68], which may bring unexpected shifts in species performance after extreme drought events in the planting design in Sardinilla. Thus, selection effects, species performing better or worse compared to their performance in monoculture [17], are expected to become more important the longer the tree communities are exposed to water limitation. Interspecific competition might move in place of species facilitation and complementarity, and persistence of species might depend on the tradeoff between drought resistance and resilience [68]. The species performing best under water limited conditions in monoculture will also become the dominant species in the mixtures and the worst performing species vice versa.

Nevertheless, mixed species stands might show a higher resilience to drought as, over the long term, the mortality was slightly lower in the mixed stands in direct comparison to monoculture [56]. Containing a mixture of various species increases the possibility of one species or a set of species surviving drought events and regaining biomass or ecosystem function after a certain recovery time [22].

This is unfortunately rather speculative and secure prediction of the drought resistance and resilience can only be made with results from further well designed research. However, no intense drought occurred since the establishment of the plantation, all dry seasons were under 150 days long and thus within the standard deviation (compare average dry season length of 131 ± 19 days; Figure 1) of a regular dry season. These questions could be addressed by monitoring the recovery or mortality rate induced by a future El Niño, similar to the studies on Barro Colorado Island in Panama [48,49], or with a manipulative drought experiment. In general, only few throughfall reduction experiments have been conducted in the tropics, especially in areas with an annual precipitation higher than 1500 mm [31,69,70]. Those areas are considered to be the most susceptible to future precipitation changes, not in the overall amount of the annual rainfall but in an increase of uneven distribution over the year and increasing dry season periods [30]. The few existing experiments were conducted in tropical old-growth forests [71–74] and in an agroforestry system in Indonesia [41]. Similar experiments in tropical tree plantations are, to our knowledge, still missing. Results from the already existing experiments cannot be directly transferred into predictions of how tree plantations will be affected by future climate change. Therefore, such a project will greatly assist the forestry sector in tropical regions to maintain highly productive and ecologically sound forest plantations in a changing climate and contribute to improving our knowledge about how tropical forests will be affected by global climate change.

4. Conclusions and Suggestions

Synthesizing results from the studies conducted in Sardinilla allows drawing some conclusions and making a few ecological generalizations regarding the resistance and resilience of mono-specific and mixed species plantations to drought. First, tree leaf phenology is a key trait in seasonal tropical forests to cope with drought stress. Trees exploiting a higher proportion of water depth also maintain a higher foliage cover in the dry season, higher sap flux densities and water use rates. Second, drought resistance of forests is promoted by species facilitation and thus forest stands with a diverse species composition containing a wide pool of tree species with different tree functional traits are more resistant. Therefore, assembling trees species differing in their leaf phenology and physiological characteristics in an artificial forest stand reduces competition and facilitates resource acquisition and, thus, influences productivity and stand water use. However, the distinct differences in productivity among monocultures and among mixtures indicate the importance of species traits and species composition. Consequently, further research should focus on physiological and morphological species traits and neighborhood effects as well as on how these might lead to an enhanced water resource complementarity in water limited periods during an annual cycle. This will be of high importance in predicting the influence of species diversity in maintaining ecosystem functions under changing climate conditions.

In conclusion, species selection and consideration of species richness and composition is crucial in the design of plantations to maximize wood production while conserving water resources in regard to changing water availability. Further research is urgently needed on drought tolerance of plantation tree species and on which tree species, species provenience or genetic variety, and finally on which tree species combination would be the most suitable for the establishment of plantations in face of climate change. For a maximum gain in biodiversity conservation, this quest for suitable native species should

happen on a very regional scale to imitate the very special features of many natural forest systems, conserve genetic variability and to achieve optimum ecosystem services. It still continues to be a major challenge to include the attained information into the development of sustainable and good forest management practices and the improvement of industrial plantation designs on a larger scale. Even though the demand for tropical plantation timber is growing, up to date, we are still limited to a very narrow assortment of timber species. With the wide variety of timber assortment produced by mixed tree species plantations, markets for the variety of produced timber have to be found to give a lucrative incentive for the establishment of such species rich plantations. This scenario would further avoid the cultivation shift to other exotic species.

Acknowledgments

We would like to thank Silvana Schott for assisting with the graphical layout of Figure 3. Further, we would like to thank two anonymous reviewers for their exceptional valuable comments and suggestion to improve the manuscript. And finally we would like to thank John H. Kim for English editing.

Author Contributions

Both authors contributed in writing and revising the manuscript. Norbert Kunert wrote the first unedited version of the manuscript.

Conflicts of Interest

The authors declare no conflict of interest.

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