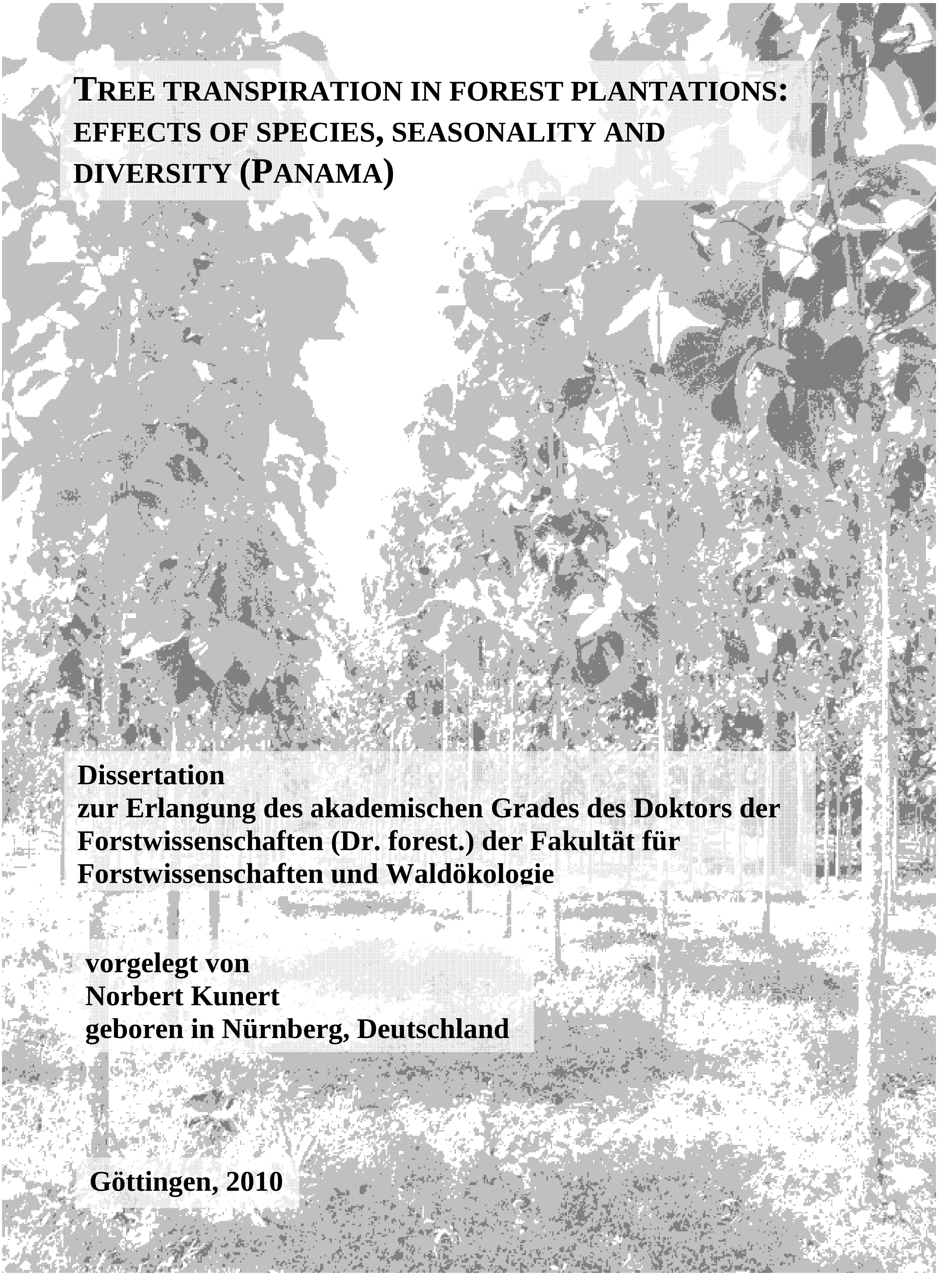


TREE TRANSPIRATION IN FOREST PLANTATIONS: EFFECTS OF SPECIES, SEASONALITY AND DIVERSITY (PANAMA)

Dissertation
zur Erlangung des akademischen Grades des Doktors der Forstwissenschaften (Dr. forest.) der Fakultät für Forstwissenschaften und Waldökologie

vorgelegt von
Norbert Kunert
geboren in Nürnberg, Deutschland

Göttingen, 2010

TREE TRANSPIRATION IN FOREST PLANTATIONS: EFFECTS OF SPECIES, SEASONALITY AND DIVERSITY (PANAMA)

Dissertation
zur Erlangung des akademischen Grades des Doktors der Forstwissenschaften (Dr. forest.) der Fakultät für Forstwissenschaften und Waldökologie
der Georg-August-Universität Göttingen

vorgelegt von
Norbert Kunert
geboren in Nürnberg, Deutschland

Göttingen, 2010

1. Gutachter: Prof. Dr. Dirk Hölscher

2. Gutachter: Prof. Dr. Christian Ammer

Tag der mündlichen Prüfung: 9. Juni 2010

TREE TRANSPIRATION IN FOREST PLANTATIONS: EFFECTS OF SPECIES, SEASONALITY AND DIVERSITY (PANAMA)

Forests serve many benefits worldwide such as providing renewable raw materials and energy, maintaining biodiversity and protecting land and water resources. However, they are threatened by fire, agricultural and urban expansion and various other disturbances. Especially in tropical areas the loss of forest cover is on an alarming high rate. Therefore the establishment of tree plantations in the tropics is of increasing importance to mitigate climate change by carbon sequestration and as a contribution to the growing demand for wood. Current research suggests that well designed forest plantations can reduce the volume of sediment, nutrients and salt transported into river systems. Nevertheless, there is a growing concern that tree plantations could potentially use high quantities of water. So far, most of afforestation and reforestation with tree plantations has been conducted with monocultures involving a limited number of species. Such traditional plantations have supplied some benefits but have made only minor contributions to the restoration of ecological functions and biodiversity. According to that, recent approaches to reforestation in the tropics emphasize the establishment of multispecies plantations consisting of native tree species. Information on species-specific water use characteristics of tropical trees is at present very limited. The few existing multispecies reforestation experiments are pointing out that tropical plantations containing higher tree diversity are likely to be more productive in biomass than monospecific stands, but possible changes in the hydrological cycle have rarely been studied. Furthermore, the effectiveness of tree species selection in stands aiming at biomass production can be questioned, as recent studies in old growth forest showed that species-independent relationships between water use and tree size exist.

The main objectives of this study were

(1) to determine the influence of species and tree structural traits on seasonal water use characteristics in trees planted monocultures,

(2) to assess the effect of tree diversity (1-, 3-, and 6-species mixtures) on the water use of tree plantations, and

(3) to compare water use characteristics of trees growing in different land use systems across the tropics.

The main part of this dissertation was conducted on an experimentally designed tree plantation in Panama. Chapters 4 and 5 of this thesis are dealing with the results gained from the field study in Panama. Chapter 6 presents data on how generalizations could be made for trees growing in different land-use systems at different locations in the tropics.

Chapter 4 is addressing water use characteristics in tree species growing in monocultures under seasonal climate. Thermal dissipation sensors were applied to measure sap flux over one entire year in nine tree species, six of which were native to the region and three were exotics widely planted throughout the tropics, growing in two plantations near the village Sardinilla, Panama. Each species was represented by four individuals with a sun-exposed crown. Simultaneously, environmental variables such as photosynthetic photon flux density, vapour pressure deficit and soil moisture were registered and aspects of tree leaf phenology were quantified. These species range in leaf phenology from evergreen to semi-deciduous and to deciduous.

Chapter 5 is presenting results from comparison of monoculture and multispecies plots consisting of native tree species. The hypothesis of this chapter was that tree diversity enhances tree transpiration of mixed tree species plots. To test this hypothesis we measured tree sap flux and estimates water useplot transpiration. Measurements were conducted in 60 trees in a seven-year-old tree plantation in Panama for one year. Trees were planted in monoculture, 3-species mixtures and 6-species mixtures. Biodiversity effects were statistically partitioned on plot level transpiration, and the importance of complementarity of species on tree water use was evaluated.

Chapter 6 is based in part on data provided by members of the research group. The dataset from the monoculture plots in Panama was combined with the datasets from mixed reforestation stands in the Philippines and an agroforestry stand in Indonesia. A simple sap flux model was applied to describe sap flux as a function of the most important environmental variables. This resulted in a synthesis covering more than 100 trees belonging to 17 species that were studied using almost identical methods. The aim of this study was to see if generalisations could be made for trees growing in different land-use systems at different locations in the tropics.

The main findings were following:

- Results from the monocultures in Panama showed that under full foliage, maximum sap flux densities varied more than two-fold among species. Time of leaf shedding and duration of leafless periods also varied strongly among the semi-deciduous and among the deciduous species. However, the relationship between percentage of foliage and normalized maximum sap flux densities can be described by a universal non species-specific function. Species means of maximum transpiration rates on a basis of projected crown area varied more than two-fold (1.2 - 2.8 mm d^{-1}). Transpiration rates between the dry and wet season differed for six of the nine species. Three species (*Acacia mangium, Anacardium excelsum,* and *Gmelina arborea*) showed enhanced transpiration in the dry season with dry to wet season ratios between 1.4 and 2.1. In contrast, the dry to wet season ratio of *Cedrela odorata, Hura crepitans,* and *Tectona grandis* ranged from 0.4 to 0.8. The results suggest that tree species choice can substantially influence water resource use in plantation forestry under such seasonal climatic conditions.

- The results of the comparison of the monoculture and multispecies plots showed that species-specific annual course of sap flux density varied little among mixture types. Annual tree water use differed significantly among species. Maximum tree water use was related to tree diameter ($r^2 = 0.54$, $p < 0.001$). Trees in most of the 3-species mixtures and in all 6-species mixtures had attained bigger diameters than those growing in monocultures, which was associated with increased tree water use rates. Accordingly, the estimated annual transpiration correlated with the basal area of the study plots. However, the 6-species mixtures had significantly higher transpiration rates per unit basal area than monocultures and 3-species mixtures (51% and 56%, respectively). An additive partitioning method suggests a positive net biodiversity effect induced by complementarity of species. We assume that enhanced transpiration rates in mixed plots might arise from complementary use of radiation and from higher canopy roughness of the mixed species plots. Our results suggest that complementarity of species influences tree water use rates in tree species mixture and can thus be used for an optimization of water resource management.

- The synthesis of data collected from more than 100 trees belonging to 17 species revealed a threefold range of maximal sap flux densities and significant differences in sap flux densities within species growing at each of the given study sites. A declining, species independent relationship between sap flux density and tree diameter, suggested in literature, could not be substantiated by this large dataset. Despite the very different study locations and large number of species included, pooled data revealed a strong linear relationship between water use rates and tree diameter ($R^2_{adj} = 0.65$). Even so, trees of different species with comparable diameter and contrasting water use (twofold differences) were found at all sites, indicating that species-identity may affect water use in a variety of land-use systems throughout the tropics.

In conclusion, it can be said that all results suggest an effect of species on tree water use characteristics and that species selection, under seasonal climate especially through the choice of tree phenolgy and species combination are helpful tools to balance water use and productivity of manmade forest.

TRANSPIRACIÓN DE ÁRBOLES EN PLANTACIONES FORESTALES: EFECTOS DE LAS ESPECIES, ESTACIONALIDAD Y DIVERSIDAD (PANAMA)

A nivel mundial, los bosques proveen muchos beneficios como materiales renovables y energía, manteniendo la biodiversidad y protegiendo recursos del suelo y agua. Sin embargo, se encuentran bajo la amenaza de expansiones urbanas y agrícolas, incendios y otro tipo de perturbaciones. La tasa de pérdida de cobertura de los bosques en areas tropicales se encuentra a niveles extremadamente altos. Por lo tanto, establecer plantaciones en zonas tropicales es de gran importancia para mitigar los cambios climáticos secuestrando carbon y para contribuir a la creciente demanda de productos madereros. Investigaciones han demostrado que el buen diseño de plantaciones forestales puede reducir el volumen sedimentos, nutrientes y volumen de sal que llegará a sistemas acuíferos. No obstante, aun se cuestiona el hecho de que plantaciones forestales pueden requerir grandes cantidades de agua. Hasta el momento la mayoría de los proyectos de aforestación y reforestación se han realizado con monocultivos, incluyendo un número limitado de especies. Este tipo de plantaciones proveen algunos beneficios materiales pero contribuyen de manera muy limitada a restorar funciones ecológicas y biodiversidad. Es por eso que recientes enfoques en investigaciones de reforestación en los trópicos hacen énfasis en establecer plantaciones con múltiples especies nativas. La información y conocimiento acerca de las carácteristicas de uso del agua específico por especie es actualmente muy limitado. Los pocos estudios de reforestación realizados utilizando múltiples especies señalan que plantaciones con una mayor diverisdad tienden a ser más productivas en cuanto a la biomasa que plantaciones de una sola especie, sin embargo no se ha tomado en cuenta el efecto de posibles cambios en el ciclo hidrológico. La efectividad en la selección de especies en base a la produción de biomasa es cuestionable, ya que estudios recientes demuestran la relación que hay entre el uso del agua y el tamaño de los árboles en bosques maduros.

Los principales objetivos de este estudio fueron:

(1) Determinar la influencia de especies y rasgos estructurales de los árboles en las características de uso del agua en plantaciones de monocultivos,

(2) Cuantificar el efecto de la diversidad de especies (mezclas de 1-, 3-, 6- especies) en el uso del agua en plantaciones forestales, y

(3) Comparar características en el uso del agua en árboles creciendo en distintos tipos de uso del suelo en zonas tropicales

El componente principal de esta tesis se llevó a cabo en una plantación experimental en Panamá. Los capítulos 4 y 5 de la tesis presentan los resultados obtenidos del trabajo de campo en Panamá. En el capítulo 6 se muestran resultados generales comparando información de árboles de diferentes sistemas ambientales en varias regiones tropicales.

En el capítulo 4 se presenta la información de monocultivos y características del uso del agua en las especies en un clima estacional. Sensores de disipación térmica se usaron para medir el flujo de savia a lo largo de un año en 9 especies de árboles, seis especies nativas a la region y 3 introducidas y comunmente utilizadas en plantaciones en zonas tropicales. Este trabajo se realizó en dos plantaciones en la localidad de Sardinilla, República de Panamá. Cada especie estaba representada por 4 individuos cuya copa estaba expuesta al sol. Igualmente se midieron variables ambientales como densidad del flujo de fotones fotosintéticos, el deficit en presión del vapor y la humedad en el suelo. También se cuantificaron aspectos de la fenológia de hojas en los árboles. Las especies estudiadas varían en fenología de hojas de siempreverdes, semicaducos a caducos.

El capítulo 5 se enfoca en la comparación de monocultivos y plantaciones con multiples especies nativas a la region, y se espera que la diversidad de árboles aumenta la perdida de agua en plantaciones con múltiples especies. Para este estudio se midió el flujo de savia y uso del agua, y estadísticamente se dividieron los efectos de biodiversidad en los niveles de transpiración por parcela. Esto permitió caracterizar la importancia de complementaridad de especies en el uso de agua por los árboles. Las medidas se hicieron durante un año en 60 árboles en una plantación establecida hace 7 años en Panamá. Los árboles se plantaron en parcelas de 1, 3, y 6 especies.

El capítulo 6 concierne datos provenientes de varios miembros del grupo de investigación. Los datos obtenidos de los monocultivos en la plantación en Panamá se utilizaron en conjunto con datos de parcelas mixtas de reforestación en las Filipinas y un sitio agroforestal en Indonesia. Un modelo simple de flujo de savia se aplica para discribir el flujo de la savia en función de las más relevantes variables ambientales. Este trabajo resulto en una sintesis de datos con más de 100 árboles representando 17 especies que se han estudiado bajo una misma metodología. El propósito de este estudio es investigar posibles generalizaciones en los árboles creciendo en diferentes sistemas en distintas localidades tropicales.

Los resultados principales son los siguientes:

- El estudio de los monocultivos en Panama muestran que la densidad de flujo máximo de la savia varía más del doble entre especies cuando el follaje es completo. El tiempo en que las hojas empiezan a caer y la duración de los periodos sin hojas tienen una fuerte variación entre las especies. Sin embargo, la relación entre el porcentaje de follaje y las densidades máximas de flojo de savia normalizadas pueden describirse con una función universal no específica por especie. La media de las tasas máximas de transpiración proyectadas en base al área de la copa varía más del doble (1.2 – 2.8 mm d^{-1}). Las tasas de transpiración entre la estación seca y la estación humeda varía para seis de las nueve especies. Tres especies (*Acacia mangium, Anacardium excelsum,* and *Gmelina arborea*) muestran aumentos en la transpiración durante la estación seca. La proporción de transpiración entre la estación seca y la estación humeda es de 1.4 a 2.1. A diferencia de las otras especies *Cedrela odorata, Hura crepitans,* y *Tectona grandis*, en donde la proporción de la estación seca a la humeda va de 0.4 a 0.8. Los resultados indican que la selección de especies para plantaciones forestales puede influenciar significativamente el uso del agua bajo estaciones climáticas similares.
- Los resultados de la comparación de monocultivos y plantaciones con múltiples especies muestran que el curso anual de la densidad de flujo de savia especifico para cada especie varía poco entre las distintas mezclas de especies. El uso anual del agua por los árboles difiere significativamente entre especies. El máximo uso del agua se relaciona al diametró del árbol ($r^2 = 0.54$, $p < 0.001$). Los árboles en la mayoría de las parcelas de mezclas de tres especies y todas las de seis especies tienen mayores

diametros que aquellos en los monocultivos, lo cual se puede relacionar con una mayor tasa de uso de agua por los árboles. Igualmente la transpiración anual estimada se correlaciona con el área basal en los sitios de estudio. Sin embargo, las parcelas con seis especies tienen tasas de transpiración significativamente más altas por unidad de área basal que los monocultivos y mezclas de tres especies (51 y 56% respectivamente). Un método de división aditiva sugiere un efecto neto positivo de la biodiversidad inducido por el efecto complementario de las especies. Suponemos que los aumentos en la tasa de transpiración en parcelas con mezcla de especies se dan por el uso complementario de la radiación y una mayor heterogeneidad en el dosel en las parcelas con mezcla de especies. Nuestros resultados sugieren un efecto domplementario de las especies que influye en las tasas de uso del agua en parcelas con múltiples especies, lo cual puede utilizarse para optimizar el manejo del agua.

- La sintesis de los datos colectados de más de 100 árboles representando 17 especies dejan ver una variación tres veces mayor en la densidad máxima del flujo de savia así como diferencias significativas en la densidad del flujo de savia dentro del grupo de especies en cada sitio de estudio. Una relación decreciente entre la densidad del flujo de savia y el diámetro del árbol, independiente de la especie, propuesto en la literatura, no puede confirmarse con el extenso conjunto de datos presentados en estudio. A pesar de la gran diferencia en sitios de estudio y en alto número de especies incluidas, el agrupamiento de los datos reveló una fuerte relación linear entre las tasas de uso de agua y diámetro de los árboles ($R^2_{adj} = 0.65$). Igualmente, los árboles de distintas especies con un diámetro similar y distinto uso del agua (differencias de doble del valor) se encontraron en todos los sitios. Esto indica que la identidad de las especies puede afectar el uso del agua en una variedad de sitios con distintos usos del suelo alrededor de las zonas tropicales.

En conclusión, puedo decir que todos los resultados indican un efecto de las especies en el uso del agua por los árboles, y que la selección de especies en sitios con un clima estacional, tomando en cuenta las distintas fenologías y combinación de especies, es una herramienta importante para equilibrar el uso del agua y la productividad en plantaciones forestales.

BAUMTRANSPIRATION IN FORSTLICHEN PLANTAGEN: EFFEKTE VON ARTEN, SAISONALITÄT UND DIVERSITÄT (PANAMA)

Die weltweit vorhandenen Wälder bieten eine Bandbreite an Nutzungsmöglichkeiten. Sie stellen erneuerbare Rohstoffe sowie Energieressourcen zur Verfügung, erhalten die Biodiversität und schützen sowohl Land- und Wasserressourcen. Jedoch sind diese durch Waldbrand, Ausbreitung landwirtschaftlicher und urbane Fläche sowie verschiedener anderer Eingriffe bedroht. Besonders in tropischen Gegenden hat der Verlust an Waldfläche alarmierende Ausmaße erreicht. Die Begründung von tropischen Holzplantagen hat daher gewisse Bedeutung erhalten, um die Auswirkungen des globalen Klimawandels durch Kohlenstofffixierung abzuschwächen und der wachsenden Nachfrage nach Holz nachzukommen. Aktuelle Forschungsergebnisse nehmen des Weiteren an, dass durch gut angelegte Holzplantagen der Eintrag von Sedimenten, Nährstoffen und Mineralien in Gewässer reduziert werden kann. Trotzdem gibt es zunehmend Bedenken ob diese Holzplantagen nicht potentiell große Wassermengen verbrauchen könnten. Bis jetzt wurden diese Aufforstungen in Form von Plantagen und zumeist mit einer sehr beschränkten Anzahl an Baumarten durchgeführt. Solche traditionellen Holzplantagen erfüllen durchaus ihren Zweck, jedoch haben sie nur einen geringen Beitrag zur Erhaltung der ökologischer Schutzfunktion und der Biodiversität geleistet. Daher empfehlen neuere Studien Wiederaufforstungen in Form von Mischbeständen mit einheimischen Arten zu gestalten, jedoch ist über die Wassernutzung der einzelnen tropischen Baumarten bis jetzt wenig bekannt. Die wenigen bereits bestehenden Experimente von Wiederaufforstungen mit Mischbeständen zeigen, dass tropische Holzplantagen mit einer höheren Artenzahl eine schnellere Biomasseproduktion als Reinbestände aufweisen. Der Einfluss von Mischbeständen auf den Wasserkreislauf wurde jedoch noch nicht untersucht. Des Weiteren ist die Artenwahl als Mechanismus zur Beeinflussung der Bestandestranspiration fragwürdig, da Forschungsergebnisse aus Naturwäldern einen artenunabhängigen Zusammenhand zwischen Wassernutzung und Baumgröße zeigen.

Die Hauptziele dieser Studie waren daher

(1) den Einfluss von Arten und Baumstrukturparameter auf die saisonale Wassernutzung von Bäumen in Reinbeständen zu bestimmen,

(2) die Auswirkung von Baumartendiversität (Reinbestand, 3- und 6-Artenmischbestand) auf die Wassernutzung von Holzplantagen zu bestimmen.

(3) einen Vergleich der Wassernutzung von Bäumen in verschiedenen Landnutzungssystemen in verschiedenen tropischen Regionen aufzustellen.

Der Hauptteil dieser Dissertation wurde auf einer experimentell angelegten Holzplantage in Panama durchgeführt. Die Kapitel 4 und 5 dieser Dissertation stellen die Ergebnisse der Feldstudie aus Panama dar. Kapitel 6 zielt darauf ab, in wie weit die Wassernutzung von Bäumen welche in verschieden Landnutzungssystemen kultiviert werden, verallgemeinert werden kann.

Kapitel 4 behandelt die Wassernutzung von verschiedenen Baumarten in Reinbeständen unter saisonalem Klima. Hierfür wurden über ein Jahr mit Xylemsaftflusssensoren (thermal dissipation sensors) die Saftflussdichte in neun Baumarten, davon sechs in der Region heimische und drei fremdländische Baumarten, auf zwei Holzplantage in der Nähe des Dorfes Sardinilla in Panama gemessen. Von jeder Baumart wurde die Saftflussdichte von vier Individuen mit sonnenexponierter Krone gemessen. Analog zu den Xylemsaftflussmessungen wurden die photosyntheseaktive Strahlung, das Wasserdampfdruckdefizit der Luft und die Bodenfeuchte gemessen sowie Änderungen in der Blattphänologie aufgenommen. Die untersuchten Bäume wurden in phänologisch immergrüne, halbimmergrüne und laubabwerfende Arten eingeteilt.

Kapitel 5 behandelt das Ergebnis aus dem Vergleich von Plantagen bestehend aus einheimischen Baumarten, begründet in Reinbeständen und Mischbeständen. Die Hypothese dieses Kapitels bestand darin, das Baumdiversität den Wasserverlust von Plantagen mit Mischbeständen erhöht. Um diese Hypothese zu beweisen wurden der Xylemsaftfluss und die Wassernutzung der Bäumen gemessen und die Biodiversitätseffekte auf die Bestandestranspiration statistisch aufgegliedert, sowie der Einfluss der Komplementarität der Arten auf die Wassernutzung der Bestände charakterisiert. Die Messungen wurden für ein Jahr an 60 Probebäumen in einer sieben Jahre alten Plantage in Panama durchgeführt. Die

Bäume stammten aus Reinbeständen bzw. aus Mischbeständen von drei und sechs Baumarten.

Kapitel 6 basierten auf Daten, die zum Teil von Kollegen der Arbeitsgruppe erhoben wurden. Die erhobenen Daten der Reinbestände der Plantage in Panama wurden mit den Daten von Aufforstungsmaßnahmen durch Mischbestände von den Philippinen und Daten aus einem „agroforestry“ Bestand in Indonesien verglichen. Ein einfaches Saftflussmodell wurde angewandt, das die wichtigsten Umweltvariablen, wie Strahlung und Wasserdampf-druckdefizit, berücksichtigt. Die Modellparameter sowie Wassernutzungsraten wurden analysiert, um die Einflüsse der Artzugehörigkeit und der Baumstrukturen inkl. Durchmesser und oberirdischer Biomasse zu identifizieren. Dies resultierte in einer Synthese basierend auf mehr als 100 Bäumen aus 17 Arten, die mit einheitlichen Methoden untersucht worden sind. In dieser Studie wurde geprüft, ob es generelle Zusammenhänge über Baumarten, Kontinente und Nutzungssysteme hinweg zwischen Baumstruktur und Wassernutzung gibt.

Die Hauptergebnisse waren folgende:

- Die Ergebnisse aus der Untersuchung der Reinbestände in Panama zeigen, dass unter voller Belaubung die sich maximale Saftflussdicht unter den Arten um das zweifache unterschied. Der Zeitpunkt und die Dauer der Entlaubung waren ebenfalls zwischen den Arten sehr unterschiedlich. Der Zusammenhang zwischen Belaubungsprozent und standardisierter maximaler Saftflussdichte kann jedoch als allgemein gültige Funktion beschrieben werden. Im Durchschnitt unterschied sich auch die maximale Transpiration auf der Basis der Kronenprojektionsfläche zwischen den Arten um das zweifache (1,2 - 2,8 mm pro Tag). Die Transpirationsraten waren von sechs der neun Arten zwischen der Trocken und Regenzeit unterschiedlich. Drei Baumarten (*Acacia mangium*, *Anacardium excelsum* und *Gmelina arborea*) zeigten eine um das 1,4- bis 2,1-fache erhöhte Transpiration in der Trockenzeit im Vergleich zur Regenzeit. Im Gegensatz dazu transpirierten *Cedrela odorata*, *Hura crepitans* und *Tectona grandis* nur das 0,4 bis 0,8 -fache in der Trockenzeit gegebüber der Regenzeit. Die Ergebnisse legen nahe, dass die Artenauswahl die Wassernutzung von Holzplantage unter wechselnden Jahreszeiten wesentlichen beeinflussen kann.

Die Ergebnisse aus dem Vergleich der Reinbestände und Mischbestände zeigen, dass sich der Jahresverlauf der Saftflussdichte sehr wenig zwischen den verschieden Mischungsverhältnissen unterscheiden. Der jährliche Wasserverbrauch unterschied sich signifikant zwischen den Arten. Die Maximale Wassernutzungsrate korrelierte mit dem Stammdurchmesser der Bäume ($r^2 = 0{,}54$, $p < 0{,}001$). Die meisten Bäume aus den Mischbeständen mit drei Baumarten sowie fast alle Bäume in den Mischbeständen mit sechs Baumarten hatten gegenüber den Reinbeständen dickere Durchmesser, was mit einer höheren Wassernutzung einherging. Dementsprechend korrelierte die jährliche Bestandestranspirationsrate mit der Bestandesgrundfläche. Die Mischbestände bestehend aus sechs Baumarten hatten jedoch bezüglich auf die Bestandesgrundfläche eine signifikant höhere Wassernutzung als die Reinbestände bzw. Mischbestände mit 3 Baumarten (51% und 56%). Die statistische Partitionierung der Biodiversitätseffekte ergab einen positiven netto-Biodiversitätseffekt, hervorgerufen durch Komplementarität der Arten. Es ist anzunehmen, dass die erhöhte Transpirationsrate der Mischkulturen von der komplimentärern Nutzung des Lichts und erhöhter Kronenrauhigkeit der Mischkulturen herrührt. Die Komplementarität der Arten kann daher zur Optimierung der Wasserressourcen herangezogen werden.

- Die Synthese der Daten von mehr als 100 Baumen und 17 Arten zeigte eine Variation der maximalen Saftflussdichte zwischen den Arten um den Faktor drei sowie signifikante Unterschiede zwischen den Arten an den jeweiligen Standorten. Eine Abnahme der Saftflussdichte mit zunehmendem Baumdurchmesser, wie sie in der Literatur postuliert wird, konnte aus diesen Daten nicht bekräftigt werden. Trotz aller Unterschiede war auch in diesem Datensatz die Zunahme der Wassernutzung mit ansteigendem Durchmesser deutlich ersichtlich ($R^2_{adj} = 0.65$). Jedoch wurden bei gleichem Durchmesser erhebliche Unterschiede in der Wassernutzung zwischen den Arten (um ein Faktor zwei) festgestellt, unabhängig von den Standorten und Landnutzungssystemen.

Aus den Ergebnissen kann gefolgert werden, dass ein Zusammenhang zwischen Art und arstspezifischer Wassernutzung besteht. Somit sind die richtige Baumartenwahl, unter saisonalen Klimaten durch Nutzung der Baumphänology, sowie Baumartenkombination, probate Mittel zur Regulierung von Wassernutzung und Zuwachsleistung in Waldsystemen antropogenen Ursprungs.

CHAPTER 1
INTRODUCTION

1.1 Plantation forestry in the tropics

„Serit arbores, quae alteri saeclo prosint.“

Caecilius Statius (219-166 B.C.)

Fig. 1: In the last decade most of reforestation has been conducted with monocultures involving a limited number of species. In Panama, 65% of the new established plantations consist of teak (*Tectona grandis*) (ANAM 2008). (photo: www.fincaleola.com)

Forests serve many benefits worldwide such as providing renewable raw materials and energy, maintaining biodiversity and protecting land and water resources. However, they are threatened by fire, agricultural and urban expansion and various other disturbances. Especially in the tropics, deforestation is continuing at an alarmingly high rate. Therefore, the establishment of tree plantations on deforested tropical land and the afforestation of grassland is of increasing importance to mitigate climate change by carbon sequestration and as a contribution to the worldwide growing demand for wood. Current research suggest that well design forest plantations can reduce the volume of sediment, nutrients and salt transported into river systems (van Dijk and Keenan 2007). Nevertheless, there is a special concern about a reduction in stream flow with plantation establishments (Jackson et al. 2005, Malmer et al. 2010). From a worldwide synthesis, it can be assumed that annual runoff can be reduced by 44% when grassland is afforested (Farley et al. 2005). However, when reviewing the existing literature on the effects of forest plantation on the hydrological cycle, information on water use rates under plantation conditions are only available for a very limited set of species and conditions (Scott et al. 2004). So far, most of reforestation has been conducted with industrial monocultures involving a small number of species. These species usually are from the genera

Pinus, *Eucalyptus* and *Acacia.* In Panama, where this study was mainly conducted 65% of the new established plantations are consisting of teak (*Tectona grandis*) (ANAM 2008) (Figure 1). These traditional single species plantations have supplied some benefits but have made only minor contributions to the restoration of ecological functions and biodiversity (Lamb et al. 2005). According to that, recent approaches to reforestation in the tropics emphasize the establishment of multispecies plantations consisting of native tree species (Montagnini and Jordan 2005, Lamb et al. 2005, Wishnie et al. 2007). These few existing multispecies reforestation experiments are pointing out that tropical plantations containing higher tree diversity are likely to be more productive than monospecific stands (Forrester et al. 2004, Bristow et al. 2006, Potvin et al. 2007, Piotto 2008), but possible changes in the hydrological cycle have rarely been studied so far.

1.2 Water use by tropical trees

In the last two decades numerous studies on the dynamics of sap flux and transpiration in old-growth tropical forests have been conducted (Granier et al. 1996, Goldstein et al. 1998, Meinzer et al. 2001, Meinzer et al. 2004, O'Brien et al. 2004, Motzer et al. 2005). Unfortunately, information of species growing under plantation conditions is still rare (Dünisch and Morais 2002, Lüttge et al. 2003, Fetene and Beck 2004, Dierick and Hölscher 2009). Differences in tree species and tree physiology have been recognized as one of the stand characteristics influencing the hydrological impacts of forest stands (van Dijk and Keenan 2007, Bigelow 2001, Bruijnzeel 1997). Hence, the transpirational water use of plantations may depend largely on the tree species planted (van Dijk and Keenan 2007). This contrasts with studies showing that water use at tree or stand level is predominantly influenced by tree size and stand structure in diverse old-growth forest (Meinzer et al. 2001, 2005, McJannet et al. 2007) and a single-species tree plantation (Cienciala et al. 2000). Trees and other wooden plants such as lianas are expected to show similar patterns of maximum sap flux densities and water use in relation to individual tree size, independent of species when operating within fixed biophysical limitation (Meinzer et al. 2005, Andrade et al 2005) (Figure 2). A comparative study on sap wood area and sap flux density in more than 20 tree species in a Panamanian old-growth forest suggests that variation in diameter at breast height accounted for 98% of the variation in sapwood area, and for 91% of the variation in total daily sap flux density in the outermost two cm of sapwood if all species are pooled (Meinzer et al. 2001).

Recent analyses including more angiosperm species basically confirmed earlier results on tree size dependence of water transport (Meinzer et al. 2005). This suggests that species-specific differences among angiosperms can mainly be reduced to differences in tree size and probably depth of the sap conducting xylem, and further differences are much less important. If these rules commonly apply, the possibilities to influence tree water use of plantations by species selection would be limited.

However, maximum rates of sap flux and water use are only achieved when trees are fully foliated and under optimal environmental conditions. Under seasonal rainfall conditions with extended drought periods, trees have to cope with water shortage and they have developed strategies to adjust at structural, physiological and chemical levels (Baldocchi and Xu 2007). Structural adjustment to dry periods includes reduction of leaf area or a deep root system, stomatal conductance may be under physiological control, and roots may respond by the chemical mechanism of osmotic adjustment.

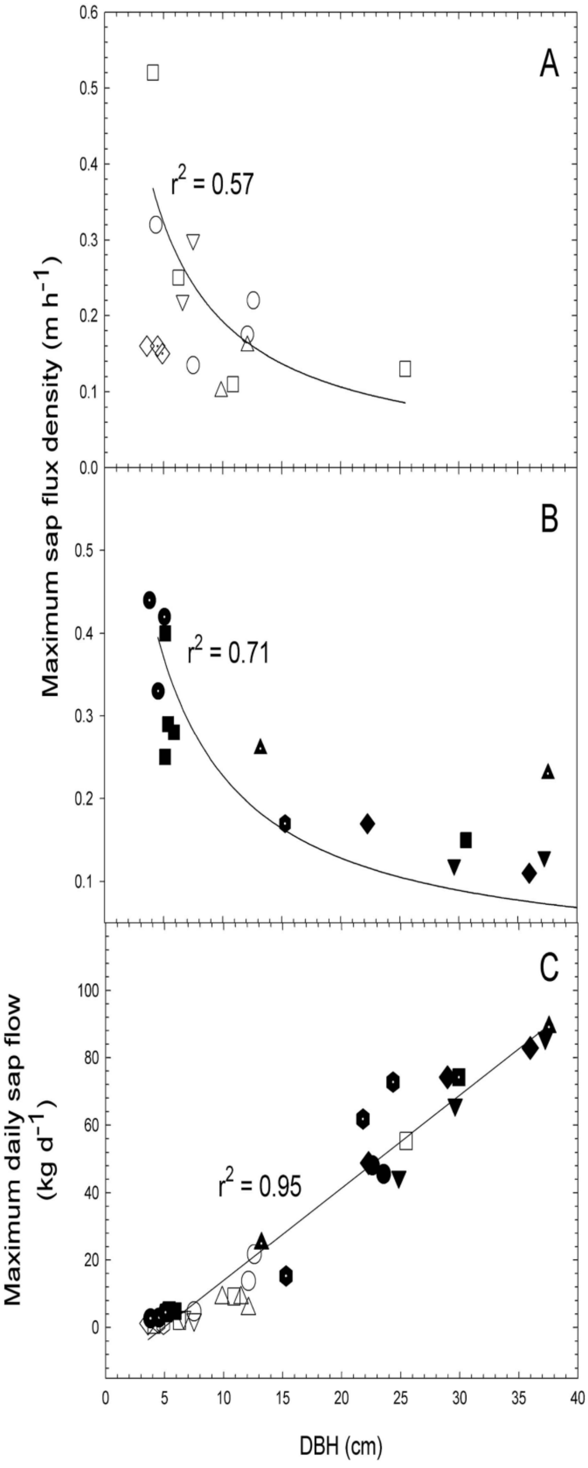


Fig. 2: Does water use universally scale? a), b), Maximum sap flux density and c) maximum daily sap flow for lianas (open symbols) and branches and trees (closed symbols) as a function to diameter at breast height. Values for tree branches from 4 to 6 cm diameter (adapted from Andrade 2005).

In the natural forest of Barro Colorado Island (BCI), Panama, where seasonal rainfall conditions prevail, tree species with a large variation in timing and duration of leafless periods co-occur (Meinzer et al. 1999), ranging from evergreen to semi-deciduous and to deciduous. Even when fully foliated, species may differ in their response to decreasing soil water availability during the dry season. In a temperate deciduous forest, among five studied co-occurring species, one showed little response to decreasing soil moisture; three were classified as being intermediate, and the species with the highest water use rate under moist soil conditions showed the most pronounced reduction in sap flow when soil moisture decreased (Hölscher et al. 2005). In an Australian Eucalyptus open-forest the evergreen tree species also exerted higher transpiration rates during the dry season than during the wet season, which was related to an increased evaporative demand and due to the use of groundwater (O’Grady et al. 1999). On BCI, trees with the ability to take up soil water from deeper layers during the dry season maintained or even increased rates of water use (Meinzer et al. 1999). Conclusions drawn from natural forests with locally adapted tree species can however not necessarily been transferred to man-made forests, and particularly monospecific plantations are usually much simple structured. Given the varied responses of tree species under seasonal rainfall distribution, a range of possibilities to influence water use by forest plantations through species selection may exist.

1.3 Plant diversity and ecosystem processes

There is evidence that biodiversity has positive effects on most ecosystem functions and biogeochemical cycles (Balvanera et al. 2006). In general the observed responses to higher diversity can be separated into two main biodiversity effects (Loreau and Hector 2001). First, in a complementarity effect that is collectively covering mechanisms like niche differentiation and facilitation process between species. Theoretically, complementarity of species occurs when resource supply allows species coexistence (Gross and Cardinale 2007). Complementarity effects often result in increasing performance of mixed communities above the expected performance of individuals (Loreau and Hector 2001). And secondly in a selection effect if the performance of mixed communities is influenced by selective processes, such as interspecific competition, which causes dominance of species with particular traits (Loreau and Hector 2001). Selective process would be the driving forces in communities where resource supply did not allow coexistence (Gross and Cardinale 2007). Selection effects can vary from positive to negative depending on whether species with lower- or higher-than-average performance dominate communities. For management purposes complementarity of species is more desirable, thus a basic understanding of patterns on species resource requirements that determine competitive ability will help to find compatible species that have an improved performance in combination.

However, most research on biodiversity effect has been carried out in grasslands and only recent studies are dealing with tree diversity (Scherer-Lorenzen et al. 2005). Similar experiments with trees have almost been absent and only a few publications deal with tree diversity effects on ecosystem processes (Orians et al. 1996, Schulze et al. 1996, Caspersen and Pacala 2001, Scherer-Lorenzen et al. 2005a). Mixing tree species may result in higher production than monocultures (Kelty 1992) and in enhanced nutrient uptake (Rothe and Binkley 2001). Positive mixture effects have also been reported from reforestation experiments in the tropics. There is some evidence that more species-rich communities are better at conserving soil nutrients than monocultures (Fölster and Khanna 1997, Montagnini 2000). From studies done in native tree plantations in the dry and wet regions of Costa Rica it was concluded that a mixed species plantation can be almost as productive if not equally productive as a monoculture, and that in some cases they will be even more productive (Menalled et al. 1998, Petit and Montagnini 2004, Piotto et al. 2004).

In general, tree diversity is affecting aboveground tree structural characteristics such as crown structure, leaf morphology and phenology and the development of a stratified canopy with increasing species diversity (Menalled et al. 1998, Bauhus et al. 2003, da Silva et al. 2009). Studies on grassland suggest that complementarity in soil water use was related to improved three-dimensional root differentiation (Verheyen et al. 2008). Although the root differentiation had a positive effect on the productivity of mixed communities, water resources were depleted earlier in the in case of water limitation (van Peer et al. 2004, Verheyen et al. 2008). On the other hand, selection effects are occurring if under severe drought stress high evapotranpiration rates are found caused by drought-tolerant species included in diverse communities (Verheyen et al. 2008).

1.4. Objectives of this study

The main part of this thesis was conducted in Central Panama, where the annual dry period lasts three months. The study site is located in the watershed of the Panama Canal, a major water way for global trade. With each ship crossing the canal, large quantities of freshwater are released into the sea, and water availability for the canal but also for the capital Panama City situated in the Canal Zone can seasonally be a problem. Degraded land is available for reforestation and research to determine appropriate tree species and species mixtures is currently underway (Wishnie et al. 2007, Potvin and Dutilleul 2009).

In view of the limited information on the relative importance of tree species and tree structural aspects on tree water use in manmade forests (including agroforestry) the following two objectives were set for this dissertation:

(1) to determine the influence of species and tree structural traits on seasonal water use characteristics in trees planted monoculture, and

(2) to assess the effect of tree diversity (1-, 3-, and 6-species mixtures) on the water use of every tree species, and

(3) to compare water use characteristics of trees growing in different land use systems across the tropics.

Working towards the first objective, it will become clear if, aside from tree structure, also species identity has a noticeable effect on water use characteristics in trees growing in different land use systems. At the same time, data on water use characteristics of a number of lesser known plantation species become available.

CHAPTER 2
STUDY SITES

2.1 Overview

The main part of this dissertation was conducted on an experimentally designed tree plantation in Panama, but it is also presenting data on tree water use gathered in different land use systems situated across the tropics. Thus a variety of results are presented from monoculture and mixed species plantations in Panama, mixed reforestation stands in the Philippines and a cacao-*Gliricidia* agroforest stand in Indonesia (Figure 3). This chapter will give a brief description of the different study sites and the species studied on the different sites. Description about methods used will follow in chapter 3. More detailed information on the study sites in Panama and on the other study sites are given in chapters 4 to 6.

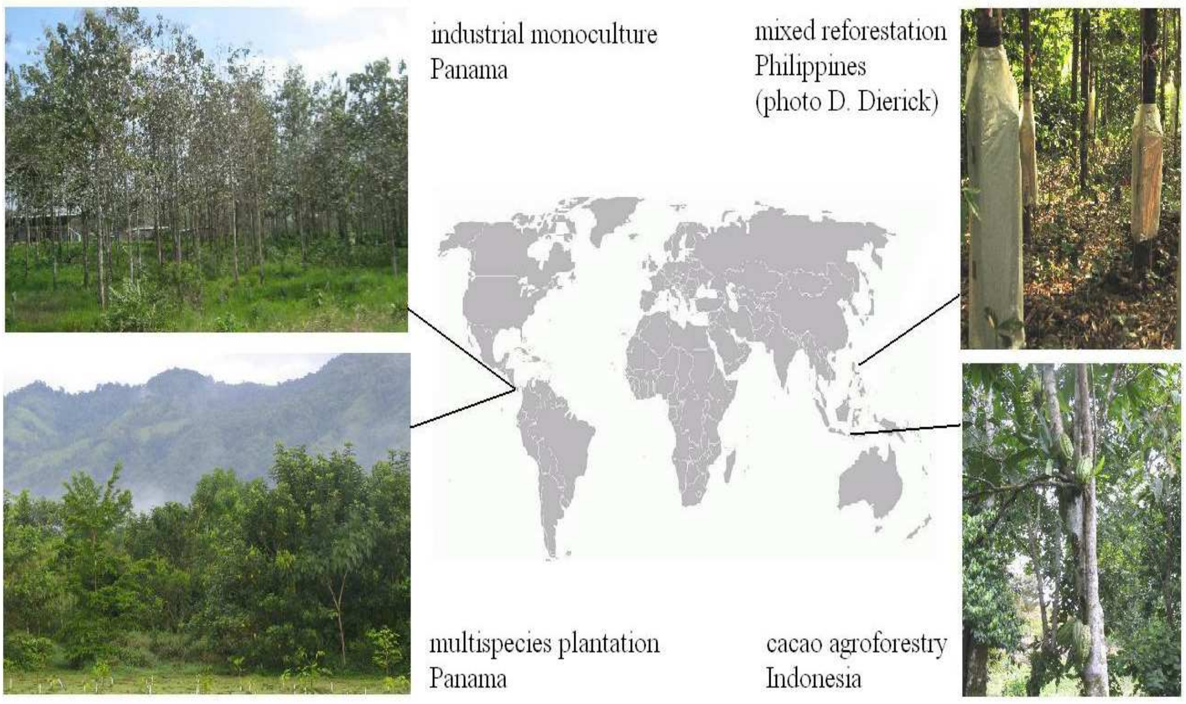


Fig. 3: Data on water use characteristics was gathered in different land-use systems across the tropics. Trees growing in monocultures and of trees growing in mixed species plantations are coming from Panama. Mixed species reforestation stands were studied in the Philippines and a cacao-*Gliricidia* agroforest stand was studied in Central-Sulawesi (map source: www.eurosino-groep.com).

2.2 Location of the study sites in Panama

The study site is located near the village of Sardinilla, Central Panama (9°19’ N, 79°38’ W), which is approximately 50 km north of Panama City (Figure 4). The elevation is 70 m above sea level. The topography is slightly undulating. Mean annual precipitation at nearby Barro Colorado Island (BCI) is 2350 mm, with 25-50 mm per month during peak dry season (January-March), 120-130 mm per month during the transition period in April and December, and 250 mm per month during the rainy season (May to November). The mean annual temperature of the region is 26.2 °C (STRI 2009). The relatively constant daily and seasonal temperatures are typical for tropical regions and annual mean daily maximum temperatures is 33.2°C with an annual mean daily minima of 21.8°C (Scherer Lorenzen et al. 2007). The bedrock in Sardinilla is belonging to the Gantuncillo formation and is characterized by silt and clay formed during the middle to upper Eocene (Potvin et al. 2004). The clay rich soils are classified as Typic and Aquic Tropudalfs with a clay content of about 65% (Potvin et al. 2004). The original vegetation around Sardinilla was probably a tropical moist forest similar to that on BCI (Holdridge and Budowski 1956) (Figure 4), 40 km west of Sardinilla (9°09’N, 79°51’W). The forest at the site was clear-cut in 1952 and 1953 and then used for agriculture. After two years in crops (probably corn, plantain and yucca) the site was changed into pasture by seeding it with a C4 African grass, *Hyparrhenia rufa* (Abraham 2004).

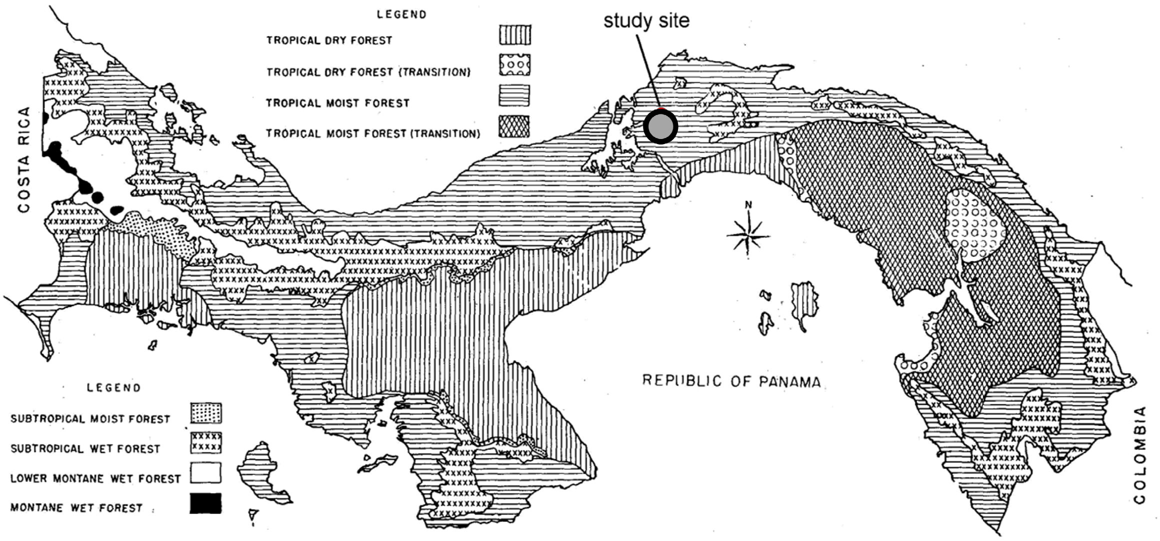


Fig. 4: Map of the natural vegetation types in Panama (adapted from Holdridge and Budowski 1956). The location of the study site in Panama is highlighted.

The main study was carried out in two tree plantations approximately 500 m apart from each other. One of the plantations is administrated by the Smithsonian Tropical Research Institute (STRI, STRI-plantation) and the other by Autoridad Nacional del Ambiente (ANAM, ANAM-plantation).

Fig. 5: Entrance to the STRI-plantation in Sardinilla, Panama.

2.3. Plantation administered by the Smithsonian Tropical Research Institute

The “Sardinilla experiment” was established as a permanent large-scale facility to study the links between biodiversity and ecosystem functioning. In July 2001, the pasture site was converted into an experimental tree plantation by Catherine Potvin. On an area of 9 ha, 24 plots were established using six native tree species. The plantation was set up with plots of 1, 3 and 6 species from different ecological groups (Figure 6): two light demanding, early successional species *Luehea seemannii* (Triana & Planch, Tiliaceae) and *Cordia alliodora* (Ruiz & Pavon, Boraginaceae), two lightintermediate species *Anacardium excelsum* (Bert. & Balb. ex Kunth, Anacardiaceae) and *Hura crepitans* (Liné, Euphorbiaceae) and two shade tolerant, late successional species *Cedrela odorata* (Liné, Meliaceae) and *Tabebuia rosea* (Bertol., DC., Bignoniaceae) (Figure 8). The tree species were selected based on relative growth rates (RGR), measured on Barro Colorado Island (respectively, 5.56% and 6.47%;

0.73% and 1.65%; 1.75% and 2.03%). *Anacardium excelsum*, *Hura crepitans*, *Luehea seemannii* and *Tabebuia rosea* can be classified as semi deciduous and *Cedrela odorata, Cordia alliodora* as deciduous.

The following types of diversity plots were established:

(a) Twelve plots with monocultures planted with one of the six different tree species; each species is replicated twice.

(b) Six plots of different three-species mixtures, each triplet containing one species, chosen randomly, from each successional group.

(c) Six plots of six-species mixtures, obtained by adding three species, each from a different successional group, to the existing triplets.

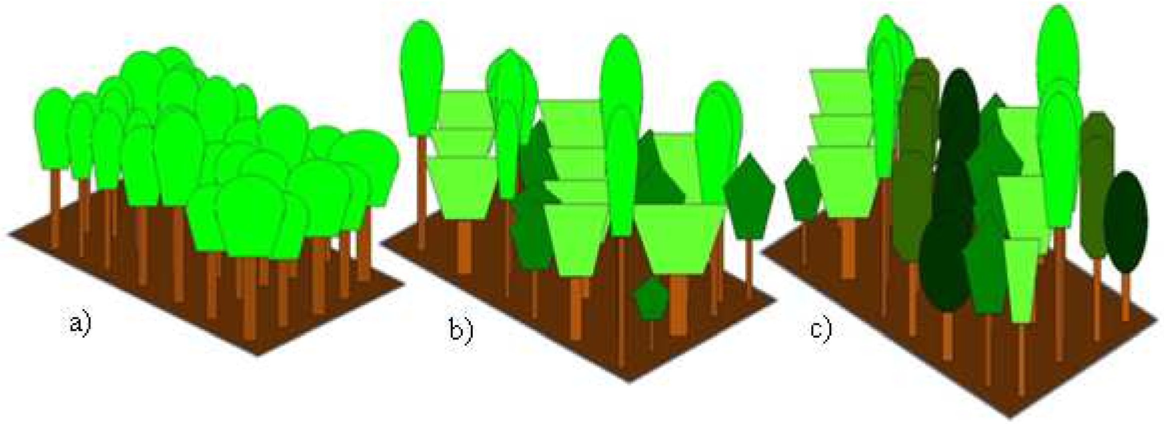


Fig. 6: Schematic diagram of the different mixture types of the biodiversity project in Sardinilla, Panama. From left to right (a) monoculture, (b) 3-species and (c) 6-species mixture plots.

Diversity treatments were randomly distributed across the site (Figure 7). Each of the plots (n=24) has a size of 45 m by 45 m and is further divided into to four subplots of 22.5 by 22.5 m. Saplings were planted with 3 m spacing what is the commercially prevalent density in Central America (225 trees per plot or 1111 trees per ha). Planting density was chosen to allow comparisons with other plantations. In total 5400 trees were planted on this plantation. Seeds were collected from forests within the Barro Colorado National Monument and germinated on-site at Sardinilla. Saplings of approximately 50 cm height were planted. The plantation is tended following standard forestry practices in Panama and Central America. In the first couple of years the understory was cut three times a year, after canopy closure only once a year. Survival of saplings was very high (> 90%), however, *Cordia alliodora* did not establish in monoculture. In the mixed plots, only some of the *Cordia* trees survived, but the number of surviving trees were too small to find enough sample trees. Therefore, this species was omitted from this study. The study was conducted between March 2007 and August 2008. Trees were about seven years old at the beginning of this study in March 2007.

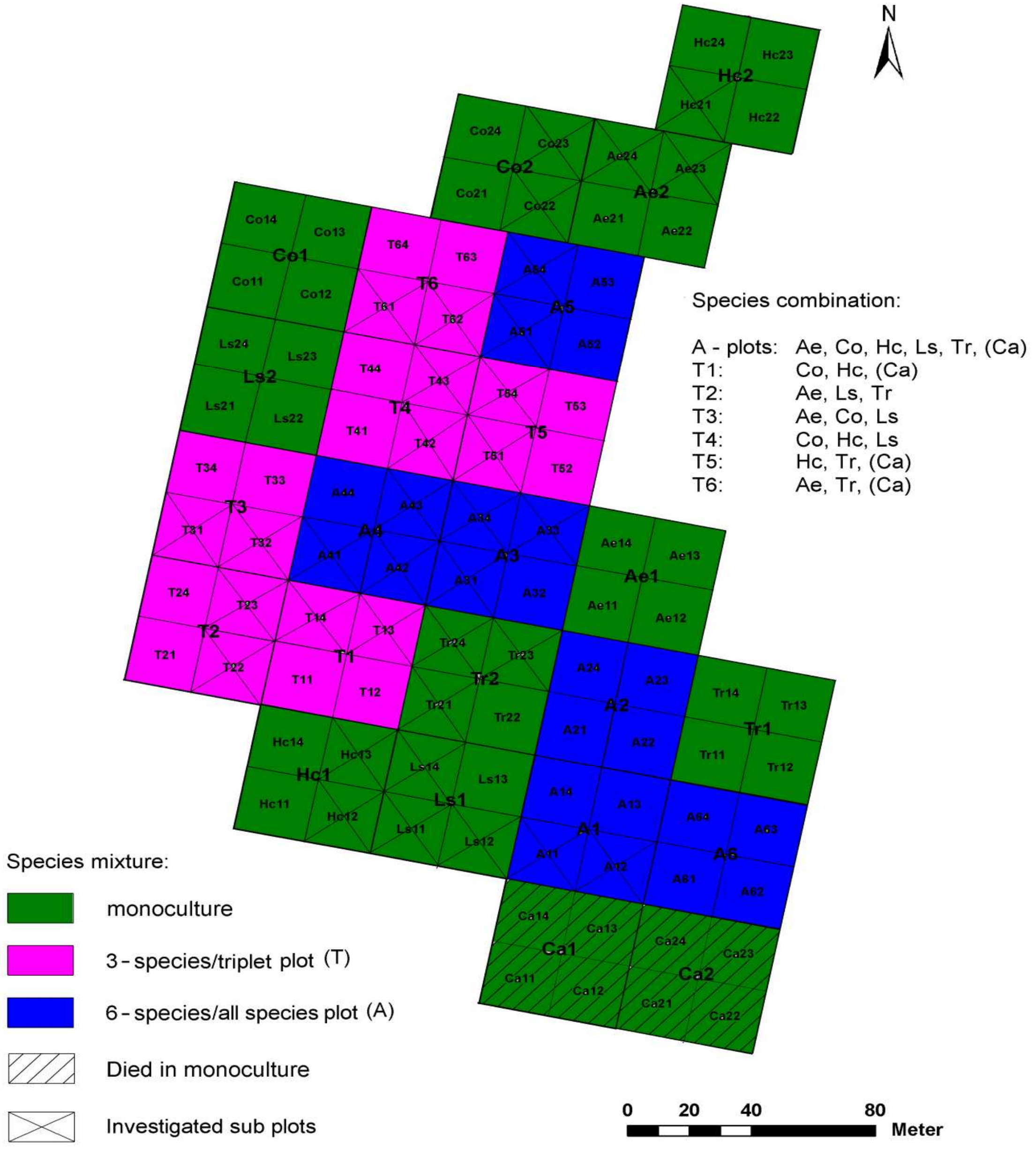


Fig. 7: Map of the design of the field experiment in Sardinilla. Basis of map data is a courtesy of Sebastian Wolf, ETH Zurich.

Fig. 8: Four of the five studied species growing on the STRI-plantation. From left to right *Anacardium excelsum* (Anacardiacea), *Cedrela odorata* (Meliacea), *Luehea seemannii* (Tiliaceae) and *Tabebuia rosea* (Bignoniaceae) (Vosso, 2003).

2.4 Plantation of the Autoridad Nacional del Ambiente

In the second plantation, three introduced species, namely *Acacia mangium* (Willd., Fabaceae), *Gmelina arborea* (Roxb., Lamiaceae), and *Tectona grandis* (Liné F., Lamiaceae) and one native species, *Terminalia amazonia* (J. F. Gmel., Exell., Combretaceae) grown in four monoculture plots were studied (Figure 9). Each of the plots was covering at least half a hectare and trees were planted with 3 m spacing. Understory was cut or burned once a year usually during the dry season. The plantation was reforested by the Autoridad Nacional del Ambiente (ANAM, ANAM-plantation) and trees were between 10 and 15 years old at the time of this study. The plantation was mainly used to collect seeds for other reforestation projects.

Fig. 9: Three of the four trees species studied growing on the ANAM-plantation. From left to right *Acacia mangium* (Fabaceae), *Gmelina arborea* (Lamiaceae) both introduced to Panama and *Terminalia amazonia* (Combretaceae) native to Panama (Vosso, 2003).

2.4 Study sites in the Philippines and in Indonesia

The study in the Philippines was conducted on Leyte Island located in the Eastern Visayas from November 2005 to September 2006 and from November 2006 to September 2007 (fieldwork was performed by Diego Dierick). The climate in the region can be described as humid tropical and annual temperature averages 27.5 °C and annual rainfall 2753 mm y^{-1} (PAGASA, 2007). Between March and May rainfall is lower than the monthly average over the year, but rainfall is never beneath 100 mm per month. The original natural vegetation of the site would be a species rich lowland dipterocarp forest (Langenberger, 2006). The study was conducted in two mixed reforestations which were 12 years old at the time of study. Water use was studied in ten tree species, eight of which were native to the region (Table 1).

The study in Indonesia, Central Sulawesi was conducted in a cacao-*Gliricidia* agroforest between February 2007 and February 2008 (fieldwork was performed by Michael Köhler). Measurements made at Gimpu (5 km away from the study site) indicated an average temperature of 25.5 °C and annual rainfall of 2092 mm y^{-1} (H. Kreilein, unpublished data). Rainfall shows a weak bimodal pattern with a rainy season (> 100 mm per month) from June to July and again from October to December. The agroforest stand was 6 years old at the time of the study and containing cacao trees growing under shade trees of the species *Gliricidia sepium*. Sap flux density was measured in 18 cacao and 18 *Gliricidia* trees distributed over the site.

Table 1: Studied tree species on the Philippines and in Indonesia

Scientific name	**Family**	**Study Location**	**Native or Exotic**
Shorea contorta S.Vidal	Dipterocarpaceae	Philippines	N
Parashorea malaanonan Merr.	Dipterocarpaceae	Philippines	N
Hopea malibato Foxw.	Dipterocarpaceae	Philippines	N
Hopea plagata S.Vidal	Dipterocarpaceae	Philippines	N
Swetenia macrophylla King	Meliaceae	Philippines	E
Vitex parviflora A.L. Juss	Verbenaceae	Philippines	N
Myrica javanica Blume.	Myricaceae	Philippines	N
Sandoricum koetjape (Burmf.) Merr.	Meliaceae	Philippines	N
Durio zibethinus Murray	Bombacaceae	Philippines	N
Gmelina arborea Roxb	Verbenaceae	Philippines	E
Theombroma cacao L.	Malvaceae	Indonesia	E
Gliricidia sepium (Jacq.) Kunth ex Steud.	Fabaceae	Indonesia	E

CHAPTER 3
METHODOLOGY

3.1 Overview

This methodology chapter provides a description about the methods used to assess water use characteristics of trees. Furthermore, methods to measure environmental, tree structural and phonological parameters are described. The description will mainly refer to the setup and the measurements on the main study site in Panama. In the Philippines and in Indonesia almost identical set ups and standardised methods were used to measure tree water use characteristics and environmental parameters. Similar methods were applied to analyse the datasets. Detailed information on the methods used in Panama and on the other study sites is given in chapters 4 to 6. Data collection in Panama was conducted by the author itself. The data collection in the Philippines and in Indonesia was conducted by the 'Tropical Silviculture and Forest Ecology' working group, namely Diego Dierick (Philippines) and Michael Köhler (Indonesia). The last part of this chapter is dedicated to the description of a method for additive portioning of biodiversity effects and a sap flux model which is used as a diagnostic tool for species comparison.

Fig. 10: Eddy flux towers in the center of the plantation and on an adjacent pasture. Micrometeorological measurements were conducted by Sebastian Wolf (photos: Sebastian Wolf).

3.2 Micrometeorological variables and soil moisture

On all sites micrometeorological data were monitored to assess their effect on tree water use. In Panama photosynthetic photon flux density, air temperature and relative humidity were measured on top of a 15 m high Eddy Covariance flux tower (Figure 10 and 11) (6-8 m above the canopy) located in the center of the STRI-plantation. Photosynthetic photon flux density (PPFD, mol m^{-2} s^{-1}) was measured with a PAR-LITE quantum sensor (Kipp & Zonen, Delft, The Netherlands), air temperature (°C) and relative humidity (%) with a thermo-hygrometer (Type MP100A, Rotronic AG, Ettlingen, Germany). Precipitation (mm) was measured with a rain gauge (Type 10116, TOSS GmbH, Potsdam, Germany) at 1.5 m above ground in an adjacent open pasture (Figure 10 and 11). Micrometeorological data were recorded every 10 seconds and average values were stored every 30 minutes. All micrometeorological data were provided by the ETH Zurich (Wolf et al. 2008). Water vapour pressure deficit (VPD, kPa) was calculated from air temperature and relative humidity.

Volumetric soil moisture content (m^3 m^{-3}) was measured using time domain reflectometry sensors (TDR; CS616, Campbell Scientific Inc., Logan, UT, USA). To cover spatial heterogeneity, sensors were installed at four locations within the STRI-plantation and at one location within the ANAM-plantation, evenly spaced throughout the site (Figure 11). The sensors were installed at 10 cm, 35 cm and 60 cm depth and hourly averages were stored (CR800 and CR1000, Campbell Scientific Inc, Logan, UT, USA). The probes were calibrated for the local soil following the procedure described in Veldkamp and O'Brien (2000).

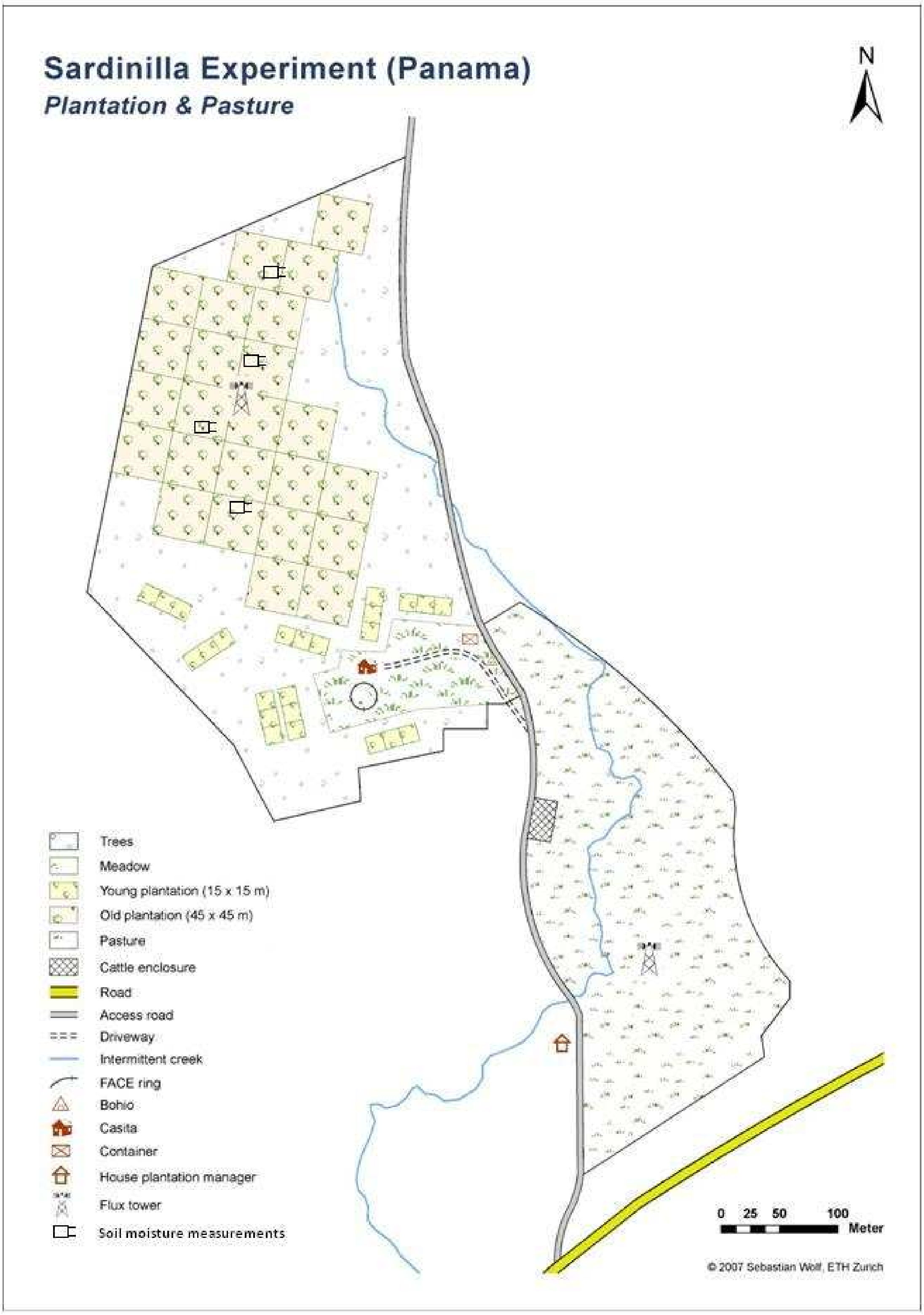


Fig.11: Surrounding of the STRI-plantation. Eddy flux towers in the center of the plantation and on an adjacent pasture. Soil moisture measurements evenly placed throughout the plantation. Basis of map data is a courtesy of Sebastian Wolf, ETH Zurich.

3.3 Measuring sap flux, tree water use and transpiration

At all three locations, the same method was used to determine the water use characteristics. On the STRI-plantation in Panama sample trees were chosen in five monoculture plots (one plot for each of the five investigated species and four sample trees per plot); six different 3-species mixture plots (one sample tree of each species in every plot and once replicated twice); and four replicates of the six-species mixture (one sample tree of each species in every plot) (Figure 7). On the ANAM-plantation, for each of the four investigated species four sample trees were chosen. Altogether 76 trees were investigated. On the Philippines, five sample trees per species were selected and in Indonesia the studied species were represented by 18 sample trees.

Sap flux density was measured with thermal dissipation sensors constructed after Granier (1985) (Figure 12). The sensors consisting of two cylindrical probes were inserted radially (0-20 mm below cambium) into the stem, with one probe placed approximately 10-15 cm vertically above the other. Every tree was equipped with two Granier sensors, one on the southern and one on the northern side of the trunk at 130 cm above the ground. The sensors were protected from thermal influences and water intrusion by a styrofoam box, reflective foil and a plastic cover. Probe output voltage was recorded every 30 seconds, and the average value stored every 15 minutes (CR800 and CR1000 datalogger; AM16/32 and AM416 multiplexer, Campbell Scientific Inc., Logan, UT, USA). This voltage difference can be related to the flux density in the sapwood around the sensor using the empirical formula (Granier 1987):

$$J_s = 3600 \times 0.0119 \times \left(\frac{\Delta V - \Delta V_{ref}}{\Delta V} \right)^{1.231}$$

where J_s is the sap flux density in the sapwood (g cm^{-2} h^{-1}); ΔV the measured voltage difference (°C); and ΔV_{ref} the reference voltage difference measured at time of zero flow (°C).

Sapwood thickness was determined for two to three individuals of all species by dye injection (Indigocarmin) into the trunk followed by taking wood cores approximately 3 cm above the injection height after two hours. The length of the coloured core section was assumed to be the conductive sapwood. For all species the sapwood thickness exceeded the lengths of the Granier sensor.

In the last two weeks of the experiment radial profile measurements of J_s were conducted. In all sample trees J_s was measured at 20 to 40 mm depth below the cambium. Sap flux density was also determined at a third depth (40-60 mm) in trees with a diameter > 8 cm. Sensors for measuring the radial profile were installed randomly on the east or west side of the trunk. J_s measured in the deeper sections was related to the concurrent measurements at reference depth (0 to 20 mm below cambium) and expressed in percentages. At least one week of good quality data were collected per depth. For each tree species an average normalised J_s profile (%) was constructed out of the four sample trees. Sap flux density data was extrapolated to tree level water use by summing up the water flow in a given number of ring-shaped stem cross sections corresponding with the respective installation depth, J_s as measured at reference depth and the normalised profile of J_s for the species considered (Edwards et al. 1996):

$$Q = \sum_{i=1}^{i=n} Q_i \quad with \quad Q_i = \frac{J_{sci}\ A_i}{1000}$$

Where Q (kg d^{-1}) is the water use per tree; Q_i is the water flow through ring i; $J_{sc\ i}$ (g cm^{-2} d^{-1}) is the cumulative sap flux density; and A_i (cm^2) is the ring-shaped area of sapwood that extends between the tip and the end of each probe for a given depth interval i. Tree level transpiration rates (mm d^{-1}) were calculated by dividing daily water use rates (kg d^{-1}) by the unit crown projection area (m^2). The plot level transpiration rate (T_{plot} mm d^{-1}) expressed per unit ground area was calculated using the relationship of tree water use and tree diameter (Garcia Santos 2007). We derived daily relationships between measured tree water use rates and tree diameters for each species separated into mixtures, inserted the known diameters of all other individuals of the plot into the respective equations, summed the calculated water use rates of all trees and divided the result by the area of the plot.

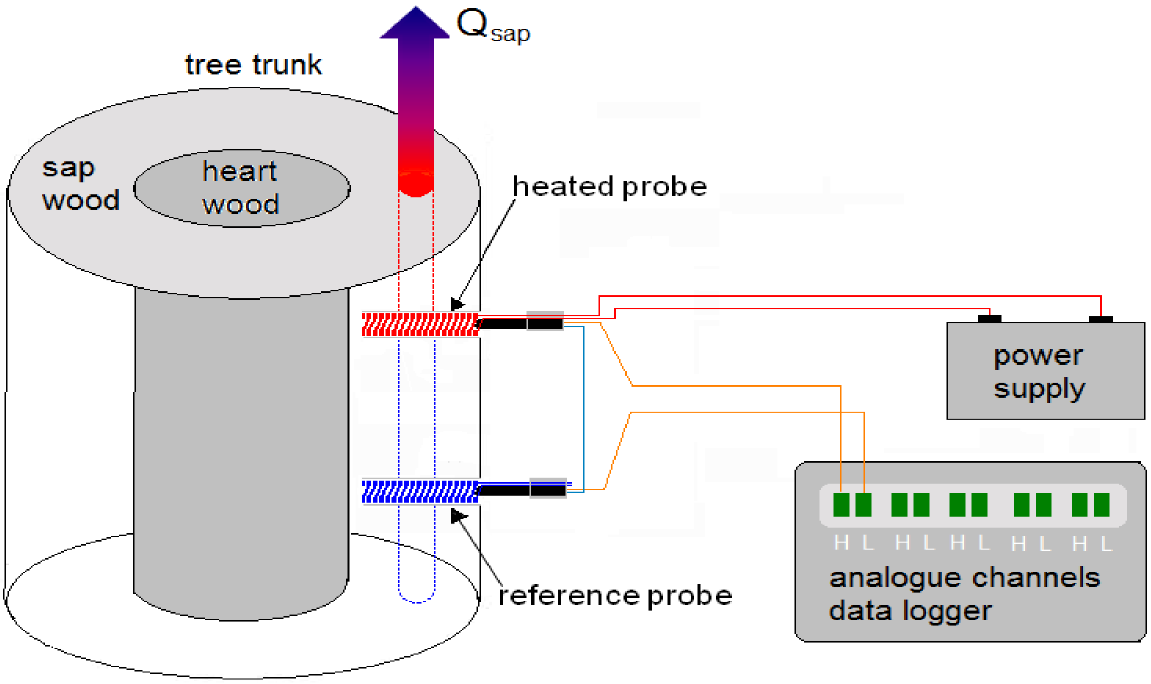


Fig. 12: Configuration of the Granier system for sap flow measurement. Each probe contains a thermocouple. Voltage difference between upper and lower probe was recorded with a data logger.

3.4 Assessing changes in tree phenology

On the study sites in Panama two methodical approaches were applied to assess changes in tree leaf phenology on individual tree level and on stand level. Individual tree leaf phenology, characterized as the percentage of foliage, was estimated on three labeled branches per tree on a monthly basis, or more frequently if changes were suspected (Figure 13). The number of leaves on each branch was counted and related to the maximum number of leaves observed during the study period (percentage of maximum). Trees were defined as being ‘defoliated’ when foliage was less than 15% of the maximum. Trees with more than 85% of foliage were classified as ‘fully foliated’. Data on percentage of foliage were collected for the five *species Anacardium excelsum, Cedrela odorata, Hura crepitans, Luehea seemannii* and *Tabebuia rosea* growing on the STRI-plantation. The percentage of foliage was not quantified for the species studied in the ANAM-plantation. However, for those species the time of major leaf shedding was assessed by visual inspection.

Stand level changes in leaf phenolgy were assed with a camera equipped with a fisheye lens. Hemispherical photographs were taken vertically with a high-resolution digital camera

(Minolta Dimage Xt, Japan) (Figure 13). The camera was equipped a 185° fish-eye lens and was placed in a leveling device (Regent Instruments, Canada), images were analyzed for the forest cover and leaf area index with Gap Light Analyzer (GLA) Version 2.0 (Simon Fraser University, Burnaby, British Columbia, Canada).

Fig. 13: On the left, labeling branches in the tree canopy in a *Tabebuia rosea* monoculture plot (photo: Rut Sanchez). On the right, hemispherical photograph of a *Luehea seemannii* monoculture plot.

3.5 Additive partitioning of biodiversity effects

Various studies have shown that that the observed responses of ecosystem processes to changes in species or functional group diversity are due to a combination of different effects (Tilman et al. 1997, Loreau 1998, 2000). These biodiversity effects can be classified into two groups. The first group of effects is induced through niche differentiation or facilitation between different species. These effects are usually resulting in a better performance of a community of species compared to the performance of a single species without competition by other species. The effects of niche differentiation and facilitation are hard to distinguish so that these two effects are commonly grouped as “complementarity” (Loreau and Hector 2001).

The second group of biodiversity effects arises from selective processes in a community of species. The selective processes can influence the performance of a species community positively or negatively. Selective processes are driven through interspecific competition, which cause dominance of species with particular traits (Loreau and Hector 2001).

In analogy with the work of Loreau and Hector (2001), we used a methodological approach based on the Price equation of evolutionary genetics (Price 1995), to measure the net biodiversity effect (ΔY) by additive partitioning a selection effect and a complementarity effect. The net biodiversity effect has the dimension of yield, where yield stands for any measurable variable in an ecosystem and is expected to be zero under the null hypothesis of no biodiversity effects. These various effects can be related by additive partitioning as follows:

$$\Delta Y = Y_O - Y_E = \sum_i RY_{O,i} M_i - \sum_i RY_{E,i} M_i$$
$$= \sum_i \Delta RY_i M_i = N \overline{\Delta RY}\, \overline{M} + N\, cov(\Delta RY, M)$$

where N = number of species in the mixture,

M_i = yield of species *i* in monoculture,

$Y_{O,i}$ = observed yield of species *i* in mixture,

$Y_O = \sum_i Y_{O,i}$ = total observed yield of the mixture,

$Y_E = \sum_i Y_{E,i}$ = total expected yield of the mixture.

Accordingly, the complementary and selection effect are expressed as a function of the deviation from the expected relative yield in the mixture (ΔRY). The yield in mixture is influenced by a complementarity effect ($N\, \overline{\Delta RY}\, \overline{M}$), if it is on average higher than the expected yield calculated out of the weighted average of the monoculture yield. The covariance between the monoculture yield of species and their change in relative yield in the mixture is explaining a selection effect ($N\, cov(\Delta RY, M)$). The additive partitioning method was applied on the data set of the STRI-plantation in Panama. Biodiversity effects for the three estimated variables stand transpiration, basal area and stand water use per basal area were partitioned.

3.6 Sap flux density model

A modified and advanced Jarvis model (Jarvis 1976, modified by O'Brien et al. 2004, advanced by Dierick and Hölscher 2009) was used to compare the large data sets of sap flux data densities from the study sites in Panama, Indonesia and the Philippines. The advantage of the sap flux model was to link measured sap flux density to key environmental variables and to condense the large data sets into a limited number of interpretable model parameters, which then could be used for further statistical analysis. The model is using global radiation (Rg) and vapour pressure deficit VPD (kPa) as explanatory variables as they exert a strong influence on sap flux density. Therefore, the model form used was:

$$J_{\mathrm{s\ model}} = a \times \frac{R_g}{b + R_g} \times \frac{1}{1 + \exp^{\frac{c - VPD}{d}}}$$

Where $J_{\mathrm{s\ model}}$ is the modelled sap flux density (g cm^{-2} h^{-1}); *a* the maximum modelled sap flux density (g cm^{-2} h^{-1}); *b* a parameter describing the R_g response; *c* and *d* parameters describing the VPD response (kPa). Parameter *b* (J m^{-2} s^{-1}, or W m^{-2}, note: 1 W = 1 J s^{-1}) can be interpreted as a measure of the light saturation level. At high Rg the function is asymptotically approaching 1 when reaching the light saturation (Cienciala el. 2000, Granier et al. 2000, Herbst et al. 1999). Under the assumption that VPD is non-limiting, sap flux density reaches 90% of the maximum value a if Rg reaches a value equal to ten times b. The response function to VPD is sigmoid shaped (O'Brien et al. 2004). The parameter c equals the VPD at which sap flux rises to half the maximum value a (Rg non-limiting), whereas d is related to the slope of the sigmoid. Parameters a, b, c and d were estimated using a Gauss Newton algorithm.

CHAPTER 4

SEASONAL DYNAMICS OF TREE SAP FLUX AND WATER USE IN NINE SPECIES IN PANAMANIAN FOREST PLANTATIONS

KUNERT, N., SCHWENDENMANN, L. & HÖLSCHER, D., 2010. SEASONAL DYNAMICS OF TREE SAP FLUX AND WATER USE IN NINE SPECIES IN PANAMANIAN FOREST PLANTATIONS. AGRICULTURAL AND FOREST METEOROLOGY 150, 411-419.

Seasonal dynamics of tree sap flux and water use in nine species in Panamanian forest plantations

Norbert Kunert*, Luitgard Schwendenmann & Dirk Hölscher

Tropical Silviculture and Forest Ecology, Burckhardt Institute, Georg-August-Universität Göttingen, Büsgenweg 1, 37077 Göttingen, Germany

Abstract. We studied nine tree species with different leaf phenologies growing in monospecific plantations in the watershed of the Panama Canal. The annual rainfall in the region averages 2,350 mm with a pronounced dry season from January to March. The atmospheric evaporative demand is usually higher in the dry season compared to the wet season. Our objectives were to 1) compare water use characteristics among the tree species, 2) analyze the response of sap flux density to changes in environmental conditions, and 3) estimate seasonal and annual tree water use and transpiration rates. Tree sap flux was monitored using the heat dissipation technique according to Granier. Under full foliage, maximum sap flux densities varied more than two-fold among species. Time of leaf shedding and duration of leafless periods also varied strongly among species. However, the relationship between percentage of foliage and normalized maximum sap flux densities can be described by a universal non species-specific function. Species means of maximum transpiration rates on a basis of projected crown area varied more than two-fold (1.2 - 2.8 mm d^{-1}). Transpiration rates between the dry and wet season differed for six of the nine species. Three species (*Acacia mangium*, *Anacardium excelsum,* and *Gmelina arborea*) showed enhanced transpiration in the dry season with dry to wet season ratios between 1.4 and 2.1. In contrast, the dry to wet season ratio of *Cedrela odorata, Hura crepitans*, and *Tectona grandis* ranged from 0.4 to 0.8. The results suggest that tree species choice can substantially influence water resource use in plantation forestry under such seasonal climatic conditions.

Keywords: deciduous, evergreen, leaf phenology, semi-deciduous, soil water content, tree transpiration

---

Kunert, N., Schwendenmann, L. & Hölscher, D., 2010. Seasonal dynamics of tree sap flux and water use in nine species in Panamanian forest plantations. Agricultural and Forest Meteorology 150, 411-419.

* Corresponding author. Tel.: +49 551 399556; Fax: +49 551 394019; E-mail address: nkunert1@gwdg.de (N. Kunert)

1 Introduction

Reforestation of degraded land in the tropics is considered as a measure to mitigate climate change by carbon sequestration and to enhance wood supply. Tree plantations are often profitable and under certain circumstances they may protect biological diversity (Lamb et al., 2005). One major concern, however, is a high water use rate of forest plantations (Jackson et al., 2005); especially where water resources are at least seasonally scarce and demand for water for other purposes is high.

Appropriate tree species selection might reduce water use rates to acceptable levels (van Dijk and Keenan, 2007) but knowledge on species-specific water use characteristics of tropical trees is rather limited. Furthermore, the effectiveness of species selection is questionable as studies in diverse old-growth forests (Meinzer et al., 2004; McJannet et al., 2007) and a single-species tree plantation (Cienciala et al., 2000) showed that tree size is the main factor influencing tree water use. Hence, trees are expected to show similar patterns of maximum sap flux densities and water use in relation to individual tree size independent of species when operating within fixed biophysical limitation (Meinzer et al., 2005). If these rules commonly apply, the possibilities to influence tree water use of plantations by species selection would be limited.

However, maximum rates of sap flux and water use are only achieved when trees are fully foliated and under optimal environmental conditions. Under seasonal rainfall conditions with extended drought periods trees have to cope with water shortage and they have developed strategies to adjust at structural, physiological and chemical levels (Baldocchi and Xu, 2007). Structural adjustment to dry periods includes reduction of leaf area or a deep root system, and stomatal conductance may be under physiological control. Chemical signal mechanisms involving the synthesis of biochemical compounds, e.g. accumulation of absisic acid, are well known as an adaptation by the plants to soil drying (Davies et al., 2000).

In the natural forest of Barro Colorado Island (BCI), Panama, where seasonal rainfall conditions prevail, tree species with a large variation in timing and duration of leafless periods co-occur (Meinzer et al., 1999), ranging from evergreen to semi-deciduous and to deciduous. Even when fully foliated, species may differ in their response to decreasing soil water availability during the dry season. In a temperate deciduous forest, among five studied co-occurring species, one showed little response to decreasing soil moisture, three were classified as being intermediate, and the species with the highest water use rate under moist soil conditions showed the most pronounced reduction in sap flow when soil moisture decreased (Hölscher et al., 2005). In Australian Eucalyptus open-forest the evergreen tree species also exerted higher transpiration rates during the dry season than during the wet season, which was related to an increased evaporative demand and due to the use of groundwater (O'Grady et al., 1999). On BCI, trees with the ability to take up soil water from deeper layers during the dry season maintained or even increased rates of water use (Meinzer et al., 1999).

Conclusions drawn from natural forests with locally adapted tree species can however not necessarily been transferred to man-made forests, and particularly monospecific plantations are usually much simple structured. Given the varied responses of tree species under seasonal rainfall distribution, a range of possibilities to influence water use by forest plantations through species selection may exist.

The present study was conducted in Central Panama, where the annual dry period lasts three months. The study site is located in the watershed of the Panama Canal, a major water way for global trade. With each ship crossing the canal, large quantities of freshwater are released into the sea, and water availability for the canal but also for the capital Panama City situated in the Canal Zone can seasonally be a problem. Degraded land is available for reforestation and research to determine appropriate tree species and species mixtures is currently underway (Wishnie et al., 2007; Potvin and Dutilleul, 2009). We studied the water use characteristics of nine tree species, six of which are native to the region and three are exotics widely planted throughout the tropics. These species range in leaf phenology from evergreen to semi-deciduous and to deciduous. Our objectives were to 1) compare water use characteristics among nine different tree species throughout a typical season, 2) analyze the response of sap flux density and leaf phenology to changes in environmental conditions, and 3) estimate seasonal and annual tree water use and transpiration rates. The results may contribute to better understanding of tree sap flux and water use rates also in relation to tree size under seasonally changing environmental conditions. It may also help stakeholders to make informed decisions on species selection especially in environments were the available water is limited.

2 Methods

2.1 Study sites

The study site was located near the village of Sardinilla, Central Panama (9°19' N, 79°38' W), approximately 50 km north of Panama City. The elevation of the site is on average 70 m, with a slightly undulating topography. Mean annual precipitation on nearby BCI is 2,350 mm, with 25-50 mm per month during the dry season (January-March), 120-130 mm per month during the transition period (April and December), and 250 mm per month during the wet season (May to November) (STRI, 2009) (Figure 1). The mean annual temperature on BCI is 26.2 °C (STRI, 2009). The bedrock in Sardinilla consists of limestone, and the clay rich soils are classified as Typic and Aquic Tropudalfs (Potvin et al., 2004). The original vegetation around Sardinilla was probably a tropical moist forest similar to that on BCI (Holdridge and Budowski, 1956). Most of the area was logged in 1952/1953, temporarily used for crop production (probably corn, plantain and yucca) and then converted into pasture with C4 grasses dominating (Potvin et al., 2004).

The study was carried out in two tree plantations approximately 500 m apart. The first plantation was converted from a pasture into an experimental tree plantation consisting of various indigenous species between June and July 2001 and is administrated by the Smithsonian Tropical Research Institute (STRI, STRI-plantation). Five native tree species, *Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels, *Cedrela odorata* Linné, *Hura crepitans* Linné, *Luehea seemannii* Triana & Planch and *Tabebuia rosea* (Bertol.) A. DC. grown in five monoculture plots were investigated in this plantation. At the beginning of this study, the trees were approximately six years old. In the second plantation, three introduced species, namely *Acacia mangium* Willd., *Gmelina arborea* Roxb., and *Tectona grandis* Linné F. and one native species, *Terminalia amazonia* (J.F. Gmel.) Exell. grown in four monoculture plots were studied. The second plantation was reforested by the Autoridad Nacional del Ambiente (ANAM, ANAM-plantation) and trees were between 10 and 15 years old at the time of this study.

2.2 Micrometeorological and soil moisture measurements

Photosynthetic photon flux density, air temperature and relative humidity were measured on top of a 15 m high flux tower (6–8 m above the canopy) located in the center of the STRI-plantation. Photosynthetic photon flux density (PPFD, mol m^{-2} s^{-1}) was measured with a PAR-LITE quantum sensor (Kipp & Zonen, Delft, The Netherlands), air temperature (°C) and relative humidity (%) with a thermo-hygrometer (Type MP100A, Rotronic AG, Ettlingen, Germany). Precipitation (mm) was measured with a rain gauge (Type 10116, TOSS GmbH, Potsdam, Germany) at 1.5 m above ground in an adjacent open pasture. Micrometeorological data were recorded every 10 seconds and average values were stored every 30 minutes. All micrometeorological data were provided by the ETH Zürich (Wolf et al., 2008). Water vapour pressure deficit (VPD, kPa) was calculated from air temperature and relative humidity.

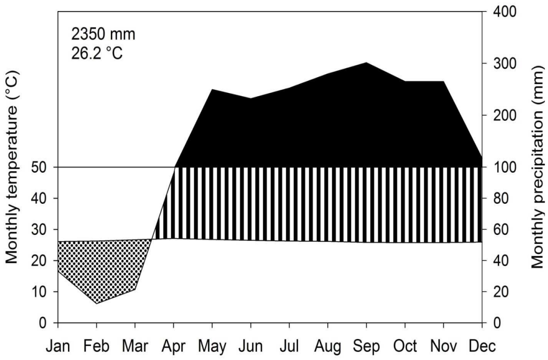


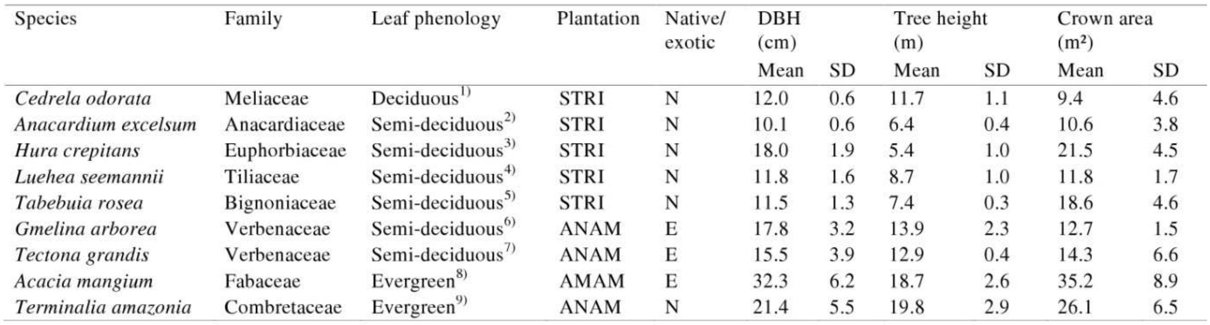
Fig. 1: Climate diagram for Barro Colorado Island (BCI) based on data obtained between 1977 and 2007 (STRI, 2009). BCI is located at a distance of approximately 30 km from Sardinilla.

Soil moisture was measured at four locations within the STRI-plantation and at one location within the ANAM-plantation using time domain reflectometry sensors (TDR; CS616, *Campbell* Scientific Inc., Logan, UT, USA). The sensors were installed at 10 cm, 35 cm and 60 cm depth and hourly averages were stored (CR800 and CR1000, Campbell Scientific Inc, Logan, UT, USA). The probes were calibrated for the local soil following the procedure described in Veldkamp and O'Brien (2000).

2.3 Tree selection, tree structural parameters, and leaf phenology

In each monoculture plot four trees were selected, resulting in a total of 36 trees. All selected trees reached the upper canopy level of a given monoculture stand. Tree diameter at breast height (DBH) was measured using a girth tape. Tree height was determined with a hypsometer (Vertex III, Haglöf, Lensele, Sweden). The crown extension was measured in each of the eight cardinal directions and the crown projection area was calculated as the sum of eight pitch circles as described by Röhle (1986). The main characteristics of the studied species are given in Table 1.

Table 1: Leaf phenology of the studied species and structural characteristics of the studied trees (mean values ± SD, n = 4 trees per species)



Species	Family	Leaf phenology	Plantation	Native/ exotic	DBH (cm)		Tree height (m)		Crown area (m²)	
					Mean	SD	Mean	SD	Mean	SD
Cedrela odorata	Meliaceae	Deciduous1)	STRI	N	12.0	0.6	11.7	1.1	9.4	4.6
Anacardium excelsum	Anacardiaceae	Semi-deciduous2)	STRI	N	10.1	0.6	6.4	0.4	10.6	3.8
Hura crepitans	Euphorbiaceae	Semi-deciduous3)	STRI	N	18.0	1.9	5.4	1.0	21.5	4.5
Luehea seemannii	Tiliaceae	Semi-deciduous4)	STRI	N	11.8	1.6	8.7	1.0	11.8	1.7
Tabebuia rosea	Bignoniaceae	Semi-deciduous5)	STRI	N	11.5	1.3	7.4	0.3	18.6	4.6
Gmelina arborea	Verbenaceae	Semi-deciduous6)	ANAM	E	17.8	3.2	13.9	2.3	12.7	1.5
Tectona grandis	Verbenaceae	Semi-deciduous7)	ANAM	E	15.5	3.9	12.9	0.4	14.3	6.6
Acacia mangium	Fabaceae	Evergreen8)	AMAM	E	32.3	6.2	18.7	2.6	35.2	8.9
Terminalia amazonia	Combretaceae	Evergreen9)	ANAM	N	21.4	5.5	19.8	2.9	26.1	6.5

1)Rocas (2003), 2)Fournier (2003a), 3)Meinzer et al. (1999), 4)Fournier (2003b), 5)Flores & Marín (2003), 6)Kijkar (2003), 7) Francis (2003a), 8)Francis (2003b), 9)Flores (2003)

Leaf phenology, characterized as the percentage of foliage, was estimated on three labelled branches per tree on a monthly basis, or more frequently if changes were suspected. The number of leaves on each branch was counted and related to the maximum number of leaves observed during the study period (percentage of maximum). Trees were defined as being 'defoliated' when foliage was less than 15% of the maximum. Trees with more than 85% of foliage were classified as 'fully foliated'. Data on percentage of foliage were collected for the five species *Anacardium excelsum, Cedrela odorata, Hura crepitans, Luehea seemannii* and *Tabebuia rosea* growing on the STRI-plantation. The percentage of foliage was not quantified for the species studied in the ANAM-plantation. However, for those species the time of major leaf shedding was assessed by visual inspection.

2.4 Sap flux density, water use and tree transpiration

The thermal dissipation method according to Granier (1985) was used to measure sap flux density. The sensors consisting of two cylindrical probes were inserted radially (0-20 mm below cambium) into the stem, with one probe placed approximately 10-15 cm vertically above the other. Every tree was equipped with two Granier sensors, one on the southern and one on the northern side of the trunk at 130 cm (DBH) above the ground. Sensors were protected from thermal influences and water intrusion by a styrofoam box, reflective foil and a plastic cover. Probe output voltage was recorded every 30 seconds, and the average value stored every 15 minutes (CR800 and CR1000 datalogger; AM16/32 and AM416 multiplexer, Campbell Scientific Inc., Logan, UT, USA). Sap flux density (J_s in g cm^{-2} h^{-1}) was calculated from differences in voltage using the calibration equation determined by Granier (1987). Sap flux density in the STRI-plantation was measured from July 2007 to June 2008 (365 days) and in the ANAM-plantation from November 2007 to June 2008 (240 days). Sensors were changed when broken or latest after approximately six month to ensure that sap flux was measured in the outermost sap wood. The new sensors were installed at the same height but moved sideways from the first installation.

Sapwood thickness was determined for two to three individuals of all species by dye (Indigo-carmin) injection into the trunk followed by taking wood cores approximately 3 cm above the injection height after two hours. The length of the coloured core section was assumed to be the conductive sapwood. For all species the sapwood thickness exceeded the lengths of the Granier sensor.

In the last two weeks of the experiment radial profile measurements of J_s were conducted. In all sample trees J_s was measured at 20 to 40 mm depth below the cambium. Sap flux density was also determined at a third depth (40-60 mm) in trees with a diameter > 8 cm. Sensors for measuring the radial profile were installed randomly on the east or west side of the trunk. J_s measured in the deeper sections was related to the concurrent measurements at reference depth (0 to 20 mm below cambium) and expressed in percentages. At least one week of good quality data were collected per depth. For each tree species an average normalised J_s profile (%) was constructed out of the four sample trees. Sap flux density data was extrapolated to tree level water use by summing up the water flow in a given number of ring-shaped stem cross sections corresponding with the respective installation depth, J_s as measured at reference depth and the normalised profile of J_s for the species considered (Edwards et al., 1996):

$$Q = \sum_{i=1}^{i=n} Q_i \quad with \quad Q_i = \frac{J_{sci} A_i}{1000}$$

Where Q (kg d^{-1}) is the water use per tree; Q_i is the water flow through ring i; $J_{sc\,i}$ (g cm^{-2} d^{-1}) is the cumulative sap flux density; and A_i (cm^2) is the ring-shaped area of sapwood that extends between the tip and the end of each probe for a given depth interval i. Tree level transpiration rates (mm d^{-1}) were calculated by dividing daily water use rates (kg d^{-1}) by the unit crown projection area (m^2).

2.5 Data analysis

Maximum sap flux density was determined as the maximum value that lasted for more than 45 min with less than 5% variation during clear days. Normalized maximum sap flux density was calculated by dividing daily maximum sap flux densities by the highest maximum daily sap flux density measured during the study period (percentage of maximum) of a given species. Normalized daily Js was estimated by dividing daily integrated Js by the highest observed daily integrated Js during the study period (percentage of maximum).

Gap filling was performed for those species and trees where only 240 days of measured data were available (ANAM plantation). Sap flux densities for missing days (J_s estimated) were calculated based on the species-specific relationships between measured sap flux densities and PPFD for the wet season ($r^2 = 0.767 – 0.830$, $p < 0.05$).

The dry season period was defined as the time when less than 100 mm rainfall was measured for the duration of three months (Dietrich et al., 1996). The starting date was set three weeks after the last major rain event. According to this definition, the dry season lasted from January 15, 2008 to April 15, 2008 (90 days). The periods from July 1, 2007 to December 14, 2007 and June 1, 2008 to June 30, 2008 were defined as wet season (195 days). Annual means are based on 365 days including the transition periods between December 15, 2007 to January 14, 2008 and April 16, 2008 to May 30, 2008.

Linear regressions were used to establish the relationship between the normalized maximum sap flux density and the proportion of foliage and between tree water use rates and environmental parameters. Differences in tree water use and tree transpiration rates between seasons were determined with a paired Student's t-test. Tree water rates among species were compared using the analysis of covariance with DBH as a covariate (ANCOVA, followed by a post-hoc Tukey HSD test). Differences in tree transpiration rates among species were assessed applying the analysis of variance (ANOVA, followed by a post-hoc Tukey HSD test). All statistical analyses were performed using SPSS 13.0 software (SPSS Inc., Chicago, USA).

3 Results

3.1 Micrometeorological and soil moisture measurements

Precipitation during the 12-month study period totalled 2,260 mm. During the dry season (January 15, 2008 to April 15, 2008), only 33.4 mm rainfall was measured (Figure 2). Mean PPFD (47.1 ± 9.7 mol m^{-2} d^{-1}) and VPD (0.81 ± 0.18 kPa) were substantially higher during the dry season compared to the wet season (29.9 ± 9.2 mol m^{-2} d^{-1} and 0.48 ± 0.27 kPa, respectively) (Figure 2). During the wet season, the average soil moisture at all depths was around 0.48 m^3 m^{-3}. A rapid decrease in soil moisture in 10 cm depth was observed during the transition period between wet and dry season, and lowest values of soil moisture (0.26 m^3 m^{-3}) were recorded at the end of the dry season. Soil moisture at 35 cm and 60 cm depths showed a different pattern with a gradual decline starting in mid January and reaching a low of 0.37 m^3 m^{-3} (35 cm) and 0.40 m^3 m^{-3} (60 cm), respectively, at the end of the dry season (Figure 2).

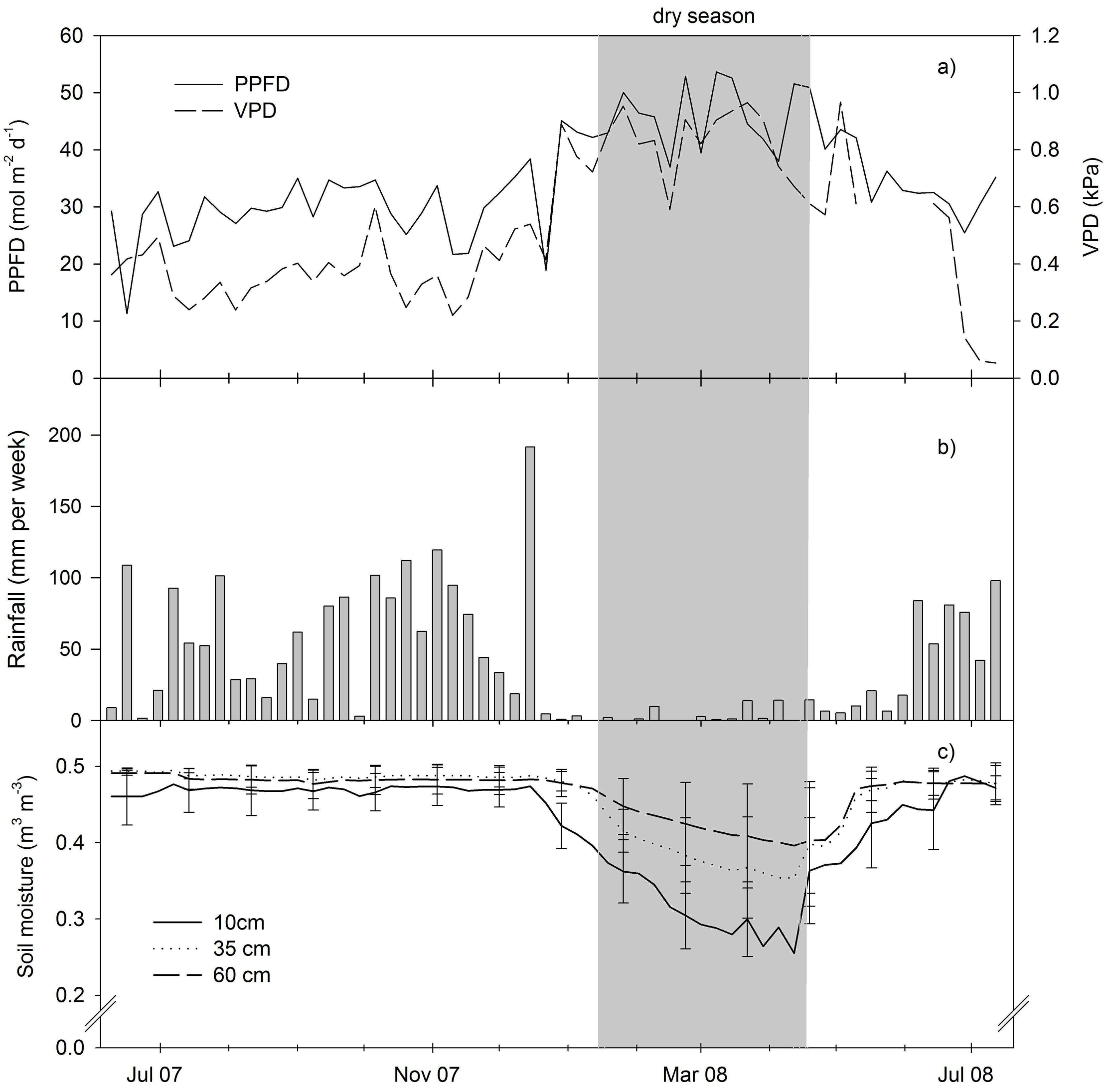


Fig. 2: a) Photosynthetic photon flux density (PPFD) and vapour pressure deficit (VPD), b) weekly rainfall, and c) soil moisture (mean of n = 4 sensors per soil depth ± SD) over the course of the study period, STRI-plantation. No VPD data were available for June 2008 due to sensor failure.

3.2 Leaf phenology

The two evergreen tree species, *Acacia mangium* and *Terminalia amazonia*, were fully foliated throughout the study period. The deciduous tree species *Cedrela odorata* was defoliated for approximately 4 months between the end of one wet season and the beginning of the next wet season (Figure 3). The semi-deciduous species were shedding their leaves at different times of the year (Figure 3) and the number of days of defoliation (over the whole observation period) ranged from 16 (*Anacardium excelsum*) to 86 days (*Tabebuia rosea*). *Hura crepitans* was defoliated during the dry season (February-March) but also shed a high number of leaves towards the end of the wet season (November). At that time, *Hura crepitans* was infested by phytopathogens (various fungi e.g. *Colletotrichum sp.;* U. Braun, personal communication) which might have led to the observed leaf loss. *Anacardium excelsum* shed most of its leaves in December/January but green flushes appeared within a couple of days. *Tectona grandis* lost a high proportion of its leaves at the beginning of the dry season, whereas *Luehea seemannii* trees gradually lost their leaves throughout the dry season. *Tabebuia rosea* trees shed most of their leaves at the end of the dry season/onset of the wet season (Figure 3). In May, *Luehea seemannii* and *Tectona grandis* were

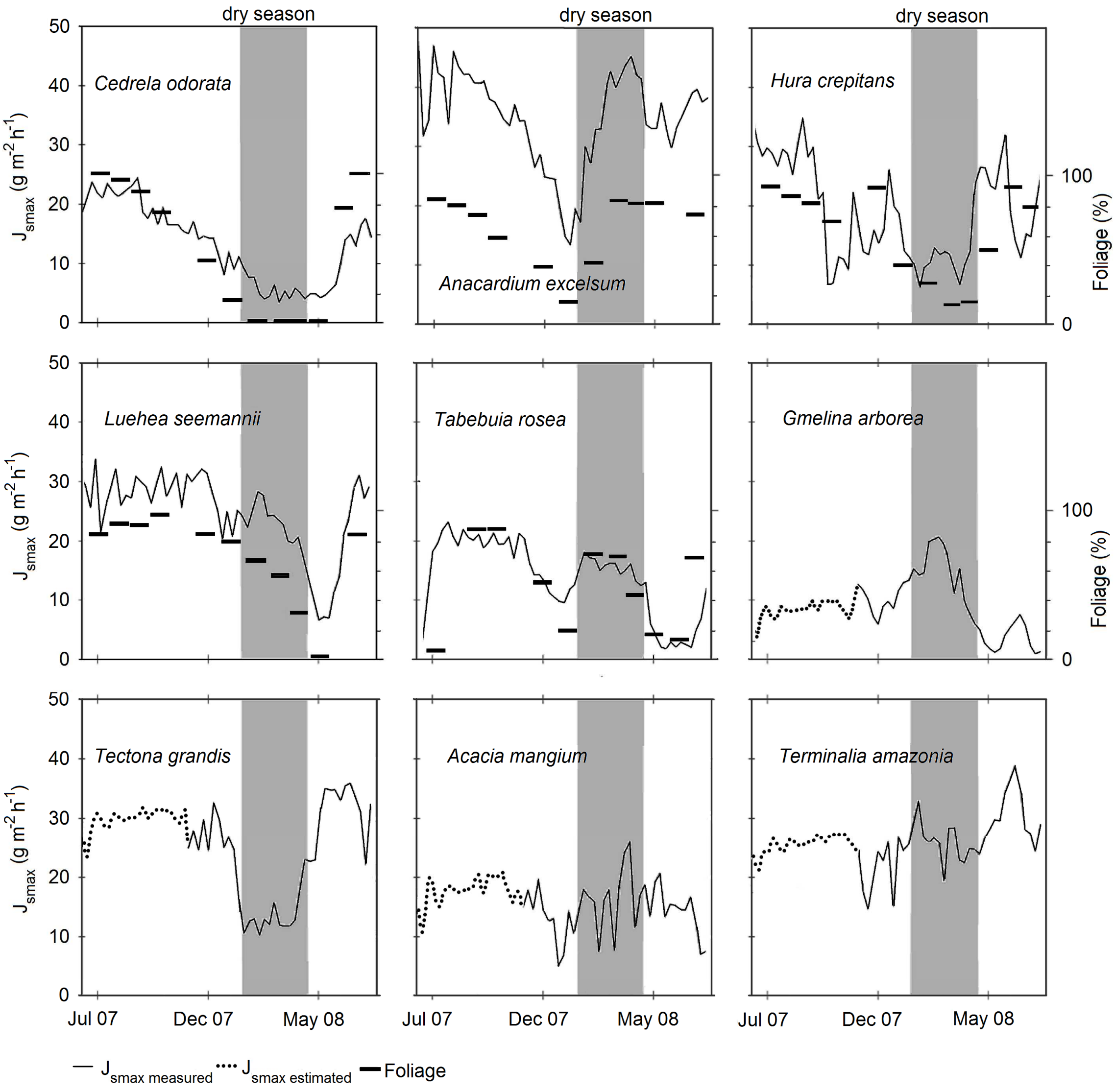


Fig. 3: Mean maximum sap flux density (J_{smax}) of the nine tree species (n = 4 trees per species) over the course of the study period.

shedding the rest of their leaves within a couple of days and green flushes appeared simultaneously. *Gmelina arborea* trees lost the majority of their leaves at the beginning of the wet season (May). At end of the wet season (November), *Gmelina arborea* trees were infested by leaf cutting ants (*Atta sp.*, H. Herz, personal communication), which may explain the additional peak in leaf loss.

3.3 Sap flux density, water use and tree transpiration

Mean maximum sap flux densities ranged from 20 g cm^{-2} h^{-1} (*Cedrela odorata* and *Gmelina arborea)* to 46 g cm^{-2} h^{-1} (*Anacardium excelsum*) and significant differences among species were found (Table 2). For the five species for which the percentage of foliage was monitored (STRI-plantation), a species-specific linear relationship between maximum sap flux densities and percentage of foliage was found (data not shown). After transforming maximum sap flux densities into normalized maximum sap flux densities and plotting these values against the percentage of foliage, the relationship between these variables remained significant and was independent of species (Figure 4). When trees had a leaf area of less than 15% the average normalized sap flux density was 20%.

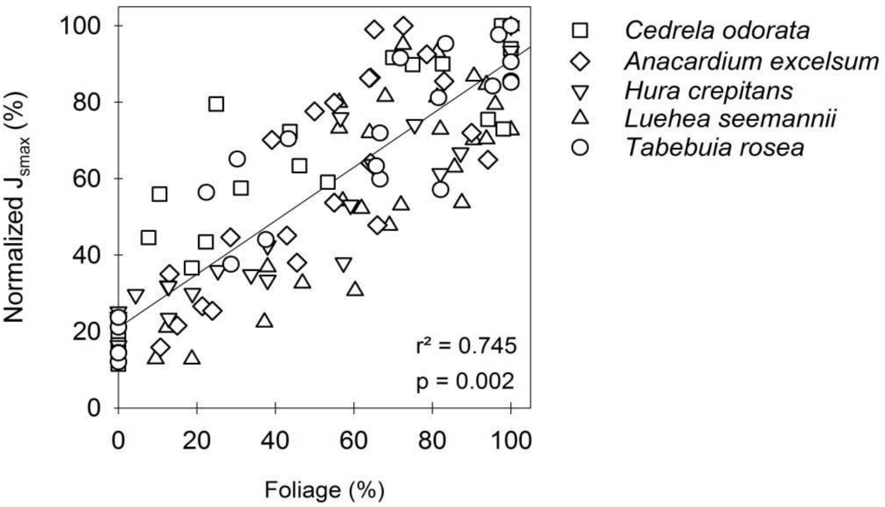


Fig. 4: Relationship between normalized maximum sap flux density (normalized J_{smax}) and percentage of foliage for five tree species (with 4 trees per species) combined (*Anacardium excelsum, Cedrela odorata, Hura crepitans, Luehea seemannii* and *Tabebuia rosea).*

The seasonal patterns of maximum sap flux density varied strongly among species (Figure 3). However, for all deciduous and semi-deciduous species, the lowest sap flux densities coincided with major leaf shedding events or periods when trees were defoliated (Figure 3).

Normalized daily *Js*, analyzed separately for dry and wet season, revealed differences in slopes and intercepts when related to PPFD (Figure 5). Except for *Gmelina arborea*, all species seemed to reduce *Js* under high PPFD. In deciduous and semi-deciduous species, this pattern may be explained by the reduced number of leaves present during the dry season whereas in evergreen species lower soil water content during the drier season may play a role.

Mean annual water use rates ranged between 5.1 kg d^{-1} (*Gmelina arborea*) and 21.9 kg d^{-1} (*Terminalia amazonia*) (Table 2). The water use rates of *Anacardium excelsum, Gmelina arborea* and *Acacia mangium* were significantly higher during the dry season compared to the wet season. In contrast, *Cedrela odorata, Hura crepitans* and *Tectona grandis* used significantly less water during the dry season than during the wet season (Table 2). Overall, maximum daily water use rates were positively correlated with tree diameter (Figure 6a). During the dry season the relationship between maximum daily water use rates and tree diameter was remaining strong over all tree species, but water use rates in the lower tree diameter class (10 - 15 cm) was wider scattered (Figure 6b). Extracting the semi deciduous tree species in the dry season, the relation between maximum daily water use rates and tree diameter was very weak (Figure 6c).

The highest and lowest maximum tree transpiration rate was measured for *Tectona grandis* (2.8 mm d^{-1}) and *Tabebuia rosea* (1.2 mm d^{-1}), respectively (Table 2). Tree transpiration of *Cedrela odorata, Anacardium excelsum, Gmelina arborea, Hura crepitans, Tectona grandis* and *Acacia mangium* differed significantly between wet and dry season (Table 2). Similarly, *Cedrela odorata, Hura crepitans* and *Tectona grandis* had significantly lower tree transpiration rates during the dry season than during the wet season, whereas *Anacardium excelsum, Gmelina arborea* and *Acacia mangium* transpired more water during the dry season as compared to the wet season (Table 2).

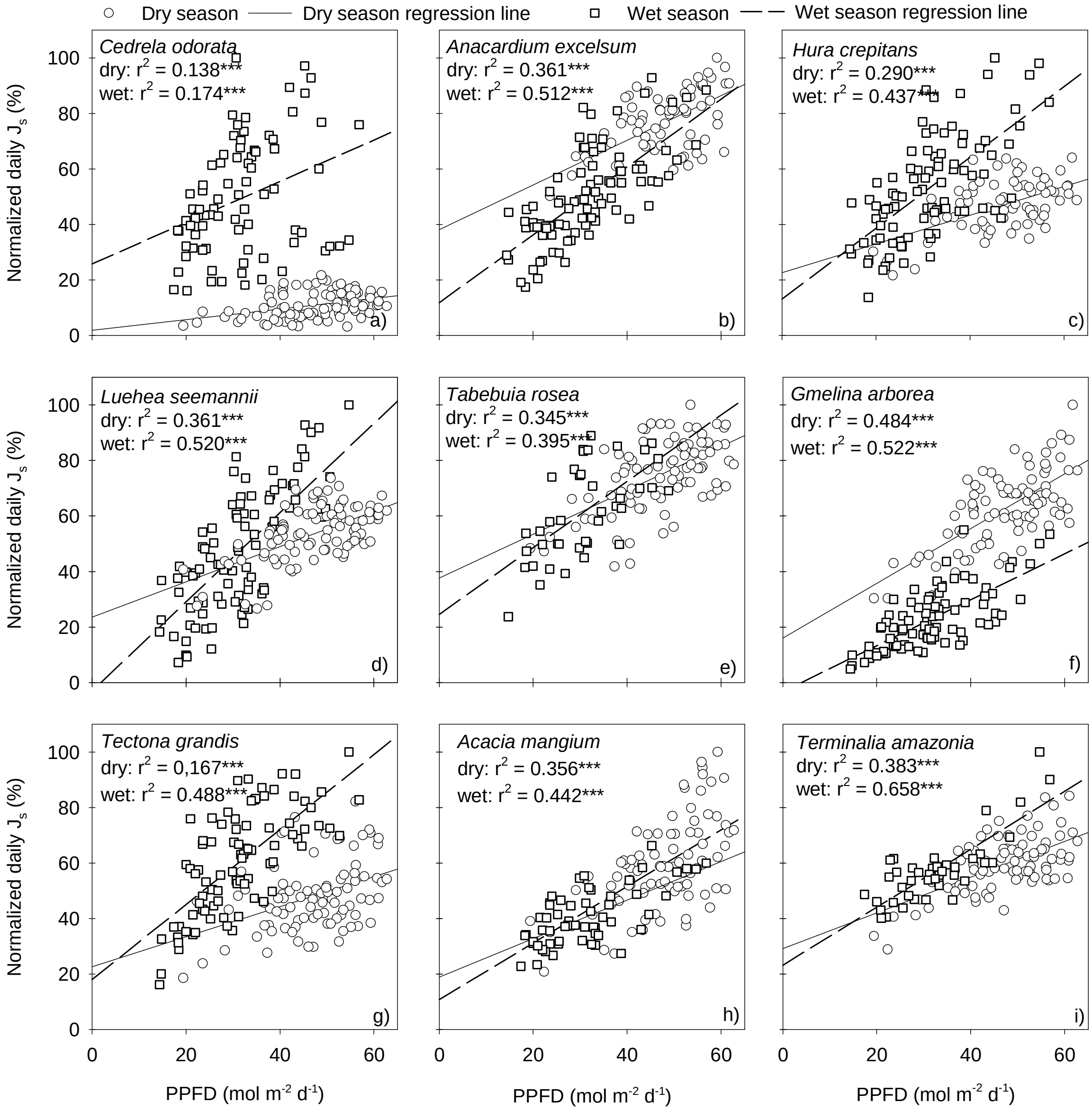


Fig. 5: Linear relationships between photosynthetic photon flux density (PPFD) and normalized daily sap flux density (Normalized daily J_s, n = 4 trees per species) during wet and dry season (significance level: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$).

4 Discussion

4.1 *Sap flux density, water use and tree transpiration*

Mean maximum sap flux density of *Acacia mangium* at Sardinilla (29 g cm^{-2} h^{-1}) was similar to values measured in a 19-year-old *Acacia mangium* plantation in South China (Ma et al., 2008). In 7-year-old *Cedrela odorata* trees growing in a plantation near Manaus, Brazil, maximum sap flux densities ranged between 12 and 22 g cm^{-2} h^{-1} (Dünisch and Morais, 2002) and are comparable to the values measured at Sardinilla. For *Gmelina arborea* (20 g cm^{-2} h^{-1}), similar maximum sap flux densities were reported from the Philippines (Dierick and Hölscher, 2009). A number of studies on tree sap flow and transpiration were conducted in species-rich Panamanian old-growth forests (Meinzer et al., 1997; Goldstein et al., 1998; Phillips et al., 1999; Clearwater et al., 2002; Andrade et al., 2005). Despite differences in tree age and canopy structure, maximum sap flux densities measured for *Luehea seemannii* in a semi-evergreen moist forest on BCI (15-30 g cm^{-2} h^{-1}; Andrade et al., 2005) and for *Anacardium excelsum* in Parque Metropolitano, Panama, (~ 22 g cm^{-2} h^{-1}; Phillips et al., 1999) were similar to the values found in our study. The water use rates that we estimated also correspond to values recorded from other stands across the tropics. For example, water use rates of 7-year-old *Cedrela odorata* trees (mean DBH 7.6 cm) in a plantation near Manaus, Brazil, ranged between 1.6 kg d^{-1} and 11.6 kg d^{-1} depending on the season (Dünisch and Morais, 2002). In contrast, the mean daily water use rates we found for *Acacia mangium* were lower than the values reported for a *Acacia mangium* plantation (80-90 kg d^{-1}) of similar DBH in Sabah, Borneo (Cienciala et al., 2000).

Our data showed a strong positive correlation between maximum daily tree water use and tree diameter (Figure 6a-c). This relationship was also observed in different species-rich old-growth tropical forests (Meinzer et al., 2004; McJannet et al., 2007) and a single-species *Acacia mangium* plantation (Cienciala et al., 2000). Despite the strong correlation between maximum water use and tree diameter in the individuals studied, considerable scatter was present around the fitted curve especially in the lower diameter range between 10 and 15 cm (Figure 6a-c). For example, annual maximum daily water use of *Luehea seemannii* (29.4 kg d^{-1}) was twice the amount of water used by *Cedrela odorata* (14.2 kg d^{-1}) trees of equal size and increased up to three times during the dry season. The variation in time of leaf shedding and duration of reduced leaf area among the semi deciduous tree species led to a weak diameter depending correlation particularly in this group in the dry season. Hence, differences in maximum water use rates among species might offer an opportunity to influence water use by species selection at the tree level. However, on the stand level, additional parameters such as stem density and the contribution of understory transpiration have to be taken into account.

4.2 Leaf phenology in relation to water use characteristics

The present study reveals that the annual course of sap flux density, tree water use, and transpiration rates differs among species (Table 2). Overall, maximum sap flux densities were only measured during periods when trees were fully foliated (Figure 3). Substantial sap flux densities (on average 20% of the maximum sap flux density) were measured when on the three study branches foliage was less than 15% of the maximum (Figure 4). Normalized daily sap flux density for the deciduous species *Cedrela odorata* was less than 6% when trees shed all their leaves (Figure 5a). In a 7-year-old plantation near Manaus, daily sap flux densities of leafless *Cedrela odorata* trees during the dry season were 14% of the maximum sap flux density measured during the wet season (Dünisch and Morais, 2002). It is thus suggested, that this species still transpires some water even without leaves. However, *Cedrela odorata* had significantly lower water use and transpiration rates during the dry season compared to the wet season. Shedding the leaves at the end of the wet season and remaining almost leafless during the dry season could be an adjustment of *Cedrela odorata* to reduced water availability. In a general assessment, *Cedrela odrorata* is characterized by a superficial root system (Cintron, 1990).

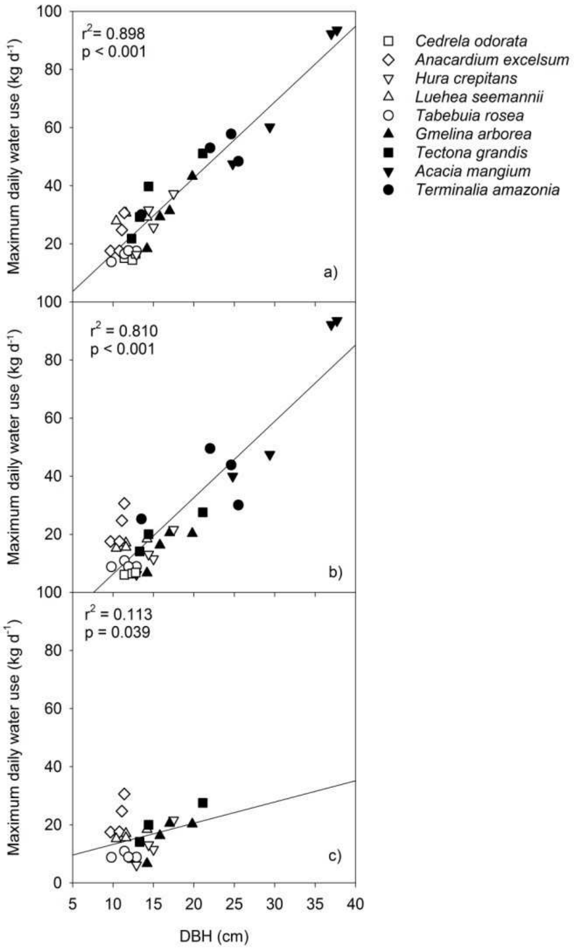


Fig. 6: a) Relationship between annual maximum daily tree water use and diameter at breast height (DBH). b) Relationship between maximum daily tree water use during the dry season and DBH. c) Relationship between maximum daily tree water use during the dry season and DBH of the semi deciduous trees species.

Table 2: Maximum sap flux densities (J_{smax}), tree water use rates and tree transpiration rates per unit crown area for different periods. Dry season, wet season and annual values are based on 90, 195 and 365 days, respectively (mean ± SD, n = 4 trees per species). Note that sap flux densities for trees in the ANAM plantation (indicated by \$) were only measured for 240 days. For the missing days sap flux densities (J_s estimated) were calculated based on the species-specific relationships between measured sap flux densities and PPFD for the wet season. Lower-case letters indicate significant differences ($p < 0.05$) for a given species between dry and wet season (paired Student t-test). Capital letters indicate significant differences among species in a given season (J_{smax} and tree transpiration: ANOVA followed by a post-hoc Tukey HSD test; water use rate: ANCOVA with DBH as covariate followed by a post-hoc Tukey HSD test, $p < 0.05$).

Species	J_{smax} ($g\ cm^{-2}\ h^{-1}$)		Water use rate ($kg\ d^{-1}$)						Tree transpiration ($mm\ d^{-1}$)							
			Dry		Wet		Annual		Dry		Wet		Annual		Maximum	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Cedrela odorata	20^{A}	4	$3.2^{a,A}$	0.8	$7.9^{b,AB}$	2.2	5.8^{A}	1.7	$0.40^{a,A}$	0.16	$0.89^{b,AB}$	0.27	0.65^{AB}	0.20	1.43^{A}	0.40
Anacardium excelsum	46^{B}	9	$13.7^{a,B}$	4.6	$10.1^{b,AB}$	2,8	10.9^{C}	3.4	$1.17^{a,B}$	0.35	$0.87^{b,AB}$	0.20	0.93^{AB}	0.22	2.13^{AB}	0.14
Hura crepitans	33^{AB}	8	$7.2^{a,AB}$	2.6	$14.2^{b,BCD}$	7.2	12.4^{B}	5.5	$0.61^{a,AB}$	0.12	$0.99^{b,AB}$	0.20	1.03^{AB}	0.38	2.04^{AB}	0.08
Luehea seemannii	43^{B}	7	$12.3^{a,AB}$	4.8	$13.3^{a,BCD}$	2.3	12.5^{B}	2.4	$1.09^{a,AB}$	0.56	$1.13^{a,B}$	0.14	1.07^{AB}	0.28	2.53^{B}	0.39
Tabebuia rosea	30^{AB}	5	$7.7^{a,AB}$	3.3	$8.5^{a,AB}$	0.9	7.5^{AB}	1.9	$0.62^{a,AB}$	0.14	$0.63^{a, AB}$	0.14	0.57^{AB}	0.26	1.21^{A}	0.28
Gmelina arborea$^{\$}$	20^{A}	5	$8.6^{a,AB}$	3.9	$4.1^{b,A}$	0.2	5.1^{A}	1.2	$0.74^{a,AB}$	0.25	$0.36^{b,A}$	0.06	0.45^{A}	0.09	2.53^{B}	0.11
Tectona grandis$^{\$}$	35^{AB}	6	$9.0^{a,AB}$	4.1	$13.0^{a,BC}$	1.5	11.6^{AB}	2.5	$0.71^{a,AB}$	0.46	$1.05^{b,B}$	0.41	0.93^{AB}	0.35	2.77^{B}	0.25
Acacia mangium$^{\$}$	29^{AB}	7	$27.5^{a,C}$	6.4	$17.8^{b,CD}$	0.9	20.9^{C}	2.2	$0.85^{a,AB}$	0.19	$0.53^{b,AB}$	0.11	0.66^{AB}	0.10	2.06^{AB}	0.26
Terminalia amazonia$^{\$}$	39^{B}	3	$20.7^{a,C}$	6.6	$19.9^{a,D}$	0.7	21.9^{C}	1.9	$1.09^{a,AB}$	0.69	$1.05^{a,B}$	0.53	1.12^{B}	0.60	2.38^{B}	0.56

It may therefore react very sensitive to changes in precipitation and soil water content. The use of stable isotope techniques (δ^2H) on the STRI plantation indicated that during the dry season, *Cedrela odorata* obtained most of its water from the upper soil layers (0-30 cm) (L. Schwendenmann and R. Sánchez Bragado, unpublished data).

The semi-deciduous species *Hura crepitans* and *Tectona grandis* also used less water during the dry season than during the wet season, which can be explained by the reduced number of leaves during the dry season. On the STRI plantation three-years-old *Hura crepitans* trees allocated a lower amount of biomass into taproots compared to Tabebuia rosea (Coll et al., 2008). In Venezuela it was observed older *Hura crepitans* tend to develop a superficial root system (Esteva, 1969 as cited in Francis, 1990). *Tectona grandis* also has a superficial root system (Schorcht, 2000).

In contrast, the semi-deciduous species *Anacardium excelsum*, which was almost fully foliated during the dry season, had significantly higher water use rates during the dry season (Table 2), possibly caused by a higher evaporative demand. Such an observation was also made in eucalypt open-forests of northern Australia, where during the dry season transpiration rates were higher than in the rainy season (O'Grady et al., 1999). This was explained with a higher atmospheric evaporative demand and due to the use of groundwater. Comparing the natural abundance of δ^2H values during the dry season suggested that *Anacardium excelsum* used water from deeper soil layers than *Cedrela odorata* and *Hura crepitans* on the STRI plantation (L. Schwendenmann and R. Sánchez Bragado, unpublished data). Access to deeper soil water may enable *Anacardium excelsum* to maintain its leaves during the dry season. On BCI, trees with the ability to take up soil water from deeper layers during the dry season maintained or even increased rates of water use (Jackson et al. 1995, Meinzer et al., 1999).

Gmelina arborea was attacked by leaf cutting ants during November 2007 and all sample trees had a reduced leaf area during this time. The leaf herbivory was leading to considerable reduced sap flux densities through this reduction in leaf area, and the extrapolation from 240 days to the full year was performed with the wet season data of November 2007. Hence, it is likely that we underestimated the wet season and annual water use and tree transpiration rates of *Gmelina arborea*. Similar situation has also been reported from an Australian Eucalyptus woodland where sap flux density of trees without insect protection was half that of protected trees (Cunningham et al., 2009).

The evergreen species *Acacia mangium* had higher water use and tree transpiration rates during the dry season, most likely due to an increased evaporative demand. In contrast, no seasonal difference in water use was found for *Terminalia amazonia*. We assume that soil water availability during the dry season may have become limiting for *Terminalia amazonia*. In *Terminalia amazonia* trees, the reduced water use under high PPFD in the dry season (Figure 5i) cannot be attributed to leaf loss but may indicate water shortage. A similar tendency is also present in *Acacia mangium*. Both species were growing in the ANAM-plantation where soil water content at all depths declined rapidly around two weeks earlier (end of December 2007) than in the STRI-plantation. A study of water use characteristics of co-existing species in a natural forest on BCI during the dry season found that trees able to develop a deep and extensive root system maintained or even increased rates of water use (Meinzer et al. 1999).

5 Conclusions

Overall, under optimal environmental conditions there was a strong correlation between tree size and tree water use. Still some tree species show the tendency to differ in daily tree water uses in the same diameter class, which was even more pronounced when dry season values were considered. Our study shows that species-specific differences in leaf phenology had a large influence on the annual course of tree water use and tree transpiration. Leaf phenological and water use differences may go along with different rooting patterns and soil water uptake depths. Our results imply that tree species selection can be used to influence tree water use in forest plantations under seasonal rainfall conditions. The respective decision may depend on specific goals and constraints.

6. Acknowledgements

We thank Catherine Potvin for the opportunity to conduct our study at the experimental tree plantation in Sardinilla and for her encouragement. Special thanks to Sebastian Wolf for providing the micrometeorological data. We thank Klaus Winter for advice, Milton Garcia for technical support, Diego Dierick and two anonymous reviewers for valuable comments on earlier versions of the manuscript and Sol Heber for critical proof reading. We are grateful to ANAM for granting access to their plantations. This study benefited from the logistical support provided by STRI and ANAM and was funded by the German Research Foundation (Ho-2119/3-1).

7. References

Andrade, J.L., Meinzer, F.C., Goldstein, G., Schnitzer, S.A., 2005. Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest. Trees 19, 282-289.

Baldocchi, D.D., Xu, L., 2007. What limits evaporation from Mediterranean oak woodlands – The supply of moisture in the soil, physiological control by plants or the demand by atmosphere? Adv. Water Res. 30, 2113-2122.

Cienciala, E., Kucera, J., Malmer, A., 2000. Tree sap flow and stand transpiration of two *Acacia mangium* plantations in Sabah, Borneo. J. Hydrol. 236, 109-120.

Cintron, B. B., 1990. *Cedrela odorata* L. Cedro hembra, Spanish cedar. In: Burns, R. M., Honkala, B. H. (Eds.), Silvics of North America: 2. Hardwoods. Agricultural. Handbook. 654. U.S. Department of Agriculture, Forest Service, Washington, DC, pp. 250-257.

Clearwater, J.S.A., M., Meinzer, F.C., Goldstein, G., 2002. Heat dissipation sensors of variable length for measurement of sap flow in trees with deep sapwood. Tree Physiol. 22, 277-283.

Coll, L., Potvin, C., Messier, C., Delagrange, S., 2008. Root architecture and allocation patterns of eight native tropical species with different successional status used in open-grown mixed plantations in Panama. Trees 22, 585-596.

Cunningham, S.A., Kimberi, R.P., Colloff, M.J., 2009. Whole-tree sap flow is substantially diminished by leaf herbivory. Oecologia 158, 633–640.

Davies, W.J., Bacon, M.A., Thomson, D.S., Sobeih, W., Gonzalez, R.L., 2000. Regulation of leaf and fruit growth in plants growing in drying soil: exploitation of the plant's own chemical signaling system and hydraulic architecture to increase the efficiency of water use in agriculture. Journal of Experimental Botany 51, 1617-1626.

Dierick, D., Hölscher, D., 2009. Species-specific tree water use characteristics in reforestation stands in the Philippines. Agric. For. Meteorol. 149, 1317-1326.

Dietrich, W.E., Windsor, M.D., Dunne, T., 1996. Geology, Climate and Hydrology of Barro Colorado Island. In: Leigh, E.G. Jr., Rand, A.S., Windsor, D.M. (Eds.), The Ecology of a Tropical Forest. Seasonal Rhythms and Annual Changes. Second edition. Smithsonian Institution Press, Washington DC, pp. 21-46.

Dünisch, O., Morais, R.R., 2002. Regulation of xylem sap flow in an evergreen, a semi-deciduous, and a deciduous Meliaceae species from the Amazon. Trees 16, 404-416.

Edwards, W.R.N., Becker, P., Cermák, J., 1996. A unified nomenclature for sap flow measurements. Tree Physiol. 17, 65–67.

Flores, E.M., 2003. *Terminalia amazonia* (J.F. Gmel.) Exell. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 748-751.

Flores, E.M., Marín, W.A., 2003. *Tabebuia rosea* (Bertol.) DC. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 737-739.

Fournier, L.A., 2003a. *Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 294-296.

Fournier, L.A., 2003b. *Luehea seemannii* Triana & Planch. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 553-554.

Francis, J.K., 1990. *Hura crepitans* L. Sandbox, molinillo, jabillo. Euphorbiaceae. Spurge family. USDA Forest Service, Southern Forest Experiment Station, Institute of Tropical Forestry. SO-ITF-SM; 38, New Orleans, LA, USA.

Francis, J.K., 2003a. *Acacia mangium* Willd. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 256-258.

Francis, J.K., 2003b. *Tectona grandis* L.f. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 745-747.

Goldstein, G., Andrade, J.L., Meinzer, F.C., Holbrook, N.M., Cavalier, J., Jackson, P., Celis, A., 1998. Stem water storage and diurnal patterns of water use in tropical forest canopy trees. Plant Cell Environ. 21, 397-406.

Granier, A., 1985. A new method of sap flow measurement in tree stems. Ann. For. Sci. 42, 193-200.

Granier, A., 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiol. 3, 309-320.

Hölscher, D., Koch, O., Korn, S., Leuschner, Ch., 2005. Sap flux of five co-occurring tree species in a temperate broad-leaved forest during seasonal soil drought. Trees 19, 628-637.

Holdridge, L.R., Budowski, G., 1956. Report on an ecological survey of the Republic of Panama. The Caribbean Forester 17, 92-109.

Jackson, P.C., Cavelier, J., Goldstein, G., Meinzer, F.C., Holbrook, N.M., 1995. Partitioning of water resources among plants of a lowland tropical forest. Oecologia 101, 197-203.

Jackson, B.J., Jobbagy, E.G., Avissar, R., Roy, S.B., Barrett, D.J., Cook, C.W., Farley, K.A., le Maitre, D.C., McCarl, B.A., Murray, B.C., 2005. Trading water for carbon with biological carbon sequestration. Science 310, 1944-1947.

Kijkar, S., 2003. *Gmelina arborea* Roxb. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 476-478.

Lamb, D., Erskine, P.D., Parrotta, J.A., 2005. Restoration of degraded tropical forest landscapes. Science 310, 1628-1632.

Ma, L., Lu, P., Zhao, P., Roa, X.-Q., Cai, X.A., Zeng, X.P., 2008. Diurnal, daily seasonal and annual patterns of sap-flux-scaled transpiration from an *Acacia mangium* plantation in South China. Ann. For. Sci. 65, 402p1-402p9.

McJannet, D., Fitch, P., Disher, M., Wallace, J., 2007. Measurements of transpiration in four tropical rainforest types of north Queensland, Australia. Hydrol. Process. 21, 3549-3564.

Meinzer, F.C., James, S.A, Goldstein, G., 2004. Dynamics of transpiration, sap flow and use of stored water in tropical forest canopy trees. Tree Physiol. 24, 901-909.

Meinzer, F.C., Bond, B.J., Warren, J.M., Woodruff, D.R., 2005. Does water transport scale universally with tree size? Funct. Ecol. 19, 558-565.

Meinzer, F.C., Andrade, J.L, Goldstein, G., Holbrook, N.M., Cavelier, J., Jackson, P., 1997. Control of transpiration from the upper canopy of a tropical forest, the role of stomatal, boundary layer and hydraulic architecture components. Plant, Cell and Environ. 20, 1242-1252.

Meinzer, F.C., Andrade, J.L., Goldstein, G., Holbrook, N.M., Cavelier, J., Wright, S.J., 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. Oecologia 21, 293-301.

O'Grady, A.P., Eamus, D., Hutley, L.B., 1999. Transpiration increases during dry season, patterns of tree water use in eucalypt open-forests of northern Australia. Tree Physiol. 19, 591-597.

Phillips, N., Oren, R., Zimmermann, R., Wright, S.J., 1999. Temporal patterns of water flux in trees and lianas in Panamanian moist forest. Trees 14, 116-123.

Potvin, C., Dutilleul, P., 2009. Neighborhood effects and size-symmetric competition in a tree plantation varying in diversity. Ecology 90, 321–327.

Potvin, C., Whidden, E., Moore, T., 2004. A case study of carbon pools under three different land-uses in Panama. Clim. Change 67, 291-307.

Rocas, A.N., 2003. *Cedrela odorata* L. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 386-389.

Röhle, H., 1986. Vergleichende Untersuchungen zur Ermittlung der Genauigkeit bei der Ablotung von Kronenradien mit dem Dachlot und durch senkrechtes Anvisieren des Kronenrandes. Forstarchiv 57, 67–71.

Schorcht, M., 2000. *Tectona grandis*. In: Schütt, P., Schuck, H.J., Lang, U., Rollof,A. (Eds.), Enzykloppädie der Holzgewächse. Handbuch und Atlas der Dendrologie. Ecomed Verlagsgesellschaft, Landsberg..

STRI, 2009. Temperature and rainfall data Barro Colorado Island, Panama 1987-2007. Online. http://striweb.si.edu/esp/meta_data/details_bci_temp1.html

van Dijk, A.I.J.M., Keenan, R.J., 2007. Planted forests and water in perspective. For. Ecol. Manage. 251, 1-9.

Veldkamp, E., O'Brien, J.J., 2000. Calibration of a FDR sensor for humid tropical soils of volcanic origin. Soil Sci. Soc. Am. J. 64, 1549-1553.

Wishnie, M.H., Dent, D.H., Mariscal, E., Deago, J., Cedeño, N., Ibarra, D., Condit, R., Ashton, P.M.S., 2007. Initial performance and restoration potential of 24 tropical tree species planted across a precipitation gradient in the Republic of Panama. For. Ecol. Manage. 243, 39-49.

Wolf, S., Eugster, W., Buchmann, N., 2008. Micrometeorological measurements of a plantation and adjacent pasture in Sardinilla, Panama. Field Measurements. ETH Zürich, Institute of Plant Sciences. Digital media.

CHAPTER 5

TREE DIVERSITY ENHANCES TREE TRANSPIRATION IN A PANAMANIAN FOREST PLANTATION

KUNERT, N., SCHWENDENMANN, L., POTVIN, C. & HÖLSCHER, D.,

(ARTICLE IN PREPARATION).

Tree diversity enhances tree transpiration a Panamanian forest plantation

Norbert Kunert[1]*, Luitgard Schwendenmann[1,2], Cathrine Potvin[3], Dirk Hölscher[1]

[1]*Tropical Silviculture and Forest Ecology, Burckhardt Institute, Georg-August-Universität Göttingen, Büsgenweg 1, 37077 Göttingen, Germany*
[2]*Present address: School of Environment, The University of Auckland, Private Bag 92019, Auckland 1142, New Zealand*
[3]*Department of Biology, McGill University, 1205 Dr Penfield, Montreal, Quebec, H3A 1B1, Canada*

Abstract:

1. Tree plantations may play an important role in carbon sequestration and wood supply but there is concern about high water use rates. Recent approaches to reforestation in the tropics emphasize the establishment of multispecies plantations. The effects of tree species mixture on water use have not yet been studied.
2. We hypothesized that tree species diversity enhances plot level transpiration rates. Tree sap flux and water use rates were assessed in monocultures (n = 5), 3-species mixtures (n = 6) and 6-species mixtures (n = 4). Therefore, sap flux densities were monitored with thermal dissipation probes in 60 trees for one year in a seven-year-old tree plantation in Panama.
3. The species-specific sap flux characteristics varied little among mixture types. The individual trees in the 3- and 6-species mixtures had attained bigger diameters than those growing in monocultures, which was associated with higher tree water use rates. Accordingly, on the plot level the estimated annual transpiration by trees increased with increasing tree basal area, and was thus highest in mixed plots.
4. A statistical additive partitioning method suggests a positive net biodiversity effect on the water use characteristics of mixed species plots, which was induced by complementarity of species.
5. Furthermore, for the 6-species mixtures a disproportional increase in tree transpiration was observed. 6-species mixtures had significantly higher transpiration rates per unit basal area than an average monocultures and 3-species mixtures (51 and 56 %, respectively). We speculate that the over-proportional high transpiration rates in the 6-species plots might arise from enhanced vegetation-atmosphere energy exchange e.g. through higher canopy roughness and/or complementary use of soil water uptake.
6. *Synthesis and applications*: The study suggests that tree species diversity enhances transpiration by trees, and the increase is almost linear to tree basal area regarding monocultures and 3-species mixtures and disproportional for 6-species mixtures. For the design of tree plantations this may be taken into account in order to balance goals with respect to biodiversity, production and the use of water resources.

Keywords: monoculture, mixtures, native species, plot transpiration, complementarity of species, selection effect

---

Kunert, N., Schwendenmann, L., Potvin, C. & Hölscher, D. (in prep.)

*Corresponding author. Tel.: +49 551 399556; Fax: +49 551 394019; E-mail address: nkunert1@gwdg.de (N. Kunert)

1 Introduction

The establishment of tree plantations in the tropics is of increasing importance to mitigate climate change by carbon sequestration and as a contribution to the growing demand for wood. Current research suggest that well designed forest plantations can reduce the volume of sediment, nutrients and salt transported into river systems (van Dijk and Keenan 2007). Nevertheless, there is concern about reduction in stream flow with plantation establishment (Jackson et al. 2005, Malmer et al. 2010), because trees may exhibit high water use rates. So far, most reforestations have been conducted with monocultures involving a limited number of species. Such traditional plantations have supplied some goods but have made only minor contributions to the restoration of ecological functions and biodiversity (Lamb et al. 2005). According to that, recent approaches to reforestation in the tropics emphasize the establishment of multispecies plantations consisting of native tree species (Montagnini and Jordan 2005, Lamb et al. 2005, Wishnie et al. 2007). The few existing multispecies reforestation experiments indicate that tropical plantations containing higher tree diversity are likely to be more productive than monospecific stands (Forrester et al. 2004, Bristow et al. 2006, Potvin et al. 2007, Piotto 2008), but possible changes in the hydrological cycle have to our knowledge not been studied.

There is evidence that biodiversity has positive effects on most ecosystem functions (Balvanera et al. 2006). In general the observed responses to higher diversity can be separated into two main biodiversity effects (Loreau and Hector 2001). First, in a complementarity effect that is collectively covering mechanisms like niche differentiation and facilitation processes among species. Complementarity effects often result in increasing performance of mixed communities above the expected performance of individuals (Loreau and Hector 2001). And secondly in a selection effect if the performance of mixed communities is influenced by selective processes, such as interspecifc competition, which causes dominance of species with particular traits (Loreau and Hector 2001). Selection effects can be positive or negative depending on whether species with lower- or higher-than-average performance dominate communities. Biodiversity effects are directly affecting intra-specific tree morphology and physiology at the individual tree level (Richards et al. 2010). However, changes in aboveground tree structural characteristics, such as canopy architecture, leaf traits (Menalled et al. 1998, Bauhus et al. 2004), and spatial, temporal or chemical stratification of roots (da Silva et al 2009) have been observed when tree species were planted in mixtures.

Tree water use and transpiration are directly linked to tree structural characteristics such as tree size, canopy structure and diameter (Meinzer et al. 1999). We hypothesized that tree species diversity enhances tree water use and plot level transpiration rates. Tree sap flux and water use rates were assessed in monocultures, 3-species mixtures and 6-species mixtures and combined with a methodological approach to identify and separate biodiversity effects. We measured sap flux densities with thermal dissipation probes in 60 trees for one year in a seven-year-old tree plantation in Panama. The results may contribute to a better understanding of biodiversity effects on the water use of tree plantations and may help to select appropriate tree species mixtures with respect to water resource management.

2 Methods

2.1 Study area

The study was conducted in an experimental plantation close to the village of Sardinilla, Central Panama (9°19’ N, 79°38’ W), which is located 50 km north of Panama City. The elevation of the site is approximately 70 m a.s.l. In the area, mean annual precipitation is about 2,350 mm (Figure 1), with a pronounced dry season from January to March. In the wet season precipitation reaches on average 250 mm per month (May - November), 120-130 mm during the transit period (April and December) and 25-50 mm during the dry season. The mean annual temperature in the region is 26.2 °C (Figure 1). The clay rich soils in Sardinilla are classified as Typic and Aquic Tropudalfs and are derived from limestone (Potvin et al. 2004). The original vegetation in the area around Sardinilla was probably a tropical moist forest similar to that on Barro Colorado Island (Holdridge and Budowski 1956). Most of the area was clear cut in the 1950th and then used for agriculture (probably corn, plantain and yucca). In the following years the site was converted into pasture (Abraham 2004).

2.2 Experimental design of the plantation

The experimental tree plantation was set-up with plots of varying tree species richness (monoculture, 3-species and 6-species mixtures) and species combinations (Figure 2). In total 24 plots were established between June and July 2001 (Figure 2). The following six native tree species were planted: *Anacardium excelsum* ((Bertero & Balb. ex Kunth) Skeels; Anacardiaceae), *Hura crepitans* (Linné; Euphorbiaceae), *Luehea seemannii* (Triana & Planch, Tiliaceae) *Tabebuia rosea* ((Bertol.) DC, Bignoniaceae), *Cordia alliodora* ((Ruiz & Pavon) Oken, Boraginaceae) and *Cedrela odorata* (Liné, Meliaceae). The first five species can be classified as semi deciduous tree species and the last as a deciduous tree species. Each plot is 45x45 m and further divided into four subplots of 22.5x22.5 m. Seedlings were planted with 3 m spacing which is the commercially prevalent planting density in Central America with 1,111 stems per ha. The plantation includes 12 monoculture plots with each of the species replicated two times, six different 3-species mixture plots with different species combination and six 6-species mixture plots containing all six species (Figure 2). Unfortunately, all *Cordia allidora* trees grown in monocultures and the majority of *Cordia allidora* in the 3-species and 6-species mixtures died within the first year. Consequently, we did not include *Cordia alliodora* in the study.

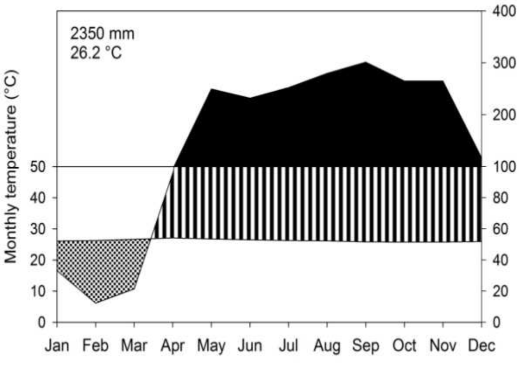


Fig. 1: Climate diagram for Barro Colorado Island (BCI) based on data obtained between 1977 and 2007 (STRI, 2009). BCI is located at a distance of approximately 30 km from Sardinilla.

2.3 Micrometeorological and soil moisture measurements

The micrometeorological data such as photosynthetic photon flux density (PPFD, mol m^{-2} s^{-1}), air temperature (C°), relative humidity (%) and precipitation (mm) were provided by the ETH Zürich (Wolf et al. 2007-2008). The photosynthetic photon flux density was measured with a PAR-LITE quantum sensor (Kipp & Zonen, Delft, The Netherlands), air temperature and relative humidity with a thermo-hygrometer (Type MP100A, Rotronic AG, Ettlingen, Germany) installed 6–8 m above the canopy on top of a 15 m high flux tower in the center of the plantation. Precipitation (mm) was measured with a rain gauge (Type 10116, TOSS GmbH, Potsdam, Germany) at 1.5 m above ground in an adjacent open pasture (Wolf et al. 2007-2008). Data were recorded every 10 seconds and half hourly averages were stored. ***Soil moisture*** content was measured with ***time*** domain reflectometry sensors (TDR, CS610, ***Campbell*** Scientific, Inc., Logan, UT, USA) at four locations within the plantation and at three depths (10 cm, 35 cm and 60 cm). Soil moisture content was recorded hourly and stored on data loggers (CR800 and CR1000 datalogger, Campbell Scientific Inc., Logan, UT, USA). Soil moisture sensors were calibrated following the procedure of Veldkamp and O'Brien (2000).

2.4 Tree selection

Sap flux measurements were conducted in the five remaining tree species (*Anacardium excelsum*, *Cedrela odorata*, *Hura crepitans, Luehea seemannii* and *Tabebuia rosea*). Sample trees were chosen in five monoculture plots (one plot for each of the five investigated species and four sample trees per plot); six different 3-species mixture plots (one sample tree of each species in every plot and once replicated twice); and four replicates of the six-species mixture (one sample tree of each species in every plot) (Figure 2). Altogether 60 trees were investigated. All sample trees had all four direct neighboring trees and were situated within those subplots that had the lowest mortality rates.

2.5 Sap flux density, tree water use and plot level transpiration

Sap flux density was measured with thermal dissipation sensors constructed after Granier (1985). The sensors consisting of two cylindrical probes were inserted radially (0-20 mm below cambium) into the stem, with one probe placed approximately 10-15 cm vertically above the

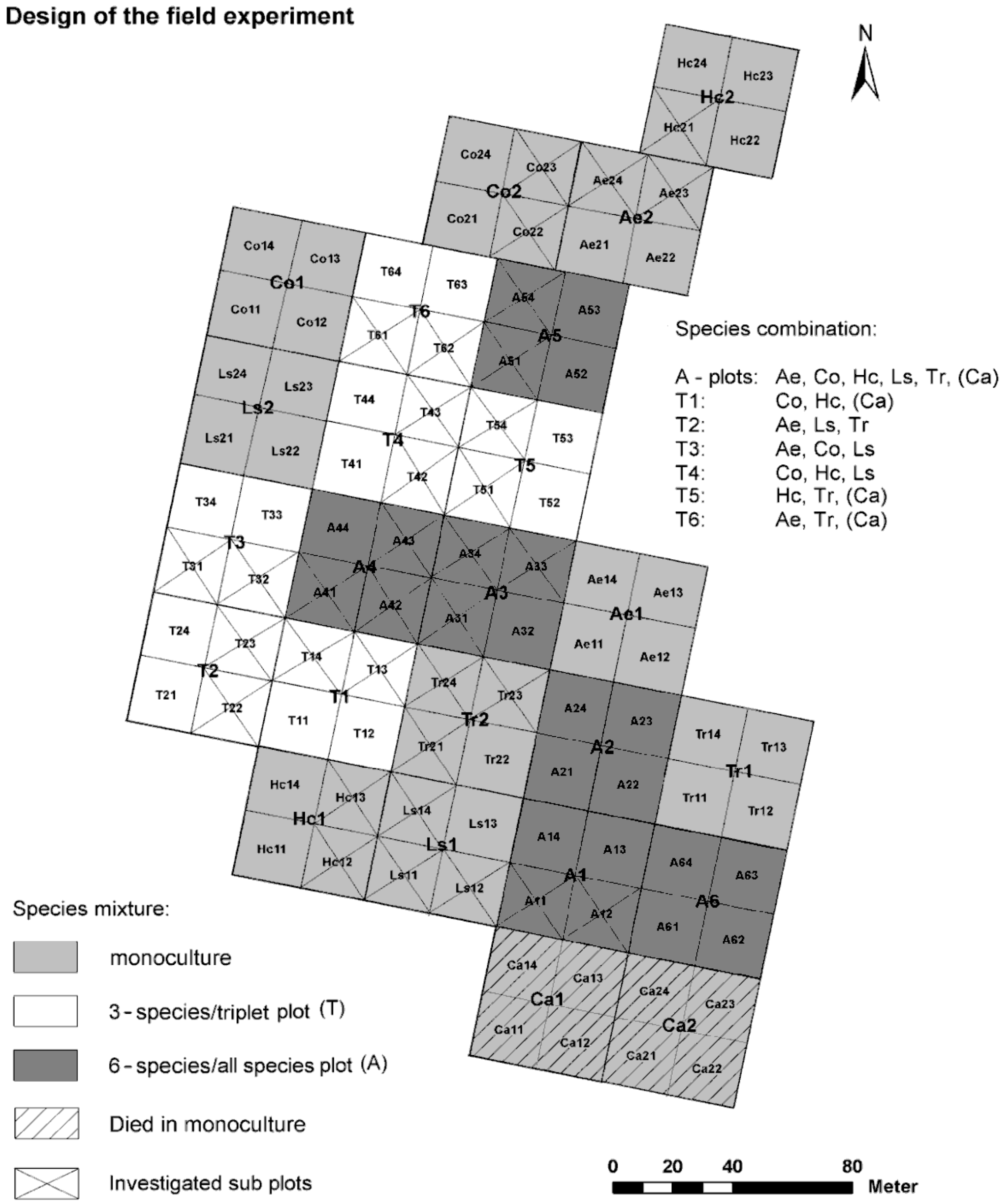


Fig. 2: Map of the design of the field experiment in Sardinilla. The basis of the map is a courtesy of Sebastian Wolf, ETH Zurich

other. Every tree was equipped with two Granier sensors, one on the southern and one on the northern side of the trunk at 130 cm above the ground. The sensors were protected from thermal influences and water intrusion by a styrofoam box, reflective foil and a plastic cover. Probe output voltage was recorded every 30 seconds, and the average value stored every 15 minutes (CR800 and CR1000 datalogger; AM16/32 and AM416 multiplexer, Campbell Scientific Inc., Logan, UT, USA). Sap flux density (J_s in g cm^{-2} h^{-1}) was calculated from differences in voltage using the calibration equation determined by Granier (1987). Sap flux density was measured from July 2007 to June 2008 (365 days). Sap flux sensors were changed when necessary to ensure that sap flux was measured in the outermost sap wood.

The estimation of the water use (Q) for individual trees was based upon the sapwood area of the tree and the radial changes in J_s present in the sapwood. Species specific xylem depth was estimated by dye injection for three trees per species. Thereby, sap wood depth of all species was found to be greater than sensor length. Changes of sap flux density with increasing xylem depth were assessed in each tree in the last two week of the experiment. For each tree species an average normalised J_s profile (%) was constructed out of the four sample trees. Sap flux density data was extrapolated to tree level water use Q [kg d^{-1}] by summing up the water flow in a given number of ring-shaped stem cross sections corresponding with the respective installation depth, J_s as measured at reference depth and the normalised profile of J_s for the species considered (Edwards et al. 1996). The plot level transpiration rate (T_{plot} mm d^{-1}) expressed per unit ground area was calculated using the relationship of tree water use and tree diameter (Garcia Santos 2007). We derived daily relationships between measured tree water use rates and tree diameters for each species separated into mixtures, inserted the known diameters of all other individuals of a given plot into the respective equations, summed the calculated water use rates of all trees and divided the result by the area of the plot.

2.6 Tree and stand structure

Diameter at breast height (DBH) was measured with a girth tape of all sample trees. Tree height and crown base height of each sample tree was determined with a hypsometer (Vertex III, Haglöf, Lensele, Sweden). The crown extension in each of eight cardinal directions was measured by vertically looking up and crown area was calculated as sum of eight pitch circles as described by Röhle (1986). A complete inventory of all plots was conducted every year at the onset of the dry season and individual tree height and diameter at breast height were measured as explained above. Hemispherical photographs were taken vertically with a high-resolution digital camera (Minolta Dimage Xt, Japan). The camera was equipped a 185° fish-eye lens and was placed in a leveling device (Regent Instruments, Canada), Images were analyzed for the forest cover and leaf area index with Gap Light Analyzer Version 2.0 (GLA, Simon Fraser University, Burnaby, British Columbia, Canada).

2.7 Additive partitioning of biodiversity effects

Following the work of Loreau and Hector (2001), we used a methodological approach based on the Price equation of evolutionary genetics (Price 1995), to measure the net biodiversity effect (ΔY) by additive partitioning a selection effect and a complementarity effect. The net biodiversity effect has the dimension of yield, where yield stands for any measurable variable in an ecosystem and is expected to be zero under the null hypothesis of no biodiversity effects. These various effects can be related by additive partitioning as follows:

$$\Delta Y = Y_O - Y_E = \sum_i RY_{O,i}M_i - \sum_i RY_{E,i}M_i$$

$$= \sum_i \Delta RY_i M_i = N\overline{\Delta RY}\,\overline{M} + N\,cov(\Delta RY, M)$$

where N = number of species in the mixture,

M_i = yield of species i in monoculture,

$Y_{O,i}$ = observed yield of species i in mixture,

$Y_O = \sum_i Y_{O,i}$ = total observed yield of the mixture,

$Y_E = \sum_i Y_{E,i}$ = total expected yield of the mixture.

Accordingly the complementary and selection effect are expressed as a function of the deviation from the expected relative yield in the mixture (ΔRY). The yield in mixture is influenced by a complementarity effect ($N\,\overline{\Delta RY}\overline{M}$), if it is on average higher than the expected yield calculated out of the weighted average of the monoculture yield. The covariance between the monoculture yield of species and their change in relative yield in the mixture is explaining a selection effect ($N\ cov(\Delta RY, M)$). The additive partitioning method was applied to the variables plot level transpiration, basal area and plot level water use per unit basal area.

2.8 Data analyses

Normalized daily J_s was calculated by dividing daily integrated J_s by the highest observed daily integrated J_s during the study period (percentage of maximum). Gap filling for missing days was done based on the species-specific relationships between measured sap flux densities and PPFD ($r^2 = 0.671 - 0.830$, $p < 0.05$). The dry season was defined following Dietrich et al. (1996) when less than 100 mm rainfall was measured for the duration of three months. We set the starting date of the dry season three weeks after the last major rain event, so that the dry season lasted from January 15, 2008 to April 15, 2008 (90 days). The time from July 1, 2007 to December 14, 2007 and June 1, 2008 to June 30, 2008 was characterized as wet season (195 days). All annual values and means are based on 365 days including the transition periods between December 15, 2007 to January 14, 2008 and April 16, 2008 to May 30, 2008. Linear regressions were used to establish the relationship between the maximum tree water use and DBH. Tree water use rates among species and mixtures were compared using the analysis of covariance with DBH as a covariate (ANCOVA, followed by a post-hoc Tukey HSD test). Differences in plot level transpiration rates between seasons were determined with a paired Student's t-test.

Statistical tests of the additive partitioning were performed following Loreau and Hector (2001). Accordingly, we used the initial planted species richness (monoculture, 3-species and 6-species mixtures) in the analysis defining the treatments in the experimental design. Values of the selection, complementarity and net biodiversity effects were square root transformed preserving the original positive or negative sign. Grand mean values across all 3-species and 6-species mixtures were tested versus zero with a one-sample t-test. Analysis of variance was used to test the relationship between over yield and species richness, partitioning the relationship into a linear regression, testing for positive or negative relationships. All statistical analyses were performed using SPSS 13.0 software (SPSS Inc., Chicago, USA).

3 Results

3.1 Micrometeorological and soil moisture measurements

Rainfall during the 12 months of the study period equaled 2,260 mm. Monthly average rainfall was 254.8 ± 88.1 mm during the wet season (July 1, 2007 to December 14, 2007 and June 1, 2008 to June 30, 2008). Total rainfall during the dry season (January 15, 2008 to April 15, 2008) was only 33.4 mm in a three month period. Higher mean PPFD (47.1 ± 9.7 mol m^{-2} d^{-1}) and VPD (0.81 ± 0.18 kPa) were recorded during the dry season than during the wet season (29.9 ± 9.2 mol m^{-2} d^{-1} and 0.48 ± 0.27 kPa, respectively). Soil moisture in 10 cm depth decreased rapidly during the wet to dry season transition period and reached its minimum (0.26 m^3 m^{-3}) at the end of the dry season. Soil moisture at 35 cm and 60 cm depths showed a different pattern with a gradual decline starting in mid January and reaching a low of 0.37 m^3 m^{-3} (35 cm) and 0.40 m^3 m^{-3} (60 cm), respectively, at the end of the dry season.

3.2 Daily sap flux density and annual courses

Maximum sap flux densities (J_{smax}) were between 20 g cm^{-2} h^{-1} (*Cedrela odorata*, monoculture) and 55 g cm^{-2} h^{-1} (*Anacardium excelsum*, 3-species mixture). Mean daily integrated sap flux densities (J_{sdaily}) ranged from 68 g cm^{-2} d^{-1} (*Cedrela odorata,* 6-species mixture) to 202 g cm^{-2} d^{-1} (*Anacardium excelsum,* monoculture). For both measures significant differences among species were found (ANOVA; $F_{4,15} < 9.372$; $p < 0.001$). In contrast, we did not find statistically significant differences among diversity level of a given species (ANOVA; $F_{2,9} > 2.402$; $p > 0.146$), except for the daily sap flux densities of *Hura crepitans* (ANOVA; $F_{2,9} = 7.088$; $p = 0.014$) (Table 2). The seasonal patterns of normalized daily sap flux density varied strongly among species, but revealed similar patterns among the different mixtures for a given species (Figure 3). Minimum sap flux densities in the annual course coincided with major leaf shedding periods of a

Table 1: Structural characteristics of the study trees (mean values ± SD, n = 4 trees per species) and mean tree diameter and tree height of the species on the study plots.

Species abbreviation and scientific name		Mixture type	Sample trees DBH (cm)		Tree height (m)		Crown area (m^2)		Plot level DBH (cm)		Tree height (m)	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Ae	*Anacardium excelsum*	1-species	10.1	0.6	6.4	0.4	10.6	3.8	8.4	4.9	5.8	1.8
		3-species	14.7	2.6	9.1	2.5	10.3	1.8	12.6	6.7	7.3	3.0
		6-species	11.2	1.7	7.5	1.2	12.2	2.4	14.2	8.0	7.9	2.3
Co	*Cedrela odorata*	1-species	12.0	0.6	11.7	1.1	9.4	4.6	9.3	3.9	9.2	3.3
		3-species	20.2	1.0	14.7	1.9	26.9	7.7	13.6	6.7	10.0	4.7
		6-species	16.0	4.0	11.2	1.7	17.6	10.0	10.9	7.2	9.0	4.5
Hc	*Hura crepitans*	1-species	18.0	1.9	5.4	1.0	21.5	4.5	6.8	4.8	4.4	2.4
		3-species	16.7	7.0	6.2	1.3	30.7	35.1	9.7	6.6	5.4	2.5
		6-species	22.0	7.2	7.4	2.0	32.4	23.4	13.3	8.6	5.6	2.5
Ls	*Luehea seemannii*	1-species	11.8	1.6	8.7	1.0	11.8	1.7	17.7	7.5	9.3	1.7
		3-species	14.1	2.6	10.2	1.2	25.2	7.1	18.2	9.8	9.8	3.1
		6-species	12.5	2.5	8.3	2.1	12.8	8.4	13.2	7.0	8.7	2.7
Tr	*Tabebuia rosea*	1-species	11.5	1.3	7.4	0.3	18.6	4.6	10.1	4.5	6.2	1.7
		3-species	10.6	2.0	8.2	2.1	13.5	4.7	9.7	5.3	6.2	2.2
		6-species	13.8	3.7	7.1	2.7	20.7	10.4	13.0	8.4	7.2	2.0

Table 2: Water use characteristics of the study trees (mean values ± SD, n = 4 trees per species). Mean daily intergrated sap flux densities (J_{sdaily}), maximum sap flux densities (J_{smax}) and tree water use rates (Q) for different periods. Dry season, wet season and annual values are based on 90, 195 and 365 days, respectively (mean ± SD, n = 4 trees per species). Capital letters indicate significant differences among species tested for each mixture and lower-case letters indicate significant differences within species (J_{sdaily} and J_{smax}: ANOVA followed by a post-hoc Tukey HSD test; water use rate: ANCOVA with DBH as covariate followed by a post-hoc Tukey HSD test, $p < 0.05$).

Species abbreviation	Mixture type	J_{sdaily} ($g\ cm^{-2} d^{-1}$)		J_{smax} ($g\ cm^{-2} h^{-1}$)		Q ($kg\ d^{-1}$)					
						Dry		Wet		Annual	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Ae	1-species	202	35	46	9	$13.7^{AB,a}$	4.6	$10.1^{B,a}$	2.8	$10.9^{B,a}$	3.4
	3-species	196	32	55	4	$28.6^{B,ab}$	5.6	$17.6^{A,ab}$	7.3	$20.7^{A,ab}$	9.6
	6-species	175	22	51	11	$29.3^{A,b}$	8.0	$19.5^{A,b}$	12.2	$22.9^{A,b}$	8.2
Co	1-species	73	24	20	4	$3.2^{A,a}$	0.8	$7.9^{A,a}$	2.2	$5.8^{A,a}$	1.7
	3-species	75	39	21	4	$6.0^{A,a}$	2.7	$14.0^{A,b}$	4.2	$13.1^{A,b}$	5.2
	6-species	68	20	23	9	$7.3^{A,a}$	5.1	$21.1^{A,b}$	1.1	$19.4^{A,b}$	6.3
Hc	1-species	86	30	33	8	$7.2^{AB,a}$	2.6	$14.2^{AB,a}$	7.2	$12.4^{AB,a}$	5.5
	3-species	73	37	30	12	$5.6^{A,a}$	6.6	$10.7^{A,a}$	5.3	$8.4^{A,a}$	6.2
	6-species	93	27	32	9	$33.6^{A,a}$	14.6	$42.2^{A,a}$	10.6	$39.7^{A,a}$	18.9
Ls	1-species	183	29	43	7	$12.3^{B,a}$	4.8	$13.3^{B,a}$	2.3	$12.5^{B,a}$	2.4
	3-species	188	24	45	6	$28.1^{B,b}$	7.4	$18.3^{A,a}$	8.3	$23.2^{A,a}$	7.2
	6-species	181	31	44	9	$21.3^{A,ab}$	5.7	$15.4^{A,a}$	8.4	$18.6^{A,a}$	7.5
Tr	1-species	93	30	30	5	$7.7^{A,a}$	3.3	$8.5^{AB,a}$	0.9	$7.5^{AB,a}$	1.9
	3-species	129	51	33	11	$9.4^{A,a}$	4.4	$3.9^{A,b}$	1.8	$7.6^{A,a}$	3.0
	6-species	122	26	32	4	$35.1^{A,b}$	13.7	$23.1^{A,c}$	11.3	$30.6^{A,b}$	16.3

given species and were independent from the type of mixture (Figure 3).

3.3 Tree water use rates in relation to tree characteristics

Maximum water use rates for individual trees were highly variable ranging from 18.9 kg d^{-1} for *Tabebeuia rosea* of 8.3 cm DBH to 101.1 kg d^{-1} for a *Hura crepitans* with a DBH of 28.2 cm (Figure 4). The observed tree water use rates were strongly correlated with tree diameter. A linear regression of maximum water use of all 60 sample trees against DBH explained 54% of the observed variation (Figure 4). In trees with a diameter between 10 and 15 cm diameter for example, we see a fourfold difference in water use rates with a pronounced effect of species and independent from diversity level. Significant differences in mean tree water use among species were found in the monoculture, 3-species and 6-species mixtures (ANCOVA; $F_{4,14} > 3.807$; $p < 0.027$) (Table 2).

3.4 Plot level transpiration rates and stand characteristics

Plot level transpiration averaged 1.3 ± 0.7 mm d^{-1} over the 12 month study period across all plots and did not differ between dry and wet season. Absolute minimum and maximum values were 0.3 and 2.6 mm d^{-1} (*Cedrela odorata* in monoculture and *Luhea seemannii* in monoculture, respectively). On average the daily plot level transpiration rate was 7% higher in the 3-species mixtures and 48% higher in the 6-species mixtures compared to monocultures. Plot level transpiration during wet season and during the wet to dry season transition period were significantly different in the 3 species and 6-species mixtures (paired Student's t-test; $p < 0.05$), but not different among the monocultures (paired Student's t-test; $p > 0.05$). The 3-species mixtures were showing an increased plot level transpiration during the transition period from wet to dry season, the 6-species mixtures a slightly reduced transpiration compared to the wet season.

Annual transpiration ranged from 175 (*Cedrela odorata*) to 806 mm yr^{-1} (*Luehea seemannii*) in the monocultures, from 125 to 748 mm yr^{-1} in the 3-species mixture and from 693 to 761 mm yr^{-1} in the 6-species mixture (Table 3). There was a positive relation between plot level water use and basal area across all study plots (Figure 5).

Nevertheless, the 6-species mixtures had significantly higher water use rates per unit basal area than the average monocultures and 3-species mixtures (annual 51 and 56 %, respectively). The relation between water use per basal area and PPFD was curvilinear and indicating an earlier light saturation of the monocultures and 3-species mixtures (Figure 6).

3.5 Partitioning of biodiversity effects

Overall, tree diversity enhanced plot level transpiration, basal area and water use per basal area (Figure 7). The additive partitioning revealed that the effect of species number on the net effect was positive for all measured variables ($p < 0.05$). The grand means of the net effect were significantly different from zero across all variables. The selection effect was generally small and only significant for the basal area. However, the selection effect was influenced by species richness for the plot level transpiration and water use per unit basal area, but the selection effect was unaffected by species richness for the basal area. Plot level transpiration and basal area were affected by complementarity. Remarkably was the strong compelementarity effect on the water use per unit basal area and the huge increase of the water use rates in the 6-species mixtures compared to zero (Figure 8c). The complementarity effect was significantly influenced by species richness and exceeded the selection effect in all cases. The grand means of all variables were significant different from zero for the complementarity effect (Figure 8).

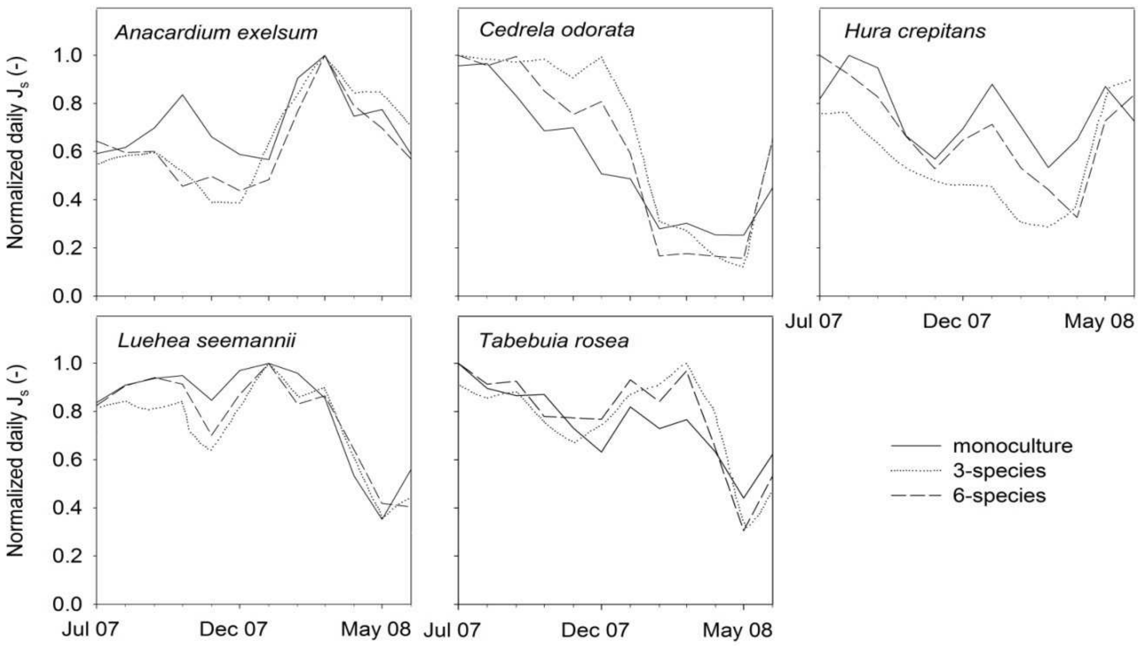


Fig. 3: Annual course of normalized daily sap flux density (species mean, n = 4) in the different species mixtures.

Table 3: Characteristics of study plot (mean values ± SD, n = 225 trees per plot, n = 5 measurements per plot for LAI), basal area and plot level transpiration (T_{plot}) rates for different periods. Wet season, transit period, and dry season transpiration rates are mean values and based on 90, 30, 195 days, respectively. Values for basal area and annual plot level transpiration (sum of 365 days) are absolute values.

Plot	Mixture type	DBH (cm)		Tree height (m)		LAI (m^2 m^{-2})		Basal area (m^2 ha^{-1})	T_{plot} (mm d^{-1})			T_{plot} (mm yr^{-1})
		Mean	SD	Mean	SD	Mean	SD		Wet season	Transit wet-dry	Dry season	Annual
AE2	Monoculture	8.1	4.8	5.8	1.8	2.44	0.65	5.1	0.62	0.55	0.82	244
CO2	Monoculture	7.9	3.8	9.2	3.3	0.80	0.60	5.4	0.60	0.41	0.26	175
LS1	Monoculture	16.3	7.7	9.3	1.7	3.22	0.60	27.4	2.36	2.63	2.27	806
HC1;2	Monoculture	5.4	4.4	3.6	1.7	1.79	0.46	4.5	0.61	0.60	0.57	366
TR2	Monoculture	10.4	5.1	6.2	1.7	1.28	0.53	11.3	0.89	0.80	0.76	297
A1	6-species	11.0	6.1	6.1	2.2	2.30	0.83	9.3	1.95	1.86	1.95	693
A3	6-species	14.3	8.2	7.9	3.1	2.95	0.59	14.3	2.23	2.01	1.87	750
A4	6-species	13.6	8.4	8.8	3.3	2.62	0.99	13.7	2.13	2.04	1.99	740
A5	6-species	10.7	6.8	7.1	2.4	2.14	0.99	8.7	2.22	2.13	1.97	761
T1	3-species	11.4	7.1	6.9	3.8	1.91	0.46	6.3	0.45	0.42	0.19	125
T2	3-species	13.2	8.6	9.2	3.1	2.74	0.58	18.6	1.86	2.25	2.60	748
T3	3-species	11.8	8.4	7.6	3.4	2.90	0.48	10.2	1.48	1.79	1.91	574
T4	3-species	12.8	7.3	9.3	4.5	2.57	1.13	14.8	1.62	1.87	1.41	544
T5	3-species	10.5	5.0	6.7	2.0	2.68	0.54	6.5	0.57	0.59	0.53	200
T6	3-species	10.0	6.3	5.0	1.6	1.64	0.59	6.5	0.60	0.63	0.92	252

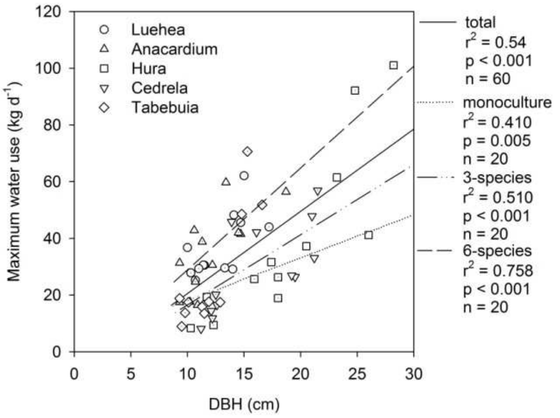


Fig. 4: Maximum daily water use for trees as a function to diameter at breast height (DBH).

4 Discussion

4.1 Sap flux density and tree water use

Measured daily and maximum sap flux densities are comparable with observations made for different tropical tree species, belonging to a large number of genera growing in natural forest and under plantation conditions (Phillip et al. 1999, Meinzer et al. 2004). As sap flux densities of the monocultures and mixture were comparable and no significant differences of the sap flux density among of the mixtures was measured, we conclude that there are no measurable effects of species mixture on the sap flux densities of trees. The water use rates that we estimated also correspond to values recorded from other stands across the tropics (Cienciala et al. 2000, Meinzer et al. 2004, McJannet et al. 2007). The variation in water use among species planted in monoculture and the opportunity to influence water use of plantations by species selection was discussed in Kunert et al. (2010). The commonly found water use and diameter relation (Meinzer et al. 2001, 2005, Andrade et al. 2005, McJannet et al. 2007) was present, but is not as strong as the reported relation in natural forests. The considerable scatter of our data in the lower diameter range between 10 and 15 cm (Figure 4) might reflect the different environmental conditions in natural forests and young plantations (Dierick and Hölscher 2009). In contrast to stratified natural forest, trees in young plantations are well exposed to sunlight. Under such conditions species specific traits to cope with light intensity, temperature, humidity, and wind speed may play a more important role. Results from monospecific and mixed *Eucalyptus grandis* and *Acacia mangium* stands in Brazil indicate that mixed species stands develop a more stratified canopy than even aged monocultures (Laclau et al. 2008).

4.2 *Basal area and transpiration in relation to tree diversity*

We found a positive net effect of tree diversity on the basal area, plot transpiration and water use per unit basal area. On average 30-58% higher tree basal area was found in the mixture plots after five years of growth (Potvin and Gotelli 2008). This difference was even more pronounced in the seven-year-old stands. In the five-year-old stands the higher basal area was explained by a significant positive complementary effect and a significant negative selection effect (Healy et al. 2008). These opposing biodiversity effects resulted in a non-significant net biodiversity effect (Healy et al. 2008). We found a significant positive complementarity effect and a negative selection effect on the basal area, but our results suggest a significant positive net biodiversity effect. The negative selection effect might be a result from the high mortality of *Cordia alliodora* as a poor performing species. Nevertheless in the 3-species mixtures (T1, T5, T6) where only two species were remaining, basal area of the remaining trees was equal to an average monoculture (Figure 7 b). Long term experiments demonstrate that complementarity of species and net biodiversity effects are increasing over time and selection effects are decreasing (Fargione et al. 2007).

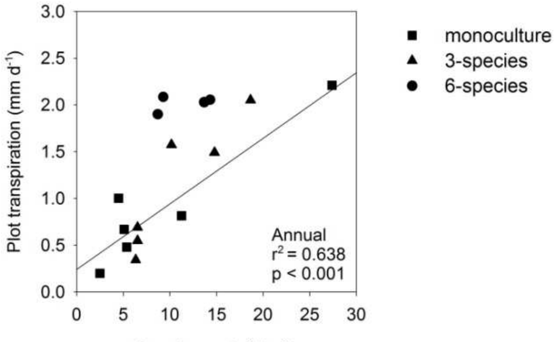


Fig. 5: Linear relationship between mean daily a annual plot level transpiration (mm d^{-1}) and basal area (m^2 ha^{-1}) of the investigated plots.

Our results support this observation as the complementarity effect in the seven-year-old plantation was higher compared to the five-year-old plantation (Healy et al. 2008).

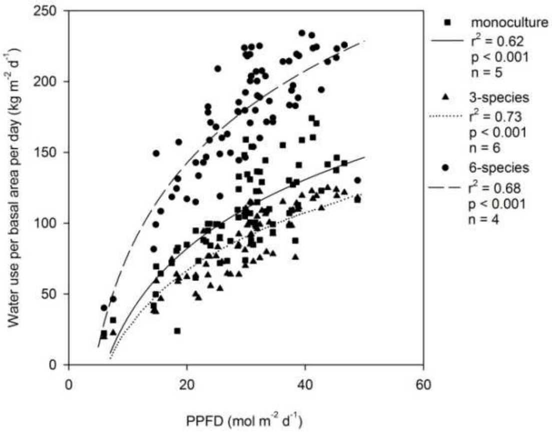


Fig. 6: Daily average water use per basal area during the wet season (monoculture: n = 5 plots, 3-Species: n = 6 plots, 6-species: n = 4 plots) as functions of daily PPFD.

Furthermore, our results show an on average higher plot level transpiration rate in the mixed species plots. Results obtained from grasslands suggest that possible explanation for higher transpiration are higher biomass of the mixed species plots, a greater representation of species that intrinsically use more water, and/or a positive influence of species diversity on transpiration (van Peer et al. 2004). In our study higher plot level transpiration was usually accompanied by higher basal area (Figure 5). Studies conducted in species rich grassland communities indicate that complementarity and/or facilitation of species accounted for enhanced transpiration (Caldeira et al. 2001, van Peer et al 2004, de Boeck et al. 2006). Remarkable is the on average over 50% higher water use rate per unit basal area of the 6-species mixtures compared to the monocultures and 3-species mixtures. This enhanced water use cannot be explained by either a higher basal area in these plots or the dominance of a single tree species with high water use rates.

4.3 The importance of complementarity of species

Our results suggest that the positive relationship between tree diversity and plot level transpiration and water use per unit basal area was explained largely by a significant positive complementarity effect (Figure 8). The higher transpiration of the mixtures in comparison to the monocultures might indicate a better use of limited resources and a better tree growth. Different resources might be limited during the wet season and during the dry season. However, the site is situated in an environment where tree growth is not water limited during the wet season, so that we assume that radiation and water vapor pressure deficit may limit tree transpiration. Potvin and Gotelli (2008) related the enhanced growth of the mixed species plots to stronger competition for light in monocultures. Recent studies show that the canopy structure of tree mixtures has a better three-dimensional canopy space filling and a more complete access to the radiation (da Silva et al. 2009). Complementary use of radiation was also made responsible for enhanced growth in mixed species grassland (Yachi and Loreau 2007). Furthermore, Baldocchi (2005) mentions higher stand transpiration rates of mixed stands due to a higher canopy roughness. The higher heterogeneity in tree heights and also mean tree height (Kelliher et al. 1993) of the mixed stands may be an indicator of canopy roughness (Table 1). Therefore the aerodynamic roughness length of the tree canopy of the mixed stands can be expected to be larger which enhances the degree of turbulent energy exchange with the atmosphere, enabling higher transpiration rates. This might even explain the oversized water use rates per unit basal area of the 6-species plots as they are representing the plots with the highest in canopy height.

In the transition periods and in the dry season trees are receiving a higher amount of radiation than in the wet season due to cloudless sky (Kunert et al. 2010). Radiation in the dry season is exceeding wet season radiation on average about 36%. Hence, trees should be able to use the increased amount of radiation for photosynthesis and should show higher transpiration rates if they are not limited by other resources such as water. Such higher tree transpiration rates during dry season were reported for a eucalypt open-forest in Northern Australia (O'Grady et al. 1999) and dry season non-deciduous monocultures in Panama (Kunert et al. 2010). Accordingly some trees have the ability to use the increased availability of radiation, but significant increased transpiration rates during the transition period from wet to dry season and during the dry season were present only in the 3-species mixtures. Significant lower transpiration rates could be observed in the 6-species mixtures during the transition period from the

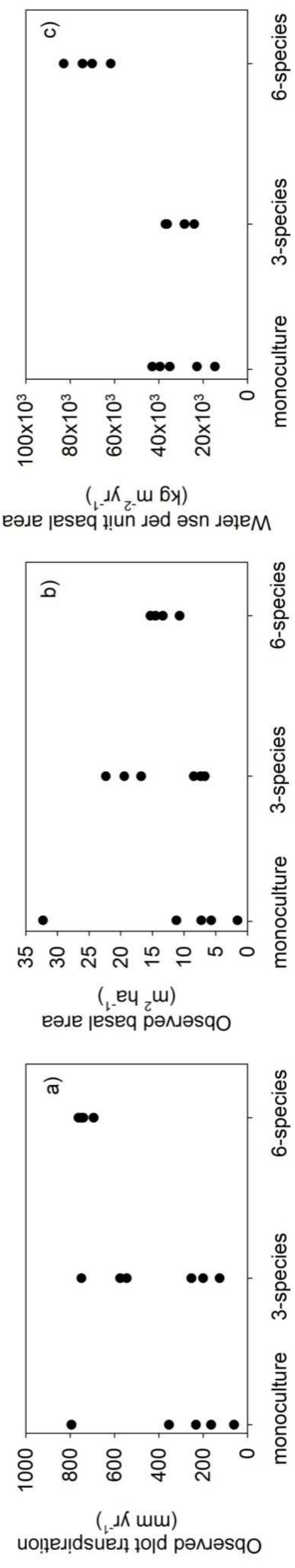


Fig. 7: Observed a) annual plot level transpiration, b) basal area per ha and c) annual plot tree water use rate per unit basal area in the different study plots.

wet to the dry season (data not shown). Nevertheless, the 6-species mixtures could maintain transpiration on a relatively constant high level compared to the other mixture types throughout the entire dry season. The wide range of species and species phenology in the 6-species mixtures might have balanced the reduction of transpiration through shedding leaves of deciduous species and the enhancement of transpiration of non deciduous species through the higher amount of radiation. Hence, an improved complementary soil water use can be assumed in the 3- and 6-species mixtures during the dry season, despite the slightly lower transpiration rates of the 6-species mixtures.

4.4 *Management considerations*

Various reasons exist for enforcing reforestation in the tropics, but a major concern is that tree planting results in a strongly reduced streamflow after reforesting deforested land (Calder et al. 2004, Farley et al. 2005, Jackson et al. 2005, Kaimowitz 2005). Hence reforestation can be critical in regions where water resources are at least seasonally scarce and demand for water for other purposes is high. Well-designed forest plantations are commonly said to positively influence the hydrological cycle by high infiltration and groundwater recharge during the wet season with a gradual release of water during the dry season (Malmer et al. 2010). The functioning of these artificial forests will largely depend on the tree species planted and species selection offers the opportunity to control tree water use in forest stands (Dierick and Hölscher 2009). The specific regional management goals will define silvicultural practices to promote best possible tree growth, land cover protection or water resource restoration. Mixed species plantations are known to attain a higher basal area in a shorter time period. Accordingly, mixed species plantations have a higher water use than monocultures, because of higher tree sizes of the individual trees. Our study suggest that with increasing species richness mixed species plantations have an enhanced water use rates per unit basal area compared to monocultures mostly due to increasing heterogeneity of the stand structure. This enhanced water use might not be problematic in non seasonal climates or during the wet season when the amount of rainfall is higher than the evaporative demand (Dietrich et al. 1996). Under seasonal climates, we suggest the establishment of suitable species mixtures containing a low number of species, to achieve high growth rates through complementarity of species and to keep water use rates on an acceptable level compared to an average monoculture through creating more homogenous stand structures.

5. Acknowledgements

We thank Sebastian Wolf for providing the micrometeorological data and Jose Monteza for taking good care of the plantation and for collecting data on tree growth. We thank Klaus Winter for advice and Milton Garcia for technical support. This study benefited from the logistical support provided by STRI and ANAM and was funded by the German Research Foundation (Ho-2119/3) and an NSERC operating grant to CP.

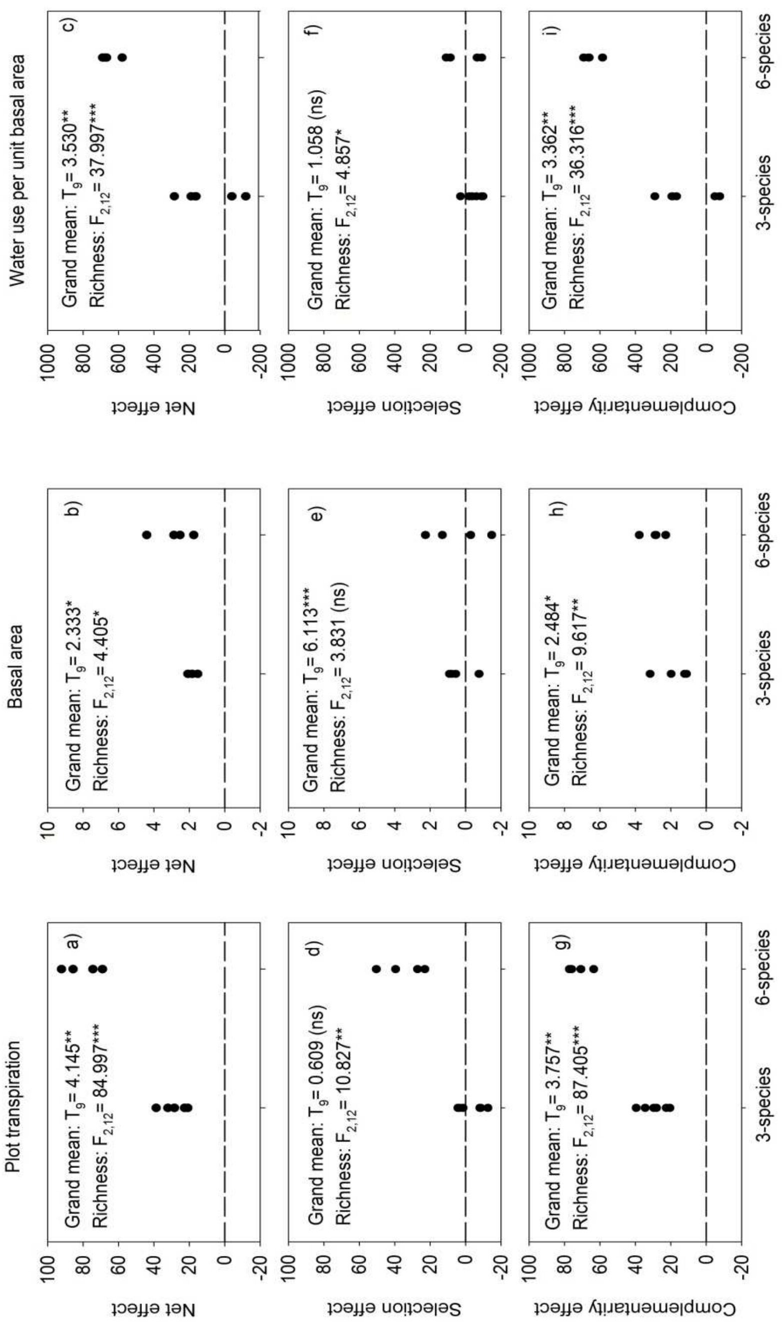


Fig. 8: Addidative partitioning of biodiversity effects (after Loreau and Hector, 2001) a,b,c) Net biodiversity effect; d,e,f) selection effect; and g,h,i) complementarity effect on annual plot level transpiration, basal area and water use rate per unit basal area, respectively. Values of the biodiversity effect, selection and complementarity effect are square-root transformed to meet the assumptions of analyses but preserve the original positive and negative signs (Single asterisk, $p < 0.05$; double asterisk, $p < 0.01$; triple asterisk, $p < 0.001$; ns: non-significant).

7. References

Andrade, J.L., Meinzer, F.C., Goldstein, G., Schnitzer, S.A., 2005. Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest. Trees 19, 282-289.

Baldocchi, D.D., Xu, L., 2007. What limits evaporation from Mediterranean oak woodlands – The supply of moisture in the soil, physiological control by plants or the demand by atmosphere? Adv. Water Res. 30, 2113-2122.

Cienciala, E., Kucera, J., Malmer, A., 2000. Tree sap flow and stand transpiration of two *Acacia mangium* plantations in Sabah, Borneo. J. Hydrol. 236, 109-120.

Cintron, B. B., 1990. *Cedrela odorata* L. Cedro hembra, Spanish cedar. In: Burns, R. M., Honkala, B. H. (Eds.), Silvics of North America: 2. Hardwoods. Agricultural. Handbook. 654. U.S. Department of Agriculture, Forest Service, Washington, DC, pp. 250-257.

Clearwater, J.S.A., M., Meinzer, F.C., Goldstein, G., 2002. Heat dissipation sensors of variable length for measurement of sap flow in trees with deep sapwood. Tree Physiol. 22, 277-283.

Coll, L., Potvin, C., Messier, C., Delagrange, S., 2008. Root architecture and allocation patterns of eight native tropical species with different successional status used in open-grown mixed plantations in Panama. Trees 22, 585-596.

Cunningham, S.A., Kimberi, R.P., Colloff, M.J., 2009. Whole-tree sap flow is substantially diminished by leaf herbivory. Oecologia 158, 633–640.

Davies, W.J., Bacon, M.A., Thomson, D.S., Sobeih, W., Gonzalez, R.L., 2000. Regulation of leaf and fruit growth in plants growing in drying soil: exploitation of the plant's own chemical signaling system and hydraulic architecture to increase the efficiency of water use in agriculture. Journal of Experimental Botany 51, 1617-1626.

Dierick, D., Hölscher, D., 2009. Species-specific tree water use characteristics in reforestation stands in the Philippines. Agric. For. Meteorol. 149, 1317-1326.

Dietrich, W.E., Windsor, M.D., Dunne, T., 1996. Geology, Climate and Hydrology of Barro Colorado Island. In: Leigh, E.G. Jr., Rand, A.S., Windsor, D.M. (Eds.), The Ecology of a Tropical Forest. Seasonal Rhythms and Annual Changes. Second edition. Smithsonian Institution Press, Washington DC, pp. 21-46.

Dünisch, O., Morais, R.R., 2002. Regulation of xylem sap flow in an evergreen, a semi-deciduous, and a deciduous Meliaceae species from the Amazon. Trees 16, 404-416.

Edwards, W.R.N., Becker, P., Cermák, J., 1996. A unified nomenclature for sap flow measurements. Tree Physiol. 17, 65–67.

Flores, E.M., 2003. *Terminalia amazonia* (J.F. Gmel.) Exell. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 748-751.

Flores, E.M., Marín, W.A., 2003. *Tabebuia rosea* (Bertol.) DC. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 737-739.

Fournier, L.A., 2003a. *Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 294-296.

Fournier, L.A., 2003b. *Luehea seemannii* Triana & Planch. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 553-554.

Francis, J.K., 1990. *Hura crepitans* L. Sandbox, molinillo, jabillo. Euphorbiaceae. Spurge family. USDA Forest Service, Southern Forest Experiment Station, Institute of Tropical Forestry. SO-ITF-SM; 38, New Orleans, LA, USA.

Francis, J.K., 2003a. *Acacia mangium* Willd. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 256-258.

Francis, J.K., 2003b. *Tectona grandis* L.f. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 745-747.

Goldstein, G., Andrade, J.L., Meinzer, F.C., Holbrook, N.M., Cavalier, J., Jackson, P., Celis, A., 1998. Stem water storage and diurnal patterns of water use in tropical forest canopy trees. Plant Cell Environ. 21, 397-406.

Granier, A., 1985. A new method of sap flow measurement in tree stems. Ann. For. Sci. 42, 193-200.

Granier, A., 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiol. 3, 309-320.

Hölscher, D., Koch, O., Korn, S., Leuschner, Ch., 2005. Sap flux of five co-occurring tree species in a temperate broad-leaved forest during seasonal soil drought. Trees 19, 628-637.

Holdridge, L.R., Budowski, G., 1956. Report on an ecological survey of the Republic of Panama. The Caribbean Forester 17, 92-109.

Jackson, P.C., Cavelier, J., Goldstein, G., Meinzer, F.C., Holbrook, N.M., 1995. Partitioning of water resources among plants of a lowland tropical forest. Oecologia 101, 197-203.

Jackson, B.J., Jobbagy, E.G., Avissar, R., Roy, S.B., Barrett, D.J., Cook, C.W., Farley, K.A., le Maitre, D.C., McCarl, B.A., Murray, B.C., 2005. Trading water for carbon with biological carbon sequestration. Science 310, 1944-1947.

Kijkar, S., 2003. *Gmelina arborea* Roxb. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 476-478.

Lamb, D., Erskine, P.D., Parrotta, J.A., 2005. Restoration of degraded tropical forest landscapes. Science 310, 1628-1632.

Ma, L., Lu, P., Zhao, P., Roa, X.-Q., Cai, X.A., Zeng, X.P., 2008. Diurnal, daily seasonal and annual patterns of sap-flux-scaled transpiration from an *Acacia mangium* plantation in South China. Ann. For. Sci. 65, 402p1-402p9.

McJannet, D., Fitch, P., Disher, M., Wallace, J., 2007. Measurements of transpiration in four tropical rainforest types of north Queensland, Australia. Hydrol. Process. 21, 3549-3564.

Meinzer, F.C., James, S.A, Goldstein, G., 2004. Dynamics of transpiration, sap flow and use of stored water in tropical forest canopy trees. Tree Physiol. 24, 901-909.

Meinzer, F.C., Bond, B.J., Warren, J.M., Woodruff, D.R., 2005. Does water transport scale universally with tree size? Funct. Ecol. 19, 558-565.

Meinzer, F.C., Andrade, J.L, Goldstein, G., Holbrook, N.M., Cavelier, J., Jackson, P., 1997. Control of transpiration from the upper canopy of a tropical forest, the role of stomatal, boundary layer and hydraulic architecture components. Plant, Cell and Environ. 20, 1242-1252.

Meinzer, F.C., Andrade, J.L., Goldstein, G., Holbrook, N.M., Cavelier, J., Wright, S.J., 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. Oecologia 21, 293-301. O'Grady, A.P., Eamus, D., Hutley, L.B., 1999. Transpiration increases during dry season, patterns of tree water use in eucalypt open-forests of northern Australia. Tree Physiol. 19, 591-597.

Phillips, N., Oren, R., Zimmermann, R., Wright, S.J., 1999. Temporal patterns of water flux in trees and lianas in Panamanian moist forest. Trees 14, 116-123.

Potvin, C., Dutilleul, P., 2009. Neighborhood effects and size-symmetric competition in a tree plantation varying in diversity. Ecology 90, 321–327.

Potvin, C., Whidden, E., Moore, T., 2004. A case study of carbon pools under three different land-uses in Panama. Clim. Change 67, 291-307.

Rocas, A.N., 2003. *Cedrela odorata* L. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 386-389.

Röhle, H., 1986. Vergleichende Untersuchungen zur Ermittlung der Genauigkeit bei der Ablotung von Kronenradien mit dem Dachlot und durch senkrechtes Anvisieren des Kronenrandes. Forstarchiv 57, 67–71.

Schorcht, M., 2000. *Tectona grandis*. In: Schütt, P., Schuck, H.J., Lang, U., Rollof,A. (Eds.), Enzykloppädie der Holzgewächse. Handbuch und Atlas der Dendrologie. Ecomed Verlagsgesellschaft, Landsberg..

STRI, 2009. Temperature and rainfall data Barro Colorado Island, Panama 1987-2007. Online. http://striweb.si.edu/esp/meta_data/details_bci_temp1.html

van Dijk, A.I.J.M., Keenan, R.J., 2007. Planted forests and water in perspective. For. Ecol. Manage. 251, 1-9.

Veldkamp, E., O'Brien, J.J., 2000. Calibration of a FDR sensor for humid tropical soils of volcanic origin. Soil Sci. Soc. Am. J. 64, 1549-1553.

Wishnie, M.H., Dent, D.H., Mariscal, E., Deago, J., Cedeño, N., Ibarra, D., Condit, R., Ashton, P.M.S., 2007. Initial performance and restoration potential of 24 tropical tree species planted across a precipitation gradient in the Republic of Panama. For. Ecol. Manage. 243, 39-49.

Wolf, S., Eugster, W., Buchmann, N., 2008. Micrometeorological measurements of a plantation and adjacent pasture in Sardinilla, Panama. Field Measurements. ETH Zürich, Institute of Plant Sciences. Digital media.

CHAPTER 6

COMPARISON OF TREE WATER USE CHARACTERISTICS IN REFORESTATION AND AGROFORESTRY STANDS ACROSS THE TROPICS

CONTRIBUTION IN: T. TSCHARNTKE, C. LEUSCHNER, E. VELDKAMP, H. FAUST, E. GUHARDJA, A. BIDIN (EDS.), TROPICAL RAINFORESTS AND AGROFORESTS UNDER GLOBAL CHANGE, SPRINGER, BERLIN, PP. 293-308.

Comparison of tree water use characteristics in reforestation and agroforestry stands across the tropics

Diego Dierick*, Norbert Kunert, Michael Köhler, Luitgard Schwendenmann & Dirk Hölscher

Tropical Silviculture and Forest Ecology, Burckhardt Institute, Georg-August-Universität Göttingen, Büsgenweg 1, 37077 Göttingen, Germany

Abstract. In the tropics, reforestations and agroforestry become increasingly important and may help mitigate climate change. However, high water use by trees may deplete water resources for associated crops or other purposes. Choice of tree species might reduce water use rates to acceptable levels, but available information on species-specific water use characteristics is scarce. We addressed the following questions: (1) do species differ in xylem sap flux response to fluctuating environmental conditions, (2) are there species-specific differences in quantities of water used, and specifically (3) do universal rules relating tree size to water use apply? This chapter combines data on tree sap flux and water use gathered in Indonesia, Panama and the Philippines. These studies applied the same methods and were conducted in recently established stands (5-12 years old when studied) characterised by small diameter trees and relatively simple stand structure. We analyse data from more than 100 trees belonging to 17 species using a simple sap flux model. Model application suggests species-specific differences in parameters such as maximal sap flux velocity and responses to radiation and vapour pressure deficit. With respect to the quantity of water used per tree, we observed a strong correlation between tree diameter and tree water use, which confirms earlier publications. However, e.g. in the stands in the Philippines where tree diameter explained 65% of observed variation, some species clearly followed distinct trajectories. For a given diameter, up to twofold differences in tree water use among species were observed. Our findings thus support the idea that species selection can be used to control tree water use of future reforestations and within agroforestry systems. This will be especially relevant in areas where water resources are limited already or where climate scenarios predict decreasing precipitation.

Keywords: Indonesia, Panama, Philippines, sap flux, tree size, tree species

1 Introduction

Natural forests in the tropics are still being converted at a high rate. Many of the former forest areas have been degraded, fail to produce goods and do not contribute to the protection of climate and biodiversity. For the management of buffer zones around remaining protected forests as well as for the restoration of degraded land, reforestation and agroforestry can be suitable measures. The re-introduction of trees into the landscape and especially reforestations have however been criticised because trees are potentially heavy water users and might deplete water resources (Jackson et al. 2005). From a global synthesis it was concluded that annual runoff was on average reduced by 44% and by 31% when reforesting grass- and shrubland, respectively (Farley et al. 2005). Also trees in agroforestry may be problematic as they may reduce

---

In: Teja Tscharntke, Christoph Leuschner, Edzo Veldkamp, Heiko Faust, Edi Guhardja, Arifuddin Bidin (editors), tropical rainforests and agroforests under global change, Springer Berlin 2009, pp 293-308.

* Corresponding author. Tel.: +49 551 399556; Fax: +49 551 394019; E-mail address: ddieric@gwdg.de (D. Dierick)

water availability for the main crops and additionally increase stand level transpiration. In Costa Rica, the estimated stand level transpiration by coffee with shade trees was on average twice as high as that of coffee grown without shade trees (van Kanten and Vaast 2006).

It has been suggested that a suitable tree species choice might reduce water use rates to acceptable levels (van Dijk and Keenan 2007). This contention is somewhat theoretical as available information on species-specific water use characteristics is scarce. Furthermore, the effectiveness of species selection is questionable as studies in diverse old-growth forests and a single-species tree plantation showed repeatedly that tree size is the main factor influencing tree water use (Cienciala et al. 2000; Meinzer et al. 2004; McJannet et al. 2007). Meinzer et al. (2005) suggested that, as a result of functional convergence, plants operating within given biophysical limitations, develop common patterns of sap flux and water use in relation to size characteristics across taxa. This would leave little room for species selection to serve as a tool to influence stand water use, at least if wood production or carbon fixation is a major goal.

A thorough analysis of the problem is difficult as single studies of sap flux and tree water use often lack sufficient replicates within a species and/or analyse a limited number of species. Comparison among studies is additionally hampered by differences in applied methods. Here we bring together data from three case studies namely from the Philippines (Dierick and Hölscher 2009), Indonesia (Köhler et al. in press) and Panama (Kunert, unpublished data), which were conducted in relatively young reforestation and agroforestry stands. Our compilation comprises 106 individual trees belonging to 17 species, which were studied and analysed using the same protocol. In this data compilation, we concentrate on time periods with ample soil water supply and on trees fully in leaves. As a diagnostic tool, we apply a model that predicts sap flux density based on meteorological parameters. The following questions were addressed: (1) do species differ in xylem sap flux response to fluctuating environmental conditions, (2) are there species-specific differences in quantities of water used, and specifically (3) do universal rules relating tree size to water use apply?

2 Methods

2.1 Study sites

In the Philippines, we worked on the island Leyte in the Eastern Visayas. Two study sites were located near the villages Marcos (10.765°N, 124.790°E) and Patag (10.736°N, 124.804°E) at an elevation of 30 and 40 m asl, respectively. Average rainfall in the region amounts to 2753 mm y^{-1} and rain is relatively evenly distributed throughout the year (PAGASA 2007). Average annual air temperature is 27.5 °C. The natural vegetation in the region is species-rich lowland dipterocarp forest (Langenberger 2006). After deforestation and intermittent cultivation, the degraded sites were reforested following the so called 'rainforestation' approach (Margraf and Milan 1996). This means reforesting with a mixture of native species, promoting the incorporation of fruit trees and combining fast growing trees with shade tolerant species. At the time of the field study, from June to August 2006 at Marcos and July to September 2007 at Patag, both stands were 12 years old. Stem density was 796 and 1367 stems ha^{-1} in Marcos and Patag, respectively. We selected ten tree species, eight of which were native to the region (Table 1). Each species was represented by five individuals selected to have well exposed crowns. Only for *Hopea plagata* S. Vidal, a species with an in general smaller stature, some individuals had little exposed crowns.

In Indonesia, our study site was located in Central Sulawesi in the vicinity of the village of Marena (1.552°S, 120.020°E) at 560 m asl. Measurements made between 2002 and 2006 at Gimpu (5 km south of Marena, 471 m asl) show that the mean air temperature is 25.5 °C and annual rainfall in the region is around 2092 mm y^{-1}. Rainfall shows a weak bimodal pattern with rainy seasons (>100 mm per month) from March to June and October to December. The structure and species composition of surrounding natural forest, which is usually only remaining at higher elevations, was described by Gradstein et al. (2007). The studied agroforest was located on former agricultural land used for cultivating annual crops such as maize and was 6 years old at the time of study. Cacao (*Theobroma cacao* L.) was growing as crop under *Gliricidia sepium* (Jacq.) Kunth ex Steud. shade trees. The stem density was 1030 stems ha^{-1} for cacao and 325 stems ha^{-1} for *Gliricidia*. Both tree species were represented by 18 individuals and studied for a one-month period in February 2007.

Table 1: Characteristics of the study trees. Scientific names are listed with the respective abbreviations used.

Species abbreviation and scientific name		Family	Study Location	Native or Exotic	Trees studied	DBH (cm)		Tree height (m)		Crown area (m^2)	
				(-)	(n)	Mean	SD	Mean	SD	Mean	SD
Sc	*Shorea contorta* S. Vidal	Dipterocarpaceae	Philippines	N	5	18.2	7.0	16.1	3.5	14.4	11.7
Pm	*Parashorea malaanonan* Merr.	Dipterocarpaceae	Philippines	N	5	12.0	0.4	13.1	1.6	12.9	3.1
Hm	*Hopea malibato* Foxw.	Dipterocarpaceae	Philippines	N	5	11.6	2.4	13.3	1.8	10.4	6.0
Hp	*Hopea plagata* S. Vidal	Dipterocarpaceae	Philippines	N	5	6.6	1.0	9.4	1.2	6.7	1.0
Sm	*Swietenia macrophylla* King	Meliaceae	Philippines	E	5	14.6	1.3	14.2	1.5	14.5	6.4
Vp	*Vitex parviflora* A. L. Juss	Verbenaceae	Philippines	N	5	20.4	5.5	12.7	1.6	33.2	15.8
Mj	*Myrica javanica* Blume.	Myricaceae	Philippines	N	5	22.1	3.7	11.2	0.6	25.5	11.6
Sk	*Sandoricum koetjape* (Burmf.) Merr.	Meliaceae	Philippines	N	5	16.3	2.7	13.2	1.1	18.0	5.0
Dz	*Durio zibethinus* Murray	Bombacaceae	Philippines	N	5	19.8	7.3	13.8	3.0	34.1	22.6
Ga	*Gmelina arborea* Roxb.	Verbenaceae	Philippines	E	5	21.9	4.0	18.1	2.4	18.6	9.5
Tc	*Theobroma cacao* L.	Malvaceae	Indonesia	E	18	10.1	1.6	4.5	0.8	23.4	9.7
Gs	*Gliricidia sepium* (Jacq.) Kunth ex Steud.	Fabaceae	Indonesia	E	18	15.0	2.5	10.9	2.1	47.3	31.5
Ls	*Luehea seemannii* Triana & Planch	Tiliaceae	Panama	N	4	11.8	1.6	8.7	1.0	11.9	1.7
Ae	*Anacardium excelsum* Beberto & Balb. ex Kunth	Anacardiaceae	Panama	N	4	10.1	0.6	6.4	0.4	9.4	5.1
Hc	*Hura crepitans* L.	Euphorbiaceae	Panama	N	4	18.0	2.3	5.4	1.0	13.7	4.7
Co	*Cedrela odorata* L.	Meliaceae	Panama	N	4	12.0	0.6	11.7	11.1	9.7	4.0
Tr	*Tabebuia rosea* (Bertol) DC	Bignoniaceae	Panama	N	4	11.5	1.3	7.4	0.3	13.4	2.1

Our site in Panama was located near the village of Sardinilla, Central Panama (9.317°N, 79.633°W), which is approximately 50 km north of Panama City. The elevation of the site is 70 m asl. Mean annual precipitation measured at Barro Colorado Island (at 30 km distance) is 2627 mm, with 25-50 mm per month during peak dry season (January-March) and 250 mm per month during the rainy season (May to November). The mean annual temperature of the region is 25.9 °C (STRI 2009). The original forest vegetation at the Sardinilla site was probably a tropical moist forest, similar to that of the Barro Colorado National Monument (Leigh et al. 1996). The study site was clear-cut in the 1950's and later used for cattle ranging. At the time of our study, the stands were 6 years old and stem density was about 1100 stems ha^{-1}. Five tree species growing in monocultures were studied with four replicates each during the rainy season between June and September 2007.

2.2 Sap flux measurements

Sap flux density J$_s$ (g cm^{-2} h^{-1}) was measured using 25 mm long thermal dissipation probes (Granier 1985). Per study tree, two sensor pairs were installed on opposite sides of the tree trunk in the outermost xylem. Sensors were shielded and protected by styrofoam boxes, reflective foil, and plastic foil. The thermocouple output from the thermal dissipation probes was measured every 30 seconds and 5 or 30 minute averages were stored using dataloggers and attached multiplexers (CR1000 and AM16/32, Campbell Scientific Inc., Logan, UT, USA). Sap flux density was calculated from raw temperature data using the calibration equation determined by Granier (1987).

2.3 Radial sap-flux profiles and water use rates

Radial profiles of sap flux density J$_s$ were used to determine tree water use. Therefore J$_s$ was measured at one or two additional depths below the cambium and expressed relatively (%) to concurrent measurements at the outer reference depth. Sap flow of ring-shaped stem cross-sections was then calculated, taking into account the cross-sectional area of the ring corresponding with the respective installation depth, J$_s$ as measured at reference depth at the outer xylem, and the normalised profile of J$_s$ for the species considered (Hatton et al. 1990; Meinzer et al. 2005). Contributions of the different cross sections were added to determine total tree sap flow (g h^{-1}) and summed over a day to give daily tree water use rates WU (kg d^{-1}). Water use rates were also expressed as transpiration rates (T, mm d^{-1}) by dividing WU by the crown projection area of the respective tree (m^2).

2.4 Sap flux density model

We used a model to capture species characteristics of sap flux density and its responses to environmental conditions in analogy with work of O'Brien et al. (2004). The sap flux model used is a modification of the Jarvis-type model (Jarvis 1976) which was originally developed to describe stomatal responses to environmental drivers. The model takes the form of a multiplication of non-linear response functions, each depending on a single environmental factor. Each individual response function takes a value between zero and one, thus limiting the overall response if one or more environmental factors become suboptimal. The fact that environmental variables appear isolated in the model enhances the interpretation of model parameters. This multiplicative type of model has been widely used in a number of variations to describe canopy conductance (Herbst et al. 1999; Granier et al. 2000; Harris et al. 2004), stand transpiration (Oren and Pataki 2001; Whitley et al. 2008) and to describe sap flow patterns in individual trees (Cienciala et al. 2000).

We opted for a sap flux density model with radiation R_g (W m^{-2}) and vapour pressure deficit VPD (kPa) as explanatory variables. Additional factors such as soil moisture conditions were not included because a preliminary exploration of the data indicated that this would not improve model fit much. The model form used was:

$$J_{s\,\mathrm{model}} = a\frac{R_g}{b+R_g}\frac{1}{1+\exp^{\frac{c-VPD}{d}}}$$

with $J_{s\ model}$ the modeled sap flux density (g cm^{-2} h^{-1}), a the maximum modeled sap flux density (g cm^{-2} h^{-1}), b a parameter describing R_g response(W m^{-2}) and c, d parameters describing the VPD response (kPa).

Modeled sap flux density $J_{s\ model}$ reaches a maximum value a when all environmental conditions are optimal. To account for the influence of radiation we introduced a commonly used hyperbolic response function which asymptotically approaches a value of 1 at high R_g. Parameter b can be interpreted as a measure of the light saturation level. Assuming VPD is non-limiting, the sap flux reaches just over 90% of *a* if radiation levels equal ten times parameter *b*. The response function used to describe the influence of VPD was taken from O'Brien et al. (2004). In this response function parameter *c* equals the vapour pressure deficit for which $J_{s\ model}$ rises to half of the maximum value (R_g non-limiting), whereas *d* is related to the slope i.e. the increase in $J_{s\ model}$ for a given increase in VPD. Model parameters *a*, *b*, *c* and *d* in the response functions were estimated by minimising the residual sum of squares using a Gauss-Newton algorithm.

2.5 Statistical analyses

Although the model is nonlinear we calculated an adjusted R^2 in analogy with linear models. Root mean square error (RMSE) is used to characterize model prediction error. When an analysis of variance indicated a significant effect of tree species on a model parameter of interest, a post-hoc Tukey HSD test was carried out to assign species to statistically different groups. The relationships between maximum tree water use rates and tree diameter were established by simple linear regression. All statistical analyses were performed with R version 2.6.2 (R Development Core Team 2008).

3 Results and discussion

3.1 Sap flux densities and environmental controls

Maximum sap flux densities between 13.2 and 52.1 g cm^{-2} h^{-1} were observed in the course of this study. This is in line with values published for tropical forest tree species which are mostly situated between 5 and 50 g cm^{-2} h^{-1} (Granier et al. 1996; Meinzer et al. 2001; Dünisch and Morais 2002), although values of up to 70 g cm^{-2} h^{-1} have been reported (Becker 1996; O'Brien et al. 2004).

Performance of the model describing sap flux density was quite satisfying, which is illustrated by high R^2_{adj} values for almost all study trees (R^2_{adj} ranged from 0.62 to 0.97, average 0.92) and low root mean square errors (RMSE, range 0.8 to 6.9, average 2.0 g cm^{-2} h^{-2}). A visual impression of the agreement between modelled and measured sap fluxes is given for a representative cacao tree in Indonesia (Fig. 1). Model performance suggests that the model form was appropriate and that vapour pressure deficit and radiation indeed exerted strong influence on sap flux of the trees in the study periods. We acknowledge that at other times of the year this could be different. Especially when rainfall is limited, soil moisture could become more influential as an explanatory variable and the need may arise to include it in the model. In particular under seasonal climatic conditions such as at our Panamanian site, this is expected to be the case. For the three study sites combined, the model parameter *a* differed threefold among species (14.4 g cm^{-2} h^{-1} for *Vitex parviflora* A. L. Juss and 47.2 g cm^{-2} h^{-1} for *Anacardium excelsum* Beberto & Balb. ex Kunth) and accurately reflected measured maximal sap flux densities in studied species. Within each of the three study sites significant species-specific differences were observed (Fig. 2). Model parameter *b*, which describes the sap flux response to radiation, differed among species at the Philippine and the Indonesian site, but not among the five species studied in Panama.

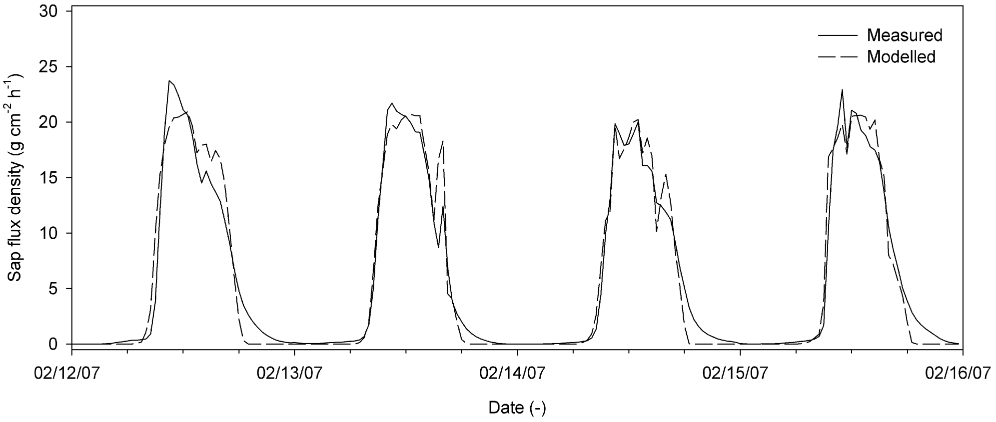


Fig. 1: Measured and modelled sap flux in a selected cacao tree (*Theobroma cacao*) for four days in February 2007, Indonesia. Note that the model form is such that modelled sap flux at night is set to zero.

High values for parameter *b* were found in species which did not have full sun exposed crowns such as *Hopea plagata* in the Philippines and *Theobroma cacao* in Indonesia. A possible explanation is that in trees growing under shade or having a layered crown structure sap flux continues to rise with additional light even at high radiation.

3.2 Sap flux density in relation to tree size

At first view our data suggests, despite a very low R^2_{adj}, a negative relation between maximum sap flux density J_{smax} and tree diameter (Fig. 3). This finding is explained by the significant decline in sap flux density with increasing diameter we observed in the dataset from Indonesia (Fig. 3 inset). Rather than by a real effect of diameter on J_{smax}, the latter is caused by the different diameter range of sampled cacao and *Gliricidia* trees in combination with the different sap flux densities observed for these species. The complete lack of a diameter-related decline of sap flux density with diameter at the two other study sites supports this interpretation. The absence of a decline of sap flux density with diameter apparently contradicts the hypothesis of functional convergence (Meinzer et al. 2001; Meinzer et al. 2005). Their work in Panama revealed a strong inverse relationship ($R^2 = 0.85$) between maximum sap flux density and tree diameter in 24 co-occurring species in a Panamanian old-growth forest. Similarly, in a patch of advanced secondary forest in Vietnam, a weak but significant ($R^2 = 0.23$) decline of mean J_s with tree diameter existed (Giambelluca et al. 2003). At the same time however, that study acknowledged the presence of large differences in J_s across and within species and the decisive role of factors such as tree exposure and environmental conditions. That our data did not reveal a similar pattern of declining J_{smax} with tree diameter could be due to the limited diameter range encompassed in comparison with the original work (Meinzer et al. 2001). The data presented by Meinzer et al. (2001) revealed considerable scatter, in particular in the lower diameter range where the steepest decline in J_{smax}

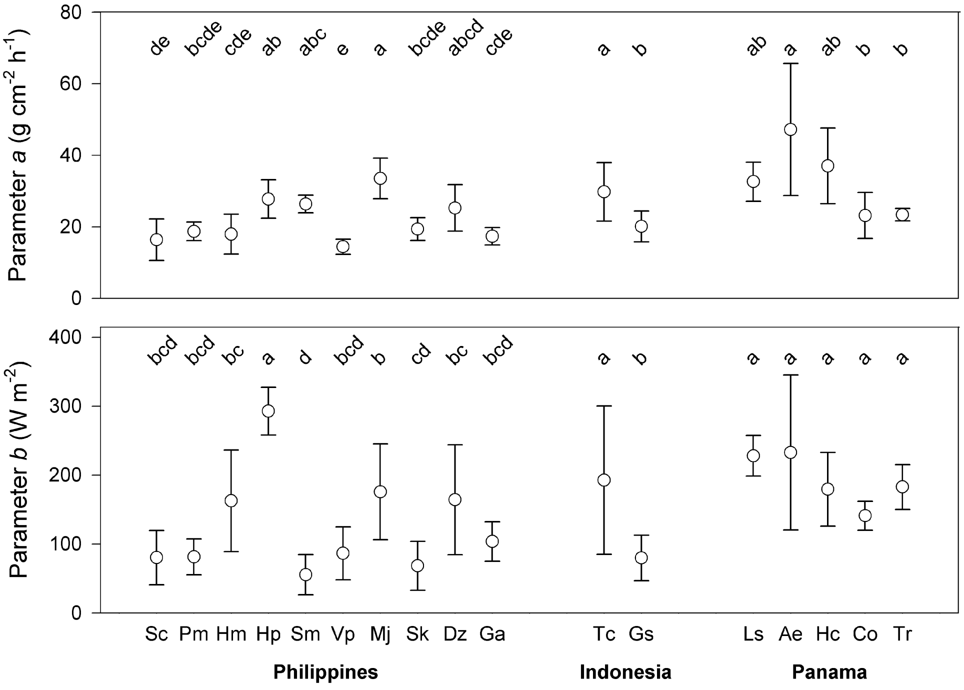


Fig. 2: Estimated model parameters *a* (upper panel) and *b* (lower panel) for the species studied (means and standard deviations, n depends on study site (see Table 1)). Significant differences ($p < 0.05$) between species within a study site are indicated by different small letters. The complete species names and abbreviations are listed in Table 1.

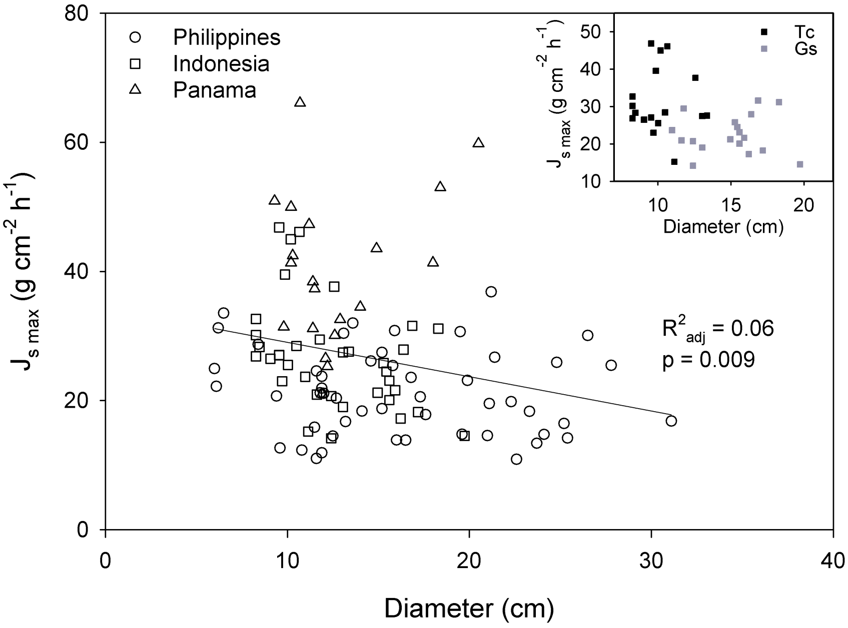


Fig. 3: Maximum sap flux density $J_{s\ max}$ for individual trees in the three studies in relation to tree diameter. The inset shows the data from the Indonesian study site

is predicted. A possible implication is that general patterns resulting from functional convergence may remain unnoticed if the range of tree diameters covered is too narrow. In our opinion the species differences we observed in $J_{s\ max}$ and responses of J_s to environmental variables do not necessarily contradict the hypothesis of functional convergence (Meinzer 2003). We hypothesise that this finding merely reflects that considerable variation remains within general patterns observed across species. This can in part be due to species-specific adaptation to a given set of growth conditions and possibly also due to stand structural differences (see also Cienciala et al. 2000).

In stands where functional convergence can be demonstrated, it would be an essential tool in assessing stand transpiration. This is particularly true in species-rich and highly structured natural forest stands (McJannet et al. 2007). However, we argue functional convergence to be less relevant in relatively young mixed reforestation or agroforest stands characterised by limited diameter ranges and stand structure. In our opinion the species-specific differences in sap flux density we observed in co-occurring trees would become relatively more important under such conditions and become a determining factor for stand water use.

3.3 Tree water use, tree diameter, and transpiration

Our data revealed a strong positive correlation between maximum daily tree water use and tree diameter (Fig. 4a). This is true for the pooled data, as well as for data from the individual study sites (Fig. 4b-d). Also Meinzer et al. (2004) found for different co-occurring species in Panama, that tree size rather than tree species was a determining factor for tree water use. Follow-up studies encompassing more species and replicates revealed similar allometric relationships between tree water use rates and tree diameter (and biomass) that were shared by species belonging to distinct species groups (Meinzer et al. 2005). The relation between tree water use and tree diameter was best described by a sigmoid relationship in 18 mainly tropical angiosperm tree species. That a simple linear regression between tree diameter and tree water use explains most of the variance in our data set, should be seen in relation to the small diameter range covered. Some theoretical relationships describing water use versus tree size characteristics might be inappropriate from a biological point of view, even though they provide an adequate fit in certain datasets (Meinzer et al. 2005). The same appears to be the case in our study.

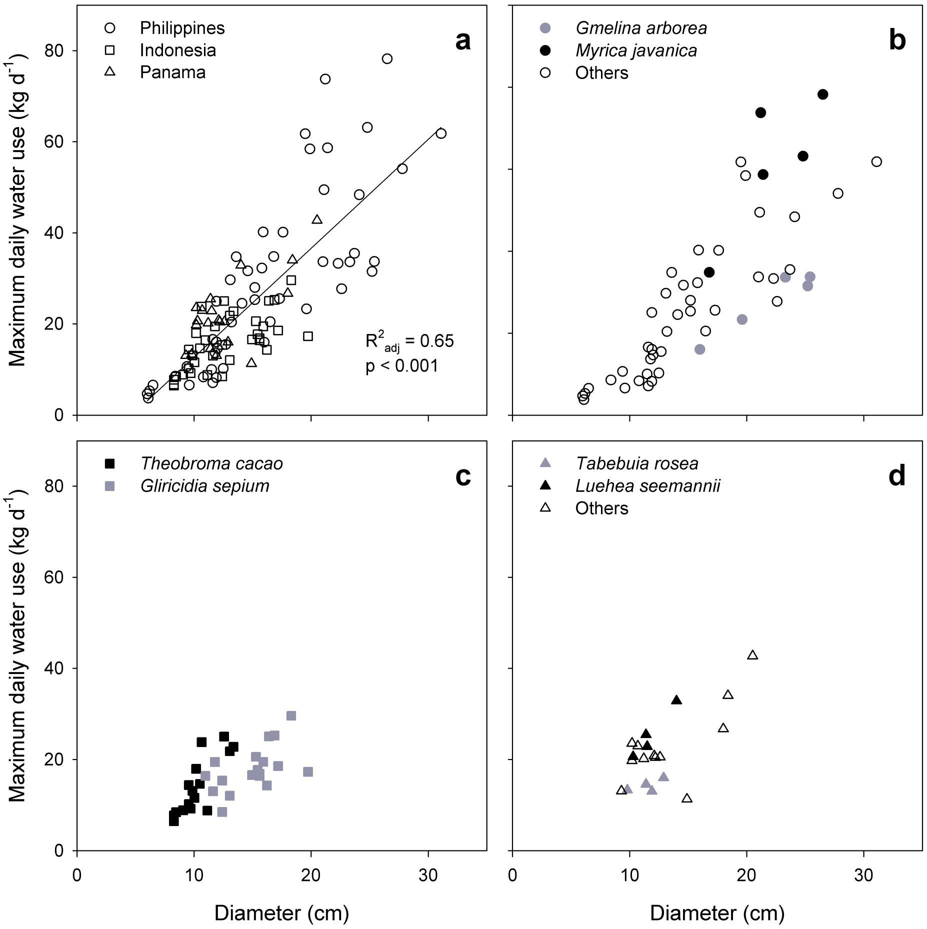


Fig. 4: Maximum daily water use rates WU_{max} for each individual in relation to tree diameter for all studied trees (a). Analogue plots show the data for species in the Philippines (b), Indonesia (c) and Panama (d). In each of the latter graphs two contrasting species are shown with a different symbol.

Despite the strong dependence of maximum water use on diameter for the individuals studied, considerable scatter was present around the fitted curve with species located on distinct trajectories (Fig. 4b-d). For a given tree diameter, tree water use differed up to twofold between some of the species studied. This resulted from a combination of both species-specific J_s and species differences in hydroactive xylem depth. Apart from these factors, the relationship would be determined strongly by cross correlation between estimated water use rates and tree diameter. This can be expected to be most pronounced in the lower diameter ranges (Meinzer et al. 2001), making the deviations from a common relationship even more significant. Maximum transpiration rates observed in individual trees varied from 0.4 to 4.9 mm d^{-1}, except for a single individual of *Swietenia macrophylla* King which had a maximum transpiration rate of 7.5 mm d^{-1}. A small crown projection area and associated larger relative error in this individual could explain the high value. Excluding this single tree, results are comparable with findings from Giambelluca et al. (2003) who measured daily transpiration rates in individual trees from 0.5 to 4.6 mm d^{-1} in a patch of advanced secondary forest in Vietnam during the wet season. In our study, mean transpiration rates over the study periods differed fourfold across species from 0.6 to 2.4 mm d^{-1} (Table 2). For the mentioned study in a forest patch in Vietnam, transpiration rates were also found to be different among species and were, in addition, influenced by crown exposure, seasonality and enhanced transpiration at the forest edge (Giambelluca et al. 2003). It is unlikely that differences in transpiration rates observed between species can be

Table 2: Maximum (WU_{max}) and mean water use (WU_{mean}) and maximum (T_{max}) and mean (T_{mean}) transpiration rates (means and standard deviations, n depends on study site (see Table 1)). Significant differences ($p < 0.05$) are indicated by different small letters.

Species	WU_{max} (kg d^{-1})		WU_{mean} (kg d^{-1})		T_{max} (mm d^{-1})			T_{mean} (mm d^{-1})		
	Mean	SD	Mean	SD	Mean		SD	Mean		SD
Shorea contorta	25.6	19.5	18.4	14.4	2.03	abcd	0.93	1.45	abc	0.70
Parashorea malaanonan	15.3	1.2	10.6	1.1	1.24	bcd	0.28	0.85	bc	0.17
Hopea malibato	13.1	8.5	9.1	6.7	1.33	bcd	0.43	0.89	bc	0.29
Hopea plagata	5.7	1.9	4.0	1.3	0.85	cd	0.18	0.59	bc	0.12
Swietenia macrophylla	33.7	4.1	25.5	3.6	3.14	a	2.46	2.38	a	1.90
Vitex parviflora	30.7	14.6	20.7	9.3	1.02	bcd	0.32	0.69	bc	0.20
Myrica javanica	61.7	17.0	43.2	12.5	2.60	ab	0.60	1.80	ab	0.38
Sandoricum koetjape	32.8	16.5	23.4	12.6	1.90	abcd	0.98	1.36	abc	0.77
Durio zibethinus	44.7	18.5	32.9	14.8	1.52	abcd	0.81	1.11	bc	0.62
Gmelina arborea	27.6	7.8	19.8	6.1	1.67	abcd	0.46	1.18	abc	0.32
Theobroma cacao	13.4	6.2	10.0	4.5	0.63	cd	0.35	0.47	c	0.25
Gliricidia sepium	17.9	5.0	13.9	4.1	0.54	d	0.36	0.42	c	0.28
Luehea seemannii	25.5	5.3	13.1	3.6	2.14	abcd	0.26	1.11	bc	0.22
Anacardium excelsum	19.8	4.8	10.5	2.8	2.64	ab	1.58	1.37	abc	0.79
Hura crepitans	28.7	13.3	14.6	7.6	2.01	abcd	0.38	1.01	bc	0.23
Cedrela odorata	20.5	0.3	9.9	2.2	2.34	abc	0.74	1.09	bc	0.29
Tabebuia rosea	14.2	1.4	7.9	0.6	1.09	bcd	0.27	0.60	bc	0.11

translated directly to transpiration at the stand level as different stand development and stand structure of contrasting species (or species mixtures) are likely to partly reduce species-specific transpiration rates. Nevertheless, we assume that the remarkable differences across tree species in both tree water use and tree transpiration rates could be exploited to manage stand water use.

4 Conclusions

We conclude that water use- and transpiration rates found in trees of tropical reforestation and agroforestry stands showed considerable variation across species. Despite the strong dependence of maximal tree water use on tree diameter for the individuals studied, considerable scatter was present around the fitted curve with species located on distinct trajectories. At a given diameter, up to twofold differences between trees of different species were observed. Species selection might thus indeed be an effective tool to control water use in reforestation and agroforestry. It can be used to optimise the balance between wood production or carbon sequestration and the use of water resources.

Acknowledgements

This study was funded by the German Research Foundation in the framework of the SFB 552 (sub-project B4) and a further grant for the study in Panama (Ho-2119/3-1).

References

Becker P (1996) Sap flow in Bornean heath and dipterocarp forest trees during wet and dry periods. Tree Physiology 16: 295-299

Cienciala E, Kucera J, Malmer A (2000) Tree sap flow and stand transpiration of two Acacia mangium plantations in Sabah, Borneo. Journal of Hydrology 236: 109-120

Dierick D, Hölscher D (2009) Species-specific tree water use characteristics in reforestation stands in the Philippines. Agricultural and Forest Meteorology 149: 1317-1326

Dünisch O, Morais RR (2002) Regulation of xylem sap flow in an evergreen, a semi-deciduous, and a deciduous Meliaceae species from the Amazon. Trees-Structure and Function 16: 404-416

Farley KA, Jobbagy EG, Jackson RB (2005) Effects of afforestation on water yield: a global synthesis with implications for policy. Global Change Biology 11: 1565-1576

Giambelluca TW, Ziegler AD, Nullet MA, Truong DM, Tran LT (2003) Transpiration in a small tropical forest patch. Agricultural and Forest Meteorology 117: 1-22

Gradstein SR, Kessler M, Pitopang R (2007) Tree species diversity relative to human land uses in tropical rain forest margins in Central Sulawesi. In: Tscharntke T, Leuschner C, Guhardja E, Zeller M (Eds.), The Stability of Tropical Rainforest Margins: Linking Ecological, Economic and Social Constraints of Land Use and Conservation. Springer, Berlin, p. 321-334

Granier A (1985) A new method of sap flow measurement in tree stems. Annals of Forest Science 42: 193-200

Granier A (1987) Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiology 3: 309-319

Granier A, Huc R, Barigah ST (1996) Transpiration of natural rain forest and its dependence on climatic factors. Agricultural and Forest Meteorology 78: 19-29

Granier A, Loustau D, Breda N (2000) A generic model of forest canopy conductance dependent on climate, soil water availability and leaf area index. Annals of Forest Science 57: 755-765

Harris PP, Huntingford C, Cox PM, Gash JHC, Malhi Y (2004) Effects of soil moisture on canopy conductance of Amazonian rainforest. Agricultural and Forest Meteorology 122: 215-227

Hatton TJ, Catchpole EA, Vertessy RA (1990) Integration of sapflow velocity to estimate plant water-use. Tree Physiology 6: 201-209

Herbst M, Eschenbach C, Kappen L (1999) Water use in neighbouring stands of beech (Fagus sylvatica L.) and black alder (Alnus glutinosa (L.) Gaertn.). Annals of Forest Science 56: 107-120

Jackson BJ, Jobbagy EG, Avissar R, Roy SB, Barrett DJ, Cook CW, Farley KA, le Maitre DC, McCarl BA, Murray BC (2005) Trading water for carbon with biological carbon sequestration. Science 310: 1944-1947

Jarvis PG (1976) The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. Philosophical Transactions of the Royal Society of London B- Biological Sciences 273: 593-610

Köhler M, Dierick D, Schwendennman L, Hölscher D (in press, DOI: 10.1002/eco.67) Water use characteristics of cacao and Gliricidia trees in an agroforest in Central Sulawesi, Indonesia. Ecohydrology

Langenberger G (2006) Habitat distribution of dipterocarp species in the Leyte Cordillera: an indicator for species-site suitability in local reforestation programs. Annals of Forest Science 63: 149-156

Leigh EG, Rand AS, Windsor DW (1996) The ecology of a tropical forest, 2nd edn, Smithsonian Press, Washington, DC

Margraf J, Milan PP (1996) Ecology of dipterocarp forests and its relevance for island rehabilitation in Leyte, Philippines. In: Schulte A, Schöne D (Eds.), Dipterocarp Forest Ecosystems: Towards Sustainable Management. World Scientific, Singapore, p. 124-154

McJannet D, Fitch P, Disher M, Wallace J (2007) Measurements of transpiration in four tropical rainforest types of north Queensland, Australia. Hydrological Processes 21: 3549-3564

Meinzer FC (2003) Functional convergence in plant responses to the environment. Oecologia 134: 1-11

Meinzer FC, Goldstein G, Andrade JL (2001) Regulation of water flux through tropical forest canopy trees: Do universal rules apply? Tree Physiology 21: 19-26

Meinzer FC, James SA, Goldstein G (2004) Dynamics of transpiration, sap flow and use of stored water in tropical forest canopy trees. Tree Physiology 24: 901-909

Meinzer FC, Bond BJ, Warren JM, Woodruff DR (2005) Does water transport scale universally with tree size? Functional Ecology 19: 558-565

O'Brien JJ, Oberbauer SF, Clark DB (2004) Whole tree xylem sap flow responses to multiple environmental variables in a wet tropical forest. Plant, Cell and Environment 27: 551-567

Oren R, Pataki DE (2001) Transpiration in response to variation in microclimate and soil moisture in southeastern deciduous forests. Oecologia 127: 549-559

PAGASA (2007) Philippine Atmospheric, Geophysical and Astronomical Services Administration, Philippines.

R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0,http://www.R-project.org (last visited 28/05/2009)

STRI (2009) Temperature and rainfall data Barro Colorado Island, Panama 1987-2006. http://striweb.si.edu/esp/physical_monitoring/download_bci.htm (last visited 28/05/2009)

Van Dijk AIJM, Keenan RJ (2007) Planted forests and water in perspective. Forest Ecology and Management 251: 1-9

Van Kanten R, Vaast P (2006) Transpiration of arabica coffee and associated shade tree species in sub-optimal, low-altitude conditions of Costa Rica. Agroforestry Systems 67: 187-202

Whitley R, Zeppel M, Armstrong N, Macinnis-Ng C, Yunusa I, Eamus D (2008) A modified Jarvis-Stewart model for predicting stand-scale transpiration of an Australian native forest. Plant and Soil 305: 35-47

CHAPTER 7

CONCLUSIONS

CONCLUSIONS

Various reasons exist for enforcing reforestation in the tropics. In the past, land has been reforested mainly for wood production, to reduce erosion, sustain soil fertility, improve quality and quantity of water supply, and for socioeconomic and conservation benefits. Recently reforestation has gained value through carbon sequestration as a potential measure to mitigate climate change. One major concern is that tree planting results in a strongly reduced streamflow after reforesting deforested land. Hence reforestation can be critical in regions where water resources are at least seasonally scarce and demand for water for other purposes is high. Well-designed forest plantations are frequently said to positively influence the hydrological cycle by high infiltration and groundwater recharge during the wet season with a gradual release of water during the dry season.

This dissertation presented three studies on water use characteristics of trees growing in different forest management systems and at different locations in the tropics. Being separate studies each of them had their specific research objectives and placed different emphases when looking into species specific tree water use or water use on plot level. Despite this, some overall conclusions can be drawn which are of importance when discussing the options to control water use from tree plantations or other man made forest stands by means of species selection and species combination. The specific regional management goals will define silvicultural practices to promote best possible tree growth, land cover protection, conservation of biodiversity or water resource restoration. The functioning of these artificial forests will largely depend on the tree species planted.

The commonly found water use and diameter relation was present in all study sites and land use systems, but was not as strong as the reported relation in natural forests. The observed tree species show the tendency to differ in daily tree water uses in the same diameter class and considerable scatter was present around the fitted curve with species located on distinct trajectories. At a given diameter, up to twofold differences between trees of different species were observed. Species selection might thus indeed be an effective tool to control water use in reforestation and agroforestry. Under seasonal climate the difference was even more pronounced when dry season values were considered. The strong differences of species under seasonal climate were mostly due to specific differences in leaf phenology and had a large influence on the annual course of tree water use and tree transpiration. Leaf phenological and water use differences may go along with different rooting patterns and soil water uptake depths.

The results from this study are confirming the findings of other multispecies reforestation experiments, which are pointing out that tropical plantations containing higher tree diversity are likely to be more productive than the average monospecific stand. The mixed species plots attained higher basal area and hence had a higher yield than monocultures. Accordingly, mixed species plantations were using a higher amount of water than monocultures. Nevertheless mixed species plots have enhanced water use rates per unit basal area compared to monocultures. However, significant higher water use rates were only observed during the wet season when the amount of rainfall was higher than the evaporative demand and high rates of surface run off may occur. In the dry season when soil water resources were limited, mean daily transpiration rates of the mixed species plots did not significantly increase compared to monocultures. The enhanced wet season water use in mixed plantations may not be evaluated negative because water is highly available anyways. The strong effects of tree diversity on plot level transpiration, basal area and water use per unit basal area were due to complementary use of resources. Differences in stand structural characteristics such as improved three-dimensional crown and root differentiation and canopy roughness must be responsible for the enhanced transpiration rates in the mixtures.

As overall conclusion it can be said that water use- and transpiration rates found in trees of tropical reforestation and agroforestry stands showed considerable variation across species. Under seasonal climate tree phenology can be an important tool to slow down transpiration rates during periods of water limitation. The establishment of mixed species plantations enhances the performance of tree growth and transpiration. Tree species selection and combination can be used to optimize the balance between wood production or carbon sequestration and the use of water resources. It is beyond question that mixed species plantations are more productive in biomass accumulation and can help to conserve biodiversity.

REFERENCES

Abraham, M., 2004. Spatial variation in soil organic carbon and stable isotope signature in a pasture and a primary forest in Central Panama. Masters Thesis, University of McGill, Montréal.

ANAM, 2008. Plan Nacional de Desarrollo Forestal: Modelo forestal sostenible. Dirección de Gestión Integrada de Cuencas Hidrográficas, Departamento de Desarrollo y Manejo Forestal. Autoridad Nacional del Ambiente. República de Panamá. p 24.

Andrade, J.L., Meinzer, F.C., Goldstein, G., Schnitzer, S.A., 2005. Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest. Trees 19, 282-289.

Baldocchi, D.D., 2005. The role of bidodiversity on the evaporation of forests. In Scherer-Lorenzen, M., Körner, C., Schulze, E.D. (Eds), Forest diversity and function. Temperate and boreal systems. Ecological Studies 176. Springer Verlag, Berlin Heidelberg, pp.131-148.

Baldocchi, D.D., Xu, L., 2007. What limits evaporation from Mediterranean oak woodlands – The supply of moisture in the soil, physiological control by plants or the demand by atmosphere? Adv. Water Res. 30, 2113-2122.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D., Schmid, B., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecol. Lett. 9, 1146–1156.

Bauhus, J., van Winden, A.P., Nicotra, A.B., 2004. Aboveground interactions and productivity in mixed-species plantations of Acacia mearnsii and Eucalyptus globulus Can. J. For. Res. 34, 686–694.

Becker, P. 1996. Sap flow in Bornean heath and dipterocarp forest trees during wet and dry periods. Tree Physiology 16: 295-299.

Bristow, M., Vanclay, J.K, Brooks, L., Hunt, M., 2006. Growth and species interactions of Eucalyptus pellita in a mixed and monoculture plantation in the humid tropics of north Queensland Forest Ecology and Management 233, 285–294.

Bruijnzeel, L.A., 1997. Hydrology of forest plantations in the tropics. In: Nambiar, E.K.S. and Brown, A.G. (Eds). Management of Soils, Nutrients and Water in Tropical Plantation Forests. ACIAR Canberra, Australia, pp. 125-167.

Calder, I., Amezaga, J., Aylward, B., Bosch, J., Fuller, L., 2004. Forest and water policies: the need to reconcile public and science conceptions. Geologica Acta, 2, 157–166.

Caldeira, M.C., Ryel, R.J., Lawton, J.H., Pereira, J.S., 2001. Mechanisms of positive biodiversity-production relationships: insights provided by delta C-13 analysis in experimental mediterranean grassland plots. Ecol. Lett. 4 , 439–443.

Caspersen, J.P., Pacala, S.W., 2001. Successional diversity and forest ecosystem function. Ecological Research 16, 895-903.

Cienciala, E., Kucera, J., Malmer, A., 2000. Tree sap flow and stand transpiration of two *Acacia mangium* plantations in Sabah, Borneo. J. Hydrol. 236, 109-120.

Cintron, B. B., 1990. *Cedrela odorata* L. Cedro hembra, Spanish cedar. In: Burns, R. M., Honkala, B. H. (Eds.), Silvics of North America: 2. Hardwoods. Agricultural. Handbook. 654. U.S. Department of Agriculture, Forest Service, Washington, DC, pp. 250-257.

Clearwater, J.S.A., M., Meinzer, F.C., Goldstein, G., 2002. Heat dissipation sensors of variable length for measurement of sap flow in trees with deep sapwood. Tree Physiol. 22, 277-283.

Coll, L., Potvin, C., Messier, C., Delagrange, S., 2008. Root architecture and allocation patterns of eight native tropical species with different successional status used in open-grown mixed plantations in Panama. Trees 22, 585-596.

Cunningham, S.A., Kimberi, R.P., Colloff, M.J., 2009. Whole-tree sap flow is substantially diminished by leaf herbivory. Oecologia 158, 633–640.

De Boeck, H.J., Lemmens, C.M.H.M., Bossuyt, H., Malchair, S., Carnol, M., Merckx, R., Nijs, I., Ceulemans, R., 2006. How do climate warming and plant species richness affect water use in experimental grasslands? Plant Soil 288, 246–261.

da Silva, E.V., de Moraes Gonçalves, J.L., de Freitas Coelho, S.R., Moreira e Moreira, R., de Miranda Mello, S.L., Bouillet, J.P., Jourdan, C., Laclau, J.P., 2009. Dynamics of fine root distribution after establishment of monospecific and mixed-species plantations of Eucalyptus grandis and Acacia mangium. Plant Soil 325, 305–318.

Dierick, D., Hölscher, D., 2009. Species-specific tree water use characteristics in reforestation stands in the Philippines. Agricultural and Forest Meteorology 149, 1317-1326.

Dietrich, W.E., Windsor, M.D., Dunne, T., 1996. Geology, Climate and Hydrology of Barro Colorado Island. In: Leigh, E.G. Jr., Rand, A.S., Windsor, D.M. (Eds.), The Ecology of a Tropical Forest. Seasonal Rhythms and Annual Changes. Second edition. Smithsonian Institution Press, Washington DC, pp. 21-46.

.

Dünisch, O., Morais, R.R., 2002. Regulation of xylem sap flow in an evergreen, a semi-deciduous, and a deciduous Meliaceae species from the Amazon. Trees-Structure and Function 16, 404-416.

Edwards, W.R.N., Becker, P., Cermák, J., 1996. A unified nomenclature for sap flow measurements. Tree Physiol. 17, 65–67.

Fargione, J., Tilman, D., Dybzinski, R., Lambers, J.H.R., Clark, C., Harpole, W.S., Knops, J.M.H., Reich, P.B., Loreau, M., 2007. From selection to complementarity: shifts in the causes of biodiversity–productivity relationships in a long-term biodiversity experiment. Proceedings Royal Society Biology 274, 871–876.

Farley, K.A., E.G. Jobbagy, Jackson, R.B., 2005. Effects of afforestation on water yield: a global synthesis with implications for policy. Global Change Biology 11, 1565-1576.

Fetene, M., Beck, E.H., 2004. Water relations of indigenous versus exotic tree species, growing at the same site in a tropical montane forest in southern Ethiopia. Trees 18, 428-435.

Fölster, H., Khanna, P.K., 1997. Dynamics of nutrient supply in plantation soils. In Nambiar, E.K.S., Brown, A.G., (eds.). Management of soil, nutrients and water in tropical plantation forests. ACIAR/CSIRO/CIFOR, Canberra, 338-378.

Flores, E.M., 2003. *Terminalia amazonia* (J.F. Gmel.) Exell. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 748-751.

Flores, E.M., Marín, W.A., 2003. *Tabebuia rosea* (Bertol.) DC. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 737-739.

Forrester, D.I., Bauhus, J., Khanna, P.K., 2004. Growth dynamics in a mixedspecies plantation of Eucalyptus globulus and Acacia mearnsii. For. Ecol. Manage. 193, 81–95.

Fournier, L.A., 2003a. *Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 294-296.

Fournier, L.A., 2003b. *Luehea seemannii* Triana & Planch. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 553-554.

Francis, J.K., 1990. *Hura crepitans* L. Sandbox, molinillo, jabillo. Euphorbiaceae. Spurge family. USDA Forest Service, Southern Forest Experiment Station, Institute of Tropical Forestry. SO-ITF-SM; 38, New Orleans, LA, USA.

Francis, J.K., 2003a. *Acacia mangium* Willd. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 256-258.

Francis, J.K., 2003b. *Tectona grandis* L.f. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 745-747.

Giambelluca, T.W., Ziegler, A.D., Nullet, M.A., Truong, D.M., Tran, L.T., 2003. Transpiration in a small tropical forest patch. Agricultural and Forest Meteorology 117: 1-22.

Garcia Santos, G., 2007. An ecohydrological and soils study in a montane cloud forest in the National Park of Garajonay, La Gomera (Canary Islands, Spain). Dissertation, Vrije Universiteit Amsterdam, The Netherlands.

Goldstein, G., Andrade, J.L., Meinzer, F.C., Holbrook, N.M., Cavalier, J., Jackson, P., Celis, A., 1998. Stem water storage and diurnal patterns of water use in tropical forest canopy trees. Plant Cell Environ. 21, 397-406.

Gradstein, S.R., Kessler, M., Pitopang, R., 2007. Tree species diversity relative to human land use in tropical rain forest margins in Central Sulawesi. In: Tscharnke, T., Leuschner, C., Guhardja, E., Zeller, M. (Eds). The Stability of Tropical Rainforest Margins: Linking Ecological, Economic and Social Constraints of Land Use and Conservation. Springer, Berlin, p. 321-334.

Granier, A., 1985. A new method of sap flow measurement in tree stems. Ann. For. Sci. 42, 193-200.

Granier, A., 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiol. 3, 309-320.

Granier, A., Huc, R., Barigah, S.T., 1996. Transpiration of natural rain forest and its dependence on climatic factors. Agricultural and Forest Meteorology 78, 19-29.

Granier, A., Loustau, D., Bréda, N., 2000. A generic model of forest canopy conductance dependent on climate, soil water availability and leaf area index. Annals of Forest Science, 57, 755-765.

Gross, K., Cardinale, B.J., 2007. Does species richness drive community production or vice versa? Reconciling historical and contemporary paradigms in competitive communities. The American Naturalist, 170, 207–220.

Harris, P.P., Huntingford, C., Cox, P.M., Gash, J.H.C., Malhi, Y., 2004. Effects of soil moisture on canopy conductance of Amazonian rainforest. Agricultural and Forest Meteorology 122: 215-227.

Hatton. T.J., Catchpole, E.A., Vertessy, R.A., 1990. Integration of sapflow velocity to estimate plant water-use. Tree Physiology 6: 201-209.

Healy, C., Gotelli, N.J., Potvin, C., 2008. Partitioning the effects of biodiversity and environmental heterogeneity for productivity and mortality in a tropical tree plantation. Journal of Ecology 96, 903–913.

Herbst, M., Eschenbah, C., Kappen, L., 1999. Water use in neighbouring stands of beech (Fagus sylvatica L.) and black alder (Alnus glutinosa (L.) Gaertn.). Annals of Forest Science, 56, 107-120.

Hölscher, D., Koch, O., Korn, S., Leuschner, Ch., 2005. Sap flux of five co-occurring tree species in a temperate broad-leaved forest during seasonal soil drought. Trees 19, 628-637.

Holdridge, L.R., Budowski, G., 1956. Report on an ecological survey of the Republic of Panama. The Caribbean Forester 17, 92-109.

Jackson, P.C., Cavelier, J., Goldstein, G., Meinzer, F.C., Holbrook, N.M., 1995. Partitioning of water resources among plants of a lowland tropical forest. Oecologia 101, 197-203.

Jackson, B.J., Jobbagy, E.G., Avissar, R., Roy, S.B., Barrett, D.J., Cook, C.W., Farley, K.A., le Maitre, D.C., McCarl, B.A., Murray, B.C., 2005. Trading water for carbon with biological carbon sequestration. Science 310, 1944-1947.

Jarvis, P.G., 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. Philosophical Transactions of the Royal Society of London: Series B Biological Sciences, 273, 593-610.

Kaimowitz, D., 2005. Useful myths and intractable truths: the politics of the link between forests and water in Central America. In eds: Bonell, M., Bruijnzeel, L.A., Forest–Water–People in the Humid Tropics. Cambridge University Press, Cambridge, UK. pp. 86–98.

Kelliher, F.M., Leuning, R., Schulze, E.D., 1993. Evaporation and canopy characteristics of coniferous forests and grasslands. Oecologia 95, 153–163.

Kelty, M.J., 1992. Comparative productivity of monocultures and mixed-species stands. In M.J. Kelty, B.C. Larson & C.D. Oliver (eds.). The ecology and silviculture of mixed-species forests. Kluwer Academic Publishers, Dordrecht, Boston, London, 125-141.

Kijkar, S., 2003. *Gmelina arborea* Roxb. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 476-478.

Köhler, M., Dierick, D., Schwendennman, L., Hölscher, D., 2009. Water use characteristics of cacao and Gliricidia trees in an agroforest in Central Sulawesi, Indonesia. Ecohydrology 2, 520- 529.

Kunert, N., Schwendenmann, L., Hölscher, D., 2010. Seasonal dynamics of tree sap flux and water use in nine species in Panamanian forest plantations. Agricultural and Forest Meteorology 150, 411-419.

Laclau, J.-P., Bouillet, J.-P., Goncçalves, J.L.M., Silva, E.V., Jourdan, C., Cunha, M.C.S, Moreira, M.R., Saint-André, L. , Maquère, V., Nouvellon, Y., Ranger, J., 2008. Mixed-species plantations of Acacia mangium and Eucalyptus grandis in Brazil 1. Growth dynamics and aboveground net primary production. Forest Ecology and Management 255, 3905–3917.

Lamb, D., Erskine, P.D., Parrotta, J.A., 2005. Restoration of degraded tropical forest landscapes. Science 310, 1628-1632.

Langenberger, G., 2006. Habitat distribution of dipterocarp species in the Leyte Cordillera: an indicator for species-site suitability in local reforestation programs. Annals of Forest Science, 63, 149-156.

Leigh, E.G., Rand, A.S., Windsor, D.W., 1996. The ecology of a tropical forest, 2nd edn, Smithsonian Press, Washington, DC.

Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. Nature, 412, 72–76.

Lüttge, U., Berg, A., Fetene, M., Nauke, P., Peter, D., Beck, E., 2003. Comparative characterization of photosynthetic performance and water relations of native trees and exotic plantation trees in an Ethiopian forest. Trees 17, 40-50.

Ma, L., Lu, P., Zhao, P., Roa, X.-Q., Cai, X.A., Zeng, X.P., 2008. Diurnal, daily seasonal and annual patterns of sap-flux-scaled transpiration from an *Acacia mangium* plantation in South China. Ann. For. Sci. 65, 402p1-402p9.

Malmer, A., Murdiyarso, D., Bruijnzeel, L.A., Ilstedt, U., 2010. Carbon sequestration in tropical forests and water: a critical look at the basis for commonly used generalizations. Global Change Biology 16, 599–604.

Margraf, J., Milan, P.P., 1996. Ecology of dipterocarp forests and its relevance for island rehabilitation in Leyte, Philippines. In: Schulte, A., Schöne, D. (Eds.), Dipterocarp Forest Ecosystems: Towards Sustainable Management. World Scientific, Singapore, p. 124-154.

McJannet, D., Fitch, P., Disher, M., Wallace, J., 2007. Measurements of transpiration in four tropical rainforest types of north Queensland, Australia. Hydrol. Process. 21, 3549-3564.

Meinzer, F.C., Andrade, J.L, Goldstein, G., Holbrook, N.M., Cavelier, J., Jackson, P., 1997. Control of transpiration from the upper canopy of a tropical forest, the role of stomatal, boundary layer and hydraulic architecture components. Plant, Cell and Environ. 20, 1242-1252.

Meinzer, F.C., Andrade, J.L., Goldstein, G., Holbrook, N.M. Cavelier, J. Wright, S.J., 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. Oecologia 121, 293–301.

Meinzer, F.C., G. Goldstein & J.L. Andrade, 2001. Regulation of water flux through tropical forest canopy trees: Do universal rules apply? Tree Physiology 21, 19-26.

Meinzer, F.C., 2003. Functional convergence in plant responses to the environment. Oecologia 134, 1-11.

Meinzer, F.C., James, S.A., Goldstein, G., 2004. Dynamics of transpiration, sap flow and use of stored water in tropical forest canopy trees. Tree Physiology 24, 901-909.

Meinzer, F.C., Bond, B.J., Warren, J.M., Woodruff, D.R., 2005. Does water transport scale universally with tree size? Functional Ecology 19, 558-565.

Meinzer, F.C., Andrade, J.L., Goldstein, G., Holbrook, N.M., Cavelier, J., Wright, S.J., 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. Oecologia 21, 293-301.

Menalled, F.D., Kelty, M.J., Ewel, J.J., 1998. Canopy development in tropical tree plantations: a comparison of species mixtures and monocultures. Forest Ecology and Management 104, 249-263.

Montagnini 2000 Montagnini, F., 2000. Accumulation in aboveground biomass and soil storage of mineral nutrients in pure and mixed plantations in a humid tropical lowland. Forest Ecology and Management 134, 257-270.

Montagnini, F., Jordan, C.F., 2005. Tropical Forest Ecology. Springer Verlag, Heidelberg.

Motzer, T., Munz, N., Küppers, M., Schmitt, D., Anhuf, D., 2005. Stomatal conductance, transpiration and sap flow of tropical montane rain forest trees in the southern Ecuadorian Andes. Tree Physiology 25, 1283-1293.

O`Brien, J.J., Oberbauer, S.F., Clark, D.B., 2004. Whole tree xylem sap flow responses to multiple environmental variables in a wet tropical forest. Plant, Cell and Environment 27, 551-567.

O'Grady, A.P., Eamus, D., Hutley, L.B., 1999. Transpiration increases during dry season, patterns of tree water use in eucalypt open-forests of northern Australia. Tree Physiol. 19, 591-597.

Oren, R., Pataki, D.E., 2001. Transpiration in response to variation in microclimate and soil moisture in southeastern deciduous forests. Oecologia 127, 549-559.

Orians, G.H., R. Dirzo & J.H. Cushman, 1996. Biodiversity and Ecosystem Processes in Tropical Forests. Ecological Studies 122. Springer Berlin.

PAGASA, 2007. Philippine Atmospheric, Geophysical and Astronomical Services Administration, Philippines, available from http://www.pagasa.dost.gov.ph (last visited: 20/08/2009).

Petit, B., Montagnini, F., 2004. Growth equations and rotation ages of ten native tree species in mixed and pure plantations in the humid neotropics. Forest Ecology and Management 199, 243-257.

Piotto, D., 2008. A meta-analysis comparing tree growth in monocultures and mixed plantations. Forest Ecology and Management, 255, 781-786.

Phillips, N., Oren, R., Zimmermann, R., Wright, S.J., 1999.Temporal patterns of water flux in trees and lianas in Panamanian moist forest. Trees 14, 116-123.

Potvin, C., Whidden, E., Moore, T., 2004. A case study of carbon pools under three different land-uses in Panama. Climate Change 67, 291-307.

Potvin, C., Tschakert, P., Lebel, F., Kirby, K., Barrios, H., Bocariza, J., Caisamo, J., Caisama, L., Cansari, C., Casamá, J., Casamá, M., Chamorra, L., Dumasa, N., Goldenberg, S., Guainora, V., Hayes, P., Moore, T., Ruíz, J., 2007. A participatory approach to the establishment of a baseline scenario for a reforestation CDM project. Mitigation and Adaptation Strategies for Global Change 12(8): 1341-1362.

Potvin, C., Gotelli, N.J., 2008. Biodiversity enhances individual performance but does not affect survivorship in tropical trees. Ecolo. Lett. 11, 217–223.

Potvin, C., Dutilleul, P., 2009. Neighborhood effects and size-symmetric competition in a tree plantation varying in diversity. Ecology 90, 321–327.

Price, G. R., 1996. The nature of selection. J. Theor. Biol. 175, 389-396.

Scherer-Lorenzen M, Körner C, Schulze E-D. 2005. The functional significance of forest diversity: a synthesis. In: Forest diversity and function. Temperate and boreal Systems. Ecological Studies, Vol. 176, Scherer-Lorenzen M, Körner C, Schulze E-D (eds); Springer: Berlin; 377–389.

R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0,http://www.R-project.org (last visited 28/05/2009)

Rocas, A.N., 2003. *Cedrela odorata* L. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Part II-Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp. 386-389.

Röhle, H., 1986. Vergleichende Untersuchungen zur Ermittlung der Genauigkeit bei der Ablotung von Kronenradien mit dem Dachlot und durch senkrechtes Anvisieren des Kronenrandes, Forstarchiv 57, 67–71.

Rothe, A., Binkley, D., 2001. Nutritional interactions in mixed species forests: a synthesis. Canadian Journal of Forest Research 31, 1855-1870.

Scherer-Lorenzen, M., Bonilla, L.B., Potvin, C., 2007.Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. Oikos 116, 2108-2124.

Schorcht, M., 2000. *Tectona grandis*. In: Schütt, P., Schuck, H.J., Lang, U., Rollof,A. (Eds.), Enzykloppädie der Holzgewächse. Handbuch und Atlas der Dendrologie. Ecomed Verlagsgesellschaft, Landsberg.

Schulze, E.-D., Bazzaz, F.A., Nadelhoffer, K.J., Koike, T., Takatsuki, S., 1996. Biodiversity and ecosystem function of temperate deciduous broad-leaved forests. In H.A. Mooney, J.H. Cushman, E. Medina, O.E. Sala & E.-D. Schulze (eds.). Functional roles of biodiversity: a global perspective. John Wiley & Sons, Chichester, New York, Brisbane, 71-98.

Scott, D.F., Bruijnzeel, L.A., Mackensen, J., 2004. The hydrological and soil impacts of forestation in the tropics. In M. Bonnell, & L.A. Bruijnzeel (eds). Forests, Water & People in the Humid Tropics. Cambridge University Press, Cambridge, 622-651.

Stocker, R., Körner, C., Schmid, B., Niklaus, P.A., Leadley, P.W., 1999. A field study of the effects of elevated Co2 and plant species diversity on ecosystem-level gas exchange in a planted calcareous grassland. Glob. Chang. Biol. 5, 95–105.

STRI, 2009. Temperature and rainfall data Barro Colorado Island, Panama 1987-2007.Online. http,//striweb.si.edu/esp/meta_data/details_bci_temp1.html

van Dijk. A.I.J.M., Keenan, R.J., 2007. Planted forests and water in perspective. Forest Ecology and Management 251, 1–9.

Van Peer, L., Nijs, I., Reheul, D., De Cauwer, B., 2004. Species richness and susceptibility to heat and drought extremes in synthesized grassland ecosystems: compositional vs physiological effects. Funct. Ecol. 18, 769–778.

Veldkamp, E., O'Brien, J. J., 2000. Calibration of a FDR sensor for humid tropical soils of volcanic origin. Soil Science Society of America Journal 64(5), 1549-1553.

Van Kanten, R., Vaast, P., 2006. Transpiration of arabica coffee and associated shade tree species in sub-optimal, low-altitude conditions of Costa Rica. Agroforestry Systems 67: 187-202.

Verheyen K, Bulteel H, Palmborg C, Olivié B, Nijs I, Raes D, Muys B. 2008. Can complementarity in water use help to explain diversity–productivity relationships in experimental grassland plots? Oecologia 156: 351-361.

Vosso, J.A., 2003 (Ed.) Tropical Tree Seed Manual: Part II – Species Descriptions. United States Department of Agriculture. Forest Service. Agriculture Handbook 721. Washington DC, pp 899.

Whitley, R., Zeppel, M., Armstrong, N., Macinnis-Ng, C., Yunusa, I., Eamus, D., 2008. A modified Jarvis-Stewart model for predicting stand-scale transpiration of an Australian native forest. Plant and Soil 305: 35-47.

Wishnie, M.H., Dent, D.H., Mariscal, E., Deago, J., Cedeño, N., Ibarra, D., Condit, R., Ashton, P.M.S., 2007.Initial performance and restoration potential of 24 tropical tree species planted across a precipitation gradient in the Republic of Panama. Forest Ecology and Management 243, 39-49.

Wolf, S., Eugster, W., Buchmann, N., 2008. Micrometeorological measurements of a Plantation and adjacent Pasture in Sardinilla, Panama. Field Measurements. ETH Zurich, Institute of Plant Sciences. Digital media.

Yachi, S., Loreau, M., 2007. Does complementary resource use enhance ecosystem functioning? A model of light competition in plant communities. Ecol. Lett. 10, 54–62.

ACKNOWLEDGMENTS

This thesis would not have been possible without the help, support, hard work and endless efforts of many.

First and foremost, I would like to thank my supervisor, Dirk Hölscher, whose encouragement, guidance and support from the initial to the final level enabled me to develop an understanding of the subject.

I am heartily thankful to Luitgard Schwendenmann. The research in this thesis would have taken far longer to complete without her. Luitgard was always there to listen and to give advice.

My particular gratitude goes to Catherine Potvin for helpful advice during my fieldwork in Panama and for sharing her insights in the Panamanian way of life.

And I want to thank Eva Siegelkow who helped me to overcome many administrative challenges and was always prepared to check the references, points and commas in my drafts.

The days would have passed far more slowly without the other PhD students of the department Mareike Roeder, Diego Dierick, Renz Come, Michael Köhler and Meik Meißner. Furthermore, I want to thank my colleagues at the field site Fabiene Zeugin, Mirco Plath and especially Sebastian Wolf (for the meteorological data).

Besides, I would like to thank the Smithsonian Tropical Research Institute for providing us with a good environment and facilities to complete this project. Especially I want to thank Klaus Winter for advice, Milton Garcia for technical support and José Monteza for his invaluable assistance during my field work.

I wish to thank my parents for their love, encouragement and support throughout the years, without whom I would never have enjoyed so many opportunities

Finally, I want to thank Alida for her love, care and patience.

DECLARATION OF HONOR

I hereby declare that I am the sole author of this dissertation entitled "*Tree transpiration in forest plantations: effects of species, seasonality and diversity (Panama)*" and that all references and data sources used have been acknowledged as such. I further declare that this work has never been submitted in any form as part of other dissertation procedures.

Göttingen, April 2010
(Norbert Kunert)

CURRICULUM VITAE

Name	**Norbert Kunert**
Date of birth	29 August 1980
Place of birth	Nürnberg, Germany
Citizenship	German

	Education
03/2007 - present	Ph.D. in Forest Science and Wood Ecology, Georg-August Universität, Germany
04/2006 - 02/2007	M.Sc. in Biology, TU-Munich, Germany
10/2005 - 05/2006	M.Sc. in Wood and Forestry Science, TU-Munich, Germany
10/2001 - 04/2006	Diploma in Forestry Science and Resource Management, TU-Munich, Germany
10/2001 - 02/2005	B.Sc. in Forestry Science, TU-Munich, Germany
09/1991 - 06/2000	Dietrich-Bonhoeffer-Gymnasium, Oberasbach, Germany
09/1987 - 06/1991	Grundschule Altenberg, Oberasbach, Germany

	Military Service
07/2000 - 04/2001	Deutsche Bundeswehr (4. GebArtBat 225), Füssen, Germany