WATER USE OF REFORESTED LANDS IN DRY TROPICAL COSTA RICA: A FUNCTIONAL TRAITS AND ECOSYSTEM SERVICES APPROACH

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AUTHORIZATION TO SUBMIT DISSERTATION

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ABSTRACT

Anthropogenic land cover change causes changes in the composition and function of ecosystems, which can impact ecosystem services and affect human welfare. A functional traits approach to ecosystem services can improve our understanding of these impacts by improving the resolution of ecosystem service assessments. The first chapter of this dissertation is a review of methods for scaling variation in functional trait composition from local to regional levels. In particular, the utility of available remote sensing methods for the regional scaling of fine-resolution functional trait variation is assessed. This is illustrated with a case study that summarizes some of the research detailed in the subsequent chapters. The second chapter of this dissertation examines the water use of reforestation strategies sponsored by government monetary incentives in seasonally dry Costa Rica, a region where water scarcity impacts human welfare. By sampling tree water use and carbon gain across paired treatment sites, I found that teak plantations have similar water use but higher water use efficiency than secondary forests of similar ecological maturity. Therefore, government policies aimed at incentivizing reforestation with secondary forests is not any better at conserving water resources than those aimed at teak plantations. The third chapter in this dissertation examines what functional traits are most related to tree and forest water use and water use efficiency across secondary forests and teak plantations in seasonally dry Costa Rica. I found that water use was strongly related to biomass at the tree stand level and that a few functional traits, namely tree sapwood depth, height and crown area, were also significantly related to tree water use. However, the relationship of traits on water use efficiency was not as significant. The capacity to remotely sense traits such as tree height and crown area makes them particularly useful for the scaling of tree water use to regional levels. Although there is strong convergence of water use with biomass, there is room for the use of functional traits to improve the resolution of tree to forest water use in ecosystem service assessments.

DEDICATION

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1. SCALING-UP SPATIAL VARIATION IN FUNCTIONAL TRAITS TO INFORM ECOSYSTEM SERVICE MANAGEMENT: CONCEPTS AND METHODS

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Abstract

Ecosystem service based approaches to land management require an accurate understanding of how land cover change influences biota and ecosystem processes. Current understanding posits that these relationships are best understood through functional traits rather than taxonomic classifications. Functional trait research occurs at many scales, applying multiple methods to quantify patterns in trait variation across scales and link functional traits to ecosystem services provisioning. In this paper, we review concepts and methods to scale-up plant and animal functional trait composition across space from individuals to populations to communities to landscapes, with the goal of assessing biotic influences on ecosystem processes and services. First, we synthesize current knowledge on the sources of variability that need be considered for capturing effect functional traits from local to regional levels. Second, we discuss three methodological approaches used to scale-up local functional trait composition to regional levels – biophysical gradient relationships, spatially explicit remote sensing, and hybrid methods. We illustrate the application using a case study to examine functional links of land cover change, ecosystem fluxes, and ecosystem service policy in an intensely human-modified landscape. We end our review by providing a brief outlook for the

application and development of these methods. This review aims to narrow the gap between ecological knowledge and ecosystem service assessments with the ultimate goal of improving ecosystem service policy and management.

Introduction

The functional traits of organisms, such as morphology and behavior, can vary substantially across time and space in response to climatic variation and environmental gradients (McGill et al. 2006; Suding et al. 2008). The resulting communities modulate ecosystem processes and fluxes through functional traits that occur at the individual organism level, termed effect functional traits (Lavorel & Garnier 2002; Violle et al. 2007). The effect trait composition of communities has shown to be altered by anthropogenic land cover change, which can alter the provisioning of ecosystem services to humans (Díaz et al. 2007, Laliberté et al. 2010).

Traditionally, methods for assessing the impact of land cover change on ecosystem services rely on correlating ecosystem properties with vegetation type (Daily et al. 2009). For example, in the Amazon basin change from forest to pasture vegetation affected local water fluxes by modifying interception and transpiration (Foley et al. 2003). These local changes have been scaled-up to basin-wide levels to assess effects on ecosystem services such as flood control (Foley et al. 2007). However, a limitation of this approach is that it does not incorporate the fine-scale functional trait variation that occurs within vegetation types, which can constitute up to 75% of the variation in trait values (Kattge et al. 2011). Individual level variation in effect traits such as tree size and leaf area can significantly affect interception and transpiration water fluxes in forest vegetation (Meinzer et al. 2005; Park & Cameron 2008). Classifications that lump heterogeneous forest communities into coarse vegetation types will miss this fine-scale trait variation, potentially resulting in inaccurate results when inferring changes in ecosystem processes at broader scales. In addition, species composition may change but functional trait composition may not, or vice-versa, within a given vegetation type (Messier et al. 2010; Albert et al. 2010).

Vegetation classifications, therefore, that are based on species compositions may miss the effect trait variation that drives ecosystem processes of interest. Current methods aim to resolve these issues by focusing on functional traits rather than vegetation types or species compositions (Westoby & Wright 2006; Kattge et al. 2011). Nevertheless, it is questionable whether it is even possible to collect high-resolution functional trait data over broad regional scales with currently available methods (Van Bodegom et al. 2012). This lack of clarity limits the use of functional traits to assess effects on ecosystem processes at regional scales where ecosystem services are delivered and managed (Fig. 1.1; Fremier et al. 2013).

The spatially explicit modeling of functional trait composition based on responses to both environmental gradients and climatic variation requires modeling complex feedbacks and is currently not a viable option for trait-based ecosystem service assessments (Suding et al. 2008; Van Bodegom et al. 2012). An alternative approach can be the direct mapping of functional trait composition by spatially explicit remote sensing of vegetation properties. Currently available remote sensing methods offer a promising link between the scales of effect functional trait variation and ecosystem service delivery because they are repeatable across time and space, and are capable of reproducing fine-scale high-resolution data at broad spatial scales (Fig. 1.1; Ustin & Gamon 2010; Asner et al. 2011a). Although many technological advances have improved the available array of remote sensing methods and their capabilities, their application to functional trait mapping at regional scales lags behind (Ustin & Gamon 2010; Homolová et al. 2013).

Current evaluation of ecosystem service policy and management requires accurate assessments of the consequences of land cover change on ecosystem processes and ecosystem services (Chazdon 2008; Daily et al. 2009). Functional trait approaches have the potential to be a more accurate approach due to the continuous nature of functional traits and the more direct link between trait and process, over species and process (McGill et al. 2006; Westoby & Wright 2006). Nevertheless, it remains to be answered whether we can accurately estimate functional trait variation at broader scales, if this gained resolution significantly improves the accuracy of process estimating, and if gained understanding can be translated to spatial levels relevant to land use planning and policymaking. The main goal of this review is to explore methods for the spatial scaling-up of local plot-scale functional trait composition to regional levels of ecosystem service delivery (Fig. 1.1).

To respond to these unknowns, we review the current conceptual understanding of functional trait-based approaches and the existing methodologies to capture variation at broader scales. Our objectives were to: 1) describe current assumptions for scaling-up effect functional traits, with emphasis on capturing the necessary sources of effect trait variation across spatial scales; and 2) describe current approaches for scaling-up effect functional trait composition across space from plot to regional levels, with emphasis on spatially-explicit remote sensing methods. We illustrate the applicability of some of these methods by utilizing a case study on how variation in functional traits of organisms in two trophic levels (i.e., forest trees and bee pollinators) affect selected ecosystem processes and services in a human-modified tropical region (Case Study). We use our case study to highlight the methodological challenges to scaling-up functional traits from plot to regional levels, and discuss on-going developments with the ultimate goal of using functional traits to inform ecosystem service policy and management.

Capturing Functional Trait Effects

Trait effects on ecosystem processes

Current approaches that quantify the relationship between effect functional traits and ecosystem processes recognize three aspects of functional traits that affect ecosystem processes, and thereby ecosystem services (*sensu* Díaz et al. 2007). The first is based on the *biomass ratio hypothesis* and states that the community-weighted mean (CWM) values of effect traits is the main driver of ecosystem properties or fluxes (Grime 1998; Lavorel & Garnier 2002). For both plants and animals, CWM values are estimated by plot-level species abundance or biomass (Lavorel et al. 2013). For plants, the relationship of CWM with ecosystem processes has consensus and is commonly regarded as the main proxy for assessing trait effects from local to broader spatial scales of ecosystem service delivery (Díaz et al. 2004; Violle et al. 2007; Lavorel et al. 2011).

The second is *functional trait diversity* of the community represents the complementarity effect of traits on ecosystem processes (Petchey & Gaston 2006; Hillebrand & Mathiessen 2009; Cadotte et al. 2011). This diversity is captured by indices of trait variation, such as evenness, divergence, and similarity. Complementarity occurs when functional trait combinations enhance or modify ecosystem properties or fluxes. In plant communities, complementarity effects on ecosystem processes are context-dependent (e.g., varying by forest type or successional status; Paquette & Messier 2011; Lasky et al. 2014) and secondary to the effects of the CWM of traits (Hooper & Vitousek 1997; Díaz & Cabido 2001; Balvanera et al. 2006; Díaz et al. 2007). Potentially, functional trait diversity is more important for ecosystem processes driven by higher trophic levels (Chapin et al. 2000; Cardinale et al. 2012). A high diversity of pollinator traits is needed to satisfy all plant pollination mechanisms, and therefore functional trait diversity of pollinators is a better indicator of pollination as an ecosystem process than a CWM (Fründ et al. 2013; Winfree 2013).

The third aspect applies in a few special context-dependent situations where one or very few species possess a special suite of traits, namely *biological engineers*. This unique species overwhelmingly drives ecosystem processes in spite contributing little to the community species abundance or biomass. In these situations, CWM or functional diversity indices would be poor indicators of ecosystem processes. In these cases, a functional trait approach may not be as helpful than a more detailed study on an individual species (Díaz et al. 2007).

Sources of trait variation

The magnitude of functional trait values can vary within an individual, a species, a community, and across a landscape. Understanding these sources of variability and the relevant scale at which they vary will improve the application of functional trait approaches to quantifying their effect on ecosystem services. Current approaches are beginning to scale-up functional trait variation. Regional trait-based ecosystem service assessments can rely on sampling species composition across land cover types and assigning effect trait values to each species using published databases of variation by species (Lavorel et al. 2008; Kattge et al. 2011; Kazakou et al. 2014). This approach may miss sources of trait variation that can affect ecosystem processes, such as variation across communities or landscapes (Violle et al. 2007; Baraloto et al. 2010; Albert et al. 2011). Although we cannot logistically measure all trait values across all scales, some understanding of the scale and magnitude of this variation will reduce uncertainty when scaling from in situ estimates of trait values.

Individuals and species

Intraspecific variation in functional trait values arises from environmental gradients occurring within and among plant and animal populations, and can rival that observed between species, or interspecific variation (Fig. 1.2; Albert et al. 2010; Bolnick et al. 2011; Violle et al. 2012). In tropical tree communities, which are characterized by high species richness, intra- and interspecific sources can account for similar magnitude of trait variation (Elias & Potvin 2003; Hulshoff & Swenson 2010; Messier et al. 2010; Ruiz & Potvin 2011).

The degree of variation attributable to intra versus interspecific sources can be species (Elias & Potvin 2003), system (e.g., plantation vs. natural forest; Ruiz & Potvin 2011), or trait dependent (Albert et al. 2010; Kattge et al. 2011; Kazakou et al. 2014). For plants, capturing intraspecific sources of effect trait variation is not necessary to assess effects on ecosystem processes at broader scales except in circumstances of high species dominance (Albert et al. 2011).

In the case of mobile animals, traits such as individual body size affect home or foraging range and resource use (Haskell et al. 2002; Kuhn-Neto et al. 2009). For example, between colonies of the same species, climate and resource availability have shown to influence bee size and morphology, which determines floral resource use (Peat et al. 2005a & b). Measuring the degree of variation attributable to intra versus interspecific sources for mobile organisms is hampered by the ability to obtain a fully random sample using trapping methods. Moreover, the variation in rare guilds compared to dominant ones will be likely be higher due to non-optimal habitat conditions (de Bello et al. 2011).

Communities and landscapes

Gradients of environmental conditions produced by soil properties, topography and climate drive the composition of functional traits across and within natural plant communities (Díaz et al. 1998; Cornwell & Ackerly 2009; Swenson et al. 2011a & b; Baraloto et al. 2012; Yang et al. 2014). This structuring has been shown to be less evident at small spatial scales within communities (≤100 m^2) due to founder effects and successional processes (Grime 1998;

Ackerly & Cornwell 2007; Swenson et al. 2007; Yang et al. 2014; *but see* Kraft & Ackerly 2010). Land cover change can disrupt the natural trait variation found within and across plant communities by altering land use history, successional status, landscape structure, and by species introductions (Fig. 1.2; Case Study; Díaz et al. 1999; Adler et al. 2004; Leishman et al. 2007; Giraõ et al. 2007). For example, the functional trait composition and diversity of tropical secondary forests is strongly dependent on successional stage and previous land use intensity (Lebrija-Trejos et al. 2010; Lasky et al. 2014). However, by accounting for this effect, patterns still emerge between environmental gradients with similar land use history and successional stage. For example, Lohbeck et al. (2013) found that the trait composition of tropical secondary forests varies across successional stages according to climatic regime (i.e., dry vs. wet). Similarly, Mayfield et al. (2005; 2006) found that the trait composition and diversity of early successional and mature tropical plant communities differ from each other yet vary predictably across landscapes with similar environment and land use history.

Overlaying environmental gradients and land use history are the confounding effect of animals on plant composition, and vice versa. Multiple studies have shown that the functional trait composition of plants can be mediated by the functional diversity of organisms at higher trophic levels, and in turn, this can modulate the trait composition of plant and animal communities across the landscape (Naeem & Wright 2002; Suding et al. 2008; Cardinale et al. 2012; Lavorel et al. 2013). Pollinators and seed dispersers, which include a wide array of animal groups going from insects (bees and beetles) to vertebrates (bats and birds), affect the trait composition of plant communities in ways that are poorly understood (Chazdon et al. 2003; Giraõ et al. 2007). For example, the plant trait composition of secondary growth for a given environment is primarily determined by previous land use intensity; yet, the trait composition of pollinators and seed dispersers is mostly determined by habitat suitability and landscape structure factors such as patch size and isolation (Lindenmayer et al. 2002; Liira et al. 2008; Tscharntke et al. 2008; Bommarco et al. 2010). This illustrates that differences in spatial mobility and resource use drive the functional trait variation of sessile plants versus highly mobile organisms at the community to landscape level. However, landscape fragmentation that results in the loss of pollinator functional groups can eventually modify the composition and diversity of functional traits of plant communities through localized extinctions (Fig. 1.2; Girañ et al. 2007; Sutton & Morgan 2009). This suggests that modulation of plant community traits by higher trophic levels comes with a time lag, which can be another reason for the disconnect in factors structuring trait composition across trophic levels.

Trait variation across scales

Although research has quantified the sources of trait variation within specific ecological or spatial scales, less is known about how this variation is partitioned across multiple scales. Knowledge of how trait variation is partitioned across scales is important for the design of trait sampling schemes. For example, if 90% of the variation in traits occurs at the species level, then accounting for intra-specific variation across communities may not be necessary. Although variance partitioning across scales remains relatively unstudied in animals, cross-scale trait variation has shown to be partitioned similarly across intraspecific, interspecific, and cross-community sources in plants (Fig. 1.2; Albert et al. 2010; Hulshof & Swenson

2010; Messier et al. 2010). Accordingly, a higher degree of trait variation exists within natural communities (alpha diversity) than across communities (beta) within a region because within community variation includes both intra and interspecific sources (Ackerly & Cornwell 2007; De Bello et al. 2009; Messier et al. 2010; Kattge et al. 2011; Freschet et al. 2012). Relatively less is known about how functional trait variation sources are partitioned across regions. This is mostly likely due to the method of using global database values that include unequal sampling schemes and sources of variation across sites to determine how trait variation is partitioned across broad to finer scales (Wright et al. 2004; Freschet et al. 2012).

Recently, Freschet et al. (2012) conducted balanced sampling to quantify the variation in selected traits (specific leaf area and leaf [N]) nested at the level of communities, regions, and biomes. They found that most trait variation sources occurred within communities (~50%) and across biomes (~35%), whereas variation across communities (i.e., regional) within a biome was relatively low (~15%). On the other hand, they found higher divergence (i.e., bimodality in trait value distribution) in traits across communities than within communities or across biomes, which was attributed to higher environmental heterogeneity and disturbances at the regional scale. This agrees with the findings of Willis et al. (2010) that show the steepness of environmental gradients within the spatial scale of interest, rather than the spatial scale itself, drives functional trait variation. Thus, environmental gradients drive functional trait variation across all spatial scales, and natural or anthropogenic disturbances can act on any spatial scale to counteract convergence in trait composition due to these gradients.

The influence of land cover change and introduced species

Land cover change can act to increase the variation in functional trait composition at the regional level by increasing trait divergence across communities (Fig. 1.2; Case Study). Across regions, gradients of increasing land use intensification are negatively related to the functional trait diversity of plant and animal communities (Hillebrand et al. 2008; Flynn et al. 2009; Laliberté et al. 2010). Therefore, variation in trait composition may be high across regions with contrasting levels of land cover change within a biome.

One mechanism behind this is the increase in species dominance within and across communities due to land cover change, which can result in higher sources of intraspecific relative to interspecific trait variation at the regional level (Fig. 1.2; Hillebrand et al. 2008). In addition, land cover change can result in the introduction of species possessing novel suites of traits for which there is no native analog (Olden et al. 2004; Leishman et al. 2007; Drenovsky et al. 2012). Some introduced species may become dominant under certain conditions (e.g., land use history or landscape fragmentation), which may lead to the emergence of novel community types (Hobbs et al. 2006). Within the novel communities they dominate, introduced species may also increase the magnitude of intraspecific relative to interspecific variation (Hillebrand et al. 2008; Drevonsky et al. 2012). In addition, managed systems, such as plantations, agriculture, and agroforestry, may perpetuate the dominance of introduced species by direct intervention, which can lead to higher trait variation sources across vegetation types (natural communities versus managed systems) within a region (Case Study). Thus, novel communities and managed systems introduced by land cover change may differ in functional trait composition from the original communities they replaced and increase the source of trait variation across communities relative to other sources within a region (Fig. 1.2). Alternatively, functional trait homogenization may occur in regions that have suffered near-complete land conversion and high rates of native species extinctions (Olden et al. 2004).

Sampling for effect traits

Whereas climate change affects the distribution of organisms at long time scales via trait responses to the environment (Suding et al. 2008), changes on effect traits are largely driven by land cover change that occurs at shorter time scales (Fig. 1.1; Foley et al. 2005; Daily et al. 2009). Therefore, the sampling of effect traits for ecosystem service assessments is usually carried out within human-modified regions that can be characterized by (1) high species dominance, (2) high cross-community trait variation, and (3) heterogeneous landscape structure. Here, we discuss what each of these conditions means for the sampling of effect functional traits.

Species dominance

Although quantifying intra-specific variation may be unnecessary for capturing trait effects on ecosystem processes (Albert et al. 2011), this variation can be of importance when one or few species dominate certain community types across environmental gradients (Violle et al. 2007; Hillebrand et al. 2008; Suding et al. 2008). In such cases, capturing the in-situ CWM of traits is an appropriate integrator of the relevant intra-specific trait variation (Albert et al. 2011). The use of database values may miss important trait effects on ecosystem processes due to intra-specific variation of regionally dominant species in regions where environmental gradients are steep and where species dominate common community or land cover types (Case Study). In addition, since species that become dominants as the result of land cover change are usually introduced, database values from regions with different environmental conditions may assign trait values disconnected from reality (Drenovsky et al. 2012).

Cross-community variation

Sampling stratification by community types of varying successional status, land use history, or management intensity is necessary to capture the modification of effect functional traits by land cover change (Garnier et al. 2007). Considering the magnitude of other sources of variation (Fig. 1.2), sampling across communities needs to be efficient at capturing cross-site variation without compromising other sources. One plot (e.g., ~500m^2 for forest tree communities) per site per community type at selected points across the environmental gradient of interest can be enough to capture the necessary effect trait variation into CWM or trait diversity indices (Ackerly & Cornwell 2007; Lavorel et al. 2008; Messier et al. 2010). Dominant species (i.e., those contributing >20% to CWM) should be adequately sampled as outlined by protocols (i.e., Cornelissen et al. 2003). For subordinate species (i.e., those contributing less than 80 to 90% of the CWM; Grime 1998; Pakeman & Quested 2007; Freschet et al. 2012) occurring in species-rich communities, such as old-growth or mature secondary forests, sampling of one individual per species per plot per site is enough to capture the necessary effect trait variation (Baraloto et al. 2010). In plant communities exhibiting high dominance and low species richness, database values may be appropriate to estimate effect traits of subordinate species (Pakeman & Quested 2007; Lavorel et al. 2008).

In the case of bees and other mobile ecosystem service providers, CWM and trait diversity indices are typically based on in-situ species abundance estimates across community types. However, measuring traits directly among the community being studied is often not possible due to logistical limitations. In such case, traits can be inferred based on phylogeny, reference works, or published keys (Moretti et al. 2009; Vandewalle et al. 2010 Wray et al. 2014). This is more acceptable when trait diversity indices are used to infer ecosystem services, as the mean trait values in a community may differ from database values depending on variables such as climate and resource availability (Peat et al. 2005a).

Landscape structure

Landscape structure can modulate the functional trait effects on ecosystem processes captured at the plot level. Increasing regional spatial extent adds landscape heterogeneity that may result in non-linear trait effects emerging across space (Fig. 1.3; Violle et al. 2007). For example, forest fragmentation increases canopy surface roughness and evaporative demand near forest edges, which can result in interception and transpiration water fluxes deviating from predictions based on CWM values of tree traits alone (*purple line in* Fig. 1.3; Case Study; Klaasen et al. 1996; Herbst et al. 2007; Briant et al. 2010). However, these effects can be constrained by the regional degree of land use intensity and landscape fragmentation as edge effects on transpiration fluxes penetrate into fragments as large as 100 ha and as far as 3 km from forest edges in human-dominated regions (Herbst et al. 2007; Briant et al. 2010). As spatial scale increases, other regions with contrasting environmental conditions, land use histories, or landscape structures are included (Fig. 1.2). This can also result in non-linear effect trait to spatial scale relationships since the effect of trait values on ecosystem processes in one region is not necessarily translated to another (Fig. 1.3; De Deyn et al. 2008). These examples illustrate that plant trait effects on ecosystem processes may not be directly transferable or equivalent across regions with varying degrees of human modification.

At higher trophic levels, landscape structure can have greater influence on trait effects by affecting dispersal capacity of highly mobile organisms (Keitt et al. 1997; Keitt 2009). In the case of plant pollinators and seed disperses, local plot-level effect trait composition does not matter as much because animals may visit unfavorable patches but not utilize them. Instead, the scale of relevant effect trait composition for such processes is determined by the organism's mobility and foraging range (Fig. 1.3; Case Study). For example, bee trait composition can display exponential effects on pollination as spatial scale increases up to their foraging distance because the proportion of native habitat within foraging range is the main factor driving pollinator trait effects (Fig. 1.3; Case Study; Kremen et al. 2004; Kremen et al. 2007). Similarly, the effect of trait composition and diversity of birds and other vertebrates on seed dispersal may exhibit a sigmoid relationship with increasing spatial scale because there may be a range of distances between patches at which dispersal is optimized (Fig. 1.3; Keitt et al. 1997). In general, sampling for animal traits needs to explicitly consider stratification at spatial scales of landscape structure whereas stratification for sampling plant traits is determined by more local scales of community types that are constrained by regional land use history.

Functional type classification

Although classification into functional types may appear to override the purpose of measuring continuous trait values, it can be useful for scaling-up trait effects for ecosystem service assessments (Quétier et al. 2007; Gillison 2013). For plants, multiple traits need to be sampled to determine functional types based on axes of resource use (e.g., Wright et al. 2004; Chave et al. 2009) and account for tradeoffs between traits that occur within individual organisms due to adaptation to the environment (Ordoñez et al. 2010a & b; Albert et al. 2011; Van Bodegom et al. 2012). For example, N-fixing and non N-fixing forest trees, and plantation trees in the dry tropics have different relationships between traits such as tree size, sapwood area, and crown diameter (Case Study). To deduce plant functional types in a given region, these trait interrelationships may be established from plot-level CWM values (Douma et al. 2012). This allows for classification based on actual trait values corresponding to the region of interest rather than *a-priori* classification schemes that can obscure effect trait relationships to ecosystem processes (Wright et al. 2006; Douma et al. 2012). In addition, since the relationships between traits can be climate dependent, sampling of multiple traits for functional type classification is necessary to remove this dependence (Wright et al. 2004; Kattge et al. 2011). Trait-to-trait relationships and functional type classifications can facilitate predicting plant trait effects on ecosystem processes, and can be useful if remote sensing is used to map variation on a subset of traits to infer changes on other effect traits of interest (Ustin & Gamon 2010; Van Bodegom et al. 2012).

There is far less work done in developing methods for dividing animals into functional types or groups based on shared traits, and most approaches focus on grouping animals based only on resource requirements (Blaum et al. 2009). The two methods for making functional groups are 1) grouping animals based on a priori knowledge of group assemblages and 2) group animals based on trait clusters using multivariate methods (Blaum et al. 2009; Moretti et al. 2009; Williams et al. 2010). Both methods are flawed, as the former can be impacted by subjectivity and, in the latter, correlation among functional traits can mask the trait response if traits assumed to be correlated respond in contradictory ways to a variable under certain conditions (Williams et al. 2010).

Scaling-up Trait Composition

Trait-based ecosystem service assessments can be improved if the captured effect trait variation is mapped across space (Lavorel et al. 2011). Eventually, dynamic vegetation models may reproduce the distribution of effect traits after their response to climatic and environmental variation but this is currently not a viable option (Suding et al. 2008; Van Bodegom et al. 2012). However, immediate changes on effect traits due to land cover change need not be modeled after complex feedback dynamics that are designed to account for climate change if tools such as scenario modeling are used to assess immediate effects on ecosystem processes and services (Fig. 1.1; Case Study; Daily et al. 2009). If the goal if to observe the relative effect of having one land cover scenario versus another on ecosystem fluxes of interest in short time scales, mapping the current "snapshot" distribution of effect traits can be enough. Therefore, instead of using response trait-mediated maps of effect trait distribution (i.e., Suding et al. 2008), mapping of effect trait spatial distribution by alternate and more viable approaches is an option. These involve (1) static statistical modeling based on trait to biophysical gradient relationships; (2) spatially explicit remote sensing of traits; and (3) a hybrid combination of these methods. Capturing regional trait variation by local plot sampling as previously discussed is required to varying degrees by all three alternatives. We review these three approaches but give emphasis to remote sensing methods because technological developments in this field offer a promising bridge to directly scale-up plot level effect trait variation to regional spatial levels with high resolution (Fig. 1.1).

Biophysical gradients

Environmental conditions regulate functional trait assembly at local to regional levels in such a way that robust statistical relationships can be used to link local trait variation to regional biophysical gradients that modulate the environment (e.g., elevation and precipitation, topography and soil moisture; Cornwell & Ackerly 2009). For example, Swenson et al. (2011) produced maps of variation in maximum height, leaf [N] and [P], specific leaf area, seed mass, and wood density for the woody vegetation of the Americas. Their method consisted on the spatial interpolation of mean trait values collected from sampling points within grid cells distributed across biophysical gradients in the continent. At a grid cell resolution of 1° to 5°, they found that latitude, elevation, temperature, and precipitation were related to each trait at varying degrees. Although these maps are unprecedented in their spatial portrayal of trait variation at broad scales, the method is limited at reproducing variation at finer scales needed for regional ecosystem service assessments because it does not incorporate variation in land cover type (e.g., stand age, land use history) and landscape structure. This limits its use for scaling-up trait variation of both plant and animals in human-modified regions. Lavorel et al. (2011) incorporated the effects of biophysical gradients on plant functional trait variation for a regional ecosystem service assessment in the Alpine prairies. Their approach was supported by an extensive sampling campaign stemming from many publications (e.g., Garnier et al. 2007; Lavorel et al. 2008) and by the use of remote sensing to facilitate land cover classifications and stratification of trait sampling across biophysical gradients.

Remote sensing

Remote sensing methods offer opportunities for mapping functional trait variation or functional types at broad spatial scales with the advantage of being spatially explicit, extensive, and repeatable over time (Figs. 1.1 & 1.4; Ustin & Gamon 2010; Schmidtlein et al. 2012; Homolová et al. 2013). Current limitations of remote sensing methods are (1) mostly restricted to sensing canopy traits at the plot-level, (2) low agreement between fine resolution in situ measurements of functional traits and coarser remote sensing data, and (3) confounding factors that affect plant spectral properties such as vegetation architecture and soil background (Ollinger 2011; Homolová et al. 2013). Fusion of remotely-sensed data types, such as passive-optical (e.g., LANDSAT) with active (e.g., LIDAR) remote sensing, and improvements of sensor spectral, directional, spatial, and temporal resolutions, can improve the resolution of leaf to canopy spectral properties for the mapping of plant functional traits (Ustin & Gamon 2010; Ollinger 2011; Homolová et al. 2013). Passive, optically-based remote sensing can be used to infer a wide range of vegetation spectral and biochemical properties while active remote sensing approaches are particularly useful for retrieving canopy and understory structural information. Here, we describe the passive optically-based remote sensing methods that may be used for mapping canopy functional traits and landscape structure, and the potential of active remote sensing methods to capture individual to plot-level traits related to vegetation structure.

Passive remote sensing

Passive optical remote sensing methods can be used for mapping discrete land cover classes, landscape structure, and vegetation or plant functional types (Fig. 1.4; Ustin & Gamon 2010). Land cover or vegetation classes are generated from relatively low resolution (e.g., 30 m) and broad extent digital imagery acquired by satellites by using a set of decision rules where each pixel is assigned to a class based on spectral properties and ancillary data such as topography. For example, optical satellite sensors such as LANDSAT, IKONOS, and AVHRR have enough spatial and temporal resolution to classify forests by successional status or phenological regime (Fig. 1.4; Vieira et al. 2003; Kalacksa et al. 2007; White et al. 2009).

As a remote sensing method, aerial photography has been used at fine resolution to map tree species based on flowering events or on individual crown properties (Fig. 1.4; Valerie &

Marie 2006; Jansen et al. 2008). Tree crown diameter, a functional trait related to tree size and water use (Case Study), has been mapped with some success using hyperspectral aerial photography processed with spatial wavelet analysis (Strand et al. 2006). This method can be affected by phenological variation and interference between the over- and understory preventing crown detection, and needs further development for use in closed canopy conditions (Garrity et al. 2008). High resolution aerial photography has been used in combination with satellite imagery (e.g., Quickbird) to map palm crown diameter by individually delineating polygons in order to estimate fruiting crop size (Jansen et al. 2008). The use of aerial photography for regional trait mapping is limited by its high cost and tradeoff with covered extent, and by the relative infancy of automated methods for image processing, interpretation, and analysis (Morgan et al. 2010).

Passive remote sensing methods can be divided by their use of empirical and physical approaches for the retrieval of plant functional traits (Homolová et al. 2013). Generally, plant traits cannot be directly retrieved from passive remotely sensed data but may be inferred by their relationship to canopy spectral properties using empirical or physical models based on statistical relationships or spectral processes, respectively (Fig. 1.4; Gray & Song 2012; Homolová et al. 2013). Empirical and physical models may be used to estimate the spatial variation of similar traits, and may be used in tandem to facilitate or improve estimation of other traits. For example, leaf mass per area (LMA), which is related to phenology and drought resistance, has been estimated from remote sensing data using empirical and physical models, and may be used to estimate leaf dry matter content based on its relationship with

LMA, leaf area index (LAI), and canopy water content (Colombo et al. 2008; Asner & Martin 2009; Homolová et al. 2013).

Empirical remote sensing approaches use regression analysis to quantify functional relationships between field observations of traits and remotely sensed data. The statistical models are then used to predict trait values across broader spatial extents (Fig. 1.4; Homolová et al. 2013). Spectral vegetation indices (e.g.; normalized difference vegetation index or NDVI) are normally used in these regressions to enhance sensitivity to canopy traits or properties. One of the most important limitations of empirical methods is that the regression relationships between remotely sensed data and field observations of traits are time, site, and species specific, lack causality, and consequently often lack robustness and transferability (Homolová et al. 2013). Concurrent ground-based measurements of canopy properties, such as LAI, canopy height, and vegetation water content, coupled with sensors that capture information at different spatial resolution and extents (i.e., 1 m and ~ 10 km for airborne LIDAR, and 30 m and >1000 km for LANDSAT, respectively) can improve the scaling of local measurements to broader scales (Fig. 1.4; Anderson et al. 2004; Williams et al. 2008). For example, Gray and Song (2012) developed a model to map effective LAI using information of multiple sensors to address limitations related to both the tendency of spectral vegetation indices to saturate at moderate levels of LAI (~ 3) and the tradeoff between spatial and temporal resolutions in remotely sensed images. They generated daily maps of effective LAI at LANDSAT spatial resolution (30 m) by combining spatial, spectral, and temporal information from IKONOS, LANDSAT, and MODIS satellite sensors.

One of the main limitations of empirical approaches is that most widely available multispectral sensors sample only a few portions of the electromagnetic spectrum at bandwidths too wide to capture subtle spectral features that are important for the discrimination of plant functional traits (Ollinger 2011). This limitation may be addressed by the use of hyperspectral data, which contain a high number of contiguous, narrow spectral bands and can be used to derive leaf and canopy chemical properties (Fig. 1.4; Malenovský et al. 2007; Asner & Martin 2008; Schlerf et al. 2010). When hyperspectral data are used, the effects of soil background, illumination, albedo, or leaf water may be reduced with spectral transformations to enhance absorption features in vegetation spectra (Schlerf et al. 2010). Also, the effects of canopy structure on leaf chemical retrieval are difficult to quantify with regression analysis, yet a solution may be to combine empirical and physical modeling approaches. For example Asner & Martin (2008) developed partial least squares regression (PLSR) models between leaf chemical properties and species leaf spectral data for the tropical forests of Australia. Subsequently, leaf spectral measurements were used in a radiative transfer model to simulate top-of-canopy reflectance (*see below*). Asner and Martin (2009) repeated the PLSR analysis at the canopy level in the forests of Hawaii using the simulated canopy reflectance to estimate leaf chemical traits (i.e., [N], [P], chlorophyll, carotenoid, & water) and LMA.

Physical remote sensing approaches are based on radiative transfer models at the leaf and canopy levels (Malenovský et al. 2007). Radiative transfer models account for absorption and scattering processes based on leaf and canopy structure and biochemistry to simulate leaf to canopy reflected or emitted optical spectral properties (Fig. 1.4; Baret & Buis 2008;

Jacquemoud et al. 2009; Ollinger 2011). The coupling of leaf and canopy radiative transfer models allows the spectral and directional variation of canopy reflectance to be described as a function of leaf biochemistry and canopy structure (Jacquemoud et al. 2009). This potentially allows the retrieval of fine-scale plant functional traits from plot-level to broader spatial scales by using inverse modeling (Colombo et al. 2008; Croft et al. 2013; Homolová et al. 2013). Coupling canopy, leaf, and soil models improves the retrieval performance by imposing a strong spectral constraint on the inversion process, decreasing drastically the number of unknown variables while providing enhanced spectral consistency (Baret & Buis 2008; Jacquemoud et al. 2009). The main drawback of this approach is that inverse modeling has high uncertainty because model solutions are not unique. This is so because several combinations of canopy traits could lead to similar signals and derive ambiguous canopy properties from remotely sensed data (Koetz et al. 2005). Using field data to help constrain the distribution and limits of the variables could help obtain more stable and reliable solutions (Baret & Buis 2008).

Since radiative transfer models do not incorporate all known sources of variability in leaf spectra (Asner et al. 2011b), the retrieval by inversion is limited to those functional traits or structural properties that are directly involved in the modeled process, such as leaf or canopy chlorophyll and water content, and LMA (Baret & Buis 2008; Asner et al. 2011c; Homolová et al. 2013). To address this limitation, Asner and Martin (2008) developed leaf-to-canopy scaling-up of multiple leaf chemical properties and specific leaf area (SLA; inverse of LMA) of 162 humid tropical forest tree species by combining field-based leaf spectra and chemical data with PLSR analysis and radiative transfer models. In a subsequent study, Asner et al.

(2011c) developed a scaling method of multiple leaf chemical components and LMA for the entire humid tropical forest biome, using a combination of a globally-distributed, consistently measured leaf spectral and chemical databases, along with canopy radiative transfer models, PLSR and high-frequency noise modeling. They showed that under conditions of varying canopy structure and spectral noise, the method consistently and accurately predicted chemical components and LMA using visible-to-shortwave infrared spectroscopy although improvements in sensing shortwave infrared (1300-2500 nm) bands could increase the accuracy of LMA estimates.

Active remote sensing

Active remote sensing methods, such as airborne LIDAR, are revolutionizing the study of vegetation structure from plot- to regional scales. LIDAR has been used in conjunction with passive remote sensing satellite images to scale plot-estimated aboveground carbon stocks in forests to regional and global scales with high accuracy (Asner et al. 2011a; Saatchi et al. 2011; Baccini et al. 2012). Besides estimating aboveground biomass, LIDAR has also been used to map individual tree functional traits such as height and crown diameter (Fig. 1.4; Case Study; Popescu et al. 2003; Popescu & Wynne 2004; Koch et al. 2006; Falkowski et al. 2006; Popescu & Zhao 2008), and stand traits such as LAI and understory vegetation density (Riaño et al. 2004; Martinuzzi et al. 2009; Zhao & Popescu 2009). LIDAR typically underestimates tree height due to the possibility of returns missing the highest point of tree crowns, although the error remains constant (~0.15m) and is mostly negligible for tall forest canopies (Asner et al. 2012). As with aerial photography, the sensing of tree crowns with

LIDAR remains limited in closed canopy conditions (>50%) cover, yet finer post-spacing of LIDAR returns (<1m) may improve the sensing of this trait (Garrity et al. 2008; Falkowski et al. 2008). Coupled with passive optical sensors, LIDAR has the potential to relate plot-level structural properties, such as canopy height, LAI, and aboveground biomass, which could be used to facilitate functional type classifications and improve the spatial scaling-up of multiple traits (Case Study; Fig. 1.4; Zhao & Popescu 2009; Asner et al. 2011a; Gray & Song 2012).

Due to its accuracy in sensing forest structure across heterogeneous terrain, LIDAR has been used to map forest type and successional status (Castillo et al. 2012; Martinuzzi et al. 2013) and has been tested to estimate forest tree species diversity (Asner & Martin 2009; Hernández et al. 2014). Recent fine-scale analyses show promising links between plant structure and function that can be derived directly from combining the 3-Dimensional location data of returned LIDAR pulses with return intensity, which is likely to open new opportunities for high resolution mapping of leaf chlorophyll, [N], and photosynthetic performance (Eitel et al., 2010, 2011; Magney et al., 2014). Other active remote sensing methods, such as satellite LIDAR (Lefsky et al. 2005), high-density laser scanning (Maltamo et al. 2004), and synthetic aperture radar (Santos et al. 2003) have been used to map forest canopy height yet their development lags behind compared to airborne LIDAR.

Remote sensing of animal traits

Remote sensing methods are used determine how landscape structure or habitat quality relate to the distribution of functional traits of animals over space and time. The use of remote sensing methods is especially helpful for studies of mobile organisms because they move within and between landscapes depending on functional traits such as foraging range and dispersal abilities (Case Study; Kremen et al. 2007). High-resolution aerial photography and passive multispectral imagery, such as LANDSAT or MODIS images, are the most common tools used to determine variables related to horizontal landscape structure or vegetation type (Case Study; Fig. 1.4; Bergen et al. 2009). Such variables correlate with bee body size and foraging range (e.g., matrix type; Wray et al. 2014), bee dispersal ability, sociality, and trophic level (e.g., habitat area and landscape heterogeneity; Steffan-Dewenter et al. 2002, Jauker et al. 2014), the diversity of beetle morphological traits and color (e.g., landscape composition; Vandewalle et al. 2010) and bird and butterfly life history traits (e.g., habitat loss; Barbaro & van Halder 2009).

At a finer scale, phenology and habitat structure predict the distribution of animal functional traits at multiple spatial extents. Remotely sensed phenological data has been used in studies of mobile organisms to understand the temporal or spatial distribution of resources among functional guilds. For example, leaf phenology, which is associated with critical blooming periods for the honeybee life cycle, was used to measure the impact of climate change and urbanization on the range of Africanized and European Honey Bees (Nightingale et al. 2008; Jarnevich et al. 2014). Leaf greening and browning was determined using vegetation indices (e.g.; NDVI), LAI, and fraction of photosynthetically active radiation (FPAR) derived from the MODIS sensor. When compared to hive weight, remotely sensed phenological data can represent the amount of resources available in the environment for Africanized bees, effectively estimating the distribution of a bee species based on foraging range and seasonality (Nightengale et al. 2008).

Airborne LIDAR has been applied to animal biodiversity and habitat studies by measuring the horizontal and vertical (3-Dimensional) composition of landscapes, and variables in forests such as understory vegetation, canopy architecture, snag size and density, and basal area, which represent resource availability (Fig. 1.4; Case Study; Turner et al. 2003; Vierling et al. 2008; Bergen et al. 2009). Researchers can combine in-situ field data with these structural characteristics to predict distributions of organisms based on field-validated models (Martinuzzi et al. 2009, Newton et al. 2009). For example, Hinsley et al. (2002) used LIDAR to estimate vegetation height for the mapping of chick mass of Blue and Great Tits in England according to foraging behavior. Chick mass of Blue Tits, which forage in upper areas of the canopy, had a positive relationship with vegetation height while the chick mass of Great Tits, which forage in lower branches or understory, had a negative relationship with the same variable (Hinsley et al. 2002).

The abundance of arthropod functional guilds has been related to 3-Dimensional habitat structure (Vierling et al. 2011, Müller et al. 2014). For example, Müller and Brandl (2009) linked local and regional scale functional trait composition of beetles by relating beetle activity, richness, and composition with habitat structural variables derived from LIDAR. They found that beetle body size was negatively related to the standard deviation of vegetation height. Their study demonstrated the high predictive power of LIDAR for habitat models with few parameters and its high cost-efficiency with surveyed ground cover and in habitats difficult to assess, illustrating its utility for scaling-up functional traits of mobile organisms from plot to regional levels (Müller & Brandl 2009).

Hybrid methods

Although remote sensing can be used to accurately map variation in several functional traits relevant to ecosystem services, remote sensing of trait variation lags behind for other relevant traits. For example, tree crown diameter can be remotely sensed at local to regional levels, but its application is so-far limited to conditions of low tree cover (Case Study; Falkowski et al. 2008). In addition, the relationships between traits that can be remotely sensed and other traits of interest can change according to the vegetation or plant functional types found in the region of interest (Case Study). Hybrid methods that rely on biophysical gradients to integrate functional trait variation into vegetation or plant functional types, which can be classified using remote sensing, have been used to spatially portray regional trait variation (akin to *hybrid models* in Van Bodegom et al. 2012). For example, Lavorel et al. (2011) mapped vegetation types based on land use trajectories using aerial photography and conducted plot-sampling to estimate functional trait CWM and diversity indices across the biophysical gradients occurring within each vegetation type. General lineal models relating trait values to abiotic variables were developed for each vegetation type and used to spatially portray the regional variation in traits relevant to ecosystem services. To our knowledge, this remains the only example where functional trait variation has been spatially mapped to inform ecosystem services management, and this was accomplished using a hybrid methods approach as described here. Clearly, there is ample space to further integrate plot-based functional trait approaches with remote sensing methods, especially to fully capitalize on current developments in the later.

Conclusion: Looking Forward

Much work remains to achieve accurate and cost-efficient portrayals of local functional trait variation at the spatial extent and resolution needed for regional ecosystem service assessments. One of the main barriers is the regional context dependency of the many relationships that are needed for this achievement: the interrelations between functional traits, between traits and ecosystem fluxes, and between traits and spectral properties that may be related to trait variation via remote sensing. At this point in time, in-situ sampling of trait variation is still needed at the regional level, and more so in human-modified regions for which ecosystem service assessments are relevant. In particular, this needs to take into account the modification of natural trait variation due to emerging regional dominant and introduced species patterns, secondary to novel community types, and ever-changing land use history and landscape structure. Incorporating higher resolution of trait variation into the mapping of vegetation or plant functional types, aided by sampling across biophysical gradients, estimates of trait variation by remote sensing, and most likely their combination in hybrid methods remain the next step for using functional trait variation to inform ecosystem service assessments in human-modified regions.

This review shows that the few examples (i.e., Lavorel et al. 2011) that have explicitly scaled-up community based functional trait variation metrics (i.e., CWM and functional diversity) to regional levels have done so using a combination of plot sampling across biophysical gradients and vegetation type classification using remote sensing. Examples that have scaled-up trait variation based exclusively on sampling across biophysical gradients (i.e., Swenson et al. 2011) have lacked sufficient resolution to be used at regional levels that are heterogeneous in land cover type and landscape structure. Further development of remote sensing methods will aid in both the resolution of land cover and plant functional type classifications, and eventually act as a direct link to scale-up in-situ local trait variation to regional levels. However, field-sampling will likely remain necessary to remove context-dependency and validate remotely sensed data at the regional level. Furthermore, frameworks for scaling-up functional traits need to consider the theoretical differences between determining the scale of biotic-physical processes and biotic-biotic processes that modulate the functional traits of sessile and mobile organisms, respectively, in heterogeneous human-modified landscapes. We foresee that, in the immediate future, hybrid methods that integrate trait sampling across gradients and remote sensing to portray trait variation of multiple trophic levels at broader regional extents will precede fully traits-based effect and response models (i.e., Van Bodegom et al. 2012) as the next trend in using functional traits to inform ecosystem service policy and management.

Case Study: Scaling-up Tree and Bee Functional Traits in Nicoya.

The Nicoya Peninsula in northwestern Costa Rica is located within the Mesoamerican dry tropical forest biodiversity hotspot (Miles et al. 2006) and the Mesoamerican drought corridor (Vega-García 2005). During the century leading up to the 1970s, the region experienced extensive land cover change from old-growth forest to near-complete deforestation primarily driven by conversion to grassland for cattle ranching. In the early 1970s, two events occurred that changed government policy and land use practices in the region. A severe drought hit the region and the price of beef for export dropped (Vega-García 2005; Calvo-Alvarado et al. 2009). Reduction of ranching and new government policies to monetarily incentivize reforestation caused reforestation of nearly 40% of the landscape by 2000 into both secondary forests and commercial tree plantations (Serrano 2005; Calvo-Alvarado et al. 2009). Plantations are now dominated by the introduced tree species *Gmelina arborea* (melina) and *Tectona grandis* (teak). Melina has naturalized and grows in the secondary forests in the region, which may be considered a novel ecosystem (Hobbs et al. 2006; Granda et al. in prep). The current landscape is a heterogeneous mosaic of old-growth, mature, and early secondary forest, novel forests, commercial plantations, pastures, and agricultural lands. The question facing the region is to what extent the new landscape provides a resilient set of ecosystems services.

The Nicoya Peninsula case study of land use change highlights how land use change influences the provisioning of ecosystem services through changes in species functional traits. In particular, we focus attention on the variation in functional traits of water use in trees and pollination traits of bees. We selected these functional traits as they influence water provision and pollination services. Changes in the provisioning of these services have been shown to have social-economic consequences in the region (Vega-García 2005; Tavárez et al. in prep). That is, land use and forest type influences availability of water through the dry season (Abelleira et al. in prep) and agricultural practices are dependent on pollination (e.g. been pollinated crops and apiculture) (Galbraith et al. in prep). Finally, we illustrate how the variability in key functional traits can be measured and scaled-up from local to the regional level.

Scaling water use from functional traits using remote-sensing proxies

Trait variation in tree trunk diameter and sapwood area affects water use in trees (Meinzer et al. 2005; Kagawa et al. 2009; Reyes-García et al. 2012). At the plot scale, researchers are able to measure these traits in the field. However, at larger scales such as a watershed, field measures are logistically difficult, particularly in areas with high trait variability such as regions that are highly diverse in forest type and tree age structure (Fig. 1.5a). The use of remote sensing tools have shown to be able to capture the spatial heterogeneity of functional traits, or their proxies, in an effort to scale ecosystem processes at scales relevant to policy (Ustin & Gamon 2010; Homolová et al. 2013).

In the case of water use, trunk diameter at breast height (DBH) and sapwood area are correlated to tree crown diameter (Fig. 1.5b & c; Kunert et al. 2012; Verma et al. 2014). Tree crown diameter can be quantified using airborne LIDAR and therefore becomes a proxy for mapping of trait variation and water flux at broad spatial levels (Popescu et al. 2003; Falkowski et al. 2006). However, there are a number of issues with this approach. Although tree trunk DBH and sapwood area are correlated with tree crown diameter, the correlations vary among other tree functional traits or types (e.g.; N-fixers vs. non-fixers; Figs. 1.5a-c). Emerging technologies do exist to map N-fixation using airborne hyperspectral sensors to help resolve this issue (Asner & Martin 2009). In addition, the regression equations between traits and proxy traits have not always been quantified. Therefore, scaling water use using trait-to-proxy correlations requires further study.

In addition to spatial variation, tree water use changes in time. Tree phenology can be remotely sensed using multispectral satellite imaging to quantify water use changes through the seasons (Kunert et al. 2010; Gray & Song 2012). Interestingly, deciduousness in dry tropical forests relates to the dominance of N-fixers (Reyes-García et al. 2012). The correlations among traits and their proxies hold promise for more resolved scaling-up of ecosystem processes, particularly to scales relevant to ecosystem service policies.

Scaling traits of pollination: habitat quality and landscape structure

For water use in trees, the magnitude of specific traits drive the ecosystem process. For pollination services in plant communities, however, trait diversity among pollinators is a key component (Williams et al. 2010; Cadotte et al. 2011; Fründ et al. 2013). For example, functional diversity of bee communities has been shown to increase the persistence of diverse plant communities (Biesmeijer et al. 2006; Fontaine et al. 2006), increase crop yield (Hoehn et al. 2008; Tsharntke et al. 2008; Martins et al. 2015), and may buffer pollination services from environmental changes (Bartomeus et al. 2013; Brittain et al. 2013; *but see* Winfree & Kremen 2009). Studies have identified bee traits that are related to pollination services, both morphological (Larsen et al. 2005; Fontaine et al. 2006; Bartomeus et al. 2013) and behavioral (Biesmeijer et al. 2006; Klein et al. 2008; Hoehn et al. 2008; Williams et al. 2010;

Bartomeus 2013; Frund et al. 2013). For example, long-tongued bees are able to access resources in flowers with a long corolla, but short-tongued bees or flies may be more efficient at accessing resources in flowers with a short corolla. If there are insects with many different mouthpart lengths within the community, pollination services will be sustained for flowering plants of diverse morphologies (Fontaine et al. 2005).

Landscape characteristics, such as proportion of native habitat, patch isolation, and land use intensity influence bee populations at different scales depending on dispersal ability and foraging range (Steffan-Dewenter et al. 2002; Kremen et al. 2004; Winfree et al. 2011). Structural and habitat data from field surveys and/or high-resolution remote sensing, such as airborne laser scanning, can be used to test additional variables that may impact bee trait diversity within plots. Standard deviation of understory plant height (Hoehn et al. 2008), tree height and DBH (Eltz & Bruhl 2002; Samejima et al. 2004), canopy openness (Lehnert et al. 2013), and plant species richness (Grass et al. 2014) have significant effects on bee diversity, richness, or trait diversity.

There are limitations to using both landscape and plot-level habitat characteristics to predict pollination services. Studies have demonstrated that there is often a scalar mismatch between service supply, demand, and decision-making, such as policy implementation (Burkhard et al. 2012). Pollination is a locally provided service, so it is critical to define the service "demand" in a given study to predict the relative pollination services received. On the other hand, the service providers (i.e., native bees) are impacted by variables from the patch up to landscape and regional scales, and the scale of these impacts depend on bee traits, as well (Kremen et al.

2004; Ricketts et al. 2008; Winfree 2013). Predicting the scale to use in pollination service assessments is made more difficult by the lack of basic ecological data on bee behaviors that are critical to their service, such as foraging, nesting, and seasonality of behavior (Zulian et al. 2013), particularly in less-studied areas, such as the Neotropics. Using spatially explicit proxies for pollination will continue to improve as more studies are done on the response of bee functional traits in different regions and contexts.

Scaled-up traits and ecosystem services

To evaluate the effectiveness of policies, such as payments for ecosystem services schemes, we need to assess simultaneously the impact of land use change on multiple services. For example, reforestation with teak may result in equal water balance as secondary forest, but provide less bee nesting and foraging habitat to support bee pollination of nearby crops. As discussed, the variables that impact the provisioning of water and pollination services work on different scales, and understanding relative impacts requires the integration of multiple disciplines and datasets. Spatial tools are particularly helpful in integrating ideas and data across subject matter (Daily et al. 2009).

Spatially explicit modeling tools are being used to quantify multiple services to show relative impacts of policy. In such models, pixels are characterized by values that correspond to service provision. Current models, such as InVEST, use land cover classifications to estimate water yield for a watershed under different land cover scenarios (Tallis et al. 2012). The use of functional traits, CWM or trait diversity, could be applied to improve estimates of water use within a watershed to estimate water yield. Similarly, the InVEST crop pollination module, which predicts relative pollination value of pixels based on spatially-explicit bee habitat, foraging quality, and crop location, has been tested on a number of landscapes, including a coffee agro-ecosystem in Costa Rica (Lonsdorf et al. 2009).

Ecosystem process models linking land cover change to ecosystem fluxes do not typically incorporate the social-economic impacts of biophysical change. Given the context dependent nature of social-economic systems, regionally specific data analysis are needed to assess the social-economic impacts of land use change. For example, to assess the impact of the modification of water fluxes and pollination in the Nicoya Peninsula, we are conducting interviews and economic choice experiments where residents outline how they would be impacted by changes in the provision of water and pollination (Tavárez et al. in prep). The next challenge is to link these types of data with generic ecosystem service tools, such as InVEST. Doing so would cover a big step for the assessment of ecosystem services at the regional scale to inform policy and management.

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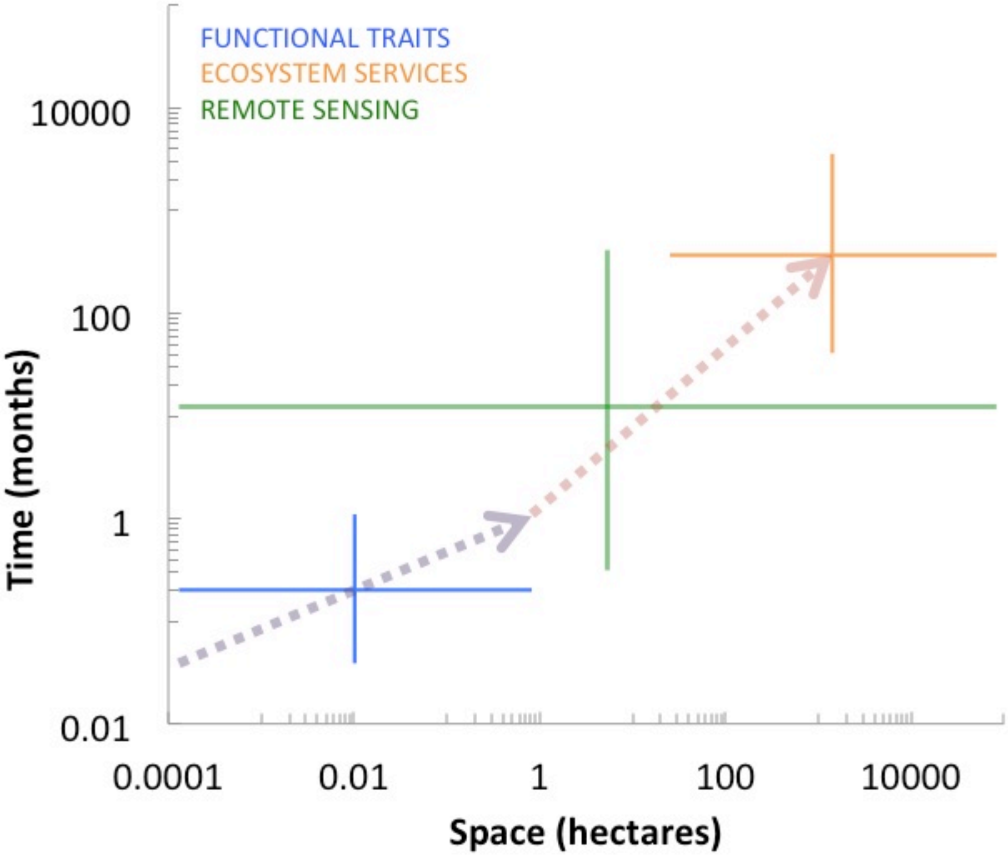

Figure 1.1. The use of functional traits to inform ecosystem service policy and management requires the scaling-up of fine-scale plot-level data from local to regional levels, and remote sensing methods offer the most promising bridge between these spatial scales. In this review, we outline (1; *purple dashed arrow*) the sampling considerations for capturing the necessary variation in effect functional trait composition from individual to community levels so that these proxies can be used for (2; *brown dashed arrow*) the high-resolution scaling of effect functional trait composition from local (i.e., plot) to regional (i.e., landscape) levels using remote sensing methods.

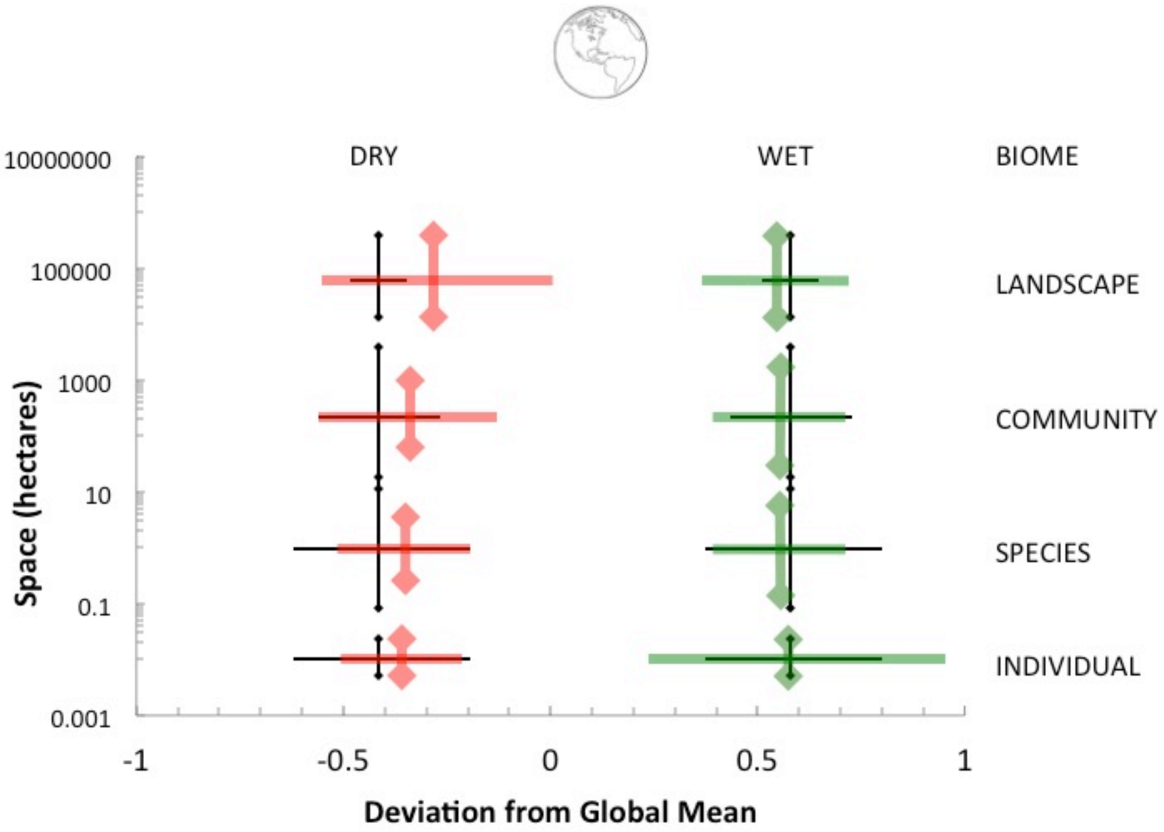

Figure 1.2. Range of hypothetical functional trait value deviation from a global mean encompassing individual to landscape ecological levels across space. Horizontal bars denote the range of deviation around the mean trait value and vertical bars represent the spatial breadth corresponding to each ecological level. Black bars represent trait variation in pristine wet and dry forest biomes, which are assumed to be similar in this example. Colored bars represent scenarios of relatively high (*red*) and low (*green*) degrees of human modification (i.e., land use intensification and landscape fragmentation) that can act to decrease or increase functional trait variation at lower relative to higher levels of ecological organization, respectively. The spatial breadth of each ecological level is relatively reduced in the highly human modified scenario (*red*) due to fragmentation.

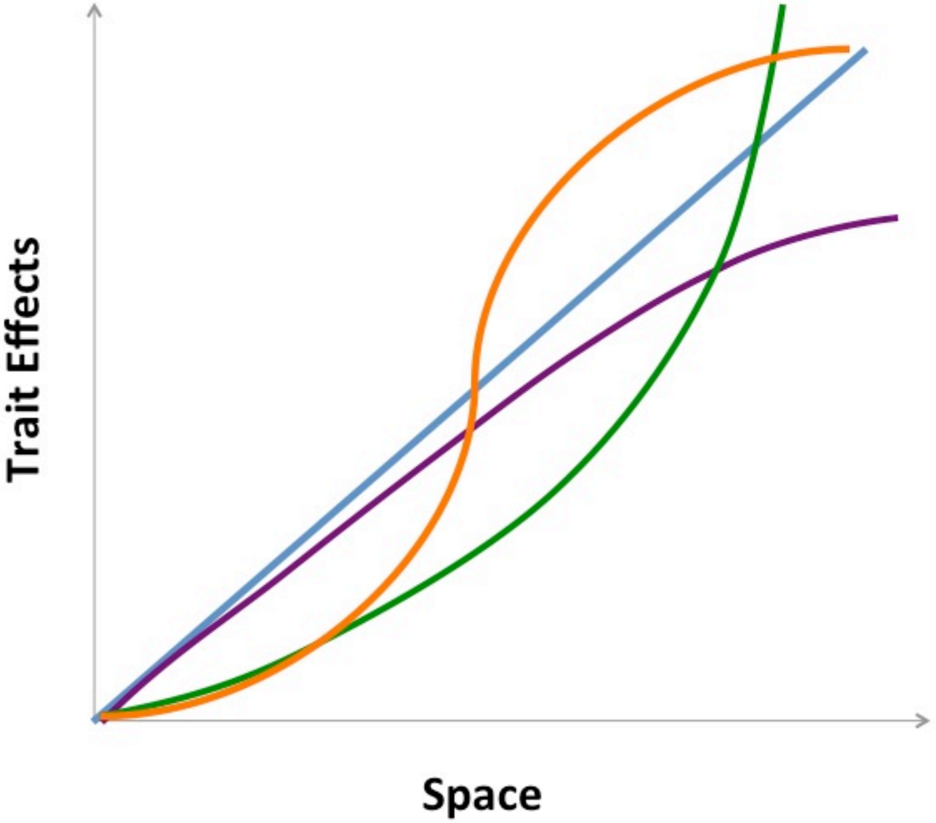

Figure 1.3. Examples of possible relationships of functional trait effects on ecosystem processes across space: a process that depends solely on functional traits across space (*blue*); a process that is dependent on functional traits at low spatial scales but modulated by other factors at increasing spatial scale (*purple*); a process that is driven by functional traits at relatively high spatial scales (*green*); and a process that is highly driven by functional traits at intermediate spatial scales (*orange*).

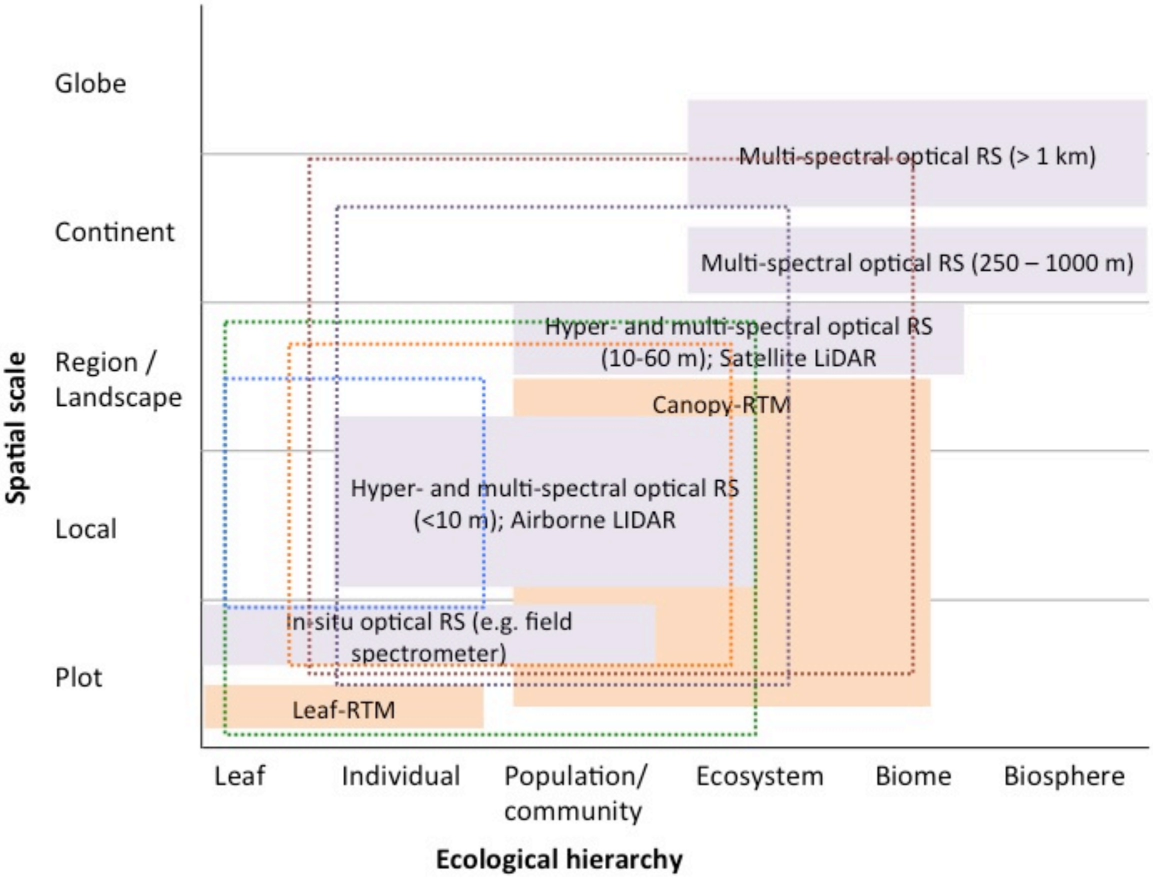

Figure 1.4. Remote sensing (RS) methods for mapping traits and their scales of operation. Radiative transfer models (RTM) use remote sensing data to infer trait values. Dashed boxes represent plant functional traits that have been mapped with remote sensing methods: crown diameter (blue), specific leaf area and leaf [N] (green), phenology (brown), leaf area index (purple), and tree height (orange).

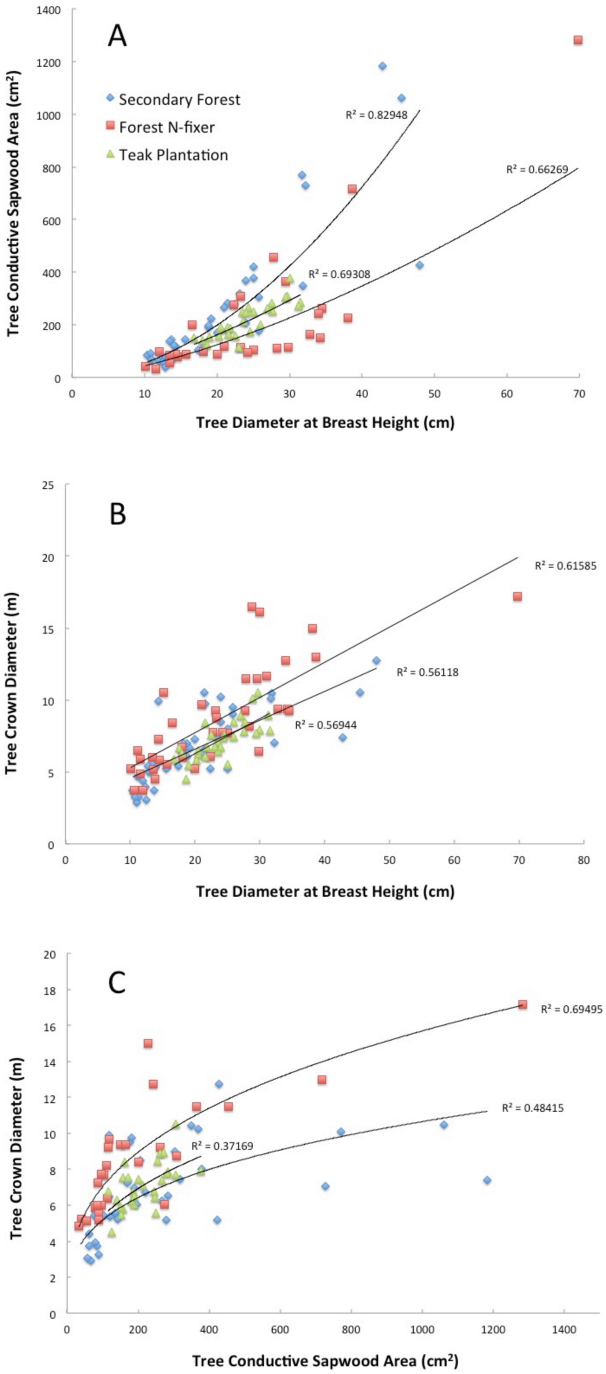

Figure 1.5. Relationships of tree trunk diameter (DBH), sapwood area, and crown diameter for secondary forest trees (non N-fixers), N-fixing trees in secondary forests, and introduced *Tectona grandis* (teak) trees in commercial plantations in the dry tropical Nicoya Peninsula, Costa Rica.

CHAPTER 2. WATER USE, CARBON FIXATION, AND WATER USE EFFICIENCY OF REFORESTATION STRATEGIES IN SEASONALLY DRY COSTA RICA

Abstract

Ecosystem service policies that incentivize reforestation for carbon sequestration may be at odds with the conservation of water supplies in seasonally dry regions and impact human welfare. In this paper, I assess the water to carbon tradeoff in reforestation strategies sponsored by the Payments for Ecosystem Services scheme in seasonally dry Costa Rica. I compared stand level water use, carbon fixation, and water use efficiency in adjacent secondary forests and teak plantations across six paired sites by estimating individual tree water use via sap flux and scaling to the stand level. I found that neither water use or carbon fixation were significantly different between paired secondary forests and teak plantations. However, water use efficiency was significantly higher in teak plantations (mean=1.7 kg C / Mg H_2O, S.E.=0.34) compared to secondary forests (mean=0.50 kg C / Mg H_2O, S.E.=0.062). Contrary to expectation, water use efficiency of secondary forests was negatively related to a gradient of elevation associated to rainfall, and no relationship was found in teak plantations. These results show that, at an annual time scale, secondary forests are not any better than managed teak plantations at conserving water in seasonally dry Costa Rica, with teak plantations fixing significantly more carbon into biomass per volume of water used than native secondary forests.

Introduction

Carbon sequestration policies aimed at climate change mitigation often involve economic incentives for the reforestation of degraded and abandoned agricultural lands. Reforestation fixes atmospheric carbon into woody tissue, which provides long-term storage as above-ground live biomass or as wood products. However, reforestation of previously cleared lands has been linked to decreased water yield in watersheds of seasonally dry regions across the world (Bruijnzeel 2004; Farley et al. 2005). This occurs because replacing pasture with forest vegetation results in higher water losses to the atmosphere through evapotranspiration (Zhang et al. 2001). The transpiration component of evapotranspiration is solely determined by water used for tree growth, which can represent up to nearly 80% of evapotranspiration losses in tropical forests and plantations (Bruijnzeel 1997). This carbon to water tradeoff in the tree water use of reforestation may negatively affect water availability for residents of seasonally dry regions, and place carbon sequestration policies at odds with other ecosystem services and with human welfare (Jackson et al. 2005).

The seasonally dry region of the Nicoya Peninsula in Costa Rica provides a tractable case where reforestation strategies coupled with socio-economic factors have resulted in the reforestation of nearly 40% of the land area in the last 30 years (Arroyo-Mora et al. 2005). Costa Rica’s reforestation strategies include a Payment for Ecosystem Services (PES) scheme where landowners are provided economic incentives to protect forested lands or to reforest previously cleared lands (Pattanayak et al. 2010). Currently, the program provides incentives for reforestation through the protection of secondary forest growth and through the planting of trees for commercial timber production.

In the Nicoya Peninsula, teak (*Tectona grandis*) has become by far the most dominant plantation tree, with about 10% of the landscape currently covered by teak plantations (Serrano 2005). Teak is a deciduous tree native to Asia, and is arguably the most popular and profitable commercial tropical hardwood in the world (Krishnapillay 2000). In Mesoamerica, teak has relatively high water transpiration rates in the growing season compared to native deciduous tree species (Kunert et al. 2010). In addition, teak has lower water use efficiency compared to native Mesoamerican tree species at the sapling stage under controlled conditions (Cernusak et al. 2007). These attributes may render teak plantations to be vigorous water users and to fix relatively less carbon per volume of water used in transpiration compared to other reforestation types, such as native secondary forests, in the Nicoya Peninsula. Therefore, the inclusion of teak plantations as a target of the PES scheme in seasonally dry Costa Rica becomes questionable when considering this region is struck periodically by droughts related to El Niño Southern Oscillation, which have already caused socio-economic changes such as human migration (Vega-García 2005).

Elsewhere in the tropics, unmanaged plantations of other tree species can have higher transpiration water use than native forest cover (e.g., Hawaii; Kagawa et al. 2009). These differences can be due to stand or species traits such as tree density or sapwood to heartwood ratio, respectively. Native forest types can also differ in water use due to the functional traits of dominant species. Such is the case of N-fixing leguminous tree species in the seasonally dry forests of Mesoamerica, which have lower water use compared to other species due to dry season deciduousness and low sapwood to heartwood ratio (Reyes-García et al. 2012). The water use efficiency of tropical secondary forests in relation to that of tree plantations remains relatively unclear in the literature. In managed plantation systems, species mixtures can have higher water use efficiency and be more productive than monocultures (Forrester et al. 2010). This substantiates the prevailing view that species diversity is positively related to productivity and efficiency of resource capture in forest systems (Paquette & Messier 2011; Kunert et al. 2012). At a global level, water use efficiency is negatively related to mean annual rainfall across the world's vegetation types (Huxman et al. 2004).

In this study, I conducted a comparison of water use, carbon fixation, and water use efficiency of secondary forests and teak plantations in the Nicoya Peninsula. I used a paired treatment experimental design to exclude climatic or edaphic differences that may influence growth and water use, and to isolate the effects of stand species composition, structural attributes, and tree functional traits. I expected that teak plantations would have higher water use in transpiration and lower water use efficiency compared to native secondary forests. I also expected that water use efficiency would be negatively related to a natural gradient of increasing elevation and precipitation across the region. I conducted a preliminary analysis to assess how stand structural attributes were related to water use and water use efficiency. This study is a contribution to informing policies destined to improve the provision of multiple ecosystem services.

Study Region

The Nicoya Peninsula in northwestern Costa Rica is located within the Mesoamerican dry tropical forest biodiversity hotspot (Miles et al. 2006) and the Mesoamerican drought corridor (Vega-García 2005). The region includes tropical dry and moist forest types, and has a four to five month dry season between January and May (Table 2.1; Costa Rica National Atlas 2008). The terrain is mostly dominated by mountains that reach up to ~800m in elevation, with wide valleys to the north and in the gulf coast. Across the study region, elevation is related to mean annual rainfall, temperature, and to length of dry season (Table 2.1; Fig. 2.1).

Methods

Site and plot selection

Six study sites were selected across a gradient of precipitation, temperature, and elevation (Table 2.1; Fig. 2.1). On each site, I located areas where near-harvest age teak plantations occurred adjacent to closed-canopy secondary forest with the help of landowners. These adjacent areas were chosen to be as similar as possible in aspect, soils, and topography on each site. A 50 x 10m plot was established on each secondary forest and teak plantation site, spaced by about 30 to 40m from each other, and by about 20m from any forest clearing edges. All trees with diameter at breast height (DBH) ≥10cm within each plot were identified to species and their DBH was recorded and marked with spray paint in the wet season of 2013. The DBH of all trees was re-measured in the dry and wet seasons of 2014.

Tree water use

Tree selection

We selected trees across the DBH range found per species on each plot, including the largest and smallest trees, to conduct tree water use measurements. For teak plantations, we selected five trees per plot distributed at roughly the same intervals across the observed DBH range. For secondary forests, the number of sampled trees per species roughly matched the plot abundance and DBH weighed species importance values (IV). At least four trees were sampled for species with IV above 50%, and at least three trees were sampled for species with IV of 20-50%, distributed at roughly the same intervals across the observed DBH range per species. In addition, at least two trees (the largest and smallest in DBH) were sampled for species with four or less individuals present in the plot. When a species occurred only once, that tree was sampled as well. Stems of multi-stemmed trees were treated as individual trees. The number of trees sampled in secondary forest plots ranged from 10 to 20.

Water use measurements

Weekly (6-8 day) wet season tree water use was measured at least once on each selected tree with manufactured sensors that use the heat ratio method to estimate sap flow velocity in cm/hr (Burgess et al. 2001; Burgess & Downey 2014). Each sensor consists of three probes that are inserted into parallel holes (~1mm in diameter spaced by 5mm) drilled into the surface of the tree (bark removed) with measurement points at 1.25 and 2.75cm depths into the tree trunk (Fig. 2.2). Measurements were taken continuously (day and night) at 15min. intervals throughout the sampling period. Two sensors were inserted at about breast height into opposite sides (roughly N and S) of all measured trees with DBH ≥15cm, and one sensor was inserted on trees between 10-15cm DBH. In addition, a special set of longer sensors with measurement points at 2.75 and 4.25cm was used to measure deeper sap flux on one side of the largest tree per species, and subsequently to conduct sap flux measurements across the radial profile of species with sap flux deeper than 6cm. All measurements were conducted during the wet seasons of 2013 and 2014.

Sap flow depth

Sap flow depth was estimated for each sampled tree by inserting green or red dye into a ~10cm drill hole at about breast height. After ~90 minutes, a tree core was retrieved at ~3cm above the drill hole and the depth of staining was used to estimate sap flow depth. For some species, the sapwood-heartwood boundary is readily visible and this was recorded as well. This procedure was done on opposite sides of trees ≥15cm DBH, and on one side of trees with DBH <15cm. Sap flow depth was estimated as the mean dyeing depth of the two cores for trees ≥15cm DBH. In some cases for some species (e.g., *Caesalpinia eriostachys*, *Lysiloma divaricata*, and *Tectona grandis*), the dyeing method underestimated sap flow depth based on actual sap flux measurements, and therefore the sapwood-heartwood boundary was used as the sap flow depth estimate in those cases (Reyes-García et al. 2012). Sampling of sap flow depth was conducted after water use was sampled on all trees to avoid damage to the tree trunk prior to sampling. Inevitably, sap flux was sampled afterwards on trees were deeper sap flux radial profiles were needed. In a few cases where sap flow depth was deeper than 8cm, a longer drill hole (~20cm) was used to estimate sap flow depth.

Radial profiles

I sampled deeper radial profiles of sap flow in trees with sap flow depth >6cm using the special set of longer sensors at increasing 1.5cm depth intervals starting from 4.25cm and up to 8.75cm depth in the tree with the highest sap flow depth (Fig. 2.2). Sampling of sap flow at and beyond the 4.25cm depth was only conducted on one side of each tree. In order to get access to depths beyond 4.25cm, I progressively removed wood disks at 1.5cm intervals so that sensors could be installed at the desired depth. Due to logistical constraints, radial sampling beyond the 4.25cm depth may have occurred at different points in time during the wet season for each tree sampled. To adjust for this temporal mismatch, sap flux at 1.25 and 2.75cm depths was conducted every time a radial profile depth was sampled so that estimates of sap flux at each radial point could be expressed as the ratio to sap flux co-occurring in the two outermost measuring points.

Individual tree water use estimation

Each tree was treated as a series of concentric rings, the midpoint of each ring located at 1.5cm increments into the tree starting from the outermost sensor, which was located at 1.25cm of depth (Fig. 2.2; Hatton et al. 1990). Sensors beyond the outer ring were located at the midpoint of each ring, and sap flux velocity from these sensors were assigned to the area of each corresponding ring to estimate sap flow rate (cm^3/hr) for that concentric ring. The sensor at 1.25cm depth was used to estimate the sap flow rate of the outermost ring in the same manner. Thus, the width of the outermost ring was 2cm and all other rings where 1.5cm in width. Sap flux beyond the innermost measured ring was estimated as a function of linear decrease of sap flux velocity in that ring to the innermost depth of sap flow. In ~90% of all cases, this area constituted less than a third of the estimated sap flow depth, and no more than 45% of the sap flow depth in all other cases (n=6 trees).

The heat ratio method uses a correction factor on the sap flow rate estimation to account for species variation in the thermal diffusivity of wood, which can be estimated from the fresh and dry mass, and fresh volume of a wood sample (Burgess et al. 2001). I collected two wood cores ~5cm deep and 5.15cm wide from opposite sides of each sampled tree ≥15 cm DBH, and one core from one side of each sampled tree trees <15cm DBH. These samples were weighed fresh and after 48 hours at 105°C in a drying oven. Fresh volume was estimated from the width and length of the borer in mm.

Cumulated water volume (cm^3) per ring was estimated for each 15 min. interval sap flow rate value and summed to estimate daily water use (cm^3/day) for each day in the sampling period. The daily water use of the two outermost rings was estimated as the sum of the mean daily water use measured by the two sensors placed on each ring for trees ≥15cm DBH. Values from one sensor was used to estimate daily water use in the outermost rings of trees <15cm DBH. Likewise, daily water use for concentric rings at and beyond 4.25cm depth were based on measurements from one sensor. In trees where one or two radial depths were sampled during different sampling periods in the wet season, the water use in those concentric rings was estimated as the product of the daily water use in the outermost rings times the ratio of daily water use of the concentric ring to that of the outermost rings during the period where that ring was sampled (n=6 trees). Finally, daily whole tree water use was estimated from the sum of daily water use for each concentric ring present in each tree, including the ring area beyond the innermost measured ring for which sap flux velocity was estimated based on linear decrease, and expressed as kg/day. All daily water use estimations were done using the Sap Flow Tool software (http://www.sapflowtool.com; ICT 2015).

Stand water use

For each plot, I developed linear and power regressions of daily tree water use to DBH for each sampled tree species. I did the same for secondary forest trees in the following three functional groups: evergreen, deciduous, and N-fixers (Table 2.2). I selected the equations with the best fit (R^2) of either linear or power relationships. In theory, power relationships better describe the relationship between DBH and water use (Enquist 2002; Meinzer et al.

2005). These were preferred in cases were the best fit was equal, or where linear relationships had negative y-intercepts when crossing the x-axis above 10cm DBH, which was not observed in these data. Secondary forest water use was estimated by applying these equations to the DBH measured in 2013 for all trees in the plot by species or functional groups, and summing the estimated daily water use per tree for each plot. In the case of species or functional groups represented by a single tree, the daily water use of that sampled tree was added to the estimate obtained by regression equations for the rest of the trees in each plot. Linear or power equations were applied in the same manner to estimate water use per plot in teak plantations. However, since the fit of equations for some teak plantations plots was low, plot water use was also estimated by assigning the mean daily water use of the five sampled teak trees to all trees in each plot.

Stand-level daily water use was expressed in kg/ha/day for the wet season based on the sum of mean daily water use per tree in each plot. Annual stand water use was estimated as the product of daily wet season water use and the length of the growing season for each species based on phenology. This was estimated to be 9 months (274 days) for deciduous, N-fixing, and teak trees, and 12 months (365 days) for evergreen trees, which only occurred at one site (Fig. 2.3; Table 2.2). Although tree water use was sampled during the dry season, and during the wet to dry and dry to wet season transitions, these data were not included in this analysis. All individual tree water use to DBH regressions were performed in Microsoft Excel.

Stand carbon fixation and water use efficiency

I searched for species-specific allometric equations to predict individual tree above-ground biomass in the FAO's Global Allometry of Trees database (http://www.globallometree.org) and in the published literature using Google scholar with the species genus and the phrase "biomass equation" as search queries. I used species to genus-specific equations when found from sources deemed reliable and when they covered the DBH range found for each species (Tables 2.2 & 2.3). For all other species in secondary forests, the equations for moist and dry forests from Chave et al. (2005) were used depending on the climate of each site (Table 2.1). For plantations, an equation developed for teak plantations in Costa Rica was used (Pérez & Kanninen 2003). Some equations used tree height and wood density to estimate biomass. I sampled tree height for all trees in the plots during the wet season of 2014. I estimated wood density based on the fresh and dry (48 hours at 105°C) mass and fresh volume of one complete core taken from the tree surface to mid-DBH of one randomly selected tree per species per site. This sample was then analyzed for total carbon (%) by combustion.

I applied each selected allometric equation to the DBH of trees in the wet seasons of 2013 and 2014. I subtracted the estimated biomass in 2013 from the 2014 estimate for each tree to estimate biomass gain (kg). Carbon fixed per tree was estimated as the product of the total carbon (%/100) for each tree species times the biomass gain for each tree between 2013 and 2014. Carbon gain per tree was summed for each plot and stand-level carbon fixation was expressed as kg/ha/yr. Stand water use efficiency was estimated by dividing stand-level carbon fixation (kg/ha/yr) by stand-level water use (Mg/ha/yr) and expressed as kg C / Mg H_2O.

Data analysis

I used paired T-tests to determine if there were significant ($p<0.05$) differences in stand level wet season water use (kg/ha/day) estimates obtained by species or functional group based regressions of individual tree water use to DBH for secondary forests plots, and between estimates obtained by regression to DBH or by tree means per plot for teak trees in plantations. I also used paired T-tests to compare stand wet season water use (kg/ha/day), annual water use (Mg/ha/yr), carbon fixed (kg/ha/yr), and water use efficiency (kg C / Mg H_2O) between secondary forests and teak plantation treatments. A goodness of fit test showed that nearly all of these data were not normally distributed but rather had log-normal distributions. Therefore, all data was log-transformed to conduct each T-test when necessary. In such cases, non-parametric Kruskal-Wallis tests were done concurrently and the results of both tests are reported. I used linear regression analysis to determine if stand wet season water use, annual water use, carbon fixed, and water use efficiency were related to gradients of elevation, temperature, and precipitation. I also used linear regression to assess how stand tree density and basal area were related to water use, carbon fixation, and water use efficiency across all sites. All statistical tests were conducted using JMP 11 statistical software (SAS Institute Inc. 2013).

Results

Tree daily water use

I measured wet season daily water use of a total of 79 secondary forest trees belonging to 22 species, and 30 teak plantation trees across all sites (Table 2.2). Mean daily water use ranged from 0.04 to 230 kg/day in secondary forest trees, and from 5 to 80 kg/day in teak plantation trees across all sites (Fig. 2.4; Appendix A). Out of 18 regressions of wet season individual tree water use to DBH performed per species across all secondary forest sites, only once did a linear fit had better predictive power (R^2) over a power fit (Appendix A). The lowest fit of species based regression equations had R^2 values of 0.2 and 0.4 respectively, and all other equations had R^2 values above 0.7 (Appendix A). Similarly, power equations performed better in seven out of eight regressions of wet season individual tree water use to DBH by functional groups across all secondary forest sites (Fig. 2.4). However, the only linear fit with higher predictive power than a power fit (R^2 of 0.8 vs. 0.9, respectively) assigned negative daily water use values to trees for which positive values were measured in the field, and therefore the power equation was used. The two lowest fits of functional group based regression equations had an R^2 value of 0.6, and all other equations had R^2 values above 0.8 (Fig. 2.4). For teak plantations, linear regressions yielded equations with higher predictive power in all but one case, and R^2 values ranged from 0.04 to 1 (Fig. 2.4). The mean of the daily water use per tree for the five teak plantation trees sampled per site ranged from 24 to 50kg/day per site.

Comparison of stand-level wet season water use estimates

For secondary forests, there were no significant differences between stand-level wet season daily water use estimates obtained by species or functional group based regressions of individual tree daily water use and DBH (Fig. 2.5a; T-test (Log): n=6, df=9.9, p=0.97; Kruskal-Wallis: df=1, p=1). Likewise, there were no significant differences between stand-level wet season water use estimates obtained by regressions of individual tree daily water use and DBH, or daily water use means by tree for teak plantations (Fig. 2.5b; T-Test: n=6, df=9.9, p=0.80). All subsequent results on stand-level water use are based on daily water use to DBH regressions for teak trees in plantations and for trees by functional groups in secondary forests. However, all statistical tests were also carried out using either species-based tree daily water use to DBH regressions for secondary forests, and mean daily water use values per tree for teak plantations (Appendix B), with virtually the same results for the significance of observed differences in each statistical test (results not shown). In addition, since evergreen species occurred only at one secondary forest site, most results for wet season and annual water use per stands are redundant. I chose to be inclusive in this case and present the results for both estimates in this paper.

Water use, carbon fixed, and water use efficiency by treatment

Wet season stand-level daily water use ranged from 8235 to 31,401 kg/ha/day in secondary forests, and from 3648 to 12,411 kg/ha/day in teak plantations (Appendix B). There were no significant differences in wet season stand-level daily water use between secondary forests and teak plantations (Table 2.4; Fig. 2.6a; T-test (Log): n=12, df=10, p=0.10; Kruskal-Wallis: n=12, df=1, p=0.11). Annual water use ranged from 2254 to 8596 Mg/ha/yr in secondary forests and from 999 to 3397 Mg/ha/yr in teak plantations, and carbon fixation ranged from 997 to 5783 kg/ha/yr in secondary forests and from 2040 to 8581 kg/ha/yr in teak plantations (Appendix B). There were also no significant differences in yearly water use (Table 2.4; Fig. 2.6b; T-test (Log): n=12, df=9.9, p=0.09; Kruskal-Wallis: n=12, df=1, p=0.11) and carbon fixation (Fig. 2.6c; T-test (Log): n=12, df=9.2, p=0.08; Kruskal-Wallis: n=12, df=1, p=0.05) between secondary forests and teak plantations. Water use efficiency was significantly higher in teak plantations compared to secondary forests (Table 2.4; Fig. 2.6d; T-test (Log): n=12, df=9.2, p=0.0008; Kruskal-Wallis: n=12, df=1, p=0.0039), and ranged from 0.26 to 0.67 kg C / Mg H_2O in secondary forests and from 0.94 to 2.84 kg C / Mg H_2O in teak plantations (Appendix B).

Gradient effects on water use, carbon fixation, and water use efficiency

Elevation was positively and significantly related to wet season daily water use of secondary forests (Fig. 2.7a; R^2=0.67, p=0.048) but unrelated to daily water use of teak plantations (R^2 =0.11, p=0.52). Annual water use of secondary forests was also positively related to elevation (Fig. 2.7b) although this relationship was only marginally significant (R^2=0.64, p=0.056). Carbon fixation in secondary forests was positively and significantly related to elevation (Fig. 2.7c; R^2=0.87, p=0.007) but not so in teak plantations (R^2=0.05, p=0.67). Water use efficiency of secondary forests was positively related to elevation (Fig. 2.7d) although this was only marginally significant (R^2=0.63, p=0.059), and not so in teak plantations (R^2=0.08, p=0.58). Neither rainfall nor temperature was significantly related to daily wet season or yearly water use, yearly carbon fixation, or water use efficiency in secondary forests or plantations.

Structural effects on water use, carbon fixation, and water use efficiency

Across all sites, wet season and annual water use was positively related to both tree density (Figs. 2.8a & b; R^2=0.58, p=0.004; and R^2=0.54, p=0.007; respectively) and stand basal area (Fig. 2.8c & 8d; R^2=0.81, p<0.0001; and R^2=0.85, p<0.0001, respectively). Neither carbon fixation or water use efficiency was related to tree density (R^2=0.09, p=0.3; and R^2=0.1, p=0.3) or basal area (R^2=0.04, p=0.5; and R^2=0.2, p=0.2; respectively).

Discussion

To my knowledge, this is the first replicated comparison of water use and water use efficiency between tropical secondary forests and tree plantations. These systems are becoming more common across Mesoamerica as a result of agricultural abandonment and reforestation incentives (Chazdon 2008). My study shows that there are no clear differences in water use between secondary forests and teak plantations in seasonally dry Costa Rica (Figs. 2.6a & b). Surprisingly, water use efficiency was consistently and significantly higher in teak plantations than the secondary forests growing right next to them (Fig. 2.6d). This contrasts with the hypothesis that productivity and the efficiency of resource capture in forested systems is increased under conditions of higher species diversity (Paquette &

Messier 2011; Kunert et al. 2012). Perhaps this pattern is not directly transferable to managed systems, such as plantations. Similar results were observed by Kunert et al. (2012) in Panamá where the water use efficiency of monocultures, which were expected to be the lowest, turned out to be higher than that of the most species rich plantation mixtures.

Contrary to expectation, the water use efficiency of secondary forests was not related to rainfall and was positively related to elevation (Fig. 2.7d), although this relationship was only marginally significant (p=0.06). This means that the secondary forests growing under the driest conditions where the least water use efficient. This may be the result of higher carbon losses to respiration in secondary forests growing in the lower and hotter part of the elevation gradient (Table 2.1). Both water use and carbon fixation had a positive and significant relation with elevation in secondary forests yet the rate of increase in carbon fixation with elevation was somewhat higher, partially offsetting the correlation and driving the increase in water use efficiency of secondary forests across the elevation gradient (Fig. 2.7). Unexpectedly, teak plantations showed no patterns of water use or water use efficiency across the studied gradient, further illustrating different rules can apply to managed systems.

Management in teak plantations can act to increase water use efficiency by pruning and thinning for high growth rates. Pruning and thinning maximize the amount of photosynthetic active radiation available for each tree by reducing shading, possibly leading to higher photosynthetic rates under the same water demand conditions as co-occurring secondary forests and resulting in higher water use efficiency. In addition, teak is native and naturally adapted to an Indian monsoon climate that is very similar to that found across the Nicoya

Peninsula, dominated by abundant summer rains and a very dry winter season. Thus, teak is potentially located within the optimum of its precipitation gradient space in the Nicoya Peninsula, which can lead to the maximization of net productivity for the resources available, in this case water in particular (Hall et al. 1992). Taking this into consideration, the finding by Cernusak et al. (2007) that teak has lower water use efficiency compared to all other Mesoamerican tree species tested in their study may have been due to controlled growing conditions that were not near teak's optimum. In all, both management and environmental conditions result in relatively low water use and high carbon fixation rates in teak plantations, which drive higher water use efficiency (Fig. 2.6).

Stand tree density and basal area were main drivers of water use across all sites (Fig. 2.8). Similar results were obtained by Kagawa et al. (2009) in their comparison of native forests and unmanaged introduced tree plantations in Hawaii. In that case higher tree density was partly the cause of higher water losses in tree plantations, not native forests. Controlling for the effects of tree density and basal area is very difficult because these are mostly the result of natural conditions in secondary forests and mostly the result of management practices in plantations. This study shows that at the tree density and basal area that secondary forests occur and teak plantations are managed for in this region (Table 2.1; Guariguata & Ostertag 2001; Bermejo et al. 2004), teak plantations are more water use efficient than natural secondary forests. The drivers of tree to stand level water use are discussed in more detail in the next chapter. However, I discuss some of these factors preliminarily in the next paragraph.

Large (>40cm DBH) trees drive high water use in secondary forest sites. In particular, large trees of the species *Anacardium excelsum* and *Schyzolobium parahyba*, which dominated the secondary forest sites Santa Marta and La Libertad, respectively, drove high water use at those sites (Tables 2.1 & 2.2; Figs. 2.4c & e; Appendix B). Not only are these trees large; they also possess relatively high sapwood to heartwood ratio. In contrast, the secondary forests dominated by the N-fixing species *Caesalpinia eriostachys* and *Lysiloma divaricata* where the only ones that displayed lower water use than their adjacent teak plantation counterparts (Table 2.1; Appendix B). The relatively low sapwood to heartwood ratio of N-fixing species acts to conserve water relative to teak plantations and other secondary forest species, as found elsewhere in Mesoamerica (Reyes-García et al. 2012). Another example further illustrates this. The largest tree in this study was an *Enterolobium cyclocarpum* tree, an N-fixer of ~70cm DBH. In spite the high capacitance brought about by tree size likely helped sustain high sap flux velocities for longer time periods in this tree (Goldstein et al. 1998), the tree with the highest daily water use was a co-occurring *Anacardium excelsum* tree of 46cm DBH (230 vs. 198 kg/day; Fig. 2.4e).

A longstanding view in ecology is that natural systems become more efficient at capturing resources as they mature (Odum 1969). In this study, sites were at near-mature conditions for each treatment based on the maxing out of tree basal area with age in secondary forests and managed teak plantations, which occurs at about 20-30 years and 10-15 years, respectively (Table 2.1; Guariguata & Ostertag 2001; Bermejo et al. 2004). In the case of teak plantations, management acts to curb basal area to a relatively constant value, meaning that these systems are still growing. The results in this study are therefore more consistent with the view that systems become more leaky and less efficient at capturing resources as they mature (Vitousek & Reiners 1975). In this case, the large size of trees in some secondary forest sites appears to drive this leakiness, but the functional traits of other tree species counteracts it in other secondary forest sites.

Water use of trees <10cm DBH and other understory vegetation were not quantified in this study. Understory vegetation constituted ~70% of the water use of native forests in Hawaii; however that native forest was dominated by a relatively small sized endemic tree species (Kagawa et al. 2009). Due to the range of tree sizes in this study, it is unlikely that understory vegetation constitutes such a large proportion of the stand-level water use. Accounting for such losses would increase secondary forest water use relative to teak plantations, as management in these plantations includes the removal of understory vegetation. An exceptional case was the teak plantation at La Cueva, where an understory *Attalea rostrata* palm tree of ~30cm DBH was present in the plot. Although sap flow was measured in this palm tree, I could not include it in this analysis because proper estimation of sap flow depth and other parameters that require stem coring was not possible due to the morphological differences of palms. La Cueva was one of the two sites where teak plantations had higher water use compared to its secondary forest counterpart (Appendix B).

The analysis presented here did not include data on tree water use collected during the dry season, and during the wet to dry and dry to wet transitions. These can be analyzed for a future version of this paper. I believe it is unlikely that the patterns described in this paper will change much when including those estimates because they represent a relatively small portion of the year where sap flux in most trees decreases significantly due to decreasing transpiration surfaces in leaf cover, and all but one secondary forest site are deciduous as are all teak plantations (Fig. 2.3). Water use preliminarily appeared to be relatively proportional to leaf cover in the dry season (data not shown), suggesting the assumption of zero water use during months of low leaf cover is not far from true. During the wet to dry and dry to wet transitions, tree water use appeared to match that of the wet season. Future analysis can yield if water use in those seasons offsets the patterns observed here. However, the differences found in water use efficiency between secondary forests and teak plantations are so striking that I believe they are not likely to change when accounting for differences in water fluxes during those periods.

All analyses presented on tree water use were based on data gathered during the wet season. Radial profiles of sap flux velocity across the tree stem can change across seasons (Jiménez et al. 2000). Since I was not able to conduct full radial profile measurements in the dry and dry to wet transitions, estimates of tree water use for those periods would suffer from relatively larger error if based on wet season sap flux radial profiles or linear decline of sap flux velocity beyond the deepest point of measurement.

Tree mortality was excluded from this analysis. Tree mortality occurred in secondary forests through the apparently natural death of some trees, possibly related to the strong dry season in 2013, and due to wood harvesting by local residents at one site. Harvesting of some trees was also done in half of the teak plantation sites during the study, and these were excluded as well. It is beyond the breadth of this study to assess the impact of natural tree mortality or tree harvest on water or carbon fluxes because these processes operate at different time scales than the focus of this study (see below).

Policy and management implications

This study shows teak plantations are as vigorous water users as are native secondary forests in seasonally dry Costa Rica. From an ecosystem service policy point of view, neither of these options is better than the other at conserving water and improving watershed water yield by decreasing water losses to the atmosphere. Although this paper focused only on the transpiration component of evapotranspiration, other data collected concurrently with this study shows that canopy interception, which constitutes the largest component of surface evaporation (non-transpiration) water loss in forest evapotranspiration (Bruijnzeel 1997), is very similar between secondary forests and teak plantations. In this case, evaporation losses due to canopy interception constituted ~10-15% of incident precipitation, which is very similar to forests and plantations elsewhere in the tropics (Bruijnzeel 1997).

There is much debate on the effects of reforestation on watershed water yield (Bruijnzeel 2004). Proponents of the "infiltration tradeoff" hypothesis suggest that the gains in water infiltration into the soil under forested relative to pasture vegetation offset the increased losses in evapotranspiration, and result in increased water yield in forested watersheds (Krishnaswamy et al. 2013). In comparative studies elsewhere in the tropics, teak plantations have infiltration rates higher than pastures and comparable to those of secondary forests (Mapa 1995; Zimmermann et al. 2006). Thus, it is unlikely that a scenario where the infiltration tradeoff hypothesis is at work will offset the patterns in water use and implications for water yield observed in this study. To be completely certain of this, studies of infiltration across secondary forests and teak plantations in this region are needed.

Ecosystem service policy requires the consideration of multiple ecosystem services. The Costa Rica PES scheme explicitly considers hydrological, carbon sequestration, scenic, and biodiversity conservation ecosystem services (Pattanayak et al. 2010). This study illustrates that as they near maturity, secondary forests are not any better than teak plantations at providing hydrological and carbon sequestration services at the annual scale. Uncertainties at longer time scales remain. For example, the fate of sequestered carbon contrasts between these treatments: in secondary forests it is largely determined by tree mortality and decomposition rates whereas in teak plantations it largely depends on the end use of commercial wood. When plantations are harvested and cleared, drastic changes in water fluxes likely occur beginning with an immediate cessation of transpiration fluxes, and an increase on soil surface evaporation fluxes. Harvesting during the wet season can also lead to significant soil erosion if proper management practices are not met. As plantations regrow, transpiration again becomes the main water loss pathway although probably never as high during early growth stages compared to mature plantations, given the positive relationship between water use, tree density, and basal area (Fig. 2.8). These changes occur at a timescale of the 15-20 year teak harvest cycle and could be further assessed by spatio-temporal modeling provided the rates of water and carbon fluxes are known across growth stages.

Differences in scenic ecosystem services between secondary forests and teak plantations can be subjective and difficult to assess. Biodiversity conservation ecosystem services are more tractable, and in this case it is evident that secondary forests harbor more native tree species biodiversity than managed teak plantations. However, the diversity of juvenile native tree species occurring in the understory of unmanaged or abandoned teak plantations is not that different from that of co-occurring native secondary forests in Mesoamerica (Wolfe et al. 2015). In a world full of novel ecological surprises, the introduction of teak and its possible naturalization in seasonally dry Costa Rica may not have negative consequences for tree biodiversity in the long-term but this remains to be seen (Hobbs et al. 2006). At an annual timescale, reforestation by managed teak plantations is as good as reforestation by native secondary forest growth if the main purposes are to conserve water supplies and sequester carbon.

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Tables

Table 2.1. Study site climate, soils, topography, and structural attributes by life zones.

Site	Elev-ation (m)	Annual rainfall (mm)	Temp. (C^o)	Dry mo.	Slope (%)*	Soil Order	Age*	Tree Density (trees/ha) *	Basal Area (m^2/ha)*	Dominant Secondary Forest Species (Importance Value in %)
						Dry				
Vigia	65	1874	26.3	5	2.5	Vertisol	35- 10	320 - 200	16.4 - 8.8	*Tabebuia guayacan* (24)
Copal	75	1902	26.4	5	27-28	Inceptisol	25 - 12	340 - 340	17.6 - 13.0	*Lysiloma divaricata* (28)
Pueblo Viejo	85	2018	26.3	5	31-14	Alfisol	20 - 10	380 - 380	18.2 - 14.2	*Lysiloma divaricata* (92)
						Moist				
Santa Marta	190	2163	23.4	4	24-33	Alfisol	25 - 14	360 - 200	27.5 - 12.4	*Anacardium excelsum* (64)
La Cueva	210	2101	25.7	4	40-60	Alfisol	20 - 12	460 - 220	19.1 - 14.3	*Caesalpinia eriostachys* (80)
La Libertad	410	2040	24.5	4	30-25	Alfisol	30 - 14	620 - 380	36.8 - 18.3	*Schyzolobium parahyba* (65)

*Values of secondary forests and teak plantations separated by a dash.

Table 2.2. Summary of trees sampled for water use in this study.

Species	Functional Group	Number of Trees	DBH Range	Number of Sites
Anacardium excelsum	Evergreen	6	10.4 – 46.0	1
Byrsonima crassifolia	Deciduous	3	14.4 – 31.8	1
Caesalpinia eriostachys	N Fixer	14	10-1 – 34.2	3
Casearia sylvestris	Evergreen	1	14	1
Cassia grandis	N Fixer	2	17.7 – 22.3	1
Cecropia peltata	Deciduous	2	11.0 – 19.2	1
Cordia alliodora	Deciduous	2	12.5 – 33.3	1
Dalbergia retusa	N Fixer	2	12 – 27.8	1
Enterolobium cyclocarpum	N Fixer	1	71.3	1
Eugenia hiraifolia	Deciduous	3	11.5 – 48.0	3
*Gmelina arborea**	Deciduous	3	10.0 – 24.0	1
Guazuma ulmifolia	Deciduous	8	10.8 – 25.8	3
Lonchocarpus felipei	N Fixer	1	12.4	1
Lonchocarpus minimiflorus	N Fixer	4	12.0 – 39.4	2
Lysiloma divaricata	N Fixer	13	10.6 – 38.1	3
Ocotea veraguensis	Evergreen	2	13.4 – 18.8	1
Pseudobombax septenatum	Deciduous	1	44.4	1
Rhedra trinervis	Deciduous	1	21.5	1
Samanea saman	N Fixer	2	17.5 – 30.0	1
Schyzolobium parahyba	Deciduous	4	17.6 – 44.2	1
Tabebuia guayacan	Deciduous	3	12.9 – 25.8	1
Ximenia americana	Deciduous	1	11.4	1
*Tectona grandis**	Deciduous	30	16.8 – 31.5	6

* Introduced species

Table 2.3. Allometric equations to predict above-ground biomass (kg) per tree used in this study.

Species or Guild	Equation	Source
Byrsonima crassifolia	e^(-1.696+2.226*Ln(DBH))	Van Breugel et al. 2011
*Caesalpinia pyramidalis**	$0.2365*DBH^{2.1928}$	Sampaio & Silva 2005
Casearia sylvestris	e^(-1.939+2.437*Ln(DBH)	Van Breugel et al. 2011
Cecropia spp.	e^(-3.78+0.95*Ln(DBH^2)+Ln(H)) +(-0.56+0.02*DBH^2-0.04H)	Uhl et al. 1988
Cordia alliodora	$0.0391*((DBH^2*H)^{0.5151})+0.0085*((DBH^2*H)^{1.045})+0.0853*((DBH^2*H)^{0.5345})$	Cole & Ewel 2006
Gmelina arborea	e^(-3.38+0.92*Ln((DBH^2)*H))	Onyekwelu 2004
Guazuma ulmifolia	e^(-1.62+2.12*Ln(DBH))	Douterlungne et al. 2013
Schyzolobium parahyba	$(4.59+0.014*(DBH^2)+0.234*H)^2$	Álvarez 2008
Tectona grandis	10^(-0.815+2.382*Log(DBH))	Pérez & Kanninen 2003
Dry Forest Trees	0.112*(WD*(DBH^2)*H)^0.916	Chave et al. 2005
Moist Forest Trees	0.0509*WD*(DBH^2)*H	Chave et al. 2005

*Surrogate for con-generic species in this study

Table 2.4. Mean water use, carbon fixation, and water use efficiency in secondary forests and teak plantations (n=6). Standard error is in parenthesis next to the mean. Values in bold are statistically different to p=0.0039.

	Secondary Forests	Teak Plantations
Wet Season Water Use (kg/day/ha)	15,488 (*3450*)	9183 (*1351*)
Annual Water Use (Mg/ha/yr)	4400 (*978*)	2514 (*370*)
Carbon Fixed (kg/ha/yr)	2281 (*745*)	4007 (*948*)
Water Use Efficiency (kg C / Mg H_2O)	**0.495** (*0.062*)	**1.700** (*0.340*)

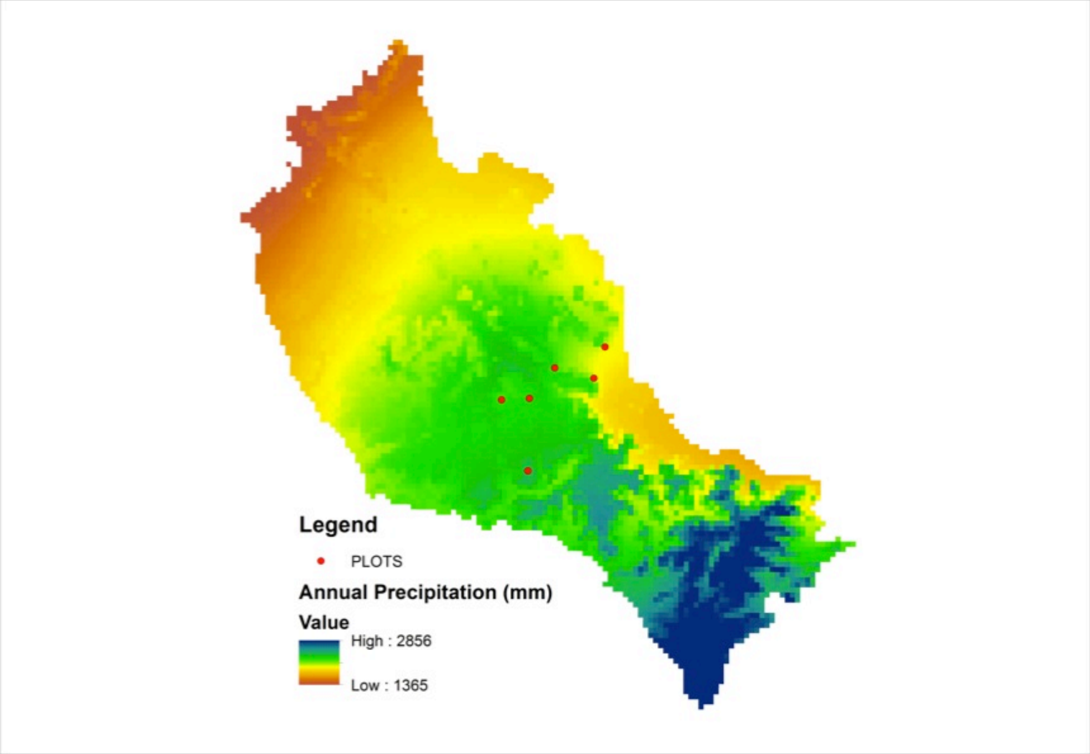

Figure 2.1. Location of study sites (plots) in the Nicoya Peninsula of Costa Rica across a gradient of mean annual precipitation (Hijmans et al. 2005).

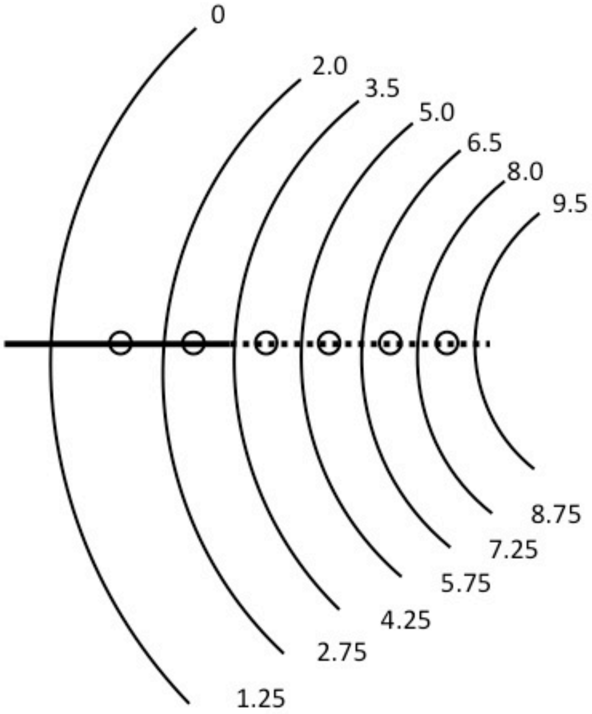

Figure 2.2. Schematic diagram of sap flow sensor installation and concentric rings used to estimate tree water use. Upper numbers indicate ring boundaries in centimeters of depth starting from the tree surface (0cm; bark removed), and lower numbers indicate the position of sap flow sensor thermistors (empty circles) in centimeters starting from the outermost sensor (1.25cm). The solid black line across the two outermost thermistors represents the sensor thermistor positions installed across all trees in this study, and the dashed line represents the sensor thermistor positions installed across trees with deeper sap flow depth. This specific example corresponds to the tree with the deepest sap flow depth in the study.

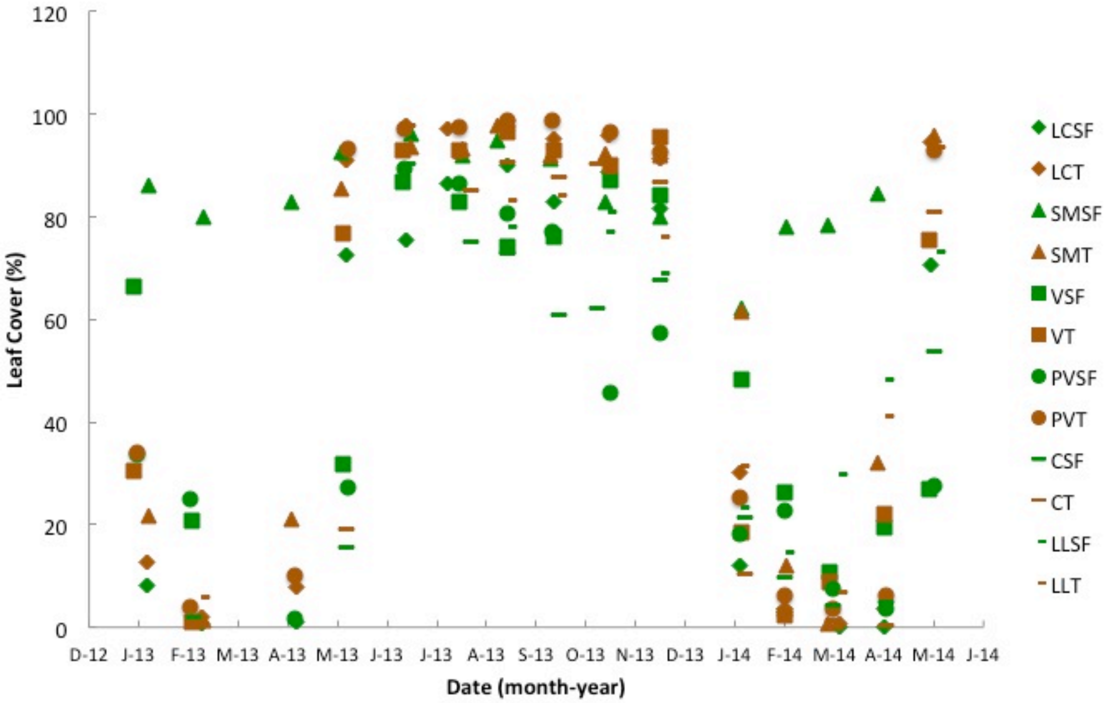

Figure 2.3. Seasonal variation in leaf phenology across all study sites. Each data point represents the mean value of leaf cover (%) for all trees in each site, visually estimated for each individual tree at approximately monthly intervals. For each secondary forest (SF; green) and teak plantation (T; brown) treatment, the site codes are: La Cueva (LC), Santa Marta (SM), Vigia (V), Pueblo Viejo (PV), Copal (C), and La Libertad (LL).

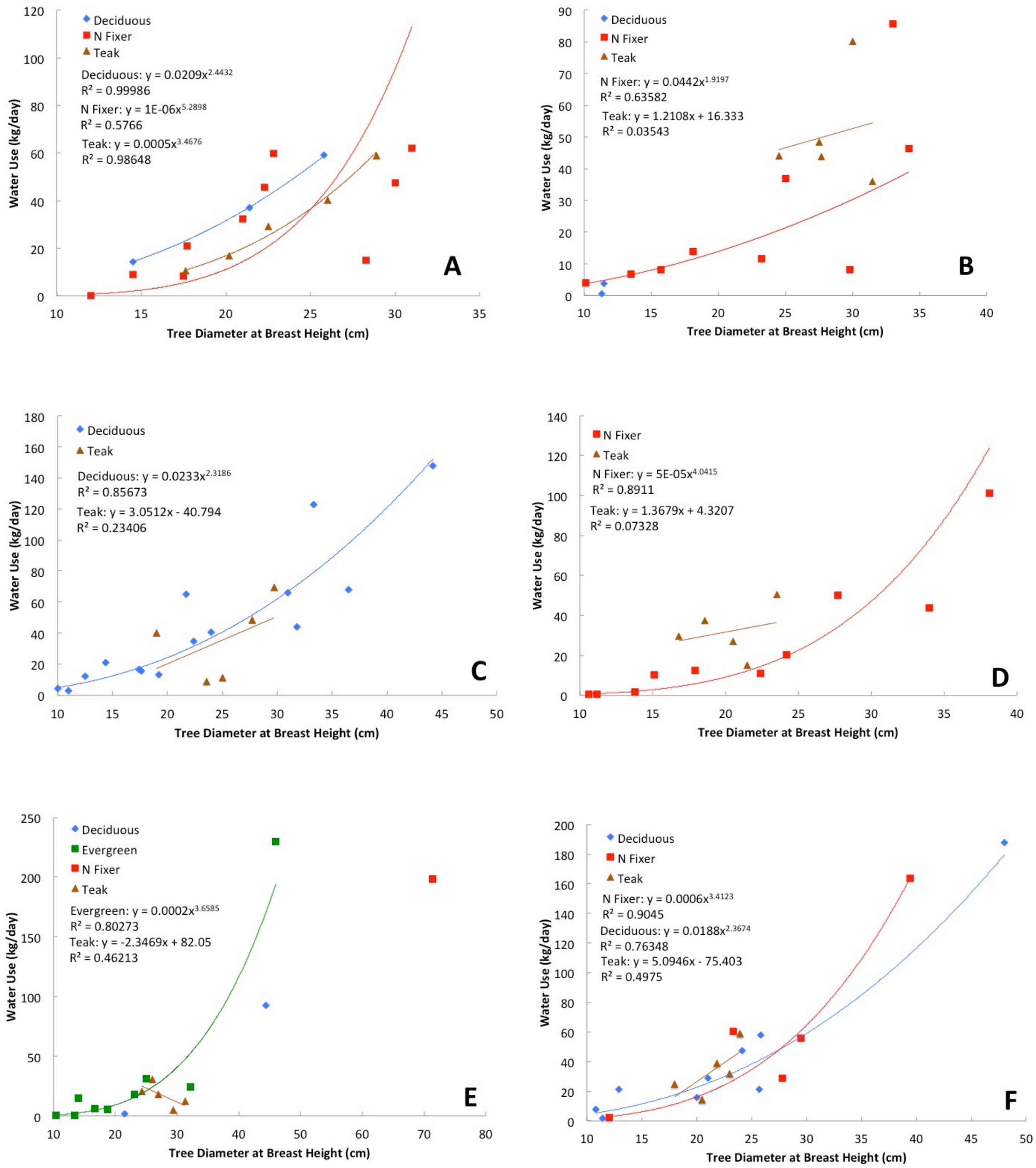

Figure 2.4. Individual tree wet season water use by functional groups for secondary forests and teak trees for plantations, and corresponding regression equations used to estimate stand-level water use for each of the following sites: Copal (A), La Cueva (B), La Libertad (C), Pueblo Viejo (D), Santa Marta (E), and Vigia (F).

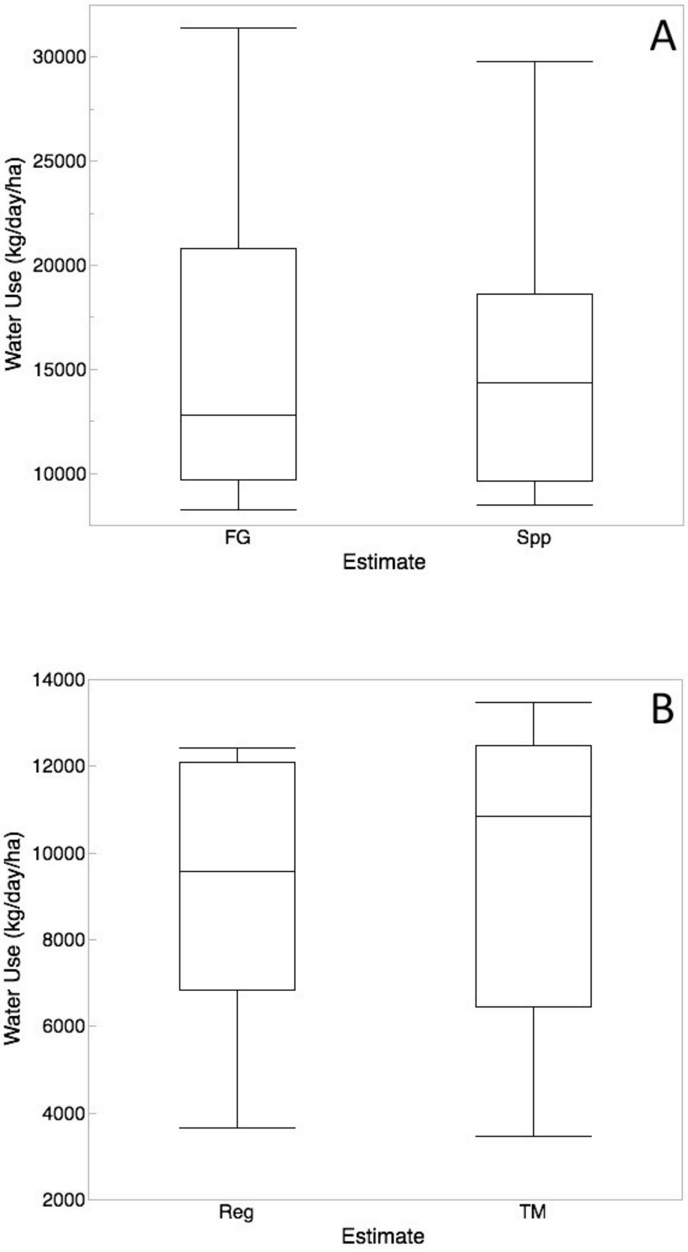

Figure 2.5. Comparison of wet season water use estimates for secondary forests (A) by species (Spp) and functional group (FG) based regression equations, and for teak plantations (B) by regression equations (Reg) and mean values (TM) for all sampled trees per site (n=6). Middle line, box limits, and outer bars correspond to the median, upper and lower quartiles, and range of the data, respectively.

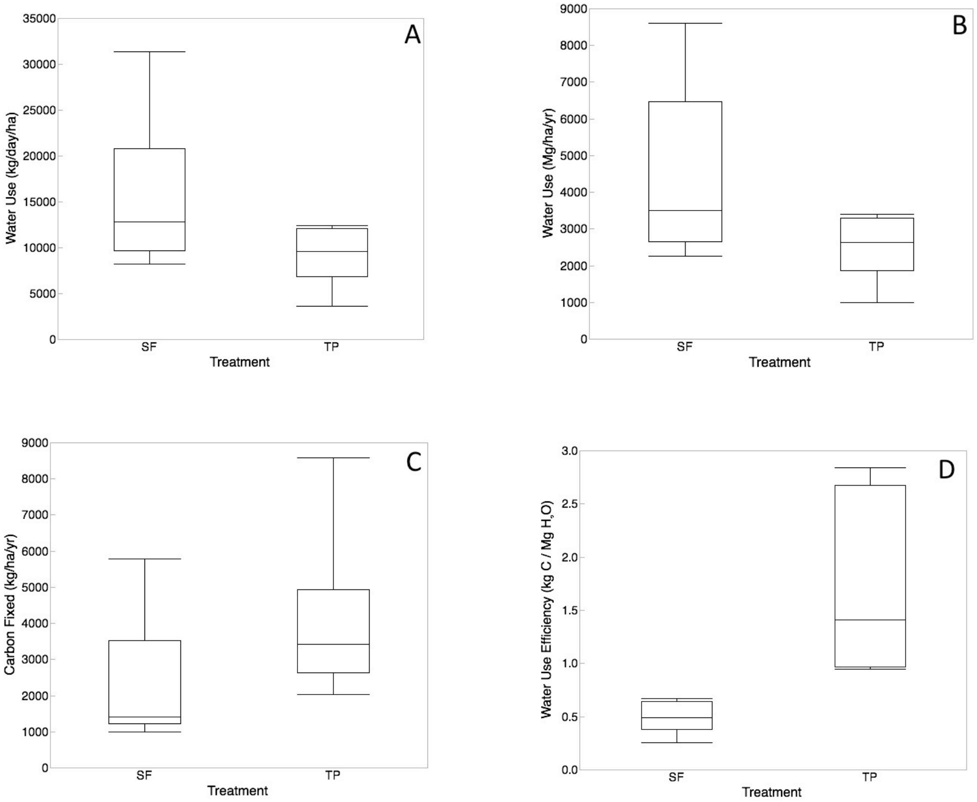

Figure 2.6. Wet season daily water use (A), annual water use (B), carbon fixation (C), and water use efficiency (D) of secondary forest (SF) and teak plantation (TP) sites (n=6). Middle line, box limits, and outer bars correspond to the median, upper and lower quartiles, and range of the data, respectively.

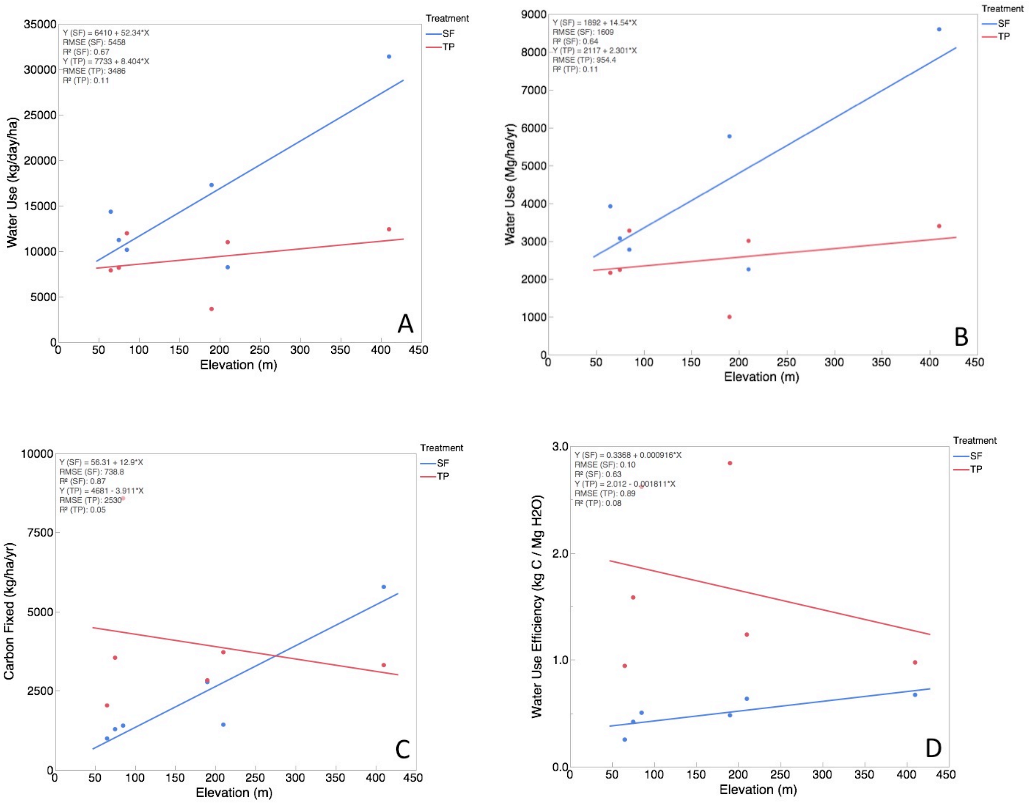

Figure 2.7. Relationship between elevation and wet season water use (A), annual water use (B), carbon fixation (C), and water use efficiency (D) across secondary forest (SF) and teak plantation (TP) sites (n=6).

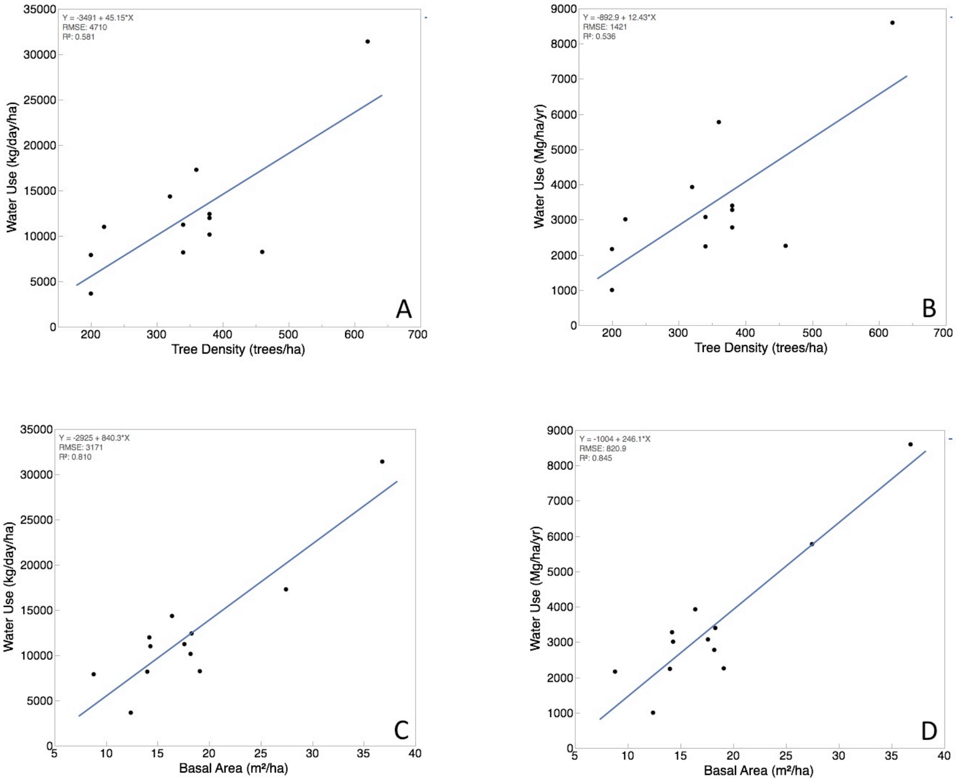

Figure 2.8. Relationship of wet season and annual water use with stand tree density (A & B; respectively) and basal area (C & D; respectively) across all site treatments (n=12).

CHAPTER 3. CONVERGENCE OF TREE TO STAND WATER USE WITH BIOMASS: IS THERE ROOM FOR FUNCTIONAL TRAITS AS INDICATORS OF WATER USE?

Abstract

A functional traits approach that identifies which traits are related to the ecosystem functions of interest at the regional level can improve the resolution of ecosystem service assessments. In this study, I assessed what traits are related to tree and stand water use and water use efficiency across secondary forests and teak plantations in seasonally dry Costa Rica. I estimated individual tree water use from sap flux measurements and water use efficiency from allometric biomass equations and wood C content, and scaled these processes to the stand level. Although there was significant convergence of stand water use with biomass and related traits across forest types, the relationship of tree water use with biomass varied according to tree functional group. Sapwood depth emerged as a functional trait related to water use at both the tree and stand level, but dependent of functional group at the tree level. Tree height, crown area, and crown depth were significantly related to water use at the tree level, and these relationships varied by tree functional group as well. Few traits, namely wood water and C content, and leaf C content, were related to tree or stand water use efficiency, but the ecological significance of these relationships deserves further research. Although the effect of biomass on tree to stand water use was overwhelming, individual tree traits such as sapwood depth, tree height and crown area can be useful for resolving differences in water use across forest types and functional groups. The potential mapping of

some of these traits using remote sensing makes them particularly useful for regional ecosystem service assessments.

Introduction

Functional traits can provide a link between local changes in ecosystem function brought about by land cover change and concomitant changes in ecosystem services at broader scales (Westoby & Wright 2006; Díaz et al. 2007). The functional traits approach to ecosystem services has been pioneered by studies conducted in grassland communities, where the community weighted mean (CWM) value of traits used in conjunction with functional diversity measures are used to asses impacts on ecosystem function (Díaz et al. 2007; Lavorel et al. 2011). However, it remains to be tested whether this approach can be used to resolve differences in ecosystem function across more structurally complex vegetation types, such as natural forests and tree plantations (Paquette & Messier 2011). The high complexity of tropical forest systems, for example, can make functional trait and ecosystem function relationships more contingent on contextual circumstances or processes, such as founder effects, natural succession, environmental conditions, or management intensity (Grime 1998; Lawton 1999; Ruiz-Jaen & Potvin 2011; Lohbeck et al. 2013). These conditions may mask, override, or modulate the effects of functional traits on ecosystem function, and make traits poor indicators of ecosystem services if the effects of these conditions on trait and function relationships are not known.

At the global scale, changes in the functional trait composition of forest vegetation types have been linked to effects on ecosystem processes, such as growth and decomposition rates, and ecosystem resilience (Díaz et al. 2004; Laliberté et al. 2010; Paquette & Messier 2011). However, some effects of functional traits on ecosystem function may not be directly translated from one region to another because environmental conditions can modulate the magnitude and direction of trait and function relationships (De Deyn et al. 2008; Ordoñez et al. 2009). The traits that drive ecosystem processes of interest may also vary according to the species and functional groups occurring within forest types, or according to forest types. For example, water use varies across trees of seasonally dry tropical forests due to differences in sapwood / heartwood area that occur between species functional groupings based on N-fixation capacity (Reyes-García et al. 2012). In addition, both stand structural and functional traits can drive differences in water use across co-occurring natural forests and tree plantations, making the utility of functional traits dependent on the sampling of other stand properties (Kagawa et al. 2009). In particular, the overwhelming effect of tree size on tree to stand water use can make functional trait approaches of limited utility if tree water use converges with biomass, regardless of differences in functional traits or groupings (West et al. 1999; Meinzer et al. 2005). Elucidating the robustness of trait to function relationships and how they vary across functional groupings or forest types at the regional level is a necessary step preceding the use of tree functional traits in ecosystem service assessments.

The objective of this study is to identify what functional traits are related to tree and stand water use and water use efficiency across and within tree functional groupings, and natural and plantation forest types. I sampled whole tree water use in naturally occurring secondary forests and managed teak (*Tectona grandis*) plantations in seasonally dry tropical Costa Rica. I sampled an array of structural and functional traits, and tested which of these were significantly related to tree and stand-level water use and water use efficiency within and across functional groups and forest types. I used a CWM approach at the stand level, and an individual approach at the tree level. I expected that water use would be most closely related to traits associated to tree biomass, such as trunk diameter or basal area, but that these relationships would be modulated by functional group and forest type at the tree and stand level, respectively. The practical utility of each trait found to be significantly related to water use and water use efficiency is discussed with particular emphasis on the potential estimation of trait values across forested regions using remote sensing technologies (Chapter 1). This study is a contribution to understanding the utility of functional trait approaches for ecosystem service management. I build upon the case of the Mesoamerican tropics, where recent land use and cover change patterns have resulted in landscape mosaics with heterogeneous forest cover of varying successional stage and management intensity (Chazdon 2008). These conditions call for the use of a functional traits approach that has enough resolution to assess the impact of biotic changes on ecosystem function and services.

Methods

Site selection

Six paired secondary forests and teak plantation sites were selected across a gradient of precipitation in the seasonally dry Nicoya Peninsula of Costa Rica (Table 2.1 & Fig. 2.1). On each site, a 50 x 10m plot was established on each adjacent secondary forest and teak plantation, spaced by about 30m, and placed at least 20m away from any forest clearings. All trees ≥10cm in diameter at breast height (DBH) within each plot were identified to species. Secondary forest species were classified into evergreen, deciduous, and N-fixing functional groupings, and teak plantation trees were considered as their own functional group.

Water use and water use efficiency

Tree water use was sampled using sensors that estimate sap flow velocity (cm/hr) by the heat ratio method (Chapter 2; Burgess et al. 2001). Trees sampled for water use were selected across the DBH range for each species in secondary forest and teak plantation plots. The amount of trees sampled per secondary forest species was roughly proportional to the abundance and basal area weighed species importance values (Chapter 2). The number of trees sampled in secondary forest plots ranged from 10 to 20, and five trees per plot were sampled in teak plantations. There was significant variation in tree size in secondary forests where DBH ranged from 10 to 71cm across all sites. This was not so in teak plantations where DBH ranged from 17 to 32cm across all sites. Therefore, the analysis of the relationship of biomass to water use across teak plantation trees is limited by not covering the range of tree sizes found in plantations younger or older than 10 or 15 years, respectively. Site selection required that teak plantation sites where at harvest age and maturity, which typically occurs at 10-15 years in the Nicoya Peninsula (Chapter 2).

Whole tree water use was estimated by integrating sap flow velocity measurements across the area of concentric circles corresponding to each sensor, and summing these for each tree across the active sapwood profile (Fig. 2.2; Hatton et al. 1990; Burgess & Downey 2014). Individual tree water use (kg/day) was estimated as the mean daily value from weekly (6-8 day) sampling periods conducted during the growing season. These values were used to construct daily water use to DBH regressions for each functional group per secondary forest plot, and for teak trees per plantation plot (Chapter 2). Stand water use (kg/ha/day) was estimated for each plot during the growing season by applying these regressions to the trees in each plot by functional group. In secondary forests, some functional groupings had one or few representatives, and in such cases the actual value sampled for those trees was added to the value obtained for all other trees based on regressions to estimate stand water use per plot.

For all trees in each plot, DBH was sampled in two consecutive growing seasons. Annual biomass increment for each tree was estimated by applying allometric equations to each DBH value, estimating the increment in tree biomass from one growing season to the next. Allometric equations were obtained from the literature to be as specific as possible for each species, and general equations for forest types were used when no specific or con-specific equations were found (Table 2.3; Chave et al. 2005). Wood C content was estimated by analyzing one tree core sample per species per plot by the combustion method. For each tree, annual C fixation was estimated as the product of wood C content and annual biomass increment. Annual C fixation was summed for all trees per plot to estimate annual stand C fixation.

Annual water use was estimated for each tree as the product of daily growing season water use and the length of the growing season. A nine month growing season was assumed for deciduous, N-fixing, and teak plantation trees, and a 12 month growing season was assumed for evergreen trees based on monthly leaf phenology observations at each site (Fig. 2.3). Stand level annual water use was estimated from the sum of annual water use of all trees per plot. Annual water use efficiency (kg C / Mg H_2O) was estimated at the tree and stand level by dividing annual C fixation by annual water use.

Sampling of traits

Stand structural traits

Stand tree density (trees/ha) and basal area (m^2/ha) were estimated from the sampling of DBH of all trees in each plot. Leaf area index (LAI) was estimated at the canopy level using a Li-Cor LAI-2000 Plant Canopy Analyzer (Li-Cor Incorporated 1990). For each plot, canopy LAI was estimated from the mean of measurements taken in during three separate days during the growing season, with five individual forest canopy measurements sampled for each day.

Tree functional traits

I sampled tree height, crown depth, crown diameter, sapwood depth, bark thickness, wood density, and wood water, C, and N content for each tree that was sampled for water use. Tree height and crown depth were sampled with a clinometer. Crown depth was estimated as the distance from the treetop to the lowermost branch. Crown diameter was measured as the distance between crown edges in two perpendicular directions, and the mean of these two measurements was used to estimate crown area (m^2) for each sampled tree.

Sapwood depth was estimated by injecting dye into a ~10cm long and ~0.5cm hole drilled into opposite sides of each tree trunk, or one side in the case of trees <15cm DBH, and retrieving a wood core ~3cm above the drill hole ~90 minutes after dye injection. This procedure was done between 9-11AM in all cases. For trees ≥15cm DBH, the mean of two measurements was used to estimate sapwood depth. In some cases were the dyeing method underestimated sapwood depth, the natural coloring changes in the sapwood-heartwood boundary was used to estimate sapwood depth (Chapter 2). Sapwood depth was used to estimate sapwood and heartwood area (cm^2) per tree. Bark thickness was estimated from the mean of measurements on opposite sides of the trunk for trees ≥15cm DBH, and from one measurement for trees <15 cm DBH.

A 5cm long wood core (bark removed) was taken from opposite sides of the tree trunk surface, or from one side in the case of trees <15cm DBH, to estimate wood density, and wood water, C and N content per sampled tree. Wood density (g/cm^3) was estimated by dividing the oven dry mass (48 hours at 105°C) by the fresh volume estimated from the core length and borer diameter (5.15mm). Wood water content (%) was estimated from the difference of fresh and oven dry mass, divided by the fresh mass of each core. Total wood C and N content (%) was estimated for each core based on the combustion method. The mean values for wood density, and water, C, and N content for the two cores taken from each tree ≥15cm DBH were used to estimate these traits for each of those trees.

Leaf functional traits

I sampled three canopy leaves from one randomly selected canopy tree per species per plot. In addition to the difficulty and cost of sampling canopy leaf traits, the relationship of leaf traits to water use was only explored at the stand level using this sampling methodology because leaf traits have relatively low variation across trees of the same species compared to across trees of different species (Baraloto et al. 2010). Canopy leaves were retrieved from each tree using a slingshot to shoot a lead weight tied to fishing line over canopy branches, and replacing the line with rope to pull and fell branches and leaves to the ground. Leaf thickness was estimated as the mean of three measurements taken with a digital caliper (Greatneck Tools, NY) around the edge of each fresh leaf (Baraloto et al. 2010). Leaf area was estimated from a photograph of each fresh leaf using ImageJ Software (http://imagej.nih.gov/ij/). Specific leaf area (SLA; cm^2/g) was estimated for each leaf by dividing leaf area by oven dry leaf mass (48 hours at 105°C). Leaf water content (%) was estimated from the difference of fresh and oven dry mass, divided by the fresh mass of each leaf. The three leaves per species per plot were combined and milled to analyze for leaf C and N content (%) by the combustion method. Leaf thickness, leaf area, SLA, and leaf water content were estimated from the mean values from the three leaves sampled per species per plot.

Stand functional traits

I estimated CWM value of each tree and leaf functional trait based on the abundance and basal area weighed importance value of each species for each plot (Grime 1998; Violle et al. 2007). For tree functional traits, the mean value of each trait for all the trees sampled per species was used to estimate the CWM of crown area / basal area (m^2/cm^2), crown depth / height (m/m), sapwood depth, sapwood / heartwood area (cm^2/cm^2), bark thickness, wood density, and wood water, C, and N content. Since crown area and depth, and sapwood area are dependent on tree size, these were normalized as ratios to basal area, height, and heartwood area per tree, respectively. Similarly, the CWM of maximum tree height was estimated from the height of the tallest tree per species per plot. The mean values of leaf thickness, leaf area, SLA, and leaf water content, and the pooled values of leaf N and C content for the three leaves sampled from one individual per species per plot were used to estimate the CWM of each leaf functional trait for each plot.

Statistical analyses

I used generalized linear models (GLMs) to identify which traits had significant effects on water use and water use efficiency at the stand and tree level across all sites (N=12) and trees (N=109), respectively. GLMs were chosen because they can be used flexibly when the error distribution between dependent and independent variables is not normal or unknown. Separate GLMs were run for testing effects of structural traits, and the CWM of tree and leaf functional traits on stand water use and water use efficiency, and for testing effects of individual tree functional traits on tree water use and water use efficiency. I chose between GLMs of normal and exponential error distributions with identity and log link functions, and identity and reciprocal link functions, respectively, based on the corrected Akaike information criterion (AICc). Traits with significant effects in GLMs were tested singly with linear regressions. I separately tested for effects of traits that were strongly correlated to the traits with the highest effects on water use and water use efficiency in GLMs using linear regression.

Analysis of covariance (ANCOVA) was used to test for effects of treatment on the relationship between each trait and water use or water use efficiency at the stand and tree level. The treatments consisted of secondary forest (n=6) or teak plantation (n=6) at the stand level, and of functional groupings at the tree level. For these analyses, evergreen and deciduous secondary forest trees were grouped together into one secondary forest functional group (n=40), in addition to secondary forest N-fixers (n=39) and teak plantation tree (n=30) functional groupings. There were only three evergreen species that occurred only at one site. Interactions were tested between treatment and each trait, and traits with significant interaction terms were excluded from ANCOVA. When there was an effect of both trait and treatment, the significance of the effects by ANCOVA was reported over those of simple linear regression. Simple linear regressions were used to test the significance of effects of traits by treatment when ANCOVA revealed significant effects for both treatment and trait, or when there was a significant effect of the interaction of trait and treatment on water use or water use efficiency. Separate ANCOVA and simple linear regression were used to test the significance of relationships of biomass with water use and water use efficiency across forest types and functional groups at the stand and tree level, respectively. All statistical tests were conducted using JMP 11 statistical software (SAS Institute Inc. 2013).

Results

Stand water use and traits

A normal error distribution with a log link function tended to yield the best-fit GLMs between stand water use, and structural and functional traits based on AICc (Table 3.1). Across all sites, basal area was the only structural trait related to stand water use in GLM (Table 3.1) showing a strong positive relationship ($p<0.0001$; Fig. 3.1a). Tree density was strongly correlated to basal area (Appendix C) and was also positively related to stand water use ($p=0.004$; Fig. 3.1b). The CWM values of sapwood depth, sapwood / heartwood, bark thickness, crown area / basal area, and wood water, N and C content were tree functional traits related to stand water use in GLMs (Table 3.1). However, only sapwood depth had a significant relationship to stand water use when the effect of each tree trait was tested singly ($p=0.012$; Fig. 3.1c). The CWM values of specific leaf area, leaf water content, and leaf N content were leaf functional traits related to stand water use in GLMs (Table 3.1), but none of these traits had a significant effect when tested singly.

ANCOVA showed that treatment had no effect on the relationships of basal area, tree density, and sapwood depth with stand water use (Table 3.2). However, ANCOVA revealed treatment-mediated effects of crown area/ basal area, wood water content, wood density, specific leaf area, and leaf thickness on stand water use (Table 3.2). Of these, the only traits that had significant effects within treatment were wood density (p=0.03; Fig. 3.2a), wood water content (p=0.03; Fig. 3.2b), and leaf thickness (p=0.03; Fig. 3.2c), all of which were only significant within secondary forests. The effect of all other traits on stand water use was not significant in ANCOVA except for maximum height and leaf area, for which there where significant effects of their interactions with secondary forest or teak plantation treatment (p=0.01 & p=0.008, respectively) and therefore were not tested in ANCOVA. Maximum height and leaf area only had significant effects on stand water use within secondary forests as well (p=0.003, Fig. 3.2d; and p=0.002, Fig. 3.2e; respectively).

Stand water use efficiency and traits

Although no relationships were found between structural traits and stand water use efficiency, a normal error distribution and log link function provided the best-fit GLMs between stand water use efficiency and functional traits based on AICc (Table 3.1). The CWM values of sapwood / heartwood, crown depth / height, crown area / basal area, and wood water, C and N content were tree functional traits related to stand water use efficiency in the best-fit GLM (Table 3.3). However, only wood water content was significantly related to stand water use efficiency when each tree trait was tested singly (p=0.01; Fig. 3.1d). The CWM of leaf C content was the only leaf functional trait significantly related to stand water use efficiency in GLM (Table 3.3) showing a significant negative relationship (p=0.009; Fig. 3.1e).

No structural, tree, or leaf-level traits had significant effects on stand water use efficiency in ANCOVA (Table 3.2). There was a significant effect of the interaction of forest type treatment with crown depth / height, wood carbon, and leaf nitrogen on stand water use efficiency (p=0.03, p=0.04, & p=0.03, respectively), and therefore these variables were not tested in ANCOVA. Of these traits, only wood C content had a significant effect on stand water use efficiency and only within the teak plantation treatment (p=0.02; Fig. 3.2f).

Tree water use and traits

A normal error distribution with a log link function provided the best-fit GLMs between tree water use and functional traits based on AICc (Table 3.3), but no distribution or link function provided a statistically significant GLM fit for tree water use efficiency. In addition, no trait had significant effects on tree-level water use efficiency in ANCOVA (Table 3.4). Therefore, only results for effects of traits on tree-level water use are presented.

Tree DBH, sapwood depth, sapwood / heartwood, and wood water and C content had significant effects on tree water use based on GLM (Table 3.3). However, only DBH and sapwood depth had significant effects on tree water use when tested singly (p<0.0001 in both cases; Fig. 3.3a & b). In addition, tree crown area was a trait highly correlated to DBH (Appendix D) that also had significant effect on tree water use when tested singly (p<0.0001, Fig. 3.3c). ANCOVA revealed that sapwood depth, crown depth, and height had effects on tree water use that were mediated by treatment (Table 3.4). The effects of these traits on tree water use were significant within secondary forest and N-fixer functional groups (p<0.0001 in all cases except for crown depth and height in secondary forests for which p=0.007 and p=0.0001, respectively), but none of these traits had significant effects on the water use of teak plantation trees (Fig. 3.4a-c). ANCOVA also revealed effects of crown area / basal area on tree water use that were not mediated by treatment (Table 3.4) but the fit of this relationship was low (R^2 adj.=0.07). There was a significant effect of the interaction of functional grouping with DBH (p=0.01) and crown area (p=0.001) on tree water use. The effect of DBH on tree water use was significant for secondary forest and N-fixer functional groups (p<0.0001 in both cases) and barely significant for teak plantation trees (p=0.07; Fig. 3.4d). The effect of crown area on tree water use was significant for all functional groups (p<0.0001 for secondary forest and N-fixers, and p=0.03 for teak plantation trees; Fig. 3.4e).

Water use and biomass

There was a significant relationship between stand water use and biomass (p=0.0002; Fig. 3.5a) with no effect of forest type treatment (ANCOVA: p=0.04). There was no effect of stand biomass on water use efficiency although there was an effect of forest type (ANCOVA: p=0.98 and p=0.03, respectively). There was a significant effect of the interaction of functional grouping and biomass on tree water use (p=0.0002) with a significant relationship for secondary forest and N-fixing trees (p<0.0001 in both cases; Fig. 3.5b). There was no effect of tree biomass on water use efficiency yet there was an effect of functional grouping (ANCOVA: p=0.4 and p=0.006, respectively).

Discussion

Biomass and related structural traits such as basal area and tree density were closely related to stand water use as expected, but this was not modulated by forest type (Figs. 3.1a & b, & 3.5a; Tables 3.1 & 3.2). On the other hand, tree water use was closely related to tree biomass and DBH, and functional grouping significantly modulated these relationships as was expected (Figs. 3.4d & 3.5b; Tables 3.3 & 3.4). The absence of significant relationships of tree water use and DBH or biomass at the tree level for teak plantation trees is likely due to the restricted tree size range sampled in the study (Figs. 3.4d & 3.5b). This limitation also applies to the relationships of most tree level traits and water use for teak plantation trees although for some traits, such as tree crown depth and crown area, significant variation in trait values was found across teak plantation trees (Figs. 3.4b & e). In spite of this limitation, these results support the idea that there is convergence in water use according to biomass across natural and plantation forest types, but highlight an effect of functional group on the water use and biomass relationship at the tree level. Meinzer et al. (2005) reported similar results for the scaling of individual tree water use with biomass of angiosperms and gymnosperms, which had distinct relationships. The contrasting results on the effect of forest type and functional group on the water use to biomass relationship at the stand and tree levels, respectively, may be due to differences in sample size and resolution across levels. Sampling resolution was higher at the tree than stand level due to larger sample size, which may have resulted in the detection of significant effects of treatment at the tree but not stand level (Figs. 3.5a & b). However, this was clearly not the case of the effect of most traits on stand water use, for which a significant effect of treatment was detected (Fig. 3.2).

Although few, functional traits emerged as better indicators of stand water use efficiency than structural traits. The lack of relationships between functional traits and individual tree water use efficiency can be due to very local microclimatic factors, such as incoming light levels or soil moisture conditions, inducing high variation on both tree carbon gain and water use. Although the CWM of two functional traits, namely wood water content and leaf C content, were significantly related to stand water use efficiency across forest types (Figs. 3.1d & e; Table 3.1), these relationships were not as strong as those found for traits related to stand water use (Fig. 3.1a & b). In addition, no known mechanisms link wood water content or leaf C content with water use efficiency. Likewise, the significant and negative relationship of wood C content and water use efficiency in teak plantations (Fig. 3.2f) was surprising since such relationship at the species level has not been reported previously (e.g., Cernusak et al. 2007). Understanding the mechanistic relationships of these functional traits to water use efficiency is beyond the scope of this study and deserves further research. The rest of the discussion focuses mostly on clarifying the mechanisms behind the significant relationships of functional traits to water use, along with the utility of each trait as indicators of water use for ecosystem service assessments.

Sapwood depth emerged as a functional trait that was consistently related to tree and stand water use across functional groups and forest types, respectively (Figs. 3.1c & 3.3b; Tables 3.1-3.4). At the tree level, the effect of sapwood depth on water use was mediated by functional group, with N-fixers having lower sapwood depth than other secondary forest species for the same amount of water use (Fig. 3.5a; Table 3.4). This replicates results found elsewhere in the seasonally dry tropics, where allocation to sapwood area drives differences in tree water use between forest N-fixers and other species (Reyes-García et al. 2012). The significant effect of sapwood depth and correlates such as sapwood area on stand water use across natural forests and plantations has also been reported previously (Kagawa et al. 2009). Sapwood depth determines the amount of actual stem basal area that transports water to the canopy and is a functional trait that is easy to measure yet appears relatively unutilized in the literature as a functional trait. Other than sapwood depth, no other functional traits were consistently related to tree or stand water use across functional groups and forest types, respectively, except for crown area at the tree level.

Tree crown area was the trait most consistently related to tree water use across and within functional groups, next to DBH and sapwood depth (Figs. 3.3c & 3.4e). Crown area relates to tree water use by being a proxy for the amount of canopy surface area exposed to transpiration. In addition, there is a close relationship between tree crown area and basal area that can vary according to species or functional groups (Appendix D; Kunert et al. 2012; Verma et al. 2014). However, establishing direct relationships between crown area and water use has eluded previous studies (Kunert et al. 2012). This relationship can be used for the scaling of forest water use from local to regional scales if continued developments in LiDAR technology and data processing allow for the mapping of individual crown area (Chapter 1; Popescu et al. 2003; Falkowski et al. 2008). Tree crown area is a relatively understudied trait related to tree water use that can have great utility for the use of functional trait approaches for ecosystem service assessments.

Similar to tree crown area, crown depth is a relatively understudied trait that was positively related to tree water use within secondary forest and N-fixer functional groups (Fig. 3.4b; Table 3.4). As with crown area, crown depth can be a proxy of the amount of canopy surface area available for transpiration, but in a vertical orientation. Crown depth is closely related to the amount of rainfall that gets past the canopy of tropical tree species (Park & Cameron 2008). However, few studies of tree water use estimate crown depth. Schäfer et al. (2000) reported crown depth and found a relationship of tree water use and height, but did not report any relationship with crown depth. Developments in LiDAR technologies may allow for the estimation of tree crown depth (Popescu & Zhao 2008), which may make this trait useful as a proxy for water use. The relationship of crown depth to tree water use, however, is not as robust as that of crown area (Fig. 3.4).

The CWM values of wood density and water content, leaf area and thickness, and maximum height were indicators of stand water use but only within secondary forests (Fig. 3.2a-e). The lack of effect in plantations can be due to the low variability of these traits across teak plantations in the studied gradient. Similar studies have found little relationship of wood density with stand water use, attributed to low variation in wood density across the trees sampled (Reyes-García et al. 2012). In this study, the large variation in wood density across secondary forests revealed that this trait is negatively related to water use at the stand level (Fig. 3.2a), most likely due to higher resistance to water flow through the stem as wood density increases (McCulloh et al. 2011). Wood density restricts water flow by being related negatively to vessel conduit diameter and positively to vessel packing density, and these relationships are modulated by functional groups (McCulloh et al. 2010; McCulloh et al.

2011). Higher wood density is also associated to increased resistance to cavitation and drought tolerance (Gotsch et al. 2010), which is consistent with lower water use in secondary forest and N-fixer species on drier sites (Chapter 2).

It was surprising to find a significant positive relationship of wood water content and stand water use in secondary forests (Fig. 3.2b). A positive relationship of wood water content with sap flow velocity was reported for temperate beech tree stands (Granier et al. 2000). This relationship can be due to higher stem water storage capacity allowing for higher tree water use rates (Goldstein et al. 1998; Phillips et al. 2003). However, wood water content was much more variable and unrelated to water use at the tree level, which undermines the stand level relationship (Table 3.4). Wood water content was also significantly related to stand water use efficiency (Table 3.2). However, the relatively low fit of this regression (Fig. 3.1) suggests this relationship is weak and maybe coincidental, making the utility of this trait as an indicator of stand water use efficiency questionable.

The positive relationship of individual leaf area and stand water use in secondary forests (Fig. 3.2e) could be explained by higher decoupling between the atmosphere and larger leaves leading to lower stomatal control of transpiration and higher tree water use (Jarvis & McNaughton 1986; Meinzer 1993; Meinzer 2003). However, this becomes questionable when considering that the largest leaves were from a compound leaf species (i.e., *Schyzolobium parahyba*) comprised of many small leaflets, for which atmospheric coupling should be higher than simple leaves of the same area and more similar to those of smaller leaves. In fact, the site with the highest CWM value for leaf area was dominated by this species and it was the only site where it occurred, undermining the significant positive relationship of leaf area and stand water use (Fig. 3.2e). Differences in individual leaf area and its effect on stomatal conductance at the leaf level may have resulted in LAI being a poor indicator of stand water use across secondary forests of differing species composition and variable individual leaf area (Table 3.2; Fig. 3.2e). It was surprising to find no positive effect of LAI on stand water use as it determines the amount of leaf surface area available for transpiration at the canopy level and it increases decoupling of the canopy and atmosphere (Waring et al. 1982; Jarvis & McNaughton 1986). On the other hand, the significant and positive relationship of leaf thickness to stand water use in secondary forests lacks any documented mechanism (Fig. 3.2c). It may be that thicker leaves with greater mesophyll space allow for higher leaf transpiration rates due to higher stomatal density and conductance (Meinzer 2003). This deserves further investigation.

The CWM of maximum tree height per species and individual tree height were both positively related to water use at the stand and tree level, respectively, but only within secondary forest types, and secondary forest and N-fixer functional groups (Figs. 3.2d & 3.4c). The absence of such relationship in teak plantations can be due to the low variability in tree height across plantations. The positive relationship of the CWM of maximum height and stand water use in secondary forests would intuitively appear to be correlated to biomass and related traits, but those correlations were not significant (Appendix C). However, height was correlated to biomass at the tree level (Appendix D). Nevertheless, taller trees and forests can have higher water use due to increased canopy surface roughness and atmospheric coupling allowing for higher stomatal conductance (Jarvis & McNaughton 1986; Schäfer et al. 2000;

Ambrose et al. 2010). Tree height can be currently estimated across forested landscapes using LiDAR (Falkowski et al. 2008; Popescu & Zhao 2008), providing a direct link for the use of this trait as an indicator of forest water use at the regional level.

Are CWM and functional trait approaches useful indicators of water use for ecosystem service assessments?

The very close relation of biomass and related traits to water use at the tree and stand level leaves some to little room for the utility of other traits as indicators of water use in ecosystem service assessments. This is not necessarily something negative for the viability of such assessments. On the contrary, the structural traits related to biomass, that is tree density and basal area are routinely estimated in forest inventories. Estimates of forest biomass that rely on allometric equations applied to these inventories can be used to calibrate LiDAR imaging so that forest biomass can be estimated at the regional level with high accuracy (Asner et al. 2011a; Asner et al. 2012). Therefore, the close relationship of water use and biomass can be a very useful indicator for ecosystem services dependent on tree to forest water use.

Aside from biomass and related structural traits, some tree level functional traits emerge as potential as indicators that can improve the resolution of tree to stand water use estimates: sapwood depth, height, and crown area. All of these traits varied significantly across the functional groups in this study (Fig. 3.4a-c & e) and all of them were correlated to biomass, the main driver of water use (Appendix D). Functional groups that capture these functional trait differences can be used to improve the resolution of water use estimates based on tree biomass. Classifications of trees or forests into these functional groups can be achieved by the remote sensing of traits such as leafing phenology and leaf N content for identifying deciduous and N-fixer functional groups, respectively (Chapter 1; Asner et al. 2011a & b). In addition, one potential flaw of this study is that two of the traits most associated to tree water use, namely DBH and sapwood area, are used in the estimation of tree water use itself. However, tree height and crown area are completely independent from the estimation of tree water use. This makes the significance of the relationships of these traits to water use more robust and highlights their utility as indicators of water use that can potentially be quantified at the regional scale by remote sensing (Falkowski et al. 2008; Popescu & Zhao 2008).

It appears that the CWM approach has little use as an indicator of forest water use for ecosystem service assessments at the regional level due to the overriding effects of tree size and biomass. The CWM of traits such as wood and leaf C content may be indicators of stand water use efficiency but further research on this is needed. Leaf C needs not be estimated via the CWM as it can be retrieved directly from canopy spectral properties (Asner et al. 2011b). Similarly, there is little utility in a CWM value of sapwood depth that cannot be easily scaled from local to regional levels, as this trait cannot be remotely sensed. The utility of sapwood depth as a trait indicative of water use then relies on its relationship to functional grouping, which can be sensed remotely via other traits. The apparent utility of the CWM as a link between local and regional variation in functional traits and ecosystem function is undermined by this study, at least for water use.

The CWM of functional traits such as sapwood depth, and wood density and water content can be useful indicators of tree to stand water use at local levels within forest types (Fig. 3.2a & b). The CWM of leaf area and thickness appear to be related to stand water use (Fig. 3.2c & e), but the mechanisms behind these relationships are uncertain and deserve further research. In addition, the relationship of the CWM of traits such as sapwood / heartwood area or crown area / basal area can have significant effects on water use and water use efficiency, respectively, if the log of the CWM value is used as proxy, as suggested by the GLM analyses (Tables 3.1 & 3.3). However, traits that are not related linearly to water use, or to the ecosystem process of interest, may have less utility as ecosystem service indicators because predicting outcomes based on their variation becomes more difficult.

This study illustrates that there is little utility in a functional traits approach that does not take ecological context into consideration. For example, bark thickness may be an indicator of resistance to fire in some regions, but fire resistance bears little relation to the variation in bark thickness if the region is not prone to fire, undermining a trait and function relationship (Paine et al. 2010). Likewise, specific leaf area may be related to succulence and drought resistance in dry regions, but may have little effect on water relations in moist to seasonally dry regions like this one where most species shed their leaves in the dry season. Ecologists that use a functional traits approach to ecosystem service management should be wary of abusing the functional trait concept by assuming that trait and function relationships hold regardless of ecological context, potentially giving unwarranted meaning to trait variation effects on ecosystem function (Viole et al. 2007; Meinzer et al. 2010). In this case, biomass emerged as a trait that could almost universally be used estimate tree to forest water use according to functional group, with some room for improving its practical use and resolution based on a few related tree functional traits such as sapwood depth, height, and crown area.

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Tables

Table 3.1. Structural, tree, and leaf level traits with significant effects on stand water use and water use efficiency according to the best-fit generalized linear models (GLM) across all study sites (N=12). All GLMs were based on a normal error distribution and log link function except for the GLM of tree trait effects on water use, which used an identity link function.

Trait	Parameter Estimate	p-Value
	Water Use (kg/ha/day)	
	Structural Traits	
Basal Area (m^2/ha)	0.054	0.001
Whole Model		<0.0001
	Tree Traits	
Sapwood Depth (cm)	8337	<0.0001
Sapwood / Heartwood Area (cm^2/cm^2)	-56	0.0002
Bark Thickness (mm)	-14163	0.001
Crown Area / Basal Area (m^2/cm^2)	-187425	0.001
Wood Water Content (%)	-1006	0.0004
Wood Nitrogen Content (%)	-32143	0.001
Wood Carbon Content (%)	3442	<0.0001
Whole Model		<0.0001
	Leaf Traits	
Specific Leaf Area (cm^2/g)	-0.047	<0.0001
Leaf Water Content (%)	0.11	0.0002
Leaf Nitrogen Content (%)	2.34	0.002
Whole Model		0.001
	Water Use Efficiency (kg C / Mg H_2O)	
	Tree Traits	
Sapwood / Heartwood Area (cm^2/cm^2)	-0.081	<0.0001
Crown Depth / Height (m/m)	4.09	0.0001
Crown Area / Basal Area (m^2/cm^2)	-32.69	<0.0001
Wood Water Content (%)	-0.11	0.0003
Wood Nitrogen Content (%)	-2.40	0.002
Wood Carbon Content (%)	-0.33	0.0003
Whole Model		<0.0001
	Leaf Traits	
Leaf Carbon Content (%)	-0.22	0.02
Whole Model		0.002

Table 3.2. Significance of effects of structural, tree, and leaf level traits, and secondary forest and teak plantation treatments on stand water use and water use efficiency by analysis of covariance (ANCOVA; N=12).

	Water Use (kg/ha/day)		Water Use Efficiency (kg C / Mg H_2O)	
Trait	Trait p-Value	Treatment p-Value	Trait p-Value	Treatment p-Value
Structural Traits				
Basal Area (m^2/ha)	0.0004	0.4	0.8	0.02
Tree Density (trees/ha)	0.02	0.8	0.7	0.02
Leaf Area Index (m^2/m^2)	0.9	0.3	0.2	0.009
Tree Traits				
Sapwood Depth (cm)	0.03	0.3	0.99	0.01
Sapwood / Heartwood Area (cm^2/cm^2)	0.9	0.2	0.99	0.01
Bark Thickness (mm)	0.5	0.6	0.7	0.03
Crown Depth / Height (m/m)	0.05	0.6	*	
Crown Area / Basal Area (m^2/cm^2)	0.03	0.01	0.7	0.04
Wood Density (g/cm^3)	0.006	0.003	0.8	0.03
Wood Water Content (%)	0.009	0.003	0.8	0.07
Wood Nitrogen Content (%)	0.3	0.07	0.6	0.03
Wood Carbon Content (%)	0.4	0.09	*	
Maximum Height (m)	*		0.5	0.01
Leaf Traits				
Leaf Thickness (mm)	0.01	0.003	0.7	0.1
Leaf Area (cm^2)	*		0.5	0.09
Specific Leaf Area (cm^2/g)	0.03	0.02	0.5	0.008
Leaf Water Content (%)	0.5	0.1	0.4	0.04
Leaf Nitrogen Content (%)	0.09	0.02	*	
Leaf Carbon Content (%)	0.2	0.06	0.2	0.1

*Significant effect of interaction of treatment and trait preclude ANCOVA.

Table 3.3. Tree traits with significant effects on tree water use (kg/day) according to the best-fit generalized linear model (GLM) across sampled trees (N=109). The GLM was based on a normal error distribution and log link function.

Trait	Parameter Estimate	p-Value
Diameter at Breast Height (cm)	0.036	0.002
Sapwood Depth (cm)	0.314	<0.0001
Sapwood / Heartwood Area (cm^2/cm^2)	-0.005	0.03
Wood Water Content (%)	0.033	0.01
Wood Carbon Content (%)	0.098	0.002
Whole Model		<0.0001

Table 3.4. Significance of effects of tree traits, and secondary forest, N-fixer, and teak plantation tree functional groupings on tree water use and water use efficiency by analysis of covariance (ANCOVA; N=12).

	Water Use (kg/ha/day)		Water Use Efficiency (kg C / Mg H_2O)	
Trait	Trait p-Value	Treatment p-Value	Trait p-Value	Treatment p-Value
Diameter at Breast Height (cm)	*		0.3	0.008
Sapwood Depth (cm)	<0.0001	0.004	0.8	0.007
Sapwood / Heartwood Area (cm^2/cm^2)	0.1	0.6	0.9	0.008
Bark Thickness (mm)	0.5	0.6	0.9	0.03
Height (m)	<0.0001	0.003	0.5	0.03
Crown Depth (m)	<0.0001	0.007	0.1	0.1
Crown Depth / Height (m/m)	0.6	0.7	0.1	0.02
Crown Area (m^2)	*		0.1	0.003
Crown Area / Basal Area (m^2/cm^2)	0.002	0.35	0.06	0.002
Wood Density (g/cm^3)	0.5	0.7	0.8	0.008
Wood Water Content (%)	0.1	0.3	0.2	0.04
Wood Carbon Content (%)	0.96	0.8	0.1	0.005
Wood Nitrogen Content (%)	0.18	0.6	0.9	0.007

*Significant effect of interaction of treatment and trait preclude ANCOVA.

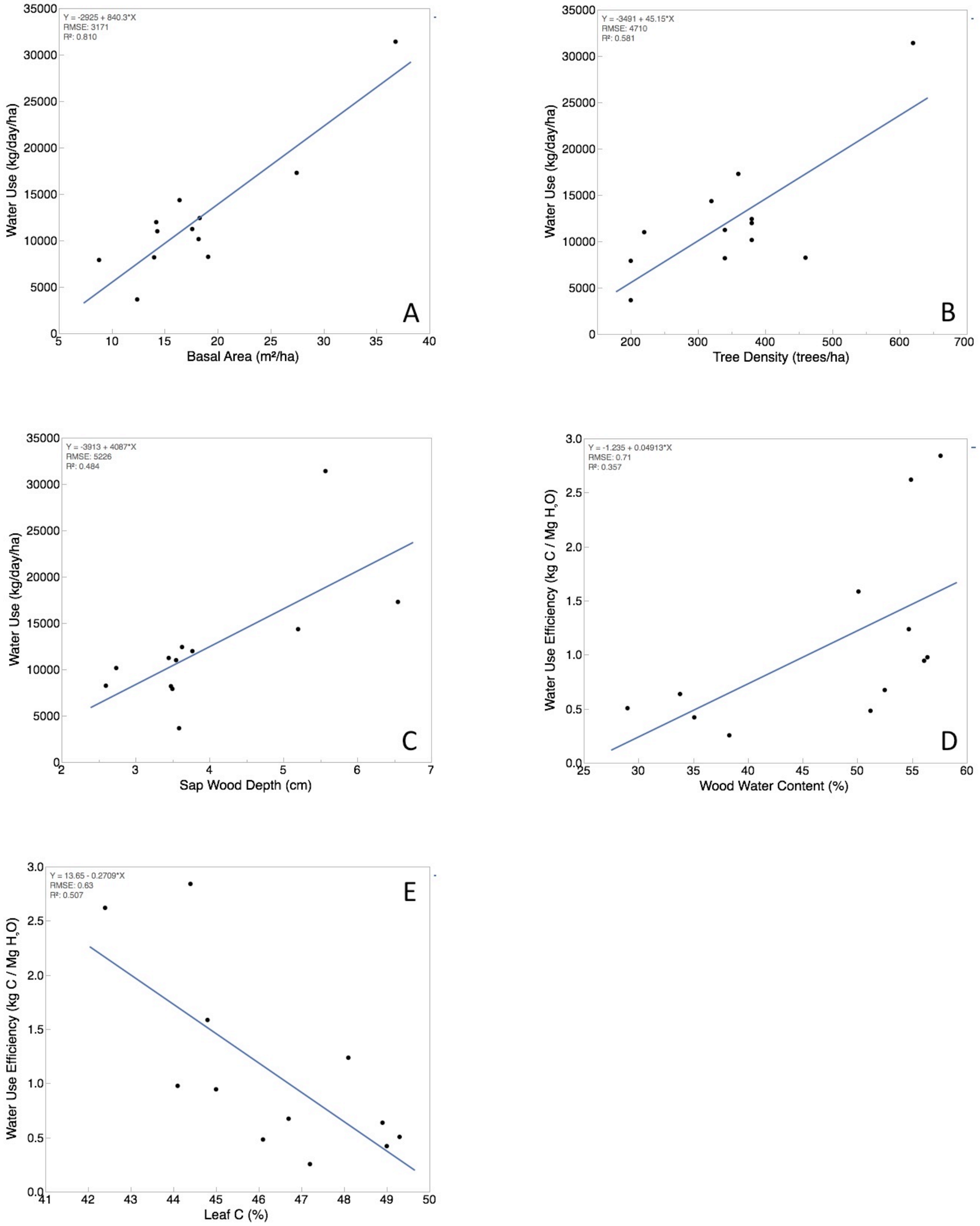


Figure 3.1. Relationships of stand basal area (A), tree density (B) and the community weighted mean value (CWM) of sapwood depth (C) to stand water use, and of the CWM of wood water content (D) and leaf C content (E) to water use efficiency across all study sites (N=12).

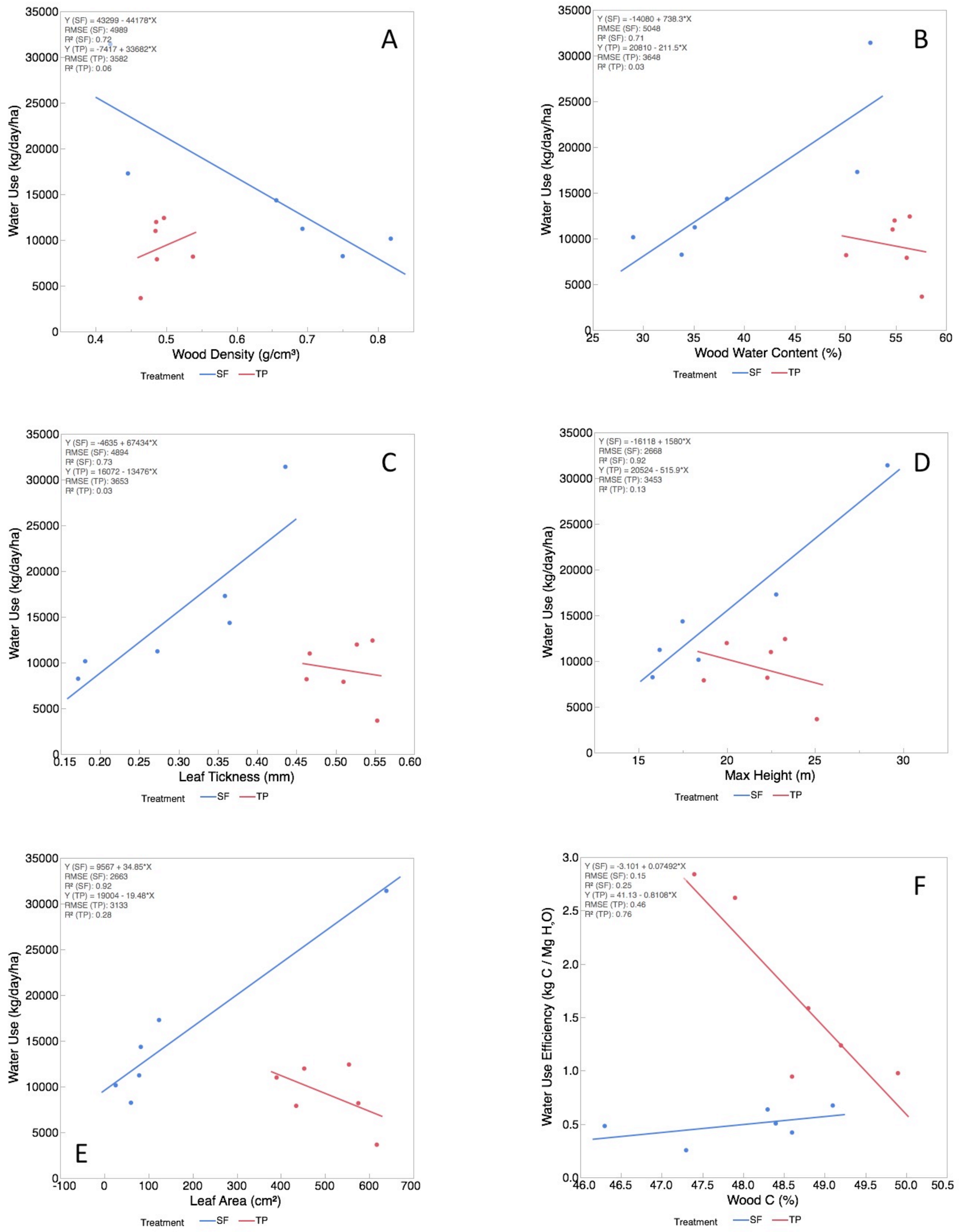


Figure 3.2. Relationships of wood density (A), wood water content (B), leaf thickness (C), maximum height (D), and leaf area (E) to stand water use, and of wood C content (F) to stand water use efficiency by secondary forest (SF) and teak plantation (TP) forest types (n=6).

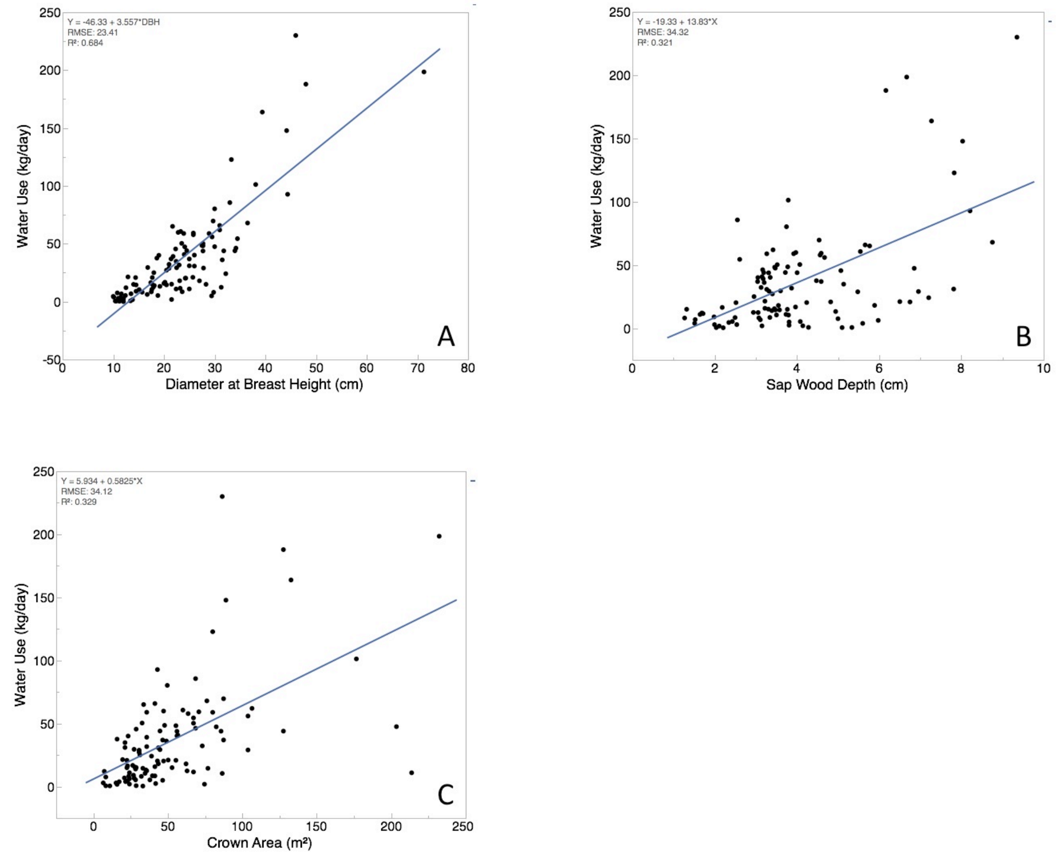


Figure 3.3. Relationships of tree trunk diameter at breast height (A), sapwood depth (B), and crown area (C) to tree water use across all sampled trees (N=109).

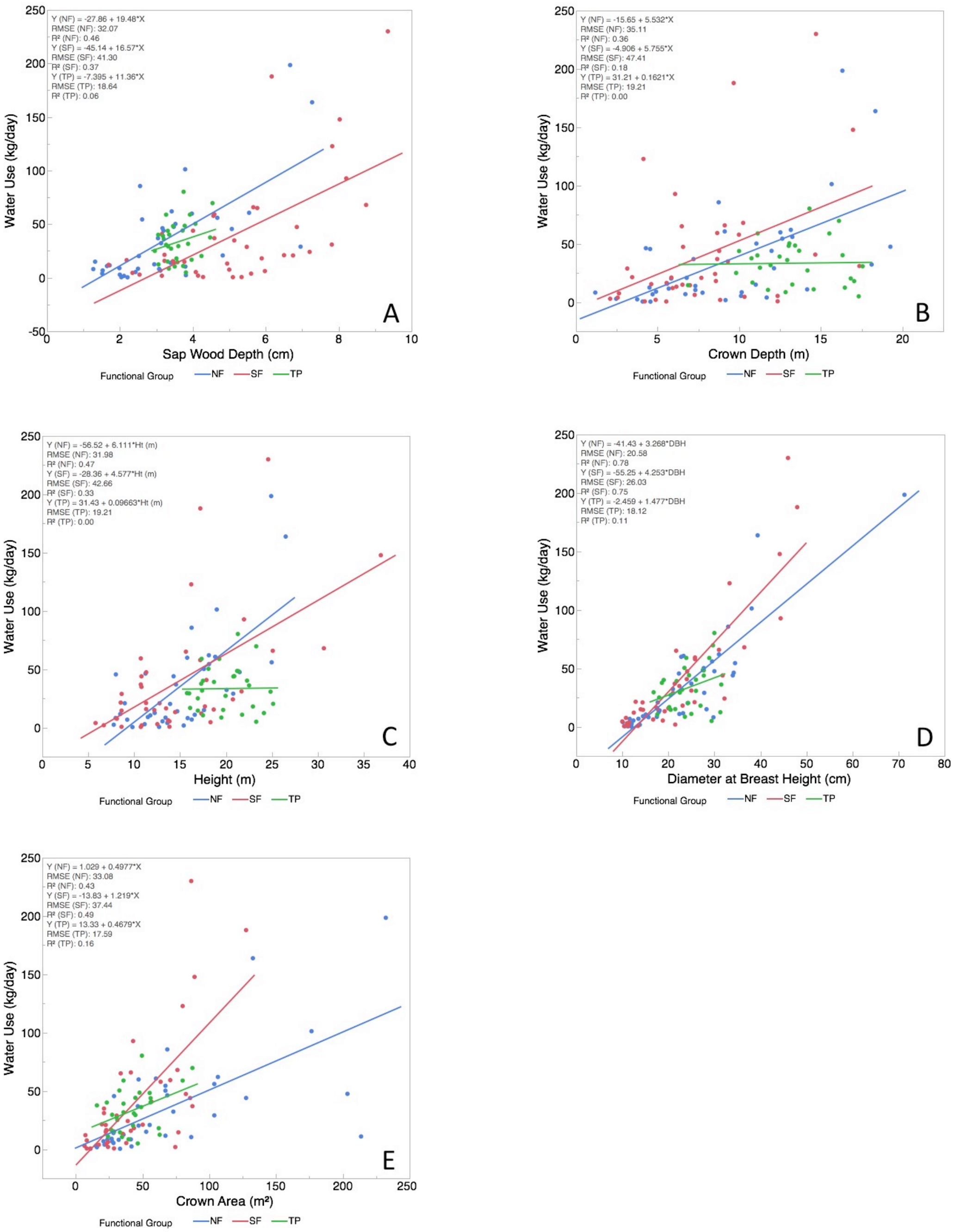


Figure 3.4. Relationships of tree sapwood depth (A), crown depth (B), height (C), trunk diameter at breast height (D), and crown area (E) to tree water use for N-fixer (NF; n=39), secondary forest (SF; n=40), and teak plantation (TP; n=30) functional groups.

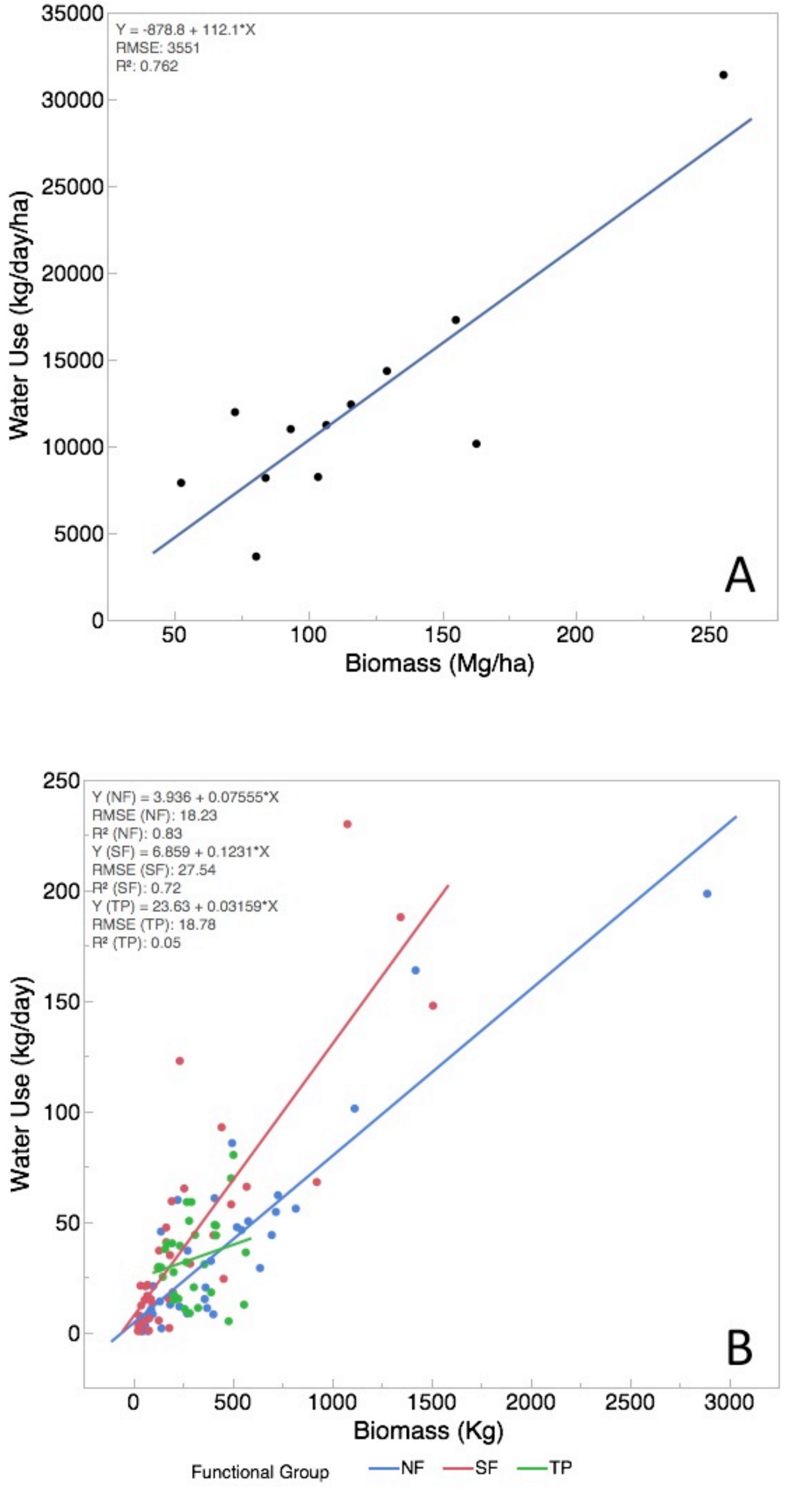
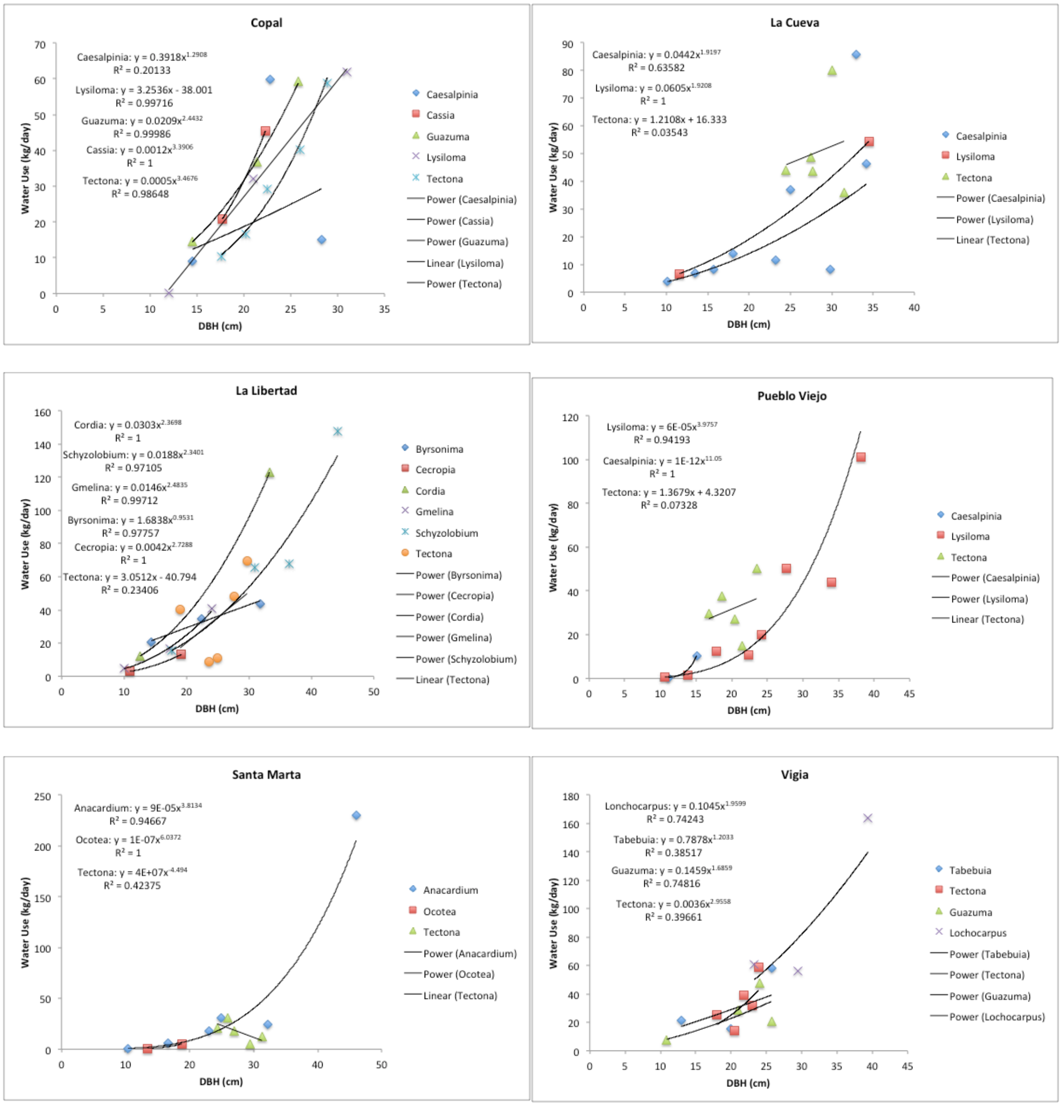


Figure 3.5. Relationship of biomass and water use at the stand level (A) across all study sites (N=12) and at the tree level (B) for N-fixer (NF; n=39), secondary forest (SF; n=40), and teak plantation (TP; n=30) functional groups.

APPENDIX A: WET SEASON WATER USE REGRESSIONS BY SPECIES



Appendix A. Individual tree wet season water use by species and corresponding regression equations used to estimate stand-level water use for each site.

APPENDIX B: WATER USE AND WATER USE EFFICIENCY ESTIMATES BASED ON DIFFERENT METHODS

Appendix B. Wet season water use (kg/ha/day), annual water use (Mg/ha/yr) and carbon fixation (kg/ha/yr), and water use efficiency (WUE; kg C / Mg H_2O) for secondary forest (SF) and teak plantation (TP) treatments by estimates based on species (Spp) or functional group (FG) regression equations, or means for teak trees (TM) per site.

Site	Treat-ment	Number of Trees	Water Use Spp (kg/day/ha)	Water Use FG (kg/day/ha)	Water Use FG-TM (kg/day/ha)	Water Use SPP (Mg/ha/yr)	Water Use FG (Mg/ha/yr)	Water Use FG TM (Mg/ha/yr)	Carbon Fixed (kg/ha/yr)	WUE Spp (kg C / Mg H_2O)	WUE FG (kg C / Mg H_2O)	WUE FG TM (kg C / Mg H_2O)
Copal	SF	23	13,791	11,228	11,228	3775	3074	3074	1291	0.342	0.420	0.420
	TP	17	8181	8181	10,579	2239	2239	2896	3547	1.584	1.584	1.225
La Cueva	SF	38	8494	8235	8235	2325	2254	2254	1434	0.617	0.636	0.636
	TP	11	10,991	10,991	11,116	3009	3009	3043	3720	1.236	1.236	1.223
La Libertad	SF	32	29,786	31,401	31,401	8154	8596	8596	5783	0.709	0.673	0.673
	TP	19	12,411	12,411	13,485	3397	3397	3691	3315	0.976	0.976	0.898
Pueblo Viejo	SF	22	9973	10,146	10,146	2730	2778	2778	1403	0.514	0.505	0.505
	TP	19	11,970	11,970	12,132	3277	3277	3321	8581	2.619	2.619	2.584
Santa Marta	SF	21	14,896	17,279	17,279	4902	5772	5772	2779	0.567	0.481	0.481
	TP	10	3648	3648	3455	999	999	946	2836	2.840	2.840	2.999
Vigia	SF	18	14,907	14,340	14,340	4081	3926	3926	997	0.244	0.254	0.254
	TP	11	7896	7896	7442	2162	2162	2037	2040	0.944	0.944	1.002

APPENDIX C: CORRELATION MATRIX OF STRUCTURAL, TREE, AND LEAF TRAITS AT THE STAND LEVEL

Appendix C. Correlation matrix of structural, tree, and leaf traits at the stand level. All correlations significant to $p<0.05$ are in bold on the upper right hand side of the matrix.

	BM	TD	BA	LAI	SWD	SWHW	BT	CD/Ht	CA/BA	WD	WWC	WN	WC	MxHt	LT	LA	SLA	LWC	LN	LC
BM	1.0000	**0.7824**	**0.9324**	0.4254	0.5429	0.2274	**-0.6153**	**-0.6933**	0.1179	-0.0047	-0.2176	0.0908	0.0261	0.4724	-0.3089	-0.0589	-0.2304	-0.3554	0.3008	0.3532
TD	0.7824	1.0000	**0.8347**	0.4523	0.2692	0.0966	-0.4675	**-0.5928**	0.0816	0.0997	-0.2669	0.0041	0.1835	0.2504	-0.3474	-0.0196	-0.0123	-0.2426	0.3261	0.1759
BA	0.9324	0.8347	1.0000	0.5095	**0.6387**	0.4226	**-0.6078**	**-0.6600**	-0.0903	-0.1671	-0.0808	-0.0140	-0.0435	0.5057	-0.2452	-0.0094	-0.2242	-0.1437	0.1373	0.2335
LAI	0.4254	0.4523	0.5095	1.0000	0.4662	**0.6556**	-0.4935	-0.4204	0.2568	0.3070	-0.4995	0.4798	**-0.6500**	-0.2129	**-0.6222**	**-0.6427**	0.4280	-0.1894	0.4914	0.3711
SWD	0.5429	0.2692	0.6387	0.4662	1.0000	**0.6515**	-0.2389	-0.4194	-0.3217	-0.5223	0.2795	-0.0296	-0.4966	0.4657	0.1776	0.0406	-0.2783	0.2277	-0.2186	-0.1581
SWHW	0.2274	0.0966	0.4226	0.6556	0.6515	1.0000	-0.3427	-0.1860	-0.1996	-0.1953	0.0305	-0.0612	**-0.6656**	0.0757	-0.2064	-0.3459	-0.0745	0.0740	-0.1590	0.0381
BT	-0.6153	-0.4675	-0.6078	-0.4935	-0.2389	-0.3427	1.0000	**0.6197**	-0.2444	-0.2544	0.4118	-0.2263	0.2208	0.0497	**0.5864**	0.4784	0.1118	0.5746	-0.4976	-0.5659
CD/Ht	-0.6933	-0.5928	-0.6600	-0.4204	-0.4194	-0.1860	0.6197	1.0000	0.0695	0.0175	0.1345	-0.2062	0.0009	-0.2253	0.2741	0.1139	0.0738	0.2134	-0.2230	-0.3391
CA/BA	0.1179	0.0816	-0.0903	0.2568	-0.3217	-0.1996	-0.2444	0.0695	1.0000	**0.9194**	**-0.9308**	**0.5985**	-0.0618	**-0.6762**	**-0.7800**	**-0.7418**	0.4967	**-0.7500**	**0.8763**	**0.6780**
WD	-0.0047	0.0997	-0.1671	0.3070	-0.5223	-0.1953	-0.2544	0.0175	0.9194	1.0000	**-0.9538**	**0.6191**	0.0007	**-0.7699**	**-0.8552**	**-0.7782**	**0.6225**	**-0.6988**	**0.8804**	**0.7032**
WWC	-0.2176	-0.2669	-0.0808	-0.4995	0.2795	0.0305	0.4118	0.1345	-0.9308	-0.9538	1.0000	**-0.6798**	0.1155	**0.6864**	**0.9407**	**0.8422**	**-0.6123**	**0.7188**	**-0.9336**	**-0.7927**
WN	0.0908	0.0041	-0.0140	0.4798	-0.0296	-0.0612	-0.2263	-0.2062	0.5985	0.6191	-0.6798	1.0000	-0.1469	-0.5602	**-0.5963**	**-0.7184**	**0.6480**	-0.2793	**0.7421**	**0.7058**
WC	0.0261	0.1835	-0.0435	-0.6500	-0.4966	-0.6656	0.2208	0.0009	-0.0618	0.0007	0.1155	-0.1469	1.0000	0.1516	0.1769	0.4072	-0.2730	-0.0830	-0.1221	0.0482
MxHt	0.4724	0.2504	0.5057	-0.2129	0.4657	0.0757	0.0497	-0.2253	-0.6762	-0.7699	0.6864	-0.5602	0.1516	1.0000	**0.5927**	**0.7737**	**-0.5870**	0.4219	**-0.5948**	-0.4112
LT	-0.3089	-0.3474	-0.2452	-0.6222	0.1776	-0.2064	0.5864	0.2741	-0.7800	-0.8552	0.9407	-0.5963	0.1769	0.5927	1.0000	**0.8602**	-0.5255	**0.6948**	**-0.8345**	**-0.8504**
LA	-0.0589	-0.0196	-0.0094	-0.6427	0.0406	-0.3459	0.4784	0.1139	-0.7418	-0.7782	0.8422	-0.7184	0.4072	0.7737	0.8602	1.0000	-0.4992	**0.6146**	**-0.7622**	**-0.7144**
SLA	-0.2304	-0.0123	-0.2242	0.4280	-0.2783	-0.0745	0.1118	0.0738	0.4967	0.6225	-0.6123	0.6480	-0.2730	-0.5870	-0.5255	-0.4992	1.0000	0.0817	0.5711	0.3936
LWC	-0.3554	-0.2426	-0.1437	-0.1894	0.2277	0.0740	0.5746	0.2134	-0.7500	-0.6988	0.7188	-0.2793	-0.0830	0.4219	0.6948	0.6146	0.0817	1.0000	**-0.6869**	**-0.6077**
LN	0.3008	0.3261	0.1373	0.4914	-0.2186	-0.1590	-0.4976	-0.2230	0.8763	0.8804	-0.9336	0.7421	-0.1221	-0.5948	-0.8345	-0.7622	0.5711	-0.6869	1.0000	**0.7221**
LC	0.3532	0.1759	0.2335	0.3711	-0.1581	0.0381	-0.5659	-0.3391	0.6780	0.7032	-0.7927	0.7058	0.0482	-0.4112	-0.8504	-0.7144	0.3936	-0.6077	0.7221	1.0000

BM=Biomass (Mg/ha); TD=Tree Density (trees/ha); BA=Basal Area (m^2/ha); LAI=Leaf Area Index (m^2/m^2); SWD=Sapwood Depth (cm); SWHW=Sapwood / Heartwood Area (cm^2/cm^2); BT=Bark Thickness; CD/Ht=Crown Depth / Height (m/m); CA/BA=Crown Area / Basal Area (m^2/cm^2); WD=Wood Density (g/cm^3); WWC=Wood Water Content (%); WN=Wood Nitrogen (%); WC=Wood Carbon (%); MxHt=Maximum Height (m); LT=Leaf Thickness (mm); LA=Leaf Area (cm^2); SLA=Specific Leaf Area (cm^2/g); LWC=Leaf Water Content (%); LN=Leaf Nitrogen (%); & Leaf Carbon (%).

APPENDIX D: CORRELATION MATRIX OF TREE TRAITS AT THE TREE LEVEL

Appendix D. Correlation matrix of tree traits at the tree level. All correlations significant to $p<0.05$ are in bold on the upper right hand side of the matrix.

	BM	DBH	SWD	SWHW	BT	Ht	CD	CD/Ht	CA	CA/BA	WD	WWC	WN	WC
BM	1.0000	**0.8896**	**0.3852**	-0.1245	0.0248	**0.6092**	**0.4887**	0.1035	**0.7170**	**-0.2519**	0.0617	-0.0088	0.1390	-0.0126
DBH	0.8896	1.0000	**0.4565**	**-0.2010**	0.0967	**0.6284**	**0.5007**	0.1237	**0.6842**	**-0.3384**	-0.0513	0.1406	0.0765	0.0066
SWD	0.3852	0.4565	1.0000	0.1206	-0.1092	**0.2948**	0.0813	-0.1242	**0.1910**	-0.1723	**-0.3822**	**0.2334**	-0.0930	**-0.2777**
SWHW	-0.1245	-0.2010	0.1206	1.0000	-0.0998	**-0.2057**	-0.1873	-0.0897	-0.1517	0.0114	-0.0865	0.0166	-0.1506	-0.1507
BT	0.0248	0.0967	-0.1092	-0.0998	1.0000	0.1082	**0.2261**	0.1577	0.0411	-0.1027	-0.0457	0.1276	0.0079	0.1149
Ht	0.6092	0.6284	0.2948	-0.2057	0.1082	1.0000	**0.7688**	0.1175	**0.3374**	**-0.3883**	**-0.2786**	**0.3868**	-0.0999	0.0598
CD	0.4887	0.5007	0.0813	-0.1873	0.2261	0.7688	1.0000	**0.6906**	**0.4666**	-0.1448	-0.0901	**0.2705**	-0.0537	0.1552
CD/Ht	0.1035	0.1237	-0.1242	-0.0897	0.1577	0.1175	0.6906	1.0000	**0.3643**	**0.2305**	0.1318	0.0100	0.0043	**0.2404**
CA	0.7170	0.6842	0.1910	-0.1517	0.0411	0.3374	0.4666	0.3643	1.0000	**0.2781**	**0.2586**	**-0.2153**	**0.2456**	0.0639
CA/BA	-0.2519	-0.3384	-0.1723	0.0114	-0.1027	-0.3883	-0.1448	0.2305	0.2781	1.0000	**0.2972**	**-0.3691**	0.1271	-0.0453
WD	0.0617	-0.0513	-0.3822	-0.0865	-0.0457	-0.2786	-0.0901	0.1318	0.2586	0.2972	1.0000	**-0.9090**	**0.4027**	0.0677
WWC	-0.0088	0.1406	0.2334	0.0166	0.1276	0.3868	0.2705	0.0100	-0.2153	-0.3691	-0.9090	1.0000	**-0.3830**	0.0913
WN	0.1390	0.0765	-0.0930	-0.1506	0.0079	-0.0999	-0.0537	0.0043	0.2456	0.1271	0.4027	-0.3830	1.0000	-0.0411
WC	-0.0126	0.0066	-0.2777	-0.1507	0.1149	0.0598	0.1552	0.2404	0.0639	-0.0453	0.0677	0.0913	-0.0411	1.0000

BM=Biomass (kg); DBH=Diameter at Breast Height (cm); SWD=Sapwood Depth (cm); SWHW=Sapwood / Heartwood Area (cm^2/cm^2); BT=Bark Thickness; Ht=Height (m); CD=Crown Depth (m); CD/Ht=Crown Depth / Height (m/m); CA=Crown Area (m^2); CA/BA=Crown Area / Basal Area (m^2/cm^2); WD=Wood Density (g/cm^3); WWC=Wood Water Content (%); WN=Wood Nitrogen (%); & WC=Wood Carbon (%).

APPENDIX E: OFFICE OF SPONSORED PROGRAMS APPROVAL FOR BORLAUG FELLOWSHIP PROPOSAL

University of Idaho

Office of Sponsored Programs

PO Box 443020
Moscow ID 83844-3020

Phone: 208-885-6651
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osp@uidaho.edu

September 13, 2012

Deb Dimmitt
Business Services
U.S. Borlaug Fellows in Global Food Security Program
Purdue Center for Global Food Security
615 W. State Street
W. Lafayette, IN 47907

Dear Ms. Dimmitt:

The University of Idaho supports the proposal prepared by Oscar J. Abelleira (US Advisor Dr. Alexander Fremier), entitled, *The impact of reforestation with plantations on water provision for agriculture in the seasonally dry tropics.*

The appropriate University of Idaho program and administrative personnel have reviewed and approved this proposal. The estimated period for this project is June 21, 2012 through July 31, 2014. The budget totals $15,000.

Contact information for the P.I. is as follows:

Dr. Alexander Kent
Fish & Wildlife Sciences Department
PO Box 441136
University of Idaho
Moscow, ID 83844-1136
email: afremier@uidaho.edu
tel. 208-885-6405
fax: 208-885-9080

Please contact Ann-Marie Bilderback, Sponsored Programs Administrator, if you require further information. She can be reached at (208) 885-6651, or by email at osp@uidaho.edu.

Sincerely,

Polly Knutson

Polly Knutson
Director
Office of Sponsored Programs
AMB 9-13-12