Foliage Turnover, Water and Carbon Relations of Three Coexisting Functional Types of Indigenous Trees in the Disturbed Natural Forest of Munessa

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This is to certify that the thesis prepared by Yigremachew Seyoum, entitled: *Foliage Turnover, Water and Carbon Relations of Three Coexisting Functional Types of Indigenous Trees in the Disturbed Natural Forest of Munessa* and submitted in fulfillment for the requirements for the Degree of Doctor of Philosophy (Biology: Botanical Science) complies with the regulations of the University and meets the accepted standards with respect to the originality and quality.

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Abstract

A good understanding of species coexistence and the extent of variations in interspecies resource utilization by investigating suits of functional traits is useful for predicting the vegetation dynamics and productivity of an ecosystem. Such documented information can be incorporated into silvicultural treatments designed to manage a natural forest towards preset social, ecological and economical targets as well as to initiate reforestation programs of a mixed forest. The present study investigated coexistence strategies of different functional types of trees in the Munessa Natural Forest by evaluating phenology, carbon and water relations of representative indigenous trees (*Podocarpus falcatus* (Thunb.) Mirb.*, Prunus africana* (Hook.f.) Kalkm., *and Croton macrostachyus* (Hochst).ex Del) between 2009 and 2011.

In the first component, foliage dynamics, growth and some ecophysiological traits were investigated. The degree of inter- and intra-individual synchronization of foliage phenophases was examined to evaluate the contributions of endogenous and external factors to the dynamics of the foliages. In the second component of the tudy, plant water status and its diurnal variation was assessed by measuring predawn and midday leaf water potentials. Moreover, sap flux at the bases of the tree trunk and of selected branches was determined using Granier type thermal dissipation sensors. Branch and basal sap flux patterns were compared to assess water movement through the stem and quantify potential water reservoirs. To that end, the daily water use by the whole trees was determined from the sap flux data and sapwood area of trees with comparable DBH. Analysis of the δ ^{18}O signatures of water samples from different soil horizons and from twigs were performed to determine the depth of the soil from which the studied functional types of trees extracted water for transpiration. Additionally, δ ^{13}C of leaf samples were used to assess gas exchange characteristics over the entire life time of the leaves. In the third component, the daily and seasonal gas exchange patterns of the leaves of the studied species were measured during the dry and wet seasons of 2009 and 2010. Water use efficiencies of carbon capture by the studied functional types of trees were also determined from the gas exchange data.

The phenological findings showed that the onset of the rain in triggering bud break depends on the functional type of the tree. Furthermore, the study proved the significance of endogenous control on the life spans of the leaves, and on the overall foliage dynamics of *P. falcatus* and *C. macrostachyus.* Moreover, leaf life-span is identified as an important trait of functional types of trees closely correlating with other functional traits. On the other hand, the water relation study showed that spatiotemporal differences in soil water use are among the ecophysiological strategies that enabled resource partitioning and coexistence among different functional types of trees. Additionally, stem tissue water storage, day-time use of that reservoir and night/day time recharging, were noted as species specific strategies stabilizing coexistence of the different functional types of trees. With respect to photosynthetic carbon capture, the study showed similar biomass production by all three functional types of trees which results from exploiting fluctuating niches of irradiance and soil moisture. The later finding emphasizes the importance of temporally changing patterns of irradiance and moisture for stabilizing the coexistence of adult individuals of different life-forms, and in turn, plant diversity.

According to this finding, the long term courses of irradiance and soil moisture could be used as a tool for predicting the impact of environmental changes on plant biodiversity and ecosystem services. Furthermore, the study implies that enrichment planting to rehabilitate degraded forests should be carried out with species representing different functional types of trees. This would guarantee an optimized carbon and hydraulic budget of the entire ecosystem. Another essential outcome is the fact that forest management plans should recognize the significance of different soil water sources for the diversity of species with respect to the hydrology of seasonally dry forests. The study also provides species-specific environmental requirements that may assist forest managers in matching planting purpose and species with site conditions.

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1 Introduction

It has been extensively documented that the forest resource bases of Ethiopia have been declining at a huge pace. However, estimates of the total land area in the past covered by natural forests remain debatable. Several authors provided variable estimates because of lack of consistency in the definition of a forest (Eshetu Yirdaw, 2002). According to Von Breitenbach (1962) 40% of the total land area was covered by forests while Sayer *et al.* (1992) reported that 87% of the highlands were forests. In the early 1950s, the remaining forest was estimated to cover 19 million hectares or 16% of the total land area (EFAP, 1994). By 2000, the coverage was estimated as only 4.2% (FAO, 2001). Despite the lack of reliable estimates of the past cover, there is unequivocal evidence of the historical deforestation that wiped out considerable portions of the forest cover of the country. Sedentary agriculture, extensive cattle herding and socio-political instability exacerbated by increasing population pressure have resulted in heavy deforestation, forest fragmentation, loss of biodiversity and impoverishment of ecosystems in general (Eshetu Yirdaw, 2002).

Rate of deforestation has been estimated as 150,000-200,000 hectares per year (FAO 2003). Pohjonen and Pukkala (1990) estimated that with this rate of deforestation, there would be no more forest in Ethiopia by the year 2020. In addition to its significance on the livelihood of the rural people, there is an increasing concern about the contribution of deforestation to increasing global atmospheric CO_2 concentration. Deforestation and conversion of tropical rain forests into agricultural ecosystems have been estimated to emit 1.6-1.7 giga tons of carbon year^{-1} into the atmosphere (IPCC, 2000). On the other hand, tropical forests have been predicted to sequester up to 80% of the total CO_2 emitted worldwide (Rotter and Danish, 2000) and play a positive role in alleviating climate change consequences. As part of tropical vegetation, the

Ethiopian highlands represent the largest mountain complex in Africa and comprise over 50% of the African land area covered by afromontane vegetation (Tamrat Bekele, 1993). Afromontane forests form one of the woodland vegetation types of Ethiopia (Friis, 1992); of which dry afromontane forests represent the largest part (Demel Teketay, 2005). The montane forests of Ethiopia received the heaviest forest depletion but still comprise most of the remnant natural forests of the country. It is this region that is being deforested most at present (Eshetu Yirdaw, 2002). Nevertheless, with sustainable management plan, in addition to their customary roles Ethiopian montane forests can also serve as carbon sink and can contribute to the global warming mitigation efforts. Among others, sustainable forest management requires knowledge on performances of trees as influenced by changing environmental conditions and their effect on ecosystem processes, such as carbon and water relation (Pohjonen and Pukkala, 1990; McJannet *et al.,* 2000).

Growth conditions in an ecosystem can be modified by anthropogenic as well as natural factors. Coexisting species of a community could reveal different phenological and physiological reactions to changes in environmental growth conditions. Consequently, differing impact of a changing environment may disrupt stabilized co-utilization of fundamental resources and eventually species diversity (Singh and Kushwaha, 2005). Such disturbances ultimately may threat economically and ecologically important species in a community. Nevertheless, with prior information on species specific requirements and physiological responses, appropriate silvicultural interventions can be implemented. Moreover, a good understanding of species coexistence and resource utilization pattern by investigating combinations of functional traits is useful in predicting the vegetation dynamics and productivity of an ecosystem. With this respect, investigating representative functional types has emerged as widely accepted approach to infer and document ecosystem functioning (Borchert, 1998; Naeem and Wright, 2003; Singh and Kushwaha, 2005). Such information can be incorporated into silvicultural treatments designed to manage a natural forest towards preset social, ecological and economical targets as well as to initiate reforestation programs of a mixed forest. In this work ecophysiological and phenological aspects of three tree functional types coexisting in the Munessa Forest are addressed. The following sections provide backgrounds for the three different components of the study.

1.1 Turnover of foliage phenophases and leaf traits

Tree foliage phenophases are common means to describe the course of a year and to follow the progression of its seasons. This holds for temperate climate zones as well as for tropical regions which are subjected to a change of dry and wet seasons. Bud break and leaf sprouting, and senescence and abscission are the most obvious foliar pheno-events, often accompanied by conspicuous coloration of the leaves. Ambient factors, such as cold or the lack or onset of precipitation are known to trigger the change of the foliar phenophases (Reich and Borchert, 1982; Do *et al.,* 2005; Singh and Kushwaha, 2005). The factors and strategies which induce these changes have been addressed in many studies but detailed knowledge is still scarce (e.g. Browse and Xin, 2001; Beck *et al.,* 2007; Bartels and Hussain, 2011). Patterns of phenophase transitions range from rapid and highly synchronous events to temporally extended, rather irregular and asynchronous processes (Borchert *et al.*, 2002). Mostly the life-spans of the leaves correspond to the periods of the seasons, resulting in one foliage exchange per year. In evergreen trees, exchange of the foliage is not obvious and may take place annually or stretch over several years. In that case, the foliage is composed of several generations of leaves whose unfolding and senescence appear irregular and asynchronous. In temperate as well as tropical forests both functional life-forms of trees, deciduous and evergreen coexist in obvious stable ecological equilibrium (Eamus, 1999; Van Oene *et al.*, 2000) which requires a high photosynthetic productivity of the deciduous species and a robust structure and physiology of the perennial leaves.

Deciduous species have commonly mesic, short-lived leaves while evergreens have coriaceous leaves whose longevity pays off the high construction costs. Such leaves must be capable to adapt to changing ambient conditions and this kind of flexibility is at the expense of productivity (e.g. Chabot and Hiks, 1982). In a broad study Givnish (2002) has reviewed the literature addressing the advantages and disadvantages of various tree functional types and has evaluated the models describing coexistence or dominance of the respective life-forms in particular habitats. Leaf life-span shows close relationship with photosynthetic carbon gain and many other physiological, anatomical and morphological traits. Usually, in those studies evergreens are compared with obligatory deciduous trees. In tropical humid and semi-humid forests, however, deciduous trees may keep their foliage all year round, at least partly, if the shortage of water during a dry season is less severe and the soils maintain sufficient moisture to allow ongoing water flux through the tree.

When considering such facultative deciduous trees, a question about the triggers for the foliage phenology and the longevity of the individual leaves arises. There is agreement that in addition to environmental cues internal physiological control may be involved in the regulation of the timing of foliage phenophases (Do *et al.*, 2005; Williams *et al.*, 2008; Valdez-Hernández *et al.,* 2010). Soil water condition represents one of the abiotic variables exhibiting pronounced fluctuations in seasonally dry forests. Thus, in such environments foliage phenophases of functional types of trees are closely related with plant water relation characteristics.

1.2 Plant-water relation

Coexisting functional types of trees may exhibit distinct water use strategies that may contribute to balanced water resource utilization. In accordance with strategy differences, functional heterogeneity can be accompanied by divergence in ecophysiological traits. Thus, plant-water related ecophysiological traits may show species-specific responses to environmental changes. Comprehensive information on the water relation characteristics of species in an ecosystem can be obtained by applying a combination of methods (Fritzsche *et al.*, 2006).

Measurements of leaf water potential have been used to assess plant water status and performance under varying soil water conditions (Williams and Araujo, 2002), with low water potential inhibiting plant growth (Sucoff, 1971). Leaf water potentials measured both during dry and wet seasons of the year allow rapid ecophysiological characterization of species (Kindeya Gebrehiwot *et al.*, 2005). Wide daily range in leaf water potential portrays trees ability to withstand high evaporative demand and extracting soil moisture which is held by strong soil matrix forces (Aster Gebrekiristos *et al.*, 2006). Differences in the daily range of leaf water potential can be associated with differences in nocturnal transpiration (Bucci *et al.,* 2005). Advances in leaf water potential research revealed that tree species of similar root architecture that have access to similar soil depths may reveal uniform dry season predawn leaf water potential, which is a surrogate measure of soil water availability (Thomas *et al.*, 1999; Aster Gebrekiristos *et al.*, 2006). But to validate such generalizations species specific hydraulic properties and variations in physiological responses to atmospheric and soil moisture conditions have to be addressed.

Understanding the whole tree water use is essential to predict the impact of removal of trees on local and regional water budget through deforestation as well as changes in forest composition by plantation and forest succession (Dawson, 1996). Quantifying whole tree water use have received increasing attention because of its use in resolving issues of water resource management, estimating variations in the water requirements of different tree species, and evaluating the role of transpiration in forest and woodland hydrology (Wullschleger *et al.*, 1998). Trees minimize the imbalance between water supply and demand by utilizing tissue stored water which is closer to the sites of evaporative demand (Goldstein *et al.*, 1998). Stem water storage is an adaptation to overcome drought stress in trees and it widely varies among species and functional types (Goldstein *et al.*, 1998; Philipps *et al.*, 2003). The contribution of stem-stored water to transpiration was estimated between 9-40% (Holbrook and Sinclair, 1992; Goldstein *et al.*, 1998; Philipps *et al.,* 2003; Meinzer *et al.*, 2004). Even if the amount of stem-stored water is small its significance on the overall water relation and carbon gain of a tree could be significant especially when it influences stomatal opening (Goldstein *et al.*, 1998).

The analysis of hydrogen and oxygen isotope ratios in water within the xylem sap serves as a strong tool for understanding the dynamics of plant water utilization (Ehleringer and Dawson, 1992). Stable isotope anlysis of Oxygen ($\delta^{18}O$) has been used to identify the soil water source of trees. Because of limited precipitation during the dry season, the upper soil layers become enriched in the heavier isotopes (^{18}O) due to evaporative fractionation, thereby creating a vertical gradient in the oxygen isotopic signature with soil depth (Queerjeta *et al.,* 2007). The oxygen isotopic signature of xylem water can therefore be compared to the $\delta^{18}O$ signature of soil water sampled from different depths of the soil profile to better understand the sources of water used by individual plants. During water uptake and transport within woody tissue, $\delta^{18}O$ of plant xylem water remains unaltered, and therefore reflects the signature of the soil water in the various depths from which plants extract soil water (Hasselquist *et al.,* 2010). Studies have revealed that extracting soil water from different sources allows co-utilization of water resources (Querejeta *et al.,* 2007). Tissue and soil $\delta^{18}O$ anlysis has been used to show that trees may exploit soil water from deeper soil layers during the dry season. The ability to switch rapidly among different water sources such as a switch from surface soil moisture to deeper soil layer puts a plant at an advantage if competition for water occurs within an ecosystem (Ehleringer and Dawson, 1992). In the literature there are contrasting reports about the relationships between soil water source and phenological groupings suggesting difficulties with generalizations. Among others, Jackson *et al.* (1995) and Meinzer *et al.* (1999) associated evergreenness with uptake of deeper soil water while Querejeta *et al.* (2007) could not find phenological association with soil water source. Regardless of such disparities, a switch to another soil depth for bulk uptake of water means a production of new fine roots at that soil horizon.

Leaf $\delta^{13}C$ values provide information on intrinsic long term integrated WUE defined as the ratio of area based CO_2 uptake and stomatal conductance or transpiration rate. Leaf $\delta^{13}C$ is useful in characterizing the ecophysiology of different functional types coexisting in an ecosystem (Sobrado and Ehleringer, 1997; Leffler and Enquist, 2002). Leaf $\delta^{13}C$ values enable the prediction of an average ratio of internal to external CO_2 concentration during a leaf's life-time which can be further interpreted with respect to the seasonal responses of the leaf gas exchange processes. The abundance of $\delta^{13}C$ in plants of the C_3-type photosynthesis depends on environmental variables such as CO_2 concentration in the air and its $\delta^{13}C$ content, CO_2 concentration in the leaf's intercellular spaces which in turn depends on physiological response of plant leaves to light, humidity and availability of moisture (Garten and Taylor, 1992; Damesin *et al.*, 1998).

Similar with the case of $\delta^{18}O$, there are contrasting reports in the literature with respect to $\delta^{13}C$ of phenological groups. Deciduous trees of tropical dry forests were reported to have less negative $\delta^{13}C$ and higher WUE than evergreen trees (Sobrado and Ehleringer, 1997; Hasselquist *et al.*, 2010). In contrast, in the deciduous temperate forest of East Tennessee a coniferous species was reported to have 2-3‰ less negative $\delta^{13}C$ than deciduous trees (Garten and Taylor, 1992). Also a study conducted in co-occurring tropical dry forest species of north-western Costa Rica revealed lack of significant $\delta^{13}C$ variation among evergreen and deciduous trees (Leffler and Enquist, 2002). These observations may underline the importance of the physiological response of plant species to the abiotic environment in comparison to genetically controlled attributes. Combining daily as well as seasonal water use characteristics of tree species with carbon gain through leaf gas exchange studies provide more comprehensive understanding about interspecies resource utilization patterns in an ecosystem.

1.3 Leaf gas exchange

Weather and environmental factors that temporally and spatially fluctuate in a forest could substantially affect physiology and, in particular, photosynthetic performance of trees. Seasonal and diurnal gas exchange characteristics of tree leaves depend on several abiotic environmental factors such as light, temperature, leaf to air vapor pressure difference, and soil moisture (Eamus *et al.*, 1999; Tucci *et al.,* 2010; Markesteijn *et al.,* 2011). Tropical forests form heterogeneous functional groups (Han *et al.,* 2010) that may show different leaf gas exchange responses to abiotic environmental conditions (Borchert, 1994; Brodribb *et al.*, 2002, Han *et al.,* 2010; Markesteijn *et al.*, 2011). These variations determine the pattern of inter-species competition for limited resources and the performance with respect to carbon gain (growth and productivity). However, to maintain stable coexistence through balanced resource utilization coexisting tree species may show diverse gas exchange strategies that allow access to different temporal and spatial niches (Hoelscher *et al.*, 2006).

The niche and ecological drift hypotheses are among widely recognized explanations of stable plant coexistence (Wright, 2002; Silvertown, 2004). Ecological niche theory suggests that a number of species coexist when there is a variation in resources through space at any point in time or through time at any point in space (Wright, 2002). It has also been well recognized that resource partitioning by exploiting differing niches stabilizes coexistence by causing species to limit themselves more than they limit their competitors (Chesson, 2000). Recent studies suggest that coexisting plant species segregate along gradients of various environmental niche axes (Araya *et al.*, 2011; Penuelas *et al.,* 2011). By occupying temporal niche axes along a resource gradient, each species may experience specific environmental conditions that favor carbon gain and growth in comparison to other species. Thus, species differing in seasonal photosynthetic rate may show temporal partitioning of resource utilization which ultimately stabilizes species coexistence (Lovelock and Feller, 2003).

1.4 Past research and gaps

Tropical tree phenology has emerged as an important area of research, not only because of its relevance with structure and function of ecosystems, but also because of its significance with respect to monitoring, modeling and predicting adverse impacts of global climate change (Singh and Kushwaha, 2005). The variation in climate seasonality and species composition of tropical forests resulted in distinct pattern of vegetative and reproductive phenology, both on large and small geographic scales (Morellato *et al.*, 2000). Several studies reported environmental triggers of phenological events. For instance, tropical deciduous forests of Costa Rica (Reich and Borchert, 1982); dry monsoon forests of Thailand (Elliott *et al.*, 2006); subtropical rainforest of Mexico (Espinosa *et al.*, 2006); dry forests of Western Brazil (Ragusa and Silva, 2007); seasonal tropical forests of Thailand (Williams *et al.*, 2008) and montane rain forest of southern Ecuador (Cueva *et al.,* 2006). Likewise, in Africa, studies were conducted in deciduous forests of Senegal (Do *et al.*, 2005) and in the tropical forests of Accra plains, Ghana (Lieberman, 1982). Similarly, in Afromontane forests of Ethiopia, Getachew Tesfaye *et al.* (2007) reported the reproductive phenology of seven indigenous species together with leaf phenology of two deciduous trees. Despite these advances, quantitative information on foliage dynamics, leaf life history, leaf traits and seasonal growth pattern from comparative studies of functional types of tress in Afromontane forests is scarce.

Seasonally dry tropical forests are characterized by pronounced seasonality in rainfall resulting in seasonal variation in soil water availability (Hasselquist *et al.,* 2010). Trees of differing functional types could have different responses to changes in abiotic conditions that can be reflected in their water relation characteristics. Several studies conducted in tropical forests addressed different plant water relation aspects of coexisting species (Sobrado, 1986, Jackson *et al.*, 1995; Stratton *et al.*, 2000; Sobrado, 2003; Meinzer et *al.*, 2004; Querejeta *et al.*, 2007). In the montane forests of Munessa, Masresha Fetene and Beck (2004); Lüttge *et al.* (2003), Fritzsche *et al.* (2006) investigated water relation characteristics of some indigenous trees mainly in comparison with exotic trees. Recently, Strobl (2012) compared the water relation characters of selected indigenous trees grown under the canopy of exotic plantations and the natural forest. However, the strategies by which coexisting functional types of trees of the Munessa Forest survive under the seasonal drought have not been comprehensively studied. Different strategies to overcome seasonal moisture limitations (Hasselquist *et al.,* 2010) decrease inter-species competition and favor species coexistence. Furthermore, coexistence among functional types of trees can be better understood by investigating their mode of water acquisition and utilization when exposed to varying soil moisture condition. Nevertheless, comparative assessment addressing these aspects of coexisting functional types of trees of the Munessa Forest is still missing.

Numerous previous studies documented that different gas exchange related leaf traits of temperate, subtropical and wet tropical forest trees may differ in their response to seasonal and diurnal rhythms of environmental conditions (Reich *et al.,* 1995; Mulkey *et al.*, 1996; Tucci *et al.,* 2010). However, despite high functional diversity in the tropics (Mulkey *et al.,* 1996) information on seasonal gas exchange characteristics of differing functional types of African tropical montane trees is lacking (Eamus *et al.,* 1999; Motzer *et al.*, 2005). There are only a few gas exchange studies conducted to investigate indigenous trees of Munessa Forest (Lüttge *et al.,* 2003; Strobl *et al.*, 2011). However, there is no comparative information on the diurnal as well as seasonal pattern of the leaf gas exchange characteristics with respect to coexistence of different functional types of trees.

Studies revealed that lack of science-directed management plan constrained previous efforts of rehabilitating degraded forests of Ethiopia (EFAP, 1994). Seed regeneration ecology, recruitment, recolonization and seedling survival of some of coexisting species of Munessa Forest have been well documented (Mullugeta Lemenih *et al.*, 2004; Demel Teketay, 2005; Getachew Tesfaye *et al.*, 2011, Strobl *et al.*, 2011). Recently, as other components of the same project of this study, Yonas Yohannes *et al.* (2011) and Krepkowski *et al.* (2011) reported the seasonality of soil respiration and cambial properties of coexisting functional groups of the Munessa Forest. Despite its significance to sound management, however, comparative information on phenological and ecophysiological characteristics of coexisting functional types of trees of the Munessa Forest is still lacking. To address this gap a project "Coexistence of different functional types of indigenous trees of the Munessa Forest, Ethiopia: Carbon, water and nutrient relations" was implemented in the Munessa Forest as an integral component of the multi disciplinary project "Functional Ecology and Sustainable Management of the Munessa Forest, Ethiopia", which was funded by the German Research Foundation. It was hypothesized that species-specific foliage turnover, water use and carbon uptake strategies would have allowed a balanced resource use and stabilized coexistence of three indigenous tree species coexisting in the disturbed Natural Forest of Munessa. The project principally envisaged information on species-specific requirements; growth and performance strategies of the investigated tree species can be used for an ecologically sound reforestation program of a mixed forest. For the first time, as integral part of the overall project, this paper presents the foliage characteristics, leaf traits, water relation and leaf gas exchange aspects of three indigenous species representing three different functional types coexisting in the Munessa Forest. Of the three chapters of this thesis the first section is published as “Foliage dynamics, leaf traits, and growth of coexisting evergreen and deciduous trees in a tropical montane forest in Ethiopia” on Trees (2012) 26:1495-1512.

1.5 Objectives of the study

1.5.1 General objective

The general objective of this study was to investigate phenological, carbon and hydraulic relations of representative indigenous trees growing in the Munessa Natural Forest and identify the strategies enabled the coexistence of differing functional types of trees.

1.5.2 Specific objectives

Specific objectives of the study were to:

1. Monitor the annual course of foliage dynamics and identify the controlling factors for three different functional types of trees ,
2. Investigate ecophysiological traits of leaves and evaluate annual stem extension growth rate of three different functional types of trees ,
3. Evaluate interspecies and seasonal trends of whole tree water consumption and tree water status,
4. Evaluate stem water storage and water resource partitioning as ecophysiological strategies contributing to the coexistence of different functional types of trees ,

5. Determine integrated long term leaf gas exchange patterns of different functional types of trees and relate it with particular traits of water relations,
6. Examine CO_2 uptake and stomatal responses of different functional types of trees to gradients of light and soil moisture, particularly with respect to niche partitioning, and
7. Investigate seasonal trends of water use efficiency and evaluate its role in enabling coexistence of functional types of trees.

2 Materials and Methods

2.1 The study site

The research area is in the Munessa Shashemene Forest (7° 27' N and 38° 53'E) on the eastern escarpment of the East African Rift valley, 240 km south of Addis Ababa (Fig. 2.1.1). In this forest, large plantations of exotic trees alternate with patches of disturbed natural forest. The vegetation, characterized as semi-humid evergreen montane forest is dominated by canopy species such as *Podocarpus falcatus* (Thunb.) Mirb., *C. macrostachyus* Hochst. ex Del., *Olea europaea* ssp. cuspidata (Wall. Ex. DE) Cifferri, *Schefflera abyssinica* Harms, *Allophylus abyssinica* (Hochst.) Radlkofer, and the co-dominant *P. africana* (Hook.f.) Kalkm. (Asferachew Abate, 2004). According to Fritzsche *et al.* (2007), the soil of the study area has been characterized as Mollic Nitisol which is rich in most of the nutrients, except phosphate (Mullugeta Lemenih *et al.,* 2004). Site conditions are homogeneous with respect to water-transport-related parameters such as porosity, texture and bulk density (Yeshanew Ashagrie, 2005). Within the depth of 150 cm the bulk density of the soils in the natural forest ranges between 0.73-1.15 g cm^{-3} and the soil matric potential can reach -

50 KPa (Fritzsche *et al.*, 2006) during the dry season. Further details of the study area are described in Asferachew Abate (2004).

2.2 Study species

Three species representing different functional types on the basis of taxonomy and foliage phenology were selected for the study. The species are known for their significant economic and ecological roles (Getachew Tesfaye *et al.*, 2010). The three species represent the dominant functional types that coexist in the Munessa natural forest and are abundant at "Kuke" (local name of the research area, see Fig. 1). The studied species were *Podocarpus falcatus* (Thunb.) Mirb., *Prunus africana* (Hook.f.) Kalkm., and *Croton macrostachyus* Hochst. ex Del.

2.2.1 Podocarpus falcatus (Thunb.) Mirb.

Podocarpus falcatus (Thunb.) Mirb. (East African yellow wood, onwards referred to as "*P. falcatus*") is an evergreen Gymnosperm, up to 46 m in height (Fig 2.2.1 A). *P. falcatus* is a wind pollinated dioecious species (Legesse Negash, 2010) whose leaves are narrow (0.4 – 0.8 cm), shiny dark green, 2-6 cm long, gradually tapering towards both ends; young leaves are brighter giving a green flush (Azene Bekele *et al.,* 1993). The tree is found at altitudes between 1500 and 2600 m.a.s.l. in areas with an annual rainfall between 700 and 1500 mm and an average temperature between 15 and 20°C (Friis, 1992). Currently, *P. falcatus* is one of the most important indigenous trees of Ethiopia, which is, however, under severe human threat (Abdela Gure *et al.*, 2005). In Ethiopia the remnants of the *P. falcatus* forests were estimated as only 0.9% of the original area (Legesse Negash, 1995). It produces high-quality softwood and is therefore used for many purposes like timber, furniture and handicrafts. In some parts of the country oil from the seeds is used for cooking and medical purposes (Legesse

Negash, 2010). Because selective logging over decades has significantly devastated genetically superior *P. falcatus* trees, this keystone species needs urgent conservation and development measures.

Fig 2.1.1 Map showing the study site in the Munessa Shashemene Forest

2.2.2 Prunus africana (Hook.f.) Kalkm.

Prunus africana (Hook.f.) Kalkm. (Red stinkwood, Mueri, Bitter almond, African Cherry, Fig 2.2.1 B, onwards referred to as "*P. africana"*) is an evergreen broad-leaf tree in the Rosaceae, 10-24 (-36) m in height (Orwa *et al.,* 2009). *P. africana* produces small white flowers in elongated clusters developing into purple fleshy drupes, about 8 mm in length and 12 mm wide (Dalitz *et al*., 2011). *P. africana* is an important fruit-bearing tree in Afromontane forests providing a food source for endemic birds (Cunninghum and Mbenkum, 1993). Leaves are simple and alternate. When crushed, leaves, twigs, fruits, and bark emit a "cherry" odor which develops from cyanogenic glycosides (Stewart, 2003). Seeds germinate well under shady conditions, but saplings require light gaps for further growth (Tsingalia, 1989; Getachew Tesfaye, 2010). Annual height increment of *P. africana* seedling is quite variable (<3–8 cm year^{-1}, Hall *et al.* 2000). The species is considered late secondary species (Stewart, 2003).

P. africana occurs mainly in lower afromontane forests together with several other broad-leaf evergreen species (Hall *et al.,* 2000). The tree occurs at altitudes between 1000 and 2500 m.a.s.l. (Stewart, 2003) where annual rainfall is between 1000 to 2000 mm (Legesse Negash, 2010). Cameroon and Madagascar contain the largest populations of the species (Hall *et al.*, 2000). Because of its heavy, hard and compact red-brown wood it is preferred for heavy construction works (Legesse Negash, 2010). An extract of the bark of *P. africana* is used to treat benign prostatic hyperplasia (BPH), an increasingly common health problem of older men (Cunninghum and Mbenkum, 1993). For that purpose the bark is taken from wild *P. africana* populations in Afromontane forests of Cameroon, Zaire, Kenya and Madagascar. Bark or the processed extracts are exported to Europe (primarily to France or Italy) for preparation of the drugs sold under the brand-names "Tadenan" (France) or "Pygenil" (Italy) (Cunninghum and Mbenkum, 1993). This has resulted in severe destruction of *P. africana* forests. By 1995, because of the growing international demand for the bark, it was included as an endangered species in Appendix II of the Convention of International Trade in Endangered Species (Stewart, 2003). There is no information if and to what extent the bark of *P. africana* trees have been commercialized in Ethiopia (Legesse Negash, 2010). Nevertheless, severe depletion of *P. africana* forests of other East African countries and poverty coupled with lack of awareness in rural Ethiopia may attract and introduce commercialization of *P. africana* bark calling for a proactive conservation schemes. The opportunity associated with planting *P. africana* as an income generating item for Ethiopian farmers and its potential contribution in poverty reduction has to be emphasized.

2.2.3 Croton macrostachyus Hochst. ex Del

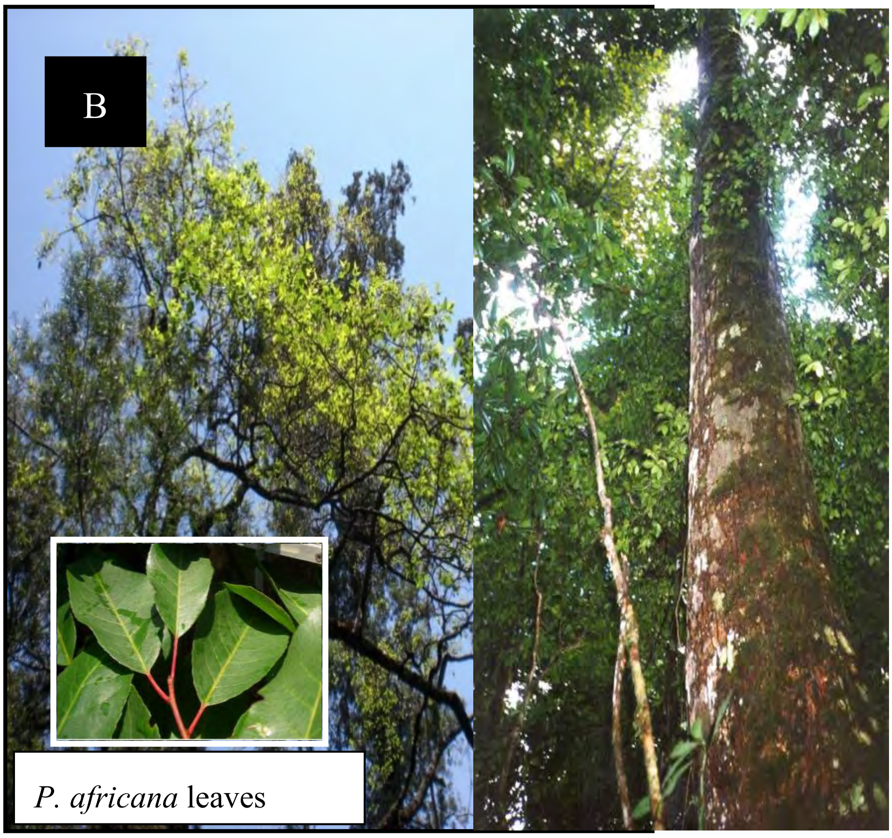
Croton macrostachyus Hochst. ex Del. (onwards referred to as "*C. macrostachyus* ") in the Euphorbiaceae is a facultatively deciduous tree up to 25 m high with an open, rounded crown (ICRAF, 2004, Noad and Birnie, 1989) (Fig 2.2.1 C). Flowers are creamy yellow, sweetly fragrant, in erect spikes of up to 25 cm in length (Dharani, 2002). It is an early successional pioneer species that grows not only in gaps of afromontane forests but also on montane wastelands (Getachew Tesfaye, 2007). *C. macrostachyus* is common in secondary forests, on forest edges along rivers, around lakes, in moist or dry evergreen upland forests, woodlands, wooded grasslands or clump bushland and along roadsides. It is associated with *Juniperus procera-P. falcatus* habitats and also occurs in the warmer parts of the montane rain forests and semi-tropical rain forests (ICRAF, 2004). The crown is rounded and open with large spreading branches. The bark of *C. macrostachyus* is pale gray or gray-brown, finely reticulate, fairly smooth, and finely fissured with age (Orwa *et al.,* 2009). The tree occurs at altitudes of 600-2500 m.a.s.l. with rainfall between 750 and 2000 mm (Dharani, 2002; Legesse Negash, 2010). Though it lacks hardness and toughness, it is used as a building material, for tool handles and saddles, for stool making and as timber (Burkill, 1985; Dharani, 2002; Legesse Negash, 2010). It is less desirable for fuel because of its bad smell and thick smoke (Legesse Negash, 2010). Implying its significance to the rural people, the tree possesses several traits of medicinal values. Its medicinal uses include antihelminthic treatments, cough, malaria, venereal diseases, blood clotting (Dharani, 2002). Moreover, this species is known not only for its use in apiculture but also its ecological roles in soil and water conservation, improving soil fertility by litter fall which provides mulch and green manure (ICRAF, 2004). A great potential of *C. macrostachyus* for sustainable beekeeping and honey production in Ethiopia has been emphasized (Legesse Negash, 2010). Moreover, owing to its un-palatability by both wild and domestic animals this species is a priority species for reforestation of degraded areas.

2.3 Climate

A climate station was established in the research station at Kuke in 2001. Over the last eight years (2001-2009) the mean annual rainfall was 1144 mm and the daily mean annual temperature was 15 °C (Strobl, 2012, Fig 2.3.1). As it is illustrated on the climadiagram the months from June to October represent the wet period while months from December to February are the driest months of the year. There is a considerable year to year and seasonal variation in the amount and distribution of rainfall in Ethiopia as a whole and the same holds true for the research site. Inter-annual changes result in a non-predictable variation of the length and timing of the dry period

Though the area has been reported to receive a bimodal rain fall (Fritzsche *et al.,* 2006), the data from the past eight years suggest lack of a clear demarcation for the short and long rainy seasons. During the two years of the study period rainfall, relative humidity, and temperature data were obtained from the research site's climate station (Pessl Instruments, Weiz, Austria), located at 100 m distance from the study plot. The climate station recorded hourly averages. Likewise, soil moisture data at 0.1 m depth were obtained from a climate station established in the natural forest in a distance of about 300 m from the investigated trees where soil water content was recorded by frequency-domain reflectometers (ECHO probe, Decagon Devices Inc., Pullman, WA, Yonnas Yohannes *et al.*, 2011).


A
P. falcatus leaves


B
P. africana leaves

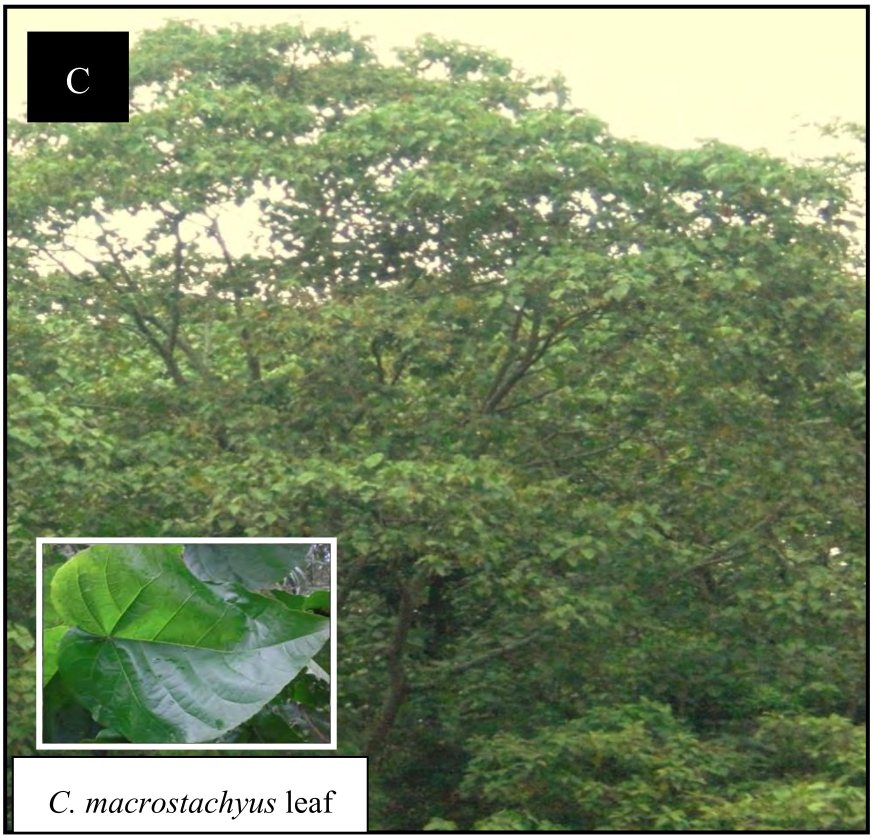


Fig 2.2.1 The studied trees and their leaves, (A) *P. falcatus*, (B) *P. africana*, (C) *C. macrostachyus. Photograph except the right side of P. africana is by Yigremachew seyoum (Y.S).*

2.4 Foliage turnover, leaf traits and growth

2.4.1 Investigation of the foliage status

Six individuals of each tree species were selected considering their representativeness in the area with respect to diameter class and height (Table 2.4.1). Foliage status of these trees was recorded monthly from February 2009 to January 2011 estimating the proportions of unfolding (light green), mature (dark green), senescent (yellow) and abscising (brown) leaves (Borchert *et al.,* 2002). The proportions of branches of the entire canopy that support foliages of different developmental status were estimated with a precision range of about 10% using a binocular. All observations were made by the same researcher (Y.S.), thus minimizing subjective estimation variability.

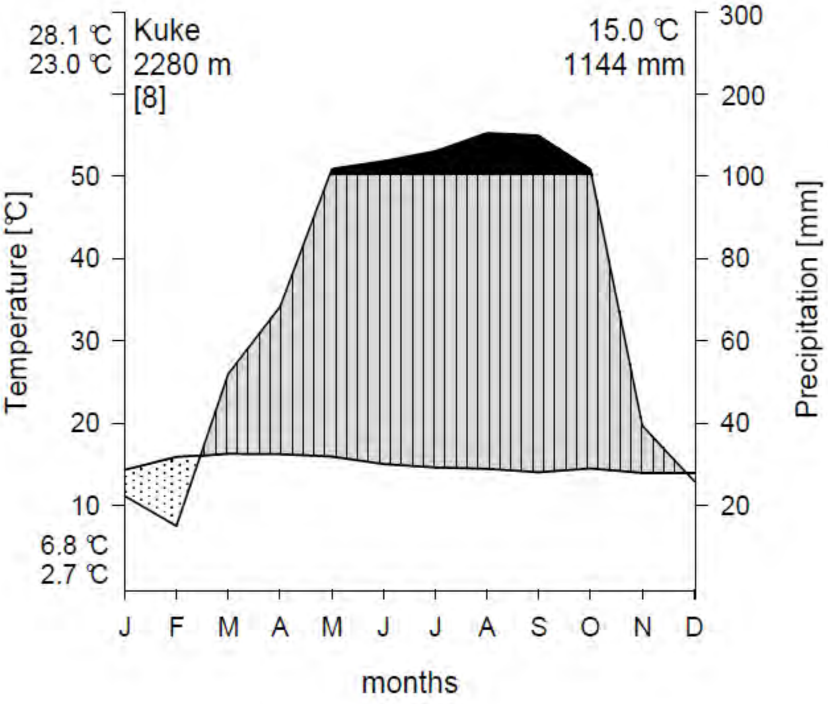


Fig 2.3.1 Climate diagram of the Munessa Forest (eight year averages 2001 to 2009 at Kuke climate station) (from Strobl *et al.*, 2011)

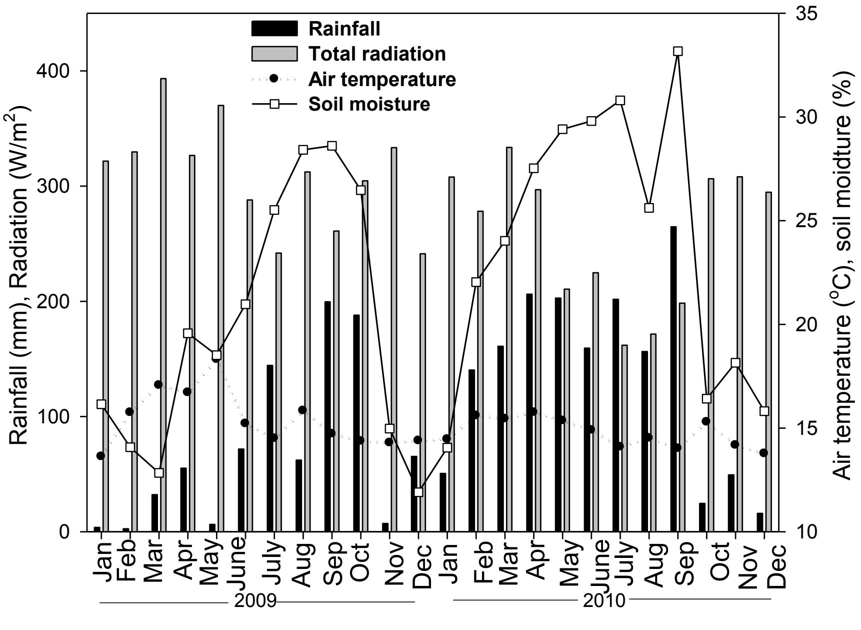


Fig 2.3.2 Weather condition and soil moisture in the Munessa Forest during the years 2009 and 2010.

Tble 2.4.1 Diameter at breast height (1.3 m) (cm) and height (m) of the six trees selected for foliage assessment.

Species	Parameter	Tree number					
		1	2	3	4	5	6
P. falcatus	Height (m)	6.30	5.40	5.00	14.90	10.50	18.00
	DBH (cm)	6.85	6.05	5.50	22.50	11.05	25.00
P. africana	Height (m)	10.00	7.25	6.00	20.00	24.00	32.00
	DBH (cm)	10.40	9.00	7.00	26.70	35.00	63.00
C. macrostachyus	Height (m)	10.00	12.80	10.80	18.20	23.50	25.00
	DBH (cm)	10.05	9.70	10.00	22.75	21.30	25.00

Fig 2.4.1 The crowns of the studied trees were accessed by a scaffold and a ladder. *Photo Y.S.*

2.4.2 Shoot foliage and leaf life-span

Shoot foliage status of each species was monitored on tagged twigs from 3 adult trees which belonged to the set of six selected trees for foliage observation in both years. On each tree 5-10 twigs were tagged. Twig-supporting branches were from top, middle and bottom positions in each cardinal direction of the crown. Crowns were accessed from scaffolds up to 20 m high or from a ladder (Fig 2.4.1). Leaf numbers on the twigs were recorded every two weeks. For recording leaf life-span twigs of additional 4 trees were also used in 2010. Individual leaves were tagged and leaf life-span was estimated from bud-break to fall, using 56, 47 and 89 tagged leaves of *P. falcatus*, *P. africana* and *C. macrostachyus*, respectively.

2.4.3 Leaf gas exchange

Measurements of CO_2 net exchange rate were made using the +Walz porometer GFS-3000 (Heinz Walz GmbH, Effeltrich, Germany) (Fig 2.4.2). Details of gas exchange measurement techniques are given in Section 2.6.1. The cuvette temperature was set to 20°C, reflecting the average of the ambient temperature during the measurements. Maximum rates of net CO_2 uptake (A_{max}) were determined at saturating light intensities which were 800 µmol PAR m^{-2} s^{-1} for *P. falcatus* and *P. africana,* and 1000 µmol PAR m^{-2} s^{-1} for *C. macrostachyus*. Dark respiration (R_{dark}) was determined after covering the leaf chamber with a black scotch-tape. Both types of measurements were conducted on 15 leaves of each species, five leaves from three individuals each. For each leaf, averages of A_{max} and R_{dark} were calculated from 3-5 stable measurements.

2.4.4 Specific leaf area (SLA)

Specific leaf area was determined at certain developmental stages. Nine to fifteen leaves were harvested from three individuals of each species at each time-point. Leaf area was measured with a leaf area meter (Am 100 ADC Ltd., England) and the weight was determined from the samples dried at 70°C to constant weight.

Fig 2.4.2 Porometer used to measure photosynthesis and dark respiration of the studied trees. *Photo Y.S.*

2.4.5 Stem extension growth

Four individuals of each tree species were equipped with plastic dendrometer bands (Grube KG, Bispingen, Germany) at 1.3 m stem height. Stem diameter increments were determined every six months during 2009 and 2010 and calculated as relative growth rates:

RGR (cm/month) = $(\ln DBH_2 - \ln DBH_1)/(t_2 - t_1)$ (Leicht *et al.*, 2005), where DBH_1 and DBH_2 were diameters at breast height at the first (t_1) and the subsequent (t_2) measurements.

2.5 Water relations

For the study of water relations three similar trees of each functional type were selected. Details of the studied trees are presented in table 2.5.1. The same trees were used to measure as many as possible water relation parameters.

Table 2.5.1 Description of individuals selected for water relation study of coexisting functional types in the Munessa Forest.

Species	Tree number	Height (m)	DBH (cm)	Sapwood area (cm^2)
P. falcatus	1	10	10.03	60.97
	2	12	11.91	75.18
	3	20	23.73	144.28
P. africana	1	10	10.19	44.13
	2	13	10.83	47.49
	3	32	63.69	405.36
C. macrostachyus	1	15	14.08	91.47
	2	14	13.38	87.54
	3	23	19.75	122.37

2.5.1 The Granier sap flux measuring system (Heat dissipation method)

The thermal heat dissipation method (TDP), after Granier (1985), was used to measure the flux of sap in trees. This is the most common technique to investigate whole tree water consumption (Fig 2.5.1). Granier's method is based on the insertion of heated and non heated probes (in flow direction) into the sapwood of the stem and the spreading of the heat in the stem which depends on the flux of the sap is measured. Each probe consists of a heating element (a copper-constantan thermocouple), with the thermo-couple tip located in the middle of the heating element (Fig 2.5.2). The voltage between the two thermocouples is measured after the application of heat

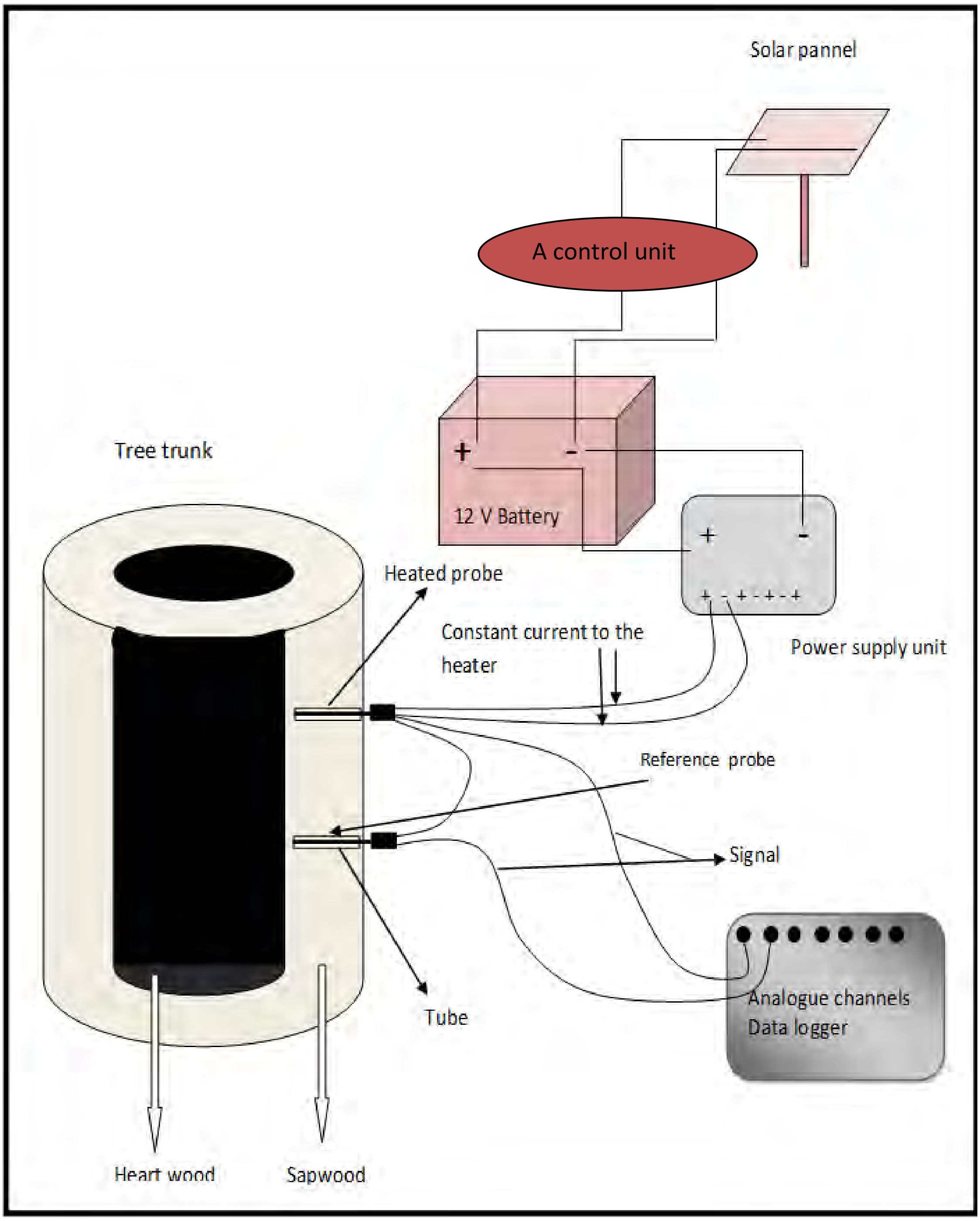


Fig 2.5.1 Schematic representation of the Granier's sap flux measuring system

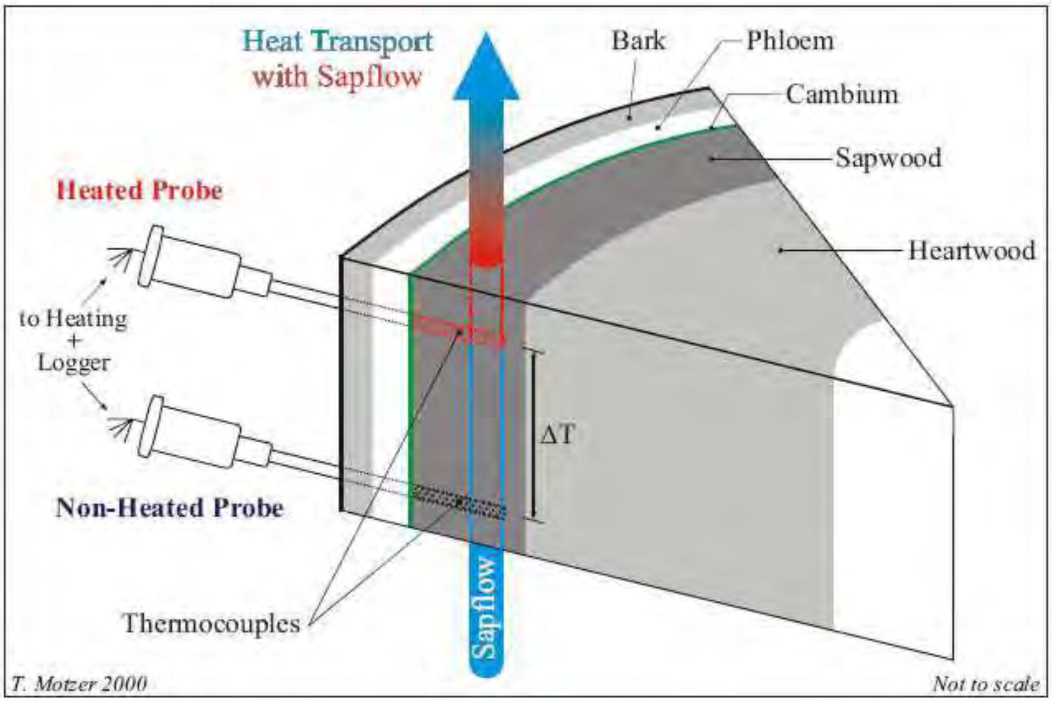


Fig 2.5.2 Schematic representation of Granier probes setup

pulses. The two needle-shaped sensors are positioned vertically 10-15 cm apart so that the temperature of the non heated needle matches that of the sapwood. The downstream (upper) probe is continuously heated at constant power (0.2 Watt) while the upstream (lower) probe is left unheated to measure the ambient temperature of the wood tissue and acts as a reference probe. Temperature difference between the two probes is under the influence of the sap flux in the vicinity of the heated probe.

The heated probe is supplied with a constant electric power and the temperature difference between the probes is monitored. Granier recommends an intensity of the electric current of 0.140 A (for an average of a conducting material with 10 Ω). The power of the heating element is about 0.20 Watts which raises its temperature by approximately 8 to 10^{o}C, when the sap flux is at or near zero. Since the Granier method determines stem flux solely from ΔT (temperature) constant power supply to the heating element is essential. The Granier system measures the electric potential difference (voltage difference) in μV (micro volt) between the two thermocouples (40 μV= 1^oC).

Thermal heat dissipation probes measures the sapwood heat dissipation, which increases with sap flow and the resulting cooling of the heat source, as the actual thermal conductance of sapwood increases with sap velocity. When the sap flux along the water transport path way is zero or minimal, the temperature difference (ΔT) between the two sensors is maximal. When the flow increases, this temperature difference decreases. This approach enables the measurement of sap flux from a known relation between ΔT and the sap flux. Granier defined a dimensionless "flow index" (U), calculated from the measured temperature difference and the maximum value thereof, occurring at zero flow velocity. He then established an empirical relation between the value of U and the actual sap flux. This exponential relation did not significantly differ among several tree species.

Granier defined the dimensionless flow index (U) as:

$$U = \frac{\Delta T^0_{max} - \Delta T^0_{act}}{\Delta T^0_{act}}$$

where $\Delta T^o{}_{max}$, is the maximum temperature difference reading. This value is often obtained during the period between midnight and pre-dawn since sap flow during this time is very little or zero. $\Delta T^o{}_{act}$, is a temperature difference reading at any given time. Sap flux can be normalized as “sap flux density” which is usually high at about noon and decreases in the course of the night. Granier found empirically that the average sap flux could be related to U by an exponential expression:

Sap flow density ($g\ m^{-2}s^{-1}$) = $119 * U^{1.231}$.

The thermal dissipation method suffers from two recognized sources of uncertainties that may result in erroneous sap flux estimation. First, the use of generalized calibration in establishing the temperature difference with the actual sap flux may over- or under-estimate the actual flux of a species. Second, what is being measured with the TDP method is an integral of the sap flux over the radial thickness of the sapwood. However, it is likely that there could be a mismatch between the length of the needle and the thickness of the sapwood. This also could lead to erroneous estimation. Calibrating and comparing the sap flux of trunks of trees under investigation solves the first uncertainty. Similarly, the second source of error can be minimized by identifying the depth of most active hydraulic part of the sapwood by differential tests along the radial profile of the sapwood. This can also be achieved by a prior dye experiment which shows the area of the most active part of the entire sapwood.

2.5.2 Basal and branch sap flux

The thermal heat dissipation method of Granier (1987) was used to monitor sap flow during the dry and wet season of 2010 (Fig 2.6.3). The sap flux sensors were installed at breast height (1.3 m) of the boles of three individuals of each species. For each tree three sensors were installed at different directions. Additionally, in order to assess the pattern of branch sap flux, upper branches (15-20 m) of one of the three individuals of each species were also equipped with sap flow sensors. Although a single branch does not seem to represent the flux of the branches in the entire crown, Phillips *et al.* (2003) showed the fairly uniform temporal pattern of within-crown flux compared to that of the bole. Crown flux that exceeded basal flux represents withdrawal of water from a reservoir in the stem, whereas basal flux that exceeded crown flux represented recharging of the reservoir.

Cylindrical aluminum tubes of 20 mm long were radially inserted into the stems or branches based on a prior experiment conducted to determine the most hydroactive zone of the sapwood of the studied trees. One probe was placed approximately 10 cm vertically above the other. The protruding parts of the three sensors were shielded to protect the probes from the external temperature fluctuations and insulated with 3 layers of aluminum foil (Fig 2.5.3 A). Constant power was applied to the heater and the difference in temperature between the two probes (ΔT) was recorded continuously every minute and averaged every 10 minutes (DL2; Delta-T Devices, Cambridge, UK) (Fig 2.5.3B). The sap flux density *Js* (g H_2O m^{-2} sapwood s^{-1}) is related to ΔT by: $Js = 119U^{1.231}$ (Granier, 1985) and $U = (\Delta T_0 – \Delta T) / \Delta T$. ΔT_0 is the value of ΔT, when there is no sap flow. It has been experimentally noted that the standard calibration developed by Granier (1985) gives reliable estimates of whole tree water use for several exotic and indigenous trees of Munessa but underestimates that of *P. falcatus* (Strobl, 2012). Hence, based on the regression developed for the actual water flow in the stem, the Granier calibration was further corrected using the relationship $Y = 1.2238X+1.3944$; where X is the flux estimated by the Granier calibration and Y is the corrected value.

The whole tree water use was determined by multiplying sap flux density by the hydroactive sapwood area (*Js* × sapwood area). Actively conducting sapwood areas of the studied trees were determined by a dying experiment performed on 15-20 individuals of differing diameter classes of each species (Meinzer *et al*., 2001). A dye (Fuchsin Acid solution 0.25% V/V; B.D.H Laboratory chemicals group, England) was injected into the boles of the trees through holes drilled (3-5 cm) by 5 mm core sampler (Fig. 2.5.3 C). The trees were injected at 1.3 m on three points in different directions. After 2 hours core samples were collected from 3-5 cm above the dye injection points (Fig. 2.5.3 D). The thickness of the core samples colored by the dye was used to calculate the area of the sap wood using a formula of concentric circles $(\prod R^{2}-\prod r^{2})$, where R and r are the radius of the big and small circles, respectively.

Fig 2.5.3 *P. falcatus* tree installed with Granier type sensors and wrapped with aluminum foil (A), sap flux DL2 datalogger (B), dye injection on *C. macrostachyus* tree (C) wood core samples being taken from injected tree of *C. macrostachyus* . *Photo Y.S and Getu Teshome.*

Based on the sapwood area of the examined trees, general relationships between sapwood area and DBH (Fig 2.5.4) were established and used to estimate actively conducting sapwood area of those trees on which sap flow was measured. Comparison of seasonal whole tree water use among functional types of trees was conducted on a representative tree of a size DBH=14 cm using a sapwood area extrapolated from the derived relationship.

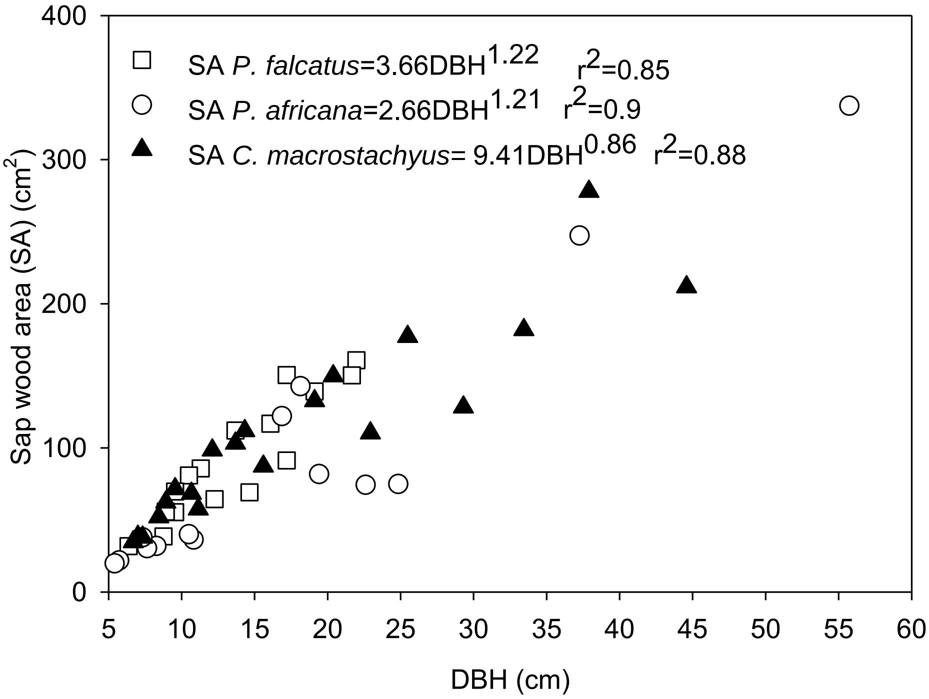


Fig 2.5.4 Sap wood area (SA) (cm^2) versus diameter (DBH) (cm) of sample trees in the Munessa Forest.

2.5.3 Leaf water potential

Midday (ψ_{midday}) and predawn ($\psi_{predawn}$) leaf/shoot water potentials were determined from 12 leaves collected from three individuals of each species in 2009 and 2010. Xylem water potential was measured using a pressure chamber (SKYE SKPM 1400, Germany) from shoots and leaf samples collected from the crowns (Scholander *et al.*, 1965) (Fig 2.5.5). Leaf samples were collected from branches approximately at similar height (10-15 m) and a similar direction of the crown. Well developed leaves or leafy twigs were collected at 4:30 Am and 1:00 Pm for $\psi_{predawn}$ and ψ_{midday} water potential measurements, respectively. During both investigation years wet and dry season measurements were conducted in January and August, respectively. From big branches collected from the crowns leaf petioles and twig samples were carefully cut under water to avoid embolism and immediately dried with tissue paper, kept in plastic bag and wrapped with aluminum foil during the measurement process.

Fig 2.5.5 The pressure chamber used to measure predawn and midday leaf water potential. *Photo Y.S and Getu Tadesse.*

2.5.4 $\delta^{18}O$ and $\delta^{13}C$ isotope signatures

Three adult trees of each species that were also used for sap flux and leaf water potential studies were selected for determination of the $\delta^{18}O$ signatures of soil and twig samples and $\delta^{13}C$ signatures of leaves. Samples were collected in triplicate from each tree after the rainy and the dry season for $\delta^{18}O$ analysis. Twigs were cut from the sun-crown and samples of 5 to 7 cm length were taken from leafless parts of the twigs. Soil samples were taken from 2 profiles per tree which were opened at the edge of the projected margin of the crowns of the sampled trees at 10 cm, 20 cm, 50 cm and 100 cm depths; samples from 200 cm depths were taken with an auger (Fig 2.5.6). Soil and twig samples were transferred into gas-tight vials, the atmosphere of which was exchanged by 1% CO_2 in Helium (Linde AG, Unterschleissheim, Germany) for direct equilibration with the sampled water (Scrimgeour, 1995). Samples were kept cold until measured. All measurements were conducted at the Centre for Environmental Research (UFZ) Halle-Leipzig with an isotope ratio mass spectrometer (IRMS, delta

S, Finnigan MAT, Bremen, Germany). Oxygen isotope ratios were expressed relative to the Vienna-Standard Mean Oceanic Water (VSMOW).

Similarly, 9 leaf samples for $\delta^{13}C$ analysis were collected from 3 individuals during the same period as for $\delta^{18}O$ samples from three different parts of the sun-crown. The dried plant material was ground with a ball mill (Retsch GmbH, Haan, Germany) and the $^{13}C/ ^{12}C$ isotope ratios were determined in the isotope laboratory of the Bayreuth Centre of Ecology and Environmental Research with an isotope ratio mass spectrometer (IRMS, delta S, Finnigan MAT, Bremen, Germany). Carbon isotope ratios are expressed in relation to the PeeDee Belemnite (PDB) standard (Ehleringer *et al.*, 1987). The average ratio of internal to external (atmospheric) CO_2 partial pressures during photosynthesis over the life time of the leaf sample (C_i/ C_a ratio) was calculated for each species from measured values of $\delta^{13}C$ following Farquhar *et al.* (1989). The relative contribution of the soil water along the soil depth was analysed using the IsoSource mixing model (Philips and Gregg, 2003).

Fig 2.5.6 Helpers opening a soil profile under a *C. macrostachyus* tree (A) and a profile ready for sampling (B). *Photo Y.S.*

2.6 Leaf gas exchange patterns of wet and dry days

2.6.1 Measurements of gas exchange

Gas exchange refers to the exchange of CO_2 and water vapor between plants and their immediate environment. Gas exchange measurement instruments are categorized in to open and closed systems. In open systems, measurements are carried out on the basis of the state of the incoming gas and after passing through the leaf specimen where the gas is then vented away (Fig 2.6.1). In closed systems, a gas sample is continuously circulated and measured over a period of time to establish rates of change in the parameters used. The gas exchange device used in the present study (Walz, GFS-3000, Heinz Walz GmbH, Effeltrich, Germany) (Fig 2.6.2) is an open gas exchange system. How gas exchange systems operate has been widely demonstrated and the principles of the GFS-3000 used in this work are schematically illustrated in Fig 2.6.1.

2.6.2 Gas exchange measurement in the 3 functional types of trees

In order to perform the measurements on homogenious conditions, northern sections of the crowns of adult trees were accessed using up to 20 m high scaffolds. Gas exchange kinetics of healthy leaves from the outer crown was measured.

The measuring head of the porometer was mounted on a tripod and leaves were inserted in leaf area adapters of 4 cm^2 (Fig 2.4.2). Because of their small sizes two leaves of *P. falcatus* were merged and inserted to completely cover the area of the leaf chamber. The measuring protocol was set to store data every minute while zero calibration of the infrared gas analyzer was performed every 20 minutes.

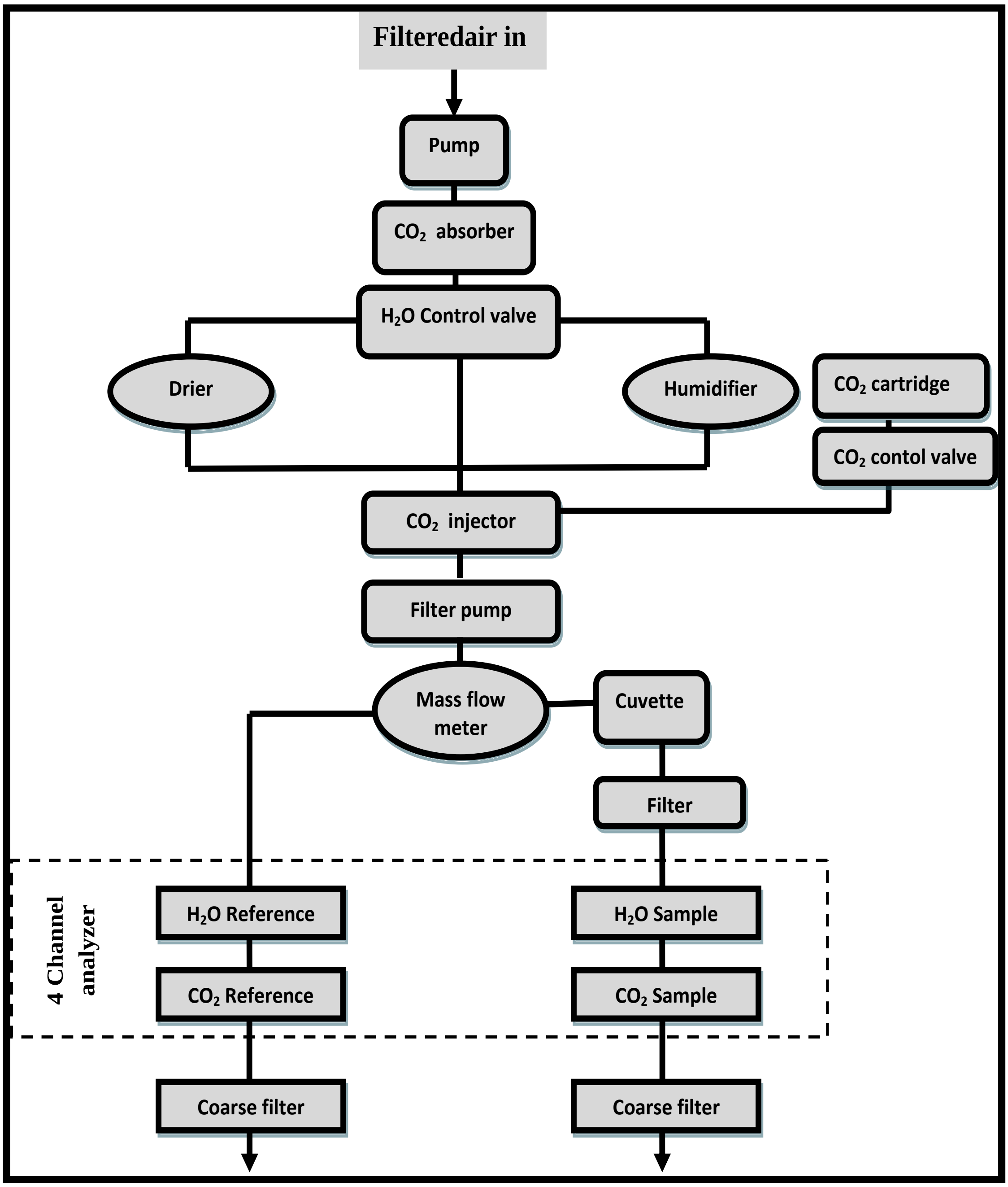


Fig 2.6.1 Principle of the GFS-3000 porometer in the CO_2 controlled mode (Walz 2007, modified sketch). When experiments made under ambient CO_2 concentration the path from the CO_2 cartridge is blocked by a solenoid pump and the CO_2 absorber must be replaced by another part termed “mixing volume 40 ml (3000-C/MV)”.

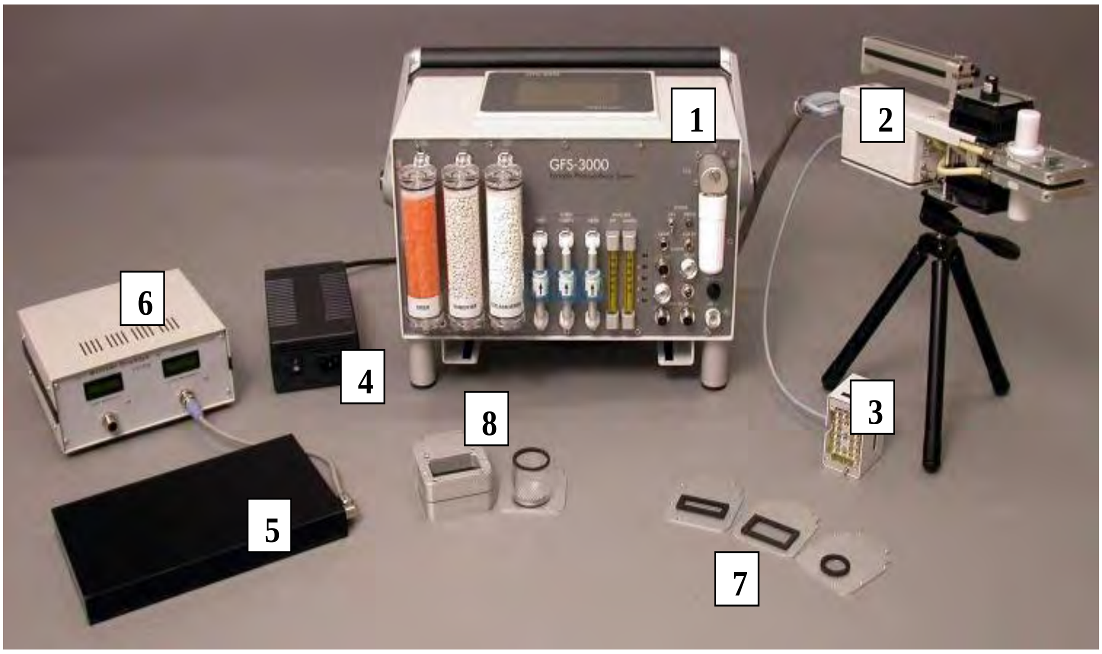


Fig 2.6.2 Overview of the essential components of GFS-3000

1. Control Unit 3000-C

2. Standard Measuring Head 3010-S

3. LED Light Source 3040-L

4. AC Power Supply 3020-N

5. Li-Ion Battery 3025-A

6. Li-Ion Battery Charger LC-03

7. Leaf Area Adapters

8. Cuvettes for Conifers or Lichens/Mosses

The measuring system stored several gas exchange parameters such as net CO_2 uptake (A_n), transpiration (E), stomatal conductance (gs), vapor pressure deficit (VPD), PAR (photosynthetically active radiation) over the entire light period of the day, from sunrise (6:30 Am) until sunset (6:00 Pm). A continuous supply of power to the porometer was achieved using two pairs of Li-Ion battery each with a power supply capacity of about 6 hours.

Because high scaffolds (up to 20 m) were necessary to get access to the crowns of adult trees, this study is a single tree assessment. Sites were selected where individuals of the three species grow in close vicinity and thus are typical for the situation in the forest. In order to compensate for shortcomings of replication, data collection was carried out during two years (2009 and 2010). During each year data were collected separately for dry and wet seasons. In 2009 wet season measurements were performed in August while dry season measurements were done in March. Likewise, in 2010 wet season measurements were performed at the end of September and beginning of October while dry season measurements were done in December. For each season and tree species a minimum of at least 3 daily courses were considered in each year.

2.6.3 Photosynthetic light response measurements

The photosynthetic light responses of leaves of the studied trees were examined during the wet season of 2010 using the auto programming facility of GFS-3000 in the mode of decreasing PAR intensities. Four to five healthy leaves were selected from accessible branches from each adult tree. Light intensities of 2000, 1750, 1500, 1250, 1000, 750, 500, 250, 100, 50, 25, 10 and 0 $\mu molm^{-2}s^{-1}$ were applied at the top of the cuvette using LED Light Source 3040-L,consisting of 24 red and 2 blue LEDs. Under each light level leaves were given 2 minutes to adapt to the new light intensity and afterwards three measurements, each for 20 seconds were stored. The averages of these three measurements were used in the calculation of photosynthetic light response of each leaf. A_{nmax} during extended dry period (January 2010) was determined in similar way from light saturation points of each tree species which were 500 µmol/m^{2}s for *P. falcatus*, and 500 µmolm^{-2}s^{-1} for both *P. africana* and *C. macrostachyus*. During an extended dry period most of the leaves of *C. macrostachyus* were senescing and finally shed. Temperature in the cuvette was set to 20°C while CO_2 concentration followed the ambient at 370±10 ppm.

2.6.4 Water use efficiencies

Water use efficiency (WUE) of the leaves was calculated from daily total A_n and daily total E. Hence WUE = $\frac{\text{An (mmol m}^{-2}\text{ day}^{-1})}{\text{E (mol m}^{-2}\text{ day}^{-1})}$

2.7 Statistical analyses

Except programs mentioned under specific studies all statistical anlyses were performed using SPSS version 13. ANOVA (Analysis of variance) was conducted to compare means of different parameters. To conform to the assumptions of ANOVA transformations were performed as necessary. When significant mean variations were detected by ANOVA, Tuckey's post hoc mean separation was applied. Variations in statistical analyses were considered significant at a level of $P \leq 0.05$.

2.7.1 Foliage turnover, leaf traits and growth

Circular statistics was used to analyze the timing of phenophases of the foliage (Morellato *et al.*, 2000; Williams *et al.*, 2008). A delay of 1 month was routinely allowed from the incidence of the environmental factor to the phenophase event.

Dates of phenological events were converted to angles using the formula:

$\mathrm{a}^{\mathrm{o}} = \frac{(360^{\mathrm{o}})\mathrm{X}}{\mathrm{K}}$ (Zar, 1996)

where a° is the angle representing the date of a particular phenophase, X is the month of observation (each month covering a circular scale of 30^{0} intervals, i.e. January 1 as 0^{o}, no.1, and December 1 as 330^{o}, no. 12) and k is the number of observations. The mean angle of each phenophase was calculated and converted to the date of the calendar. Moreover, the length of the vector (r) as a measure of the degree of concentration around the mean, i.e. synchronization, was also determined. A value of 1 means complete synchronization. The Rayleigh test (Z) for uniformity (Zar, 1996) was performed to determine whether mean angles of phenophases were uniformly distributed among observed individual trees (inter-individual synchronization). Likewise, intra-individual synchronization of the foliage of the tagged shoots of the individual trees was examined. Moreover, considering the fact that phenological events are time dependent data, time series analysis was employed. Autoregression analysis was performed and Prais-Winsten algorithm was used to transform the regression equation and remove autocorrelation of phenological events. In order to meet the stationary assumption of autoregression a lag transformation was performed with 1 order difference between pheonphases and climate variables. One-factor nested ANOVA was used to analyze ecophysiological traits in relation to leaf age. T-tests were also conducted to examine inter-annual variations in growth and foliage characteristics. The circular data was analyzed using version 4 of Oriana (Kovach Computing Services).

2.7.2 Water relations

ANOVA was performed to estimate the degree of variation in whole tree water use, leaf water potential, and $\delta\ ^{13}C$ values of the studied functional types of trees. Similarly, wet and dry season variability of these parameters was analysed using independent sample t-tests. Regression anlyses between DBH and sapwood area of the trees which was determined by dying experiment was performed by SigmaPlot for windows version 11.0; Systat software Inc.

2.7.3 Leaf gas exchange patterns of wet and dry days

T-tests were carried out to assess wet-to-dry season variations of gas exchange parameters. A_{nmax}, gs_{max} and WUE differences among functional types were analyzed using one way ANOVA. The patterns of relationships among the daily courses of different gas exchange parameters and environmental variables were estimated by regression analysis using (SigmaPlot for windows version 11.0; Systat software Inc.). Furthermore, regression analyses were performed to evaluate stomatal responses to different intensities of PAR.

3 Results

3.1 Foliage turnover, growth and leaf traits

3.1.1 Species specific response to climate variability

Because the tropical montane climate entails only little changes of the monthly temperatures over the year, plant leaf phenology is expected to respond in the first place to the seasonal distribution and amounts of precipitation. In the research area precipitation differed considerably between 2009 and 2010 and with it soil moisture (Fig 2.3.2). The dynamics of both variables were closely correlated over the 2 years. The short dry season in April and May failed completely in 2010 and precipitation was about 94% higher than in 2009 concomitantly with a 20% higher soil water content (Fig 2.3.2). Due to such variations phenological reactions of the trees cannot be predicted from one year to the other. Instead, the reactions to climate variability of the three representative species of the montane forest could be evaluated.

P. falcatus

The growth phase of an average leaf (2.5 cm^2) of *P. falcatus* was about 3 months (Table 3.1.1). Continuous leaf production by the *P. falcatus* trees held up for three months each in 2009 (July - September, maximum of soil moisture), and 2010 (March - May, identical soil moisture, but still increasing) when all 6 investigated trees synchronously developed new leaves (Table 3.1.2 and Fig. 3.1.1). In the course of the very humid year 2010, individual *P. falcatus* trees additionally produced leaves during short periods (August, October, and November) but not during the subsequent dry season 2010/2011 (Fig 3.1.2).

Table 3.1.1 Leaf area development (cm^2) of the three coexisting functional types of trees over the first 3 months. Values indicate means (n=15) while numbers in brackets represent ± S.E.

	Leaf age			
Species	<1mo	1mo	2mo	3mo
P. falcatus	1.62 (0.05)	2.04 (0.10)	1.95(0.09)	2.55(0.43)
P. africana	10.35(0.88)	21.15(1.76)	19.75(2.38)	19.47(4.67)
C. macrostachyus	29.05(2.23)	57.4(4.93)	140.18(14.32)	141.06(25.53)

The period of leaf flush during the first year was also reflected by the sudden increase in the number of leaves from 4 to 17 on the individually tagged shoots in July and August 2009 (Fig 3.1.3). The subsequent small decrease by 2 leaves per shoot indicated some leaf shedding towards the end of the year. In 2010 the main peak of leaf flush on the tagged shoots was overlaid by an enhanced rate of precocious leaf abscission as described below. At large, however, both first and peak flush were simultaneous and well synchronized between the individual trees (Table 3.1.2). In contrast, leaf flush on the examined twigs of individual trees was not strongly synchronized (r<1 for all trees for the peak of leaf flush) as observed for the individual trees though the events showed a uniform tendency (Table 3.1.3). Likewise, both first fall and peak fall were not completely synchronized among tree individuals in 2009. Thus inter-individual synchronization was high while intra-individual synchronization was low, as indicated also by high scattering of the leafiness data of the tagged twigs. With regard to the clear inter-individual synchronization of leaf production, autoregression analysis showed a significant impact of soil moisture only for the first year but not for the humid second year. Likewise, from the foliage data, leaf fall in 2009 was strongly and negatively associated with soil moisture while in 2010 air temperature and to some extent also radiation appeared to play a major role (Table 3.1.4).

Table 3.1.2 Circular statistics for major phenophases of the three coexisting functional types of trees of Munessa Forest in 2009 and 2010.

	P. falcatus				*P. africana*				*C. macrostachyus*			
	First flush	Peak flush	First fall	Peak fall	First flush	Peak flush	First fall	Peak fall	First flush	Peak flush	First fall	Peak fall
	2009											
Observations	6	6	6	6	6	6	6	6	6	6	6	6
Mean angle	210	240	10.89	10.89	90	297.11	128.8	230.6	120	180	60	60
Calendar date	Jul 30	Aug 30	Jan 10	Jan 10	Mar 30	Oct 27	May 09	Aug 21	Apr 30	Jun 30	Feb 30	Feb 30
Standard deviation			27.38	27.38	29.48	40.78	77.18	27.11		14.99		
Length of mean vector (r)	**1.00**	**1.00**	**0.89**	**0.89**	**0.87**	**0.77**	**0.4**	**0.89**	**1.00**	0.96	**1.00**	**1.00**
Rayleigh test (Z)	6	6	2.38	2.38	4.6	3.61	0.97	4.79	6	5.60	6	6
Rayleigh test (P)	**<0.00**	**<0.00**	**NS**	**NS**	**<0.00**	**<0.01**	**NS**	**<0.00**	**<0.00**	**<0.00**	**<0.00**	**<0.00**
	2010											
Observations	6	6	6	6	6	6	6	6	6	6	6	6
Mean angle	90	90	90	90	79.62	315	172.08	230.6	90	101.31	60	60
Calendar date	Mar 30	Mar 30	Mar 30	March 30	March 18	Nov 15	June 21	Aug 21	Mar 30	Apr 12	Feb 30	Feb 30
Standard deviation					20.75	12.34	56.74	27.11		31.54		
Length of mean vector (r)	**1.00**	**1.00**	**1.00**	**1.00**	**0.87**	**0.97**	**0.61**	**0.97**	**1.00**	0.96	**1.00**	**1.00**
Rayleigh test (Z)	6	6	6	6	5.26	5.72	2.25	5.72	6	4.43	6	6
Rayleigh test (P)	**<0.00**	**<0.00**	**<0.00**	**<0.00**	**<0.00**	**<0.00**	**NS**	**<0.00**	**<0.00**	**<0.00**	**<0.00**	**<0.00**

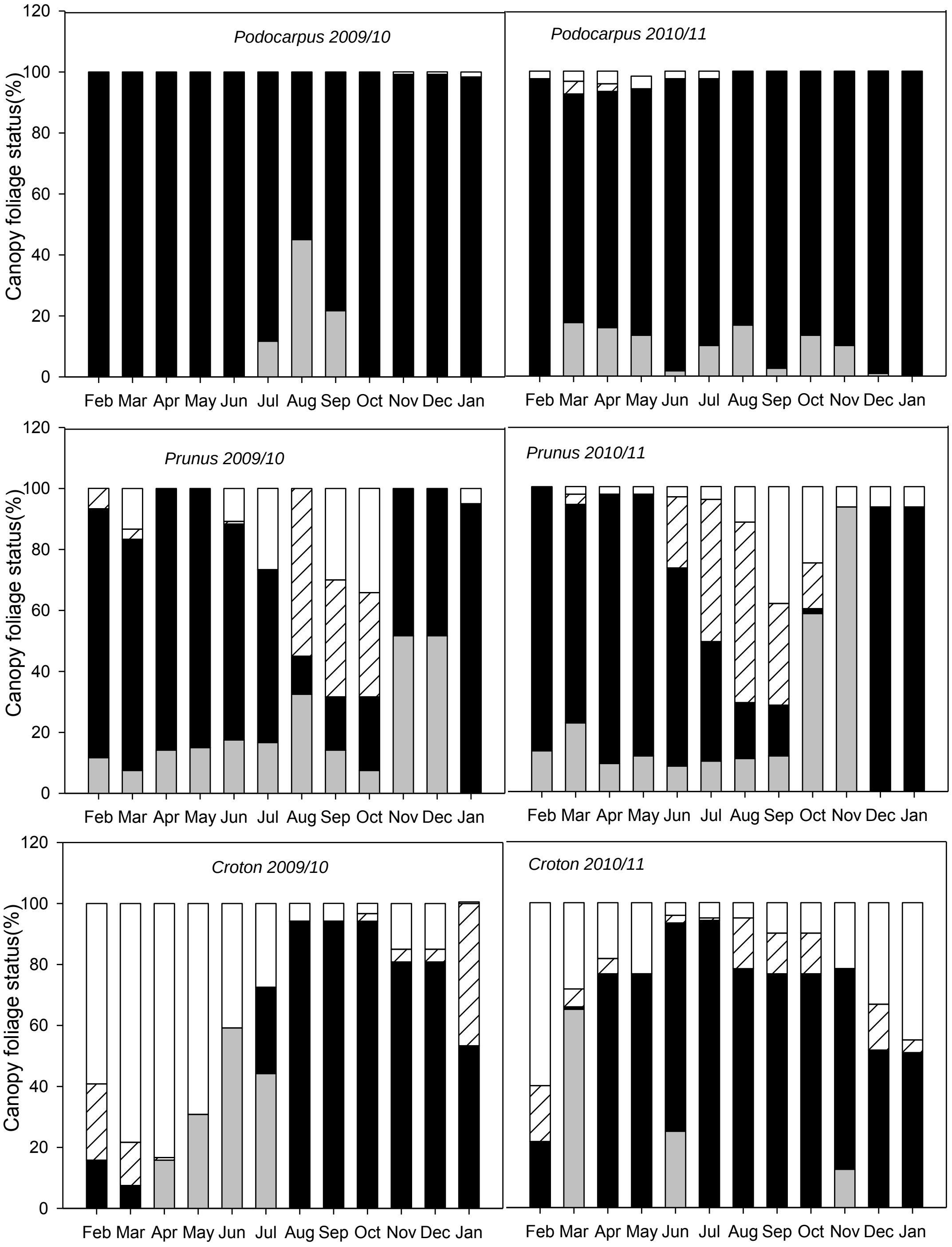


Fig 3.1.1 Dynamics of the foliage of the crowns of *P. falcatus*, *P. africana*, and *C. macrostachyus* during the years 2009 and 2010. The differentiated developmental stages of the foliage, presented as percent of the entire crowns were: Young leaves (sprouting, grey), mature leaves (black), senescing leaves (yellow leaves, hatched) and leafless (open). For each species 6 adult trees were investigated.

Examining the number of leaves on individual twigs revealed negative impact of temperature in 2009 and positive contribution of total radiation in 2010, with the corresponding model predicting only 43% and 37%, respectively of the variation in leafiness (Table 3.1.5).

Precocious leaf fall in 2010, as mentioned above, may have obscured the dynamics of leafiness on the twigs. It took place soon after unfolding of the new leaves and 95 percent of the abscised were young leaves which were shed shortly after unfolding. Apart from a loss of chlorophyll no obvious symptom could be observed, nor could an unusual microclimatic event be associated with that reaction of the trees. It should, however, be mentioned that precocious leaf shedding was observed on all investigated individuals and thus appears as a general phenomenon that requires in-depth studies. Part of the individually monitored leaves of *P. falcatus* remained healthy and green for the entire observation period suggesting a potential life-span of this evergreen gymnosperm that exceeds the two years of recording (Table 3.1.6). In general, *P. falcatus* maintained its foliage without remarkable thinning year-round as only 5-10% of the leaves appeared to become replaced year for year.

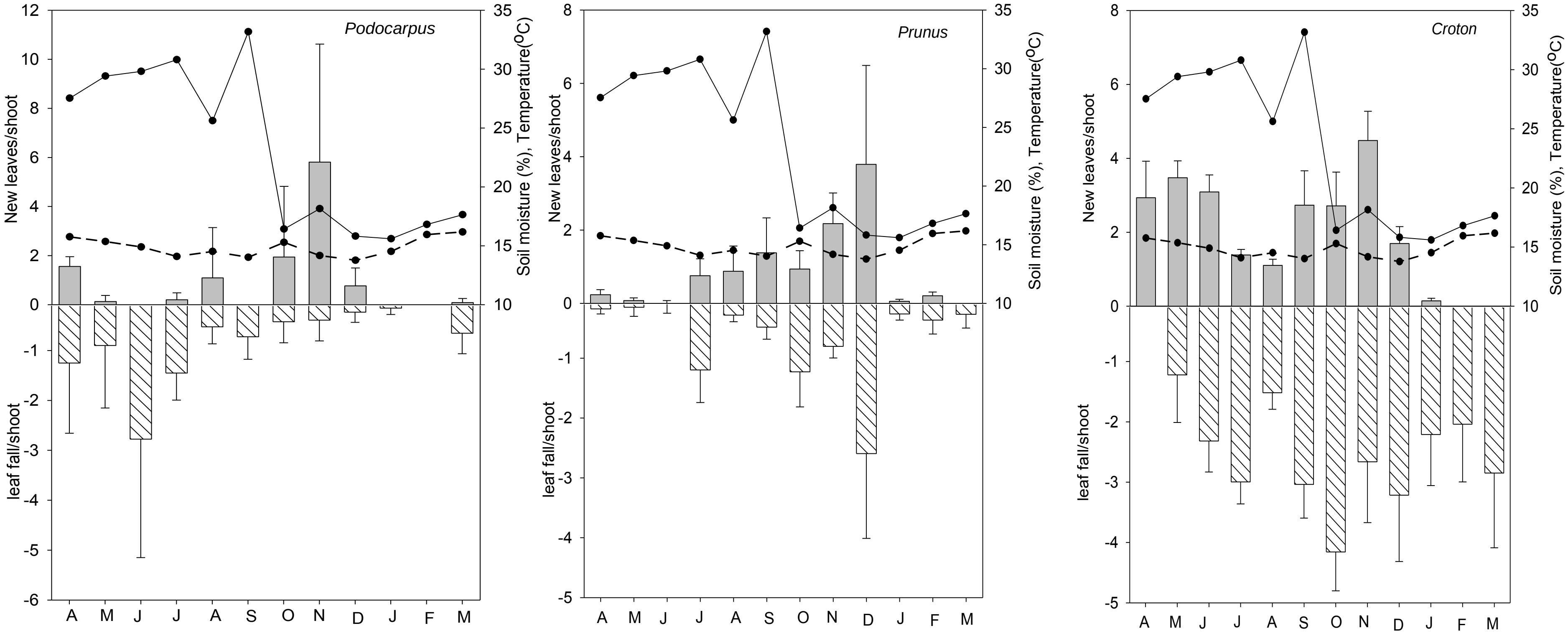


Fig 3.1.2 Leaf development and abscission dynamics of individually tagged shoots of the studied three coexisting species (*P. falcatus*, *P. africana*, and *C. macrostachyus*) plotted with air temperature and soil moisture. For each species 6-10 shoots were tagged on 4 trees and individual leaves were monitored bimonthly from emergence to fall. Grey bars, mean leaf flush; hatched bars, mean leaf fall; dashed line, temperature; solid line, soil moisture.

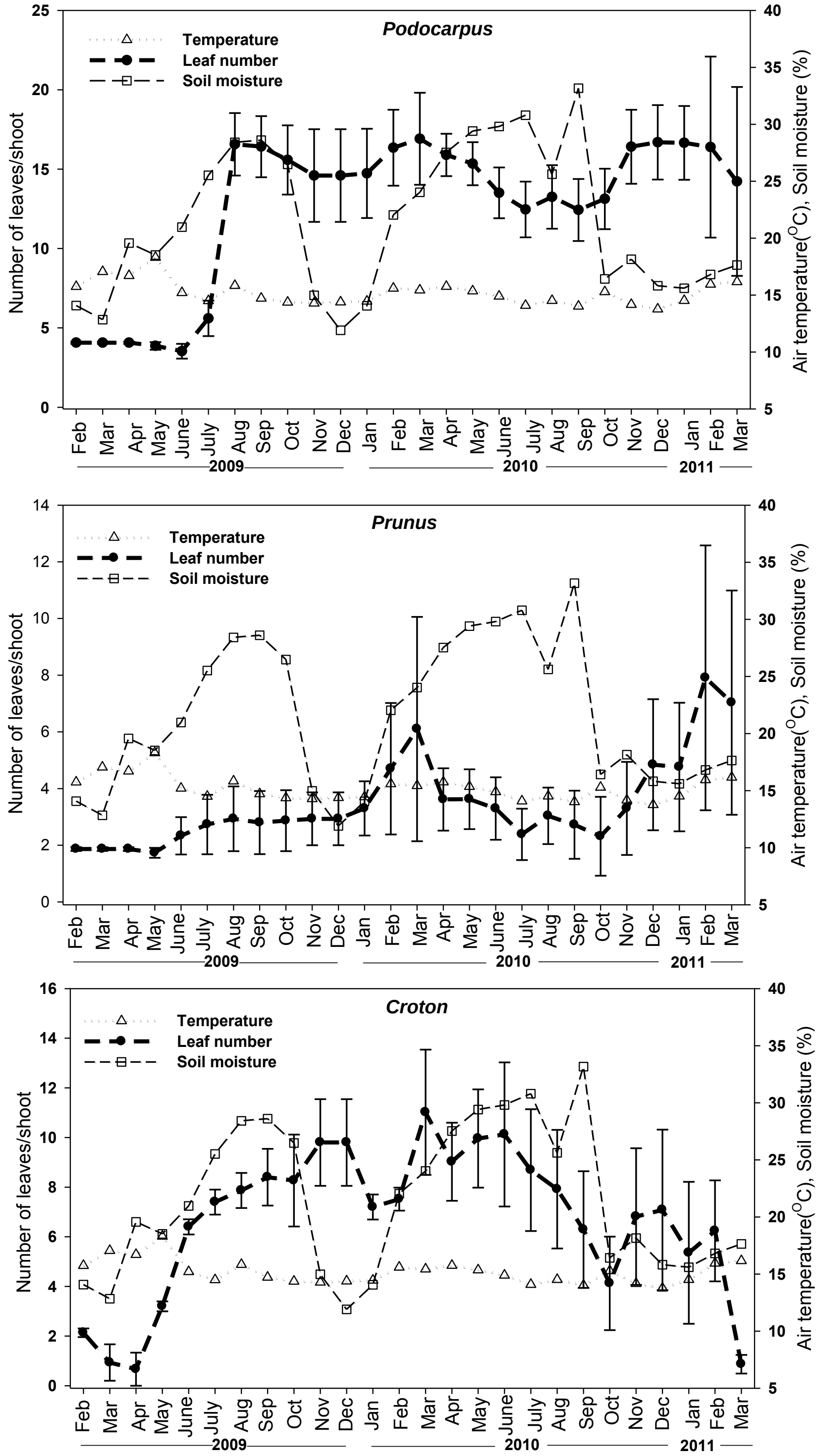


Fig 3.1.3 Monthly dynamics of leaf numbers (leafiness) on individual shoots of *P. falcatus, P. africana,* and *C. macrostachyus* with respect to monthly means of soil moisture and temperature, recorded for 2 years. Numbers of investigated twigs were 15 for all tree species during 2009 and 40 for *P. falcatus* and *P. africana,* and 36 for *C. macrostachyus* during the second year.

Table 3.1.3 Circular statistics for major phenophases of branches within individuals (intra-individual) trees of the three coexisting tree functional types of trees in Munessa Forest.

	Tree 1				Tree2				Tree3				Tree4			
	First flush	Peak flush	First fall	Peak fall	First flush	Peak flush	First fall	Peak fall	First flush	Peak flush	First fall	Peak fall	First flush	Peak flush	First fall	Peak fall
P. falcatus																
Observations	10	10	10	10	11	10	11	11	10	11	10	12	10	12	10	10
Mean angle	75	69.04	108.5	188.2	74.87	77.87	175.35	195.6	75	53.06	133.18	178.86	75	72.3	135	162.2
Standard deviation		31.56	26.94	45.15	32.7	35.45	39.78	46.25		53.13	37.38	58.49		50.9		67.35
Length of mean vector (r)	**1.00**	**0.85**	**0.89**	**0.73**	**0.85**	**0.82**	**0.78**	**0.72**	**1.00**	**0.65**	**0.8**	**0.59**	**1.00**	**0.67**	**1.00**	**0.50**
Rayleigh test(Z)	10	6.9	8.01	5.37	7.94	6.81	6.79	5.73	10	4.65	6.53	4.23	10	5.44	10	2.51
Rayleigh test (P)	**<0.00**	**<0.00**	**<0.00**	**<0.00**	**<0.00**	**<0.00**	**<0.00**	**<0.00**	**<0.00**	**<0.00**	**<0.00**	**=0.01**	**<0.00**	**<0.00**	**<0.00**	**NS**
P. africana																
Observations	10	10	10	10	10	10	10	10	9	9	9	10	10	10	10	11
Mean angle	75	350.13	218.88	350.88	75	229	179.95	0	75	10.27	211.46	270.28	81.36	339.2	153.31	108.93
Standard deviation		44.31	70.98	51.69		73.8	31.25				52.14	34.66	42.52	71.36	75.44	90.3
Length of mean vector (r)	**1.00**	**0.74**	**0.46**	**0.66**	**1.00**	**0.43**	**0.86**	**1.00**	**1.00**	**0.57**	**0.66**	**0.833**	**0.75**	**0.46**	**0.42**	**0.28**
Rayleigh test (Z)	10	5.49	2.15	4.43	10	1.9	7.42	10	9	2.97	3.93	6.93	5.76	2.11	1.76	0.91
Rayleigh test (P)	**<0.00**	**<0.00**	**NS**	**<0.00**	**<0.00**	**NS**	**<0.00**	**<0.00**	**<0.00**	**0.04**	**0.015**	**<0.00**	**0.00**	**NS**	**NS**	**NS**
C. macrostachyus																
Observations	6	6	6	8	10	13	10	14	12	11	10	12	10	10	8	9
Mean angle	75	100.4	148.9	232.2	75	317.4	162.9	163.09	75	262	180.9	258.58	75	107.9	156.03	314
Standard deviation		84.18	14.02	73.62		100.9		117.37		75.4	31.77	75.58		86	12.09	76.81
Length of mean vector (r)	**1.00**	**0.34**	**0.971**	**0.43**	**1.00**	**0.21**	**1.00**	**0.123**	**1.00**	**0.42**	**0.85**	**0.41**	**1.00**	**0.32**	**0.97**	**0.4**
Rayleigh test (Z)	6	0.69	5.65	1.53	10	0.58	10	0.211	12	1.94	7.35	2.106	10	1.04	7.65	1.49
Rayleigh test (P)	**<0.00**	**NS**	**<0.00**	**NS**	**<0.00**	**<0.00**	**<0.00**	**NS**	**<0.00**	**NS**	**<0.00**	**NS**	**<0.00**	**NS**	**<0.00**	**NS**

Table 3.1.4 Summary of multi variable autoregression of phenophases with climate variables and soil moisture during 2009 and 2010. A delay of 1 month was assumed between the climate variables and the phenophases.

Species	Phenophases	P-values of factors				Best model	R^2
		SM	T	RF	RD		
						2009	
P. falcatus	Leaf flush	0.013				0.097(SM)-1.524	0.55
	Leaf fall	0.006			0.012	-0.006(SM)-0.001(RD)+0.383	0.77
P. africana	Leaf flush	0.159			0.018	-0.036(SM)-0.009(RD)+4.470	0.6
	Leaf fall	0.062	0.009		0.021	0.098(SM)-1.036(T)+0.24(RD)	0.75
C. macrostachyus	Leaf flush	0.039		0.064	0.166	0.172(SM)-0.016(RF)-0.011(RD)+1.973	0.58
	Leaf fall	0.352	0.169			0.281(T)-0.047(SM)-1.197	0.4
						2010	
P. falcatus	Leaf flush	0.21				0.031(SM)-0.144	0.16
	Leaf fall		0.006		0.045	0.418(T)-0.004(RD)-4.789	0.65
P. africana	Leaf flush	0.21	0.005		0.007	0.066(SM)-1.171(T)+0.017(RD)+20.64	0.80
	Leaf fall					NS	
C. macrostachyus	Leaf flush					NS	
	Leaf fall				0.024	0.01(RD)-1.015	0.41

Note: SM-Soil moisture, T-air temperature, RF-rainfall and RD-total radiation. P-values are not shown for variables that do not contribute to explain the dependent variable. NS shows that the indicated factors are too weak for being used for predicting phenophases

P. africana

Compared to the evergreen gymnosperm *P. falcatus* the evergreen broad leaf species *P. africana* produced less leaves during both years (Table 3.1.7). Sprouting and extension growth of the 20 cm^2 large *P. africana* leaf took about 1 month (Table 3.1.1). In this species a basic rate of leaf production was observed over 8-9 months per year, overtopped by higher rates during 2 months at the transition from the wet to the dry season (Fig 3.1.1). A similar, though less sharp annual pattern was recorded for leaf fall during the wettest period of the years.

Table 3.1.5 Summary of multi variable autoregression of leaf numbers on tagged shoot with climate variables and soil moisture during 2009 and 2010. A delay of 1 month was assumed between the climate variables and the phenophases.

Species	P-values of factors				Best model	R^2
	SM	T	RF	RD		
					2009	
P. falcatus		0.037			-2.85(T)+53.15	0.43
P. africana		0.019			0.262(T)+6.46	0.51
C. macrostachyus		0.001			-2.368(T)+42.26	0.83
					2010	
P. falcatus	0.16			0.029	0.133(SM)+0.023(RD)+5.72	0.37
P. africana	0.045			0.017	0.016(RD)+0.126(SM)-3.52	0.45
C. macrostachyus		0.12		0.014	1.19(T)-0.022(RD)	0.47

Note: SM-Soil moisture, T-air temperature, RF-rainfall and RD-total radiation. P-values are not shown for variables that do not contribute to explain the dependent variable.

Table 3.1.6 Leaf life spans of the three coexisting functional types of trees.

Species	No of trees	No of shoots	No of leaves	LLS	S.E
P. falcatus	4	19	56	> 2 years	
P. africana	4	20	47	178 days	16
C. macrostachyus	4	25	89	85 days	4

As inferred from lower r values and high circular standard deviations, dates of first and peak flushing were not strongly synchronized between individuals (Table 3.1.2). A slight increase of the leafiness of the tagged twigs was observed during the first phase of the long rains from May to August 2009. A second boost of leaf formation was recorded four months later during the short and relatively humid dry period from December 2009 to March 2010. Thereafter, leaf number decreased during the following wet season. A third wave of leaf production commenced at the end of the wet season in October 2010, and extended into the next dry season.

Table 3.1.7 Mean numbers of leaves per individually tagged shoot of the three coexisting tree species in the Munessa Forest.

Species	Growing period	
	Jan 2009-Feb 2010 (13 months)	February 2010-March 2011 (14 months)
P. falcatus	10.31 (1.64) C	14.87 (0.482) D
P. africana	2.68 (0.0003) E	4.22 (0.0021) F
C. macrostachyus	6.12 (0.89) A	7.19 (0.76) A

Means followed by similar uppercase letters are statistically not different with respect to the growing periods for a given species at P≤0.05. Values in bracket represent ±S.E.

Table 3.1.8 Annual total mean leaf production and abscission per shoot in 2010/11.

Tree species	leaf production	Leaf fall
P. falcatus	11.49	8.84
P. africana	10.47	7.56
C. macrostachyus	23.74	28.22

While autoregression model (Table 3.1.4) using soil moisture and total radiation as factors explaining leaf flush by 60% in 2009, a model that included temperature could explain 80% of leaf flush in 2010 (Table 3.1.4). Likewise, leaf fall was predicted particularly by low air temperature and to some extent by total radiation in 2009, whereas no variable could significantly predict it in 2010. This is most probably due to a serious fungal infestation (Fig 3.1.4) of more than 80% of the *P. africana* leaves during that year. Due to an annually changing extent of the pathogen attack, the degree of synchronization of the foliage phenophases of *P. africana* changed from year to year as in November 2010 more than 90% of the twigs of the crowns had produced new leaves (after the heavily attacked leaves had been shed) while in the drier year 2009 fungal attack was less serious and only 50% of the foliage was subsequently replaced by young leaves. Irrespective of an annual variation of the biotic (the fungal infestation) events or the effects of abiotic environmental factors, the dynamics of the entire foliage suggested a turnover by which it was replaced at least once per year. This idea is corroborated by the average life-span of 6 months of the leaves (Table 3.1.6). Because production of new leaves was at minimum or even ceased during the dry months, at least part of the wave of leaf aging and abscission in July, August and September (Fig 3.1.1) may be attributable to the life-span of the leaves, i.e. to endogenous control.

Fig 3.1.4 Fungus attacked (shothole disease) leaves of *P. africana*

C. macrostachyus

In contrast to the 2 evergreen species, foliage dynamics of the facultative deciduous *C. macrostachyus* showed clear oscillations with a nearly leafless phase at the end of the dry season 2008/2009 (February, March), and a reduced foliage at the end of the dry seasons 2009/2010 and 2010/2011 (Fig 3.1.1). Especially the dry season 2009/2010 was very short and the trees maintained about 40% of their foliage. During both years leaf flush as well as leaf fall was strongly synchronized between the individual trees (Table 3.1.2). Development of a *C. macrostachyus* leaf with an average area of 140 cm^2 requires up to 2 months (Table 3.1.1). Leaf sprouting was preceded by leaf shedding during or at the end of the dry seasons (Fig 3.1.1).

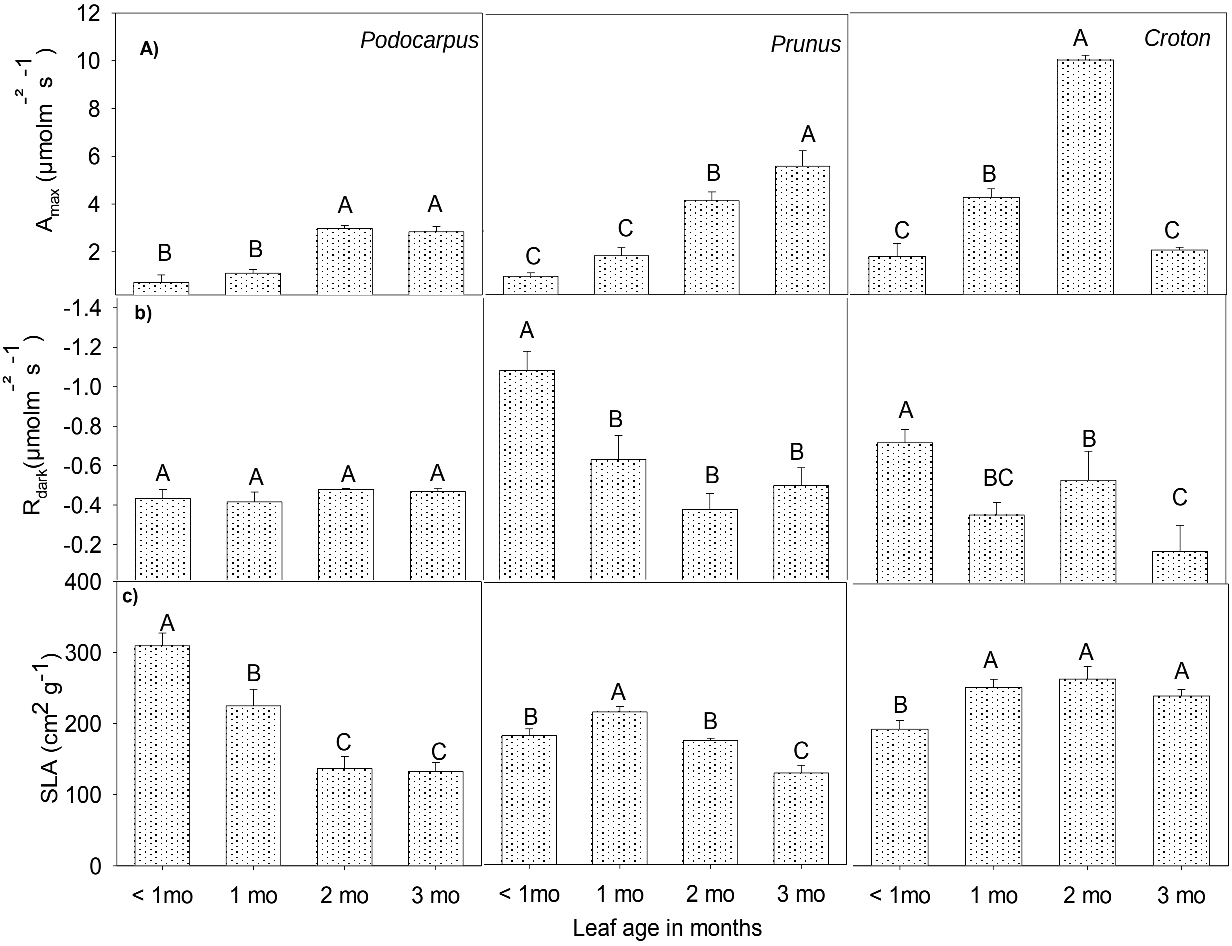


Fig 3.1.5 Ecophysiological traits of developing leaves of the three functional types of trees (*P. falcatus, P. africana and C. macrostachyus*) recorded for the first 3 months after sprouting: (A) Maximum assimilation rate under ambient conditions (A_{max}), (B) Dark respiration during the day (R_{dark}), and (C) Specific leaf area (SLA). Different letters indicate statistically significant differences ($P \leq 0.05$). Error bars represent standard errors.

When combining the environmental variables soil moisture, rainfall and total radiation in the model, leaf flush was fairly (58%) predictable, with soil moisture contributing a statistically significant share in 2009. However, no variable or combinations of variables explained leaf flushing in 2010 (Table 3.1.4). Leaf fall was only weakly (40%) predictable by soil moisture and temperature in 2009, whereas in 2010 only total radiation was correlated with leaf shedding.

Table 3.1.9 Nested ANOVA for some leaf traits of three coexisting functional types of trees in Munessa Forest

Species	Variables	Assimilation (A_{max})			Dark respiration (R_{dark})			Specific leaf area (SLA)		
		DF	F-value	Sig	DF	F-value	Sig	DF	F-value	Sig
P. falcatus	*Leaf age*	3	115	<0.000	3	2.10	0.155	3	126.49	<0.000
	Tree	2	9.00	0.002	2	3.08	0.067	2	5.39	0.011
	Leaf age (Tree)	6	2.76	0.030	4	1.34	0.283	6	2.32	0.061
	Leaf age(replicates)	12	0.82	0.630	9	0.71	0.725	14	0.62	0.829
P. africana	*Leaf age*	3	96.06	<0.000	3	28.39	<0.000	3	34.87	<0.000
	Tree	2	0.71	0.360	2	2.70	0.088	2	0.68	0.510
	Leaf age (Tree)	6	5.13	0.006	6	0.90	0.507	6	3.98	0.005
	Leaf age(replicates)	12	1.36	0.327	12	0.59	0.827	16	1.56	0.139
C. macrostachyus	*Leaf age*	3	133.80	<0.000	3	14.68	<0.000	3	7.84	0.002
	Tree	2	3.73	0.044	2	0.42	0.665	2	4.37	0.026
	Leaf age (Tree)	6	5.18	0.003	6	3.41	0.015	6	3.51	0.014
	Leaf age(replicates)	12	1.52	0.204	12	1.33	0.268	14	0.91	0.559

As shown in Fig (3.1.2) leaves were produced in a first flush from (March) April to June and a second flush from September to December while leaf fall was continuing from May 2010 until March 2011 with peaks in July and October. From July to March leaf fall exceeded leaf production, except November and therefore the total number of leaves on the tagged twigs decreased, again with the exception of November (Fig 3.1.2). Thus, considering the leafiness of the individual twigs, 2009 appeared as a year of foliage accumulation whereas in 2010 leaf abscission exceeded leaf production by about 15% (Fig 3.1.3 and Table 3.1.8).

3.1.2 Ecophysiological assessment of the leaf types of the investigated trees

Leaf traits are widely considered as indicators of the degree of adaptation of plants to their environment. In order to characterize the respective physiological traits of the leaves and to assess their significance for the performance of the trees the following three corner marks were measured over a period of 3 months following unfolding: Specific leaf area (SLA) as an indicator for leaf growth, maximal photosynthetic CO_2-net uptake for carbon assimilation and dark respiration (measured during day-time) for non-photosynthetic metabolic activity (Table 3.1.9 and Fig 3.1.5). SLA of *P. falcatus* leaves decreased until an age of 3 months, when the leaves had attained their final size (2.5 cm^2) and biomass. Leaf development is also reflected by the maximum rates of photosynthetic net CO_2 uptake which more than doubled until the end of the second month, attaining the known maximum rates of between 3 and 4 µmol CO_2 m^{-2} s^{-1} (Strobl *et al.,* 2011; Lüttge *et al.*, 2003). Dark respiration did not substantially change in the course of the three months. Transition from growth respiration to maintenance respiration was not accompanied by a change of the rate on the leaf area basis, whereas it was reflected by a decrease of 50% on the biomass basis. Specific leaf area of the much bigger *P. africana* leaves (20 cm^2) initially increased until the first month and then decreased continuously to a final value of 131 cm^2 g^{-1} which is similar to that of adult *P. falcatus* leaves (128 cm^2 g^{-1}, determined from a random sample). Thus development of an average *P. africana* leaf takes about 3 months. The rate of maximum photosynthesis of *P. africana* increases concomitantly with unfolding, attaining finally a significantly higher rate (~6 µmol CO_2 m^{-2}s^{-1}) than a *P. falcatus* leaf.

The rate of dark respiration clearly shows the transition from growth respiration to maintenance respiration after 2 months. It is assumed that these rates are typical of the adult leaves and may persist until senescence commences after 6 months. In contrast to both evergreens the corner marks of *C. macrostachyus* when recorded for three months, include both leaf development and senescence which is evident from the kinetics of photosynthetic CO_2 net uptake. This parameter increased to a maximum value above 10 µmol CO_2 m^{-2} s^{-1} until a leaf age of 2 months but subsequently strongly decreased, indicating rapid onset of senescence. Thus *C. macrostachyus* leaves do not maintain a longer phase of a high photosynthetic capacity. Pronounced dynamics in the development of the *C. macrostachyus* leaves is also reflected by the course of the dark respiration which changed from growth respiration to a period when growth and maintenance respiration overlap before a second peak indicated the onset of senescence. In contrast to the evergreens, specific leaf area of the mesic *C. macrostachyus* leaves increased during expansion. The small decrease observed with the 3 months old leaves is not statistically significant (Fig 3.1.5).

3.1.3 Stem growth

Stem growth expressed as relative rates of diameter increment at breast height, was recorded to compare annual growth of the three investigated tree species. Examination by t-tests showed that all investigated trees had considerably higher relative stem diameter growth rates during the second, humid year than during the first, drier year (Table 3.1.10). For *P. africana*, the difference in growth rates was biggest, however, due to a high statistical error, it was not significant. The data show that the annual growth rates were in the range known for tropical upland trees (Murphy and Lugo, 1986) and that the differences between the 3 species are small especially during the more humid year 2010. In principle all investigated functional tree species reacted positively to moisture (Table 3.1.10).

Table 3.1.10 Mean annual diameter relative growth rates (mm month^{-1}) of the three coexisting tree species in the Munessa Forest

Species	Growing period	
	Jan 2009-Feb 2010 (13 dry months)	February 2010-March 2011 (14 wet months)
P. falcatus	0.0150 (0.007) C	0.0450 (0.005) D
P. africana	0.0056 (0.003) E	0.0390 (0.021) E
C. macrostachyus	0.0124 (0.004) A	0.046(0.006) B

Means followed by similar uppercase letters are statistically not different with respect to the growing periods for a given species at P≤0.05.Values in bracket represent ±S.E.

3.2 Water relations

3.2.1 Seasonal variation in leaf water potential

Measurements of leaf water potential have been widely used as a proxy to estimate the daily and seasonal dynamics of plant water status. In this study leaf water potentials of the investigated functional tree types were estimated from samples collected on subsequent 2-3 typically representative dry and wet season days of 2009 and 2010. The wet season data was collected in August, when the area received the highest rainfall while the dry season measurements were conducted in January, which is a typical of the dry months. The investigated tree species showed different patterns of seasonal leaf water potential. The data collected during the two years are summarized in Table 3.2.1. The measured leaf water potentials were between -0.55 and -2.94 MPa and thus in the ranges known from other trees (Larcher, 2003). Expectedly, the potentials varied in the course of the day and with the seasons. Despite some inter-annual variations, most of the data show the expected trends, i.e. a decline of the leaf water potentials from predawn to midday and from the wet to the dry seasons. With respect to the daily fluctuations, irrespective of the seasons and the years, the mesic *C. macrostachyus* leaves showed the smallest variation in leaf water potential. The size of predawn to midday fluctuations of both sclerophyllous evergreens was statistically higher than the mesic *C. macrostachyus* (Table 3.2.1).

3.2.2 Seasonal sap flux and whole tree water use

For describing the kinetics of the flow of xylem sap through the stem of a tree the unit sap-flow density (g m^{-2} s^{-1}) is used which is spatially normalized for a direct measure of the flow rate. For an ecophysiological assessment, the total water consumption (gs^{-1}) of the investigated trees must be determined which can be calculated by multiplying sap-flow density by the area of the conducting sap-wood. For comparing the water relations of various tree species or functional types, both units can be used. Fig. 3.2.1 shows daily courses of sap-flow (as sap-flow densities) of the three investigated tree species on typical days of the dry and the rainy seasons. The data show that sap-flow is higher on a dry than on a rainy day, especially in *P. falcatus* and *C. macrostachyus,* and the difference was less pronounced in *P. africana*. After shedding the bulk of its foliage, the flow-rate in *C. macrostachyus* is only a small fraction (2-3 gm^{-2}) of that of the foliated tree and the temporal course does hardly show diurnal fluctuation.

Table 3.2.1 Leaf water potential (MPa) of three functional types of trees of Munessa Forest during wet and dry seasons of 2009 and 2010. Values represent mean of 12 leaves collected from 3 trees while values given in brackets show ±S.E. Mean values followed by uppercase letters are significantly different among functional types of trees while means followed by different lower case letters are significantly different between predawn and midday values within species and season.

Species	Wet season			Dry season		
	Predawn	Midday	Range	Predawn	midday	Range
			2010			
P. falcatus	-0.9(0.05)Aa	-1.01(0.06)Ba	0.12(0.1)AB	-1.53(0.11)Aa	-2.33(0.05)Ab	0.8(0.13)A
P. africana	-0.55(0.03)Bb	-0.98(0.12)Ba	0.43(0.13)A	-1.98(0.13)Ba	-2.37(0.11)Ab	0.38(0.14)A
C. macrostachyus	-0.63(0.02)Ba	-0.63(0.04)Aa	0.00(0.04)B	-2.94(0.10)Ca	-2.7(0.11)Ba	0.27(0.14)B
			2009			
P. falcatus	-0.58(0.027)Aa	-1.21(0.19)ABb	0.71(0.21)A	-0.88(0.04)Aa	-1.38(0.07)Ab	0.50(0.08)AB
P. africana	-1.44(0.20)Ba	-1.8(0.26)Ba	0.55(0.15)A	-1.07(0.07)ABa	-1.89(0.07)Bb	0.82(0.12)A
C. macrostachyus	-0.71(0.11)Aa	-0.91(0.06)Aa	0.23(0.09)A	-1.09(0.04)Ba	-1.32(0.05)Ab	0.23(0.07)B

Fig. 3.2.2 presents the actual water flow through the xylem of equal-sized individuals of the three functional types which in principle confirms the above mentioned water relations during the major seasons. It also shows the levels of daily water consumption of medium-sized trees which is in the range of 5-10 liters on a dry and 4-6 liters on a rainy day. Under wet season conditions water consumption of equal-sized individuals of the three species was similar but in the dry season *P. falcatus* as well as *C. macrostachyus* doubled their water demand.

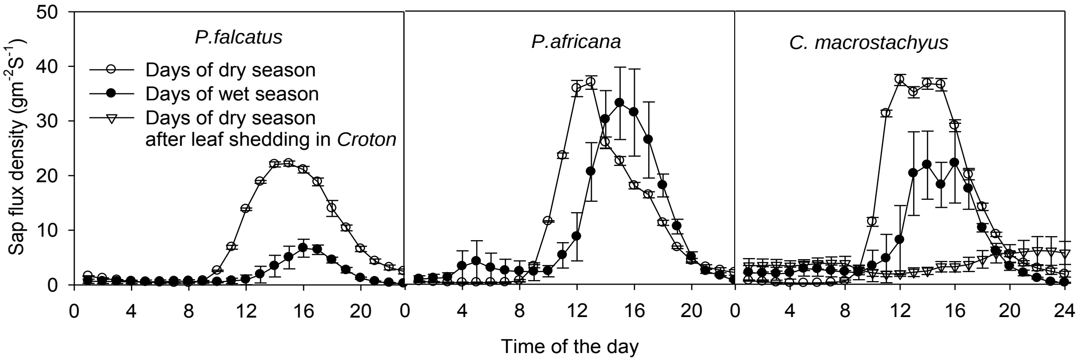


Fig 3.2.1 Diurnal pattern of sap flux density during 3 dry and wet season days of 2010 for the three functional types of trees (*P. falcatus, P. africana and C. macrostachyus*) coexisting in the Munessa Forest. The dry season days' data for the leaf shed *C. macrostachyus* tree was collected from 3 trees in 2009.

3.2.3 The dynamics of stem and branch sap flux

Transpiration is considered as the source of pressure gradient for xylem sap flow along the water transport path way. If trees conduct water storage in the axial tissues the three components of its water regime: transpiration, sap-flow in the branches and sap-flow in the stem should exhibit different time kinetics. In this section the diurnal kinetics of sap-flow densities in the stem and the lowermost big branches are compared. Transpiration triggered sap flow should first become effective in the branches and with some delay in the stem.

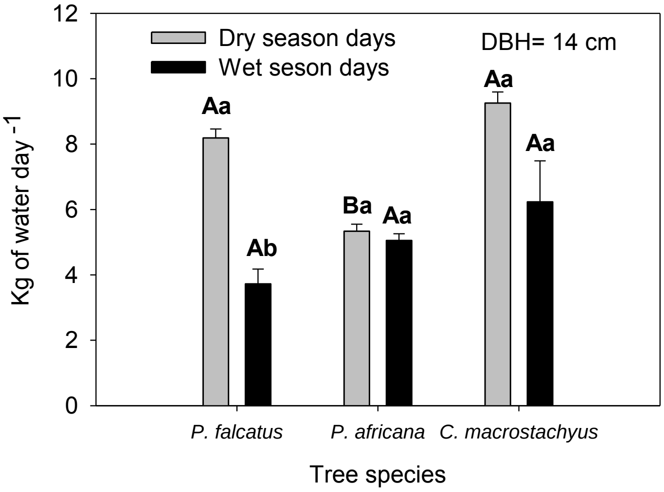


Fig 3.2.2 Total daily whole tree water use (Kg day^{-1}) in dry and wet season days by three functional types of trees *(P. falcatus, P. africana and C. macrostachyus*) coexisting in the Munessa Forest. Values represent mean values of 3 trees over 3 days during each season. Within a season functional types of trees with the same uppercase letters are not significantly different. For a species seasonal values designated with the same lowercase letters are not significantly different. For *C. macrostachyus* the dry seaon measurement was performed when the trees were with their full foliages. Error bars represent ±S.E.

Such delay of several hours between the onset of sap flow in the branch and the stem is quite obvious in *P. falcatus* and *C. macrostachyus* (Figs. 3.2.3 and 3.2.4) during the morning hours of both rainy season and dry season days, but not at all in *P. africana*. The delay of basal sap flow as compared with branch sap flow of *P. falcatus* was up to 4 hours during sunny days. The daily courses of branch and stem sap flow densities were similar but not identical. Apparently the actual stem sap flow whose volume must be bigger than that of the individual branches homogenized to some extent the individual branch sap flow kinetics. This is quite obvious from the midday depression which is more pronounced in the branch sap flow than in the stem. Respective of the afternoon section of the sap flow kinetics, *P. falcatus* differs from *C. macrostachyus* in so far as branch sap flow ceased hours before stem sap flow whereas in *C. macrostachyus* both flows stopped simultaneously.

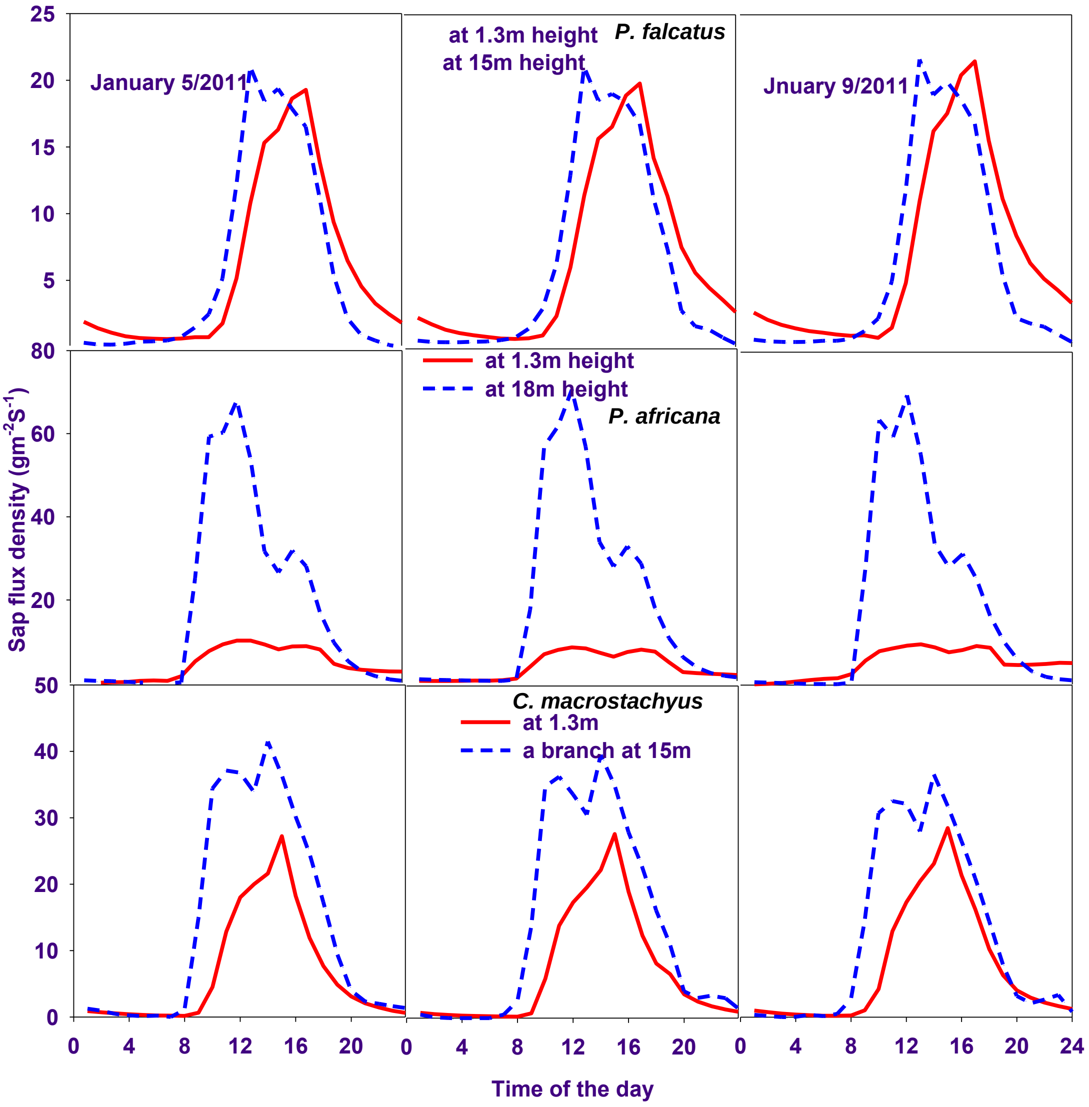


Fig 3.2.3 Diurnal patterns of basal and branch sap flux density during three dry season days for the three functional types of trees *(P. falcatus, P. africana and C. macrostachyus*) coexisting in the Munessa Forest.

The lingering sap flow in the *P. falcatus* stem during the entire night until dawn may indicate replenishment of a stem water reservoir. Interestingly, night time stem sap flux which was observed during the dry season (Fig 3.2.4) was not evident during the wet season evidencing seasonal variation in nocturnal water flow.

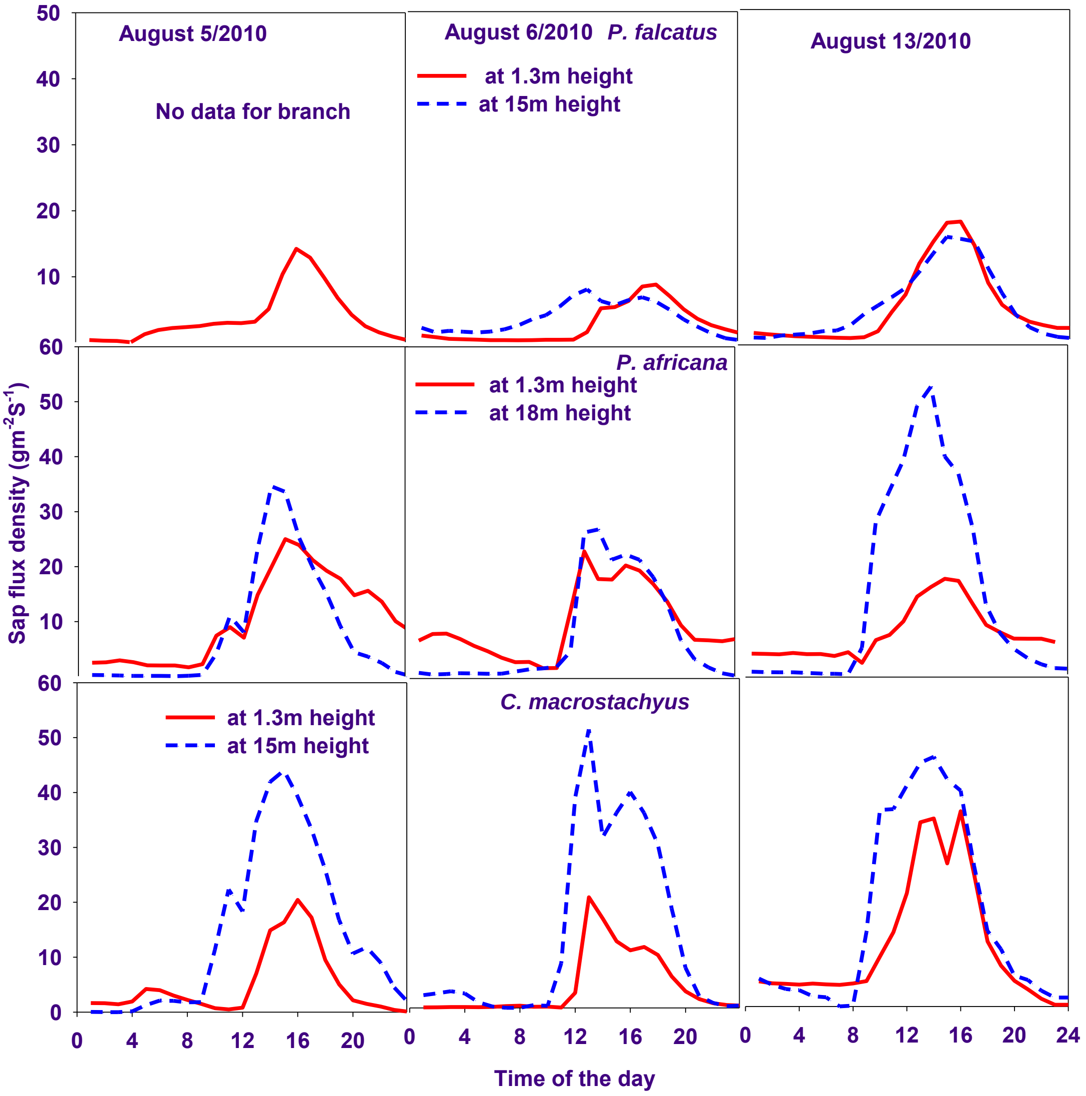


Fig 3.2.4 Diurnal pattern of basal and branch sap flux during three wet season days for the three functional types of trees (*P. falcatus, P. africana, C. macrostchyus*) coexisting in the Munessa Forest.

Nocturnal sap flow could not be observed with *C. macrostachyus* whose stem reservoir may have been refilled still during day-time. Unfortunately, time kinetics of sap flow in the branches and the stem do not allow estimations on the respective volumes. Therefore, further conclusions on the size of the water reservoirs in the axial tissues cannot be drawn from the data of Figs 3.2.3 and 3.2.4. In *P. africana* branch and stem sap flow commenced and terminated almost simultaneously, at least in the dry season, and thus did not indicate the presence of a substantial water reservoir in the stem or branches. Nevertheless, some nocturnal sap flow could be observed, especially on rainy season days.

3.2.4 Soil water source and long term water use

Niche partitioning with regard to water resources refers to different soil layers from which a tree extracts water for transpiration (Araya *et al.*, 2011; Penuelas *et al.,* 2011). Ascending soil water movement; due to evapotranspiration results in enrichment with the heavier and less volatile $H_2{}^{18}O$ as compared with the signature from a rain water. As far as evapotranspiration affects soil water movement, a gradient of decreasing ^{18}O content of the soil water can be expected (Melayah *et al.,* 1996). Deeper soil layers may be influenced by the ground water from which a corresponding gradient is unlikely. This situation is shown in Fig. 3.2.5 for the soil under the crowns of the three investigated tree species measured after spells of dry and rainy days. Unfortunately the isotope signature of the rain water was not determined, but there was no rain during dry season sampling. The data show a strong effect of evapotranspiration which after several rainless days resulted not only in a less negative value as under wet conditions but even an enrichment of ^{18}O. Since water uptake by roots is not known to discriminate between $H_2{}^{18}O$ and $H_2{}^{16}O$, the ^{18}O signature of the xylem sap can be used to identify the soil depth from which a tree extracts the bulk of its water (Hasselquist *et al.,* 2010). Irrespective of a methodological error of up to 10% of the values, the ^{18}O signatures indicate that neither *P. falcatus*, nor *P. africana* extracted a major part of the daily consumed water from the topsoil whereas *C. macrostachyus* could collect water mainly (up to 60%) from the deeper layer during rainy conditions and as well from the topsoil during the dry days.

Parameterizing the IsoSource mixing model (Philips and Gregg, 2003) with the data presented in Fig. 3.2.5 indicated that during both seasons about 80% of the water resource of *P. africana* was from the soil depth between 100 and 200 cm (Table 3.2.3).

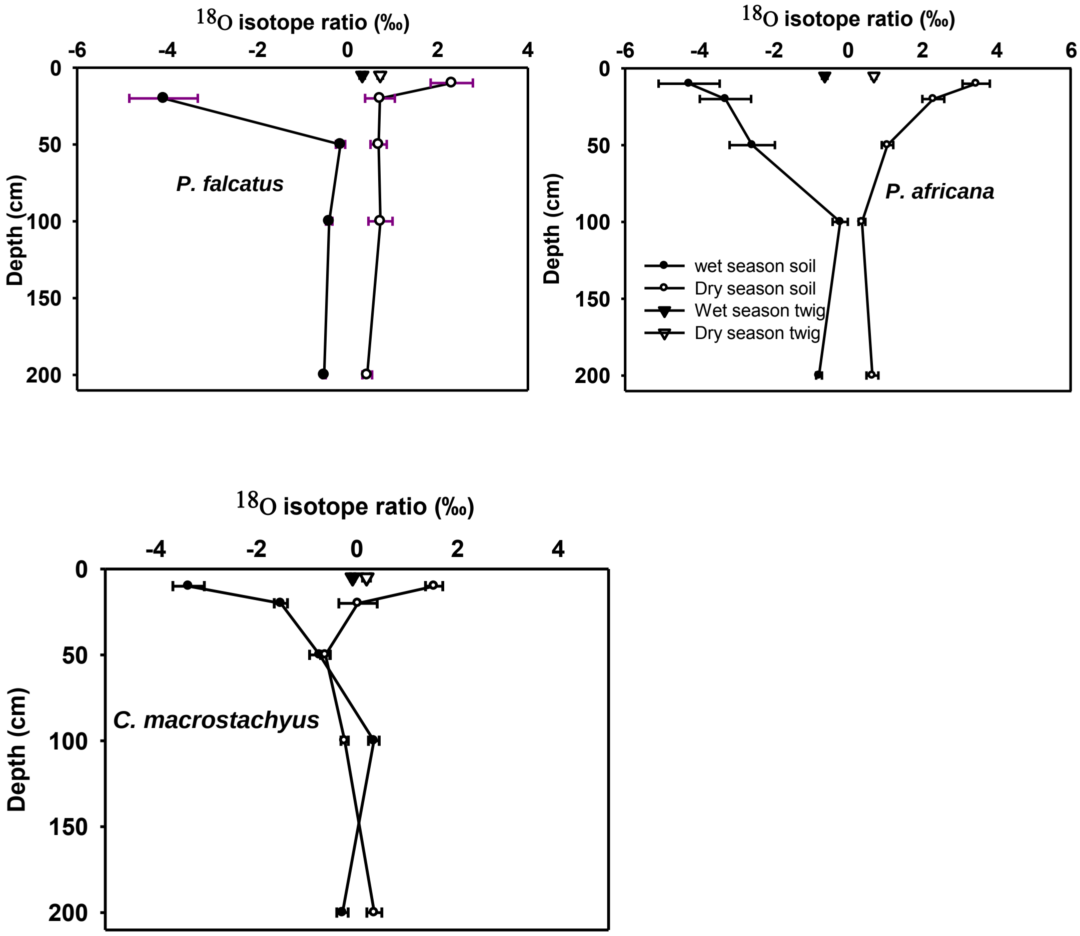


Fig 3.2.5 ^{18}O signatures of soil samples under the selected trees of the three functional tree types (*P. falcatus, P. africana*, and *C. macrostachyus)*, and twig samples collected under dry-season and wet-season conditions.

During the wet season *C. macrostachyus* extracts mainly from the depth between 100 and 200 cm. However, indicating seasonal variation in water source, the twig signatures of *C. macrostachyus* matched with soil sample signatures of all depths during the dry season. In contrast to the wet season, dry season signatures of *C. macrostachyus* twigs suggest the tendency of extracting a third of its water demand from the upper soil layer (<20 cm). During the dry season, *P. falcatus* appeared to extract soil water uniformly from all depths below 20 cm, while the ^{18}O-signature of the xylem sap collected under wet season conditions did not closely match with any of the ^{18}O-signatures of the soil water.

Table 3.2.2 Proportions (%) of water sources for three coexisting functional types of trees in the Munessa Forest. Values represent the average while numbers in parenthesis show the maximum and minimum values. Proportions were determined using the IsoSource mixing model (freely available, http://www.epa.gov/wed/pages/models/stableIsotopes/isotopes.htm, Philips and Gregg, 2003).

	Proportions of feasible water sources during wet and dry season dates					
Depth (cm)	*P. falcatus*[a]		*P. africana*		*C. macrostachyus*	
	wet	dry	wet	dry	wet	dry
10	-	4(0-15)	2.4(0-10)	2.4(0-10)	2.6(0-11)	15.8(0-37)
20	-	25(0-100)	3.3(0-13)	4.1(0-17)	5.7(0-23)	22.8(0-89)
50	-	24.6(0-98)	4.5(0-18)	12.1(0-47)	10.1(0-39)	16.1(0-62)
100	-	25.1(0-100)	70(26-89)	51.4(0-89)	64.1(32-88)	19.6(0-76)
200	-	21.3(0-85)	19.7(0-75)	29.8(0.98)	17.6(0-68)	25.7(0-84)

[a] For *P. falcatus* wet season partitioning of water uptake from certain soil depths were not determined because of mismatches between xylem and soil δ^{18}O signatures.

Long-term water relations of a plant can be concluded from the δ^{13}C isotope signature of its organs, in particular its leaves. As long as there is an effective gas exchange between the leaf and its surrounding atmosphere, the heavier and slowly diffusing $^{13}CO_2$ is discriminated in photosynthetic carbon assimilation. On the long run, however, if stomatal resistance is high, discrimination is less effective. Therefore, the δ^{13}C value of a leaf is also a measure of its long-term average of the interior to exterior CO_2 ratio (Ci/Ca) (Farquhar *et al.,* 1989). Leaves of all three investigated species showed only some level of discrimination during wet season days but less discrimination when collected during the dry season days (Table 3.2.3). In that respect *P. falcatus* and *C. macrostachyus* behaved almost identical whereas the leaves of *P. africana* were obviously less affected from dry spells, showing the highest ^{13}C-discrimination and only a small effect of a dry environment. In summary, the $\delta\ ^{13}C$-values of all three species were rather similar and only that of *C. macrostachyus* from the dry season was statistically different from the others.

Table 3.2.3 ANOVA for leaf internal to external CO_2 partial pressure (C_i/C_a) and leaf carbon isotope ratio ($\delta\ ^{13}C$) for three coexisting functional types of trees in the Munessa Forest. Values represent means (n=3 trees, 18 leaves each collected during the wet and during the dry season) while numbers in parenthesis show ±S.E. Mean values followed by similar upper and lower case letters are not significantly different ($P \leq 0.05$) between functional types of trees and seasons, respectively.

	Wet season		Dry season	
Species	C_i/C_a	$\delta\ ^{13}C$(‰)	C_i/C_a	$\delta\ ^{13}C$(‰)
P. falcatus	0.71(0.02)Aa	-27.94(0.58)Aa	0.66(0.02)ABa	-26.94(0.62)ABa
P. africana	0.81(0.03)Aa	-30.00(0.70)Aa	0.77(0.04)Aa	-29.25(0.86)Aa
C. macrostachyus	0.71(.02)Aa	-28.05(0.43)Aa	0.63(0.01)Bb	-26.33(0.18)Bb
n	3	3	3	3
F-value	4	3.91	6.05	6.03
P-value	0.08	0.08	0.036	0.037

3.3 Leaf gas exchange patterns of wet and dry days

3.3.1 Seasonality of climate

Table 3.3.1. Weather and soil moisture conditions of dry and wet season during the two investigation years in the Munessa Forest.

Month of the year	Year	Season	Relative humidity (%)	Temperature (^oC)	Total radiation (w/m)	Rain fall (mm)	Soil moisture (%)
March	2009	Dry	63.35	17.06	393.29	32.20	12.83
September	2009	Wet	91.29	14.88	285.76	199.67	28.60
December	2010	Dry	74.16	13.76	294.65	16	15.81
January	2011	Dry	73.87	14.52	311.10	12.80	15.59
September	2010	Wet	97.50	14.01	198.40	300.30	33.16

During both investigated years dry season days were characterized by high total radiation, low relative humidity, little to no precipitation and low soil moisture at least towards the end of that season. Variations between the wet and the dry seasons were higher in 2009 than in 2010. Soil moisture during the wet season was higher than the dry season by 133% in 2009 and 56% in 2010 (Table 3.3.1). Since measurements of daily courses of the dry period were performed before the deciduous *C. macrostachyus* completely shed its foliage, the data represent the earlier phase of the dry period.

3.3.2 Daily and seasonal patterns of A_n

Of a total of 18 daily courses of CO_2 uptake measured during the two investigated years Fig 3.3.1 shows 6 selected examples of ecophysiological performance and abiotic environmental parameters (one for each season), which are typical for the three functional types of trees. Daily accumulated values were determined from three selected daily courses each representing dry and wet season conditions and reactions in 2009 and 2010. For each species the relationships between PAR, A_n and gs were analyzed using linear and non linear regressions of different functions for daily courses of six days from each season (Fig 3.3.2). Transpiration rates closely followed the patterns of gs for all species while temperature showed negligible difference.

3.3.3 P. falcatus

The daily courses showed that on days of the wet season both gs and A_n followed the course of PAR (Fig 3.3.1). Analyses of the relationships between the three variables revealed stronger correlation of PAR with both A_n and gs under wet condition (Fig 3.3.2). Under wet condition gs showed strong relationship with PAR suggesting the control of light on stomatal aperture, PAR considered as a surrogate of light. Moreover, gs was comparatively higher during days of the wet season permitting an increase in A_n with an increase in PAR. The relationships between A_n and gs were linear during days of both seasons but stronger during days of the wet period because of less stomatal limitation of assimilation which allowed extended relationship between these traits (Fig 3.3.2). The daily courses of the wet season, the regression of gs to different intensities of PAR (the light response) and the relationships between A_n, PAR and gs, suggest that CO_2 uptake and stomatal aperture follow the patterns of PAR. However, during days of the dry season these relationships were weaker. The patterns of daily accumulated A_n closely correspond with the patterns of the total PAR (Fig 3.3.3). The leaves of *P. falcatus* showed contrasting total seasonal A_n during the dry and wet periods of the two investigated years. Total A_n was significantly higher during days of the dry than days of the wet season of 2009 while a reversed trend was observed during 2010. Lower A_n during days of the wet season of 2009 resulted from the lower levels of irradiation.

The contrasting result is attributed to significantly lower total PAR during days of the wet season of 2009 but significantly higher values during days of the wet season of

2010. This observation confirms the previous suggestion that carbon gain during days of the wet season was mainly modulated by PAR. Significantly lower mean gs during days of the dry than the wet season in 2010 and the narrow range of stomatal aperture in the scatter plot demonstrate the importance of stomatal limitation during drier months.

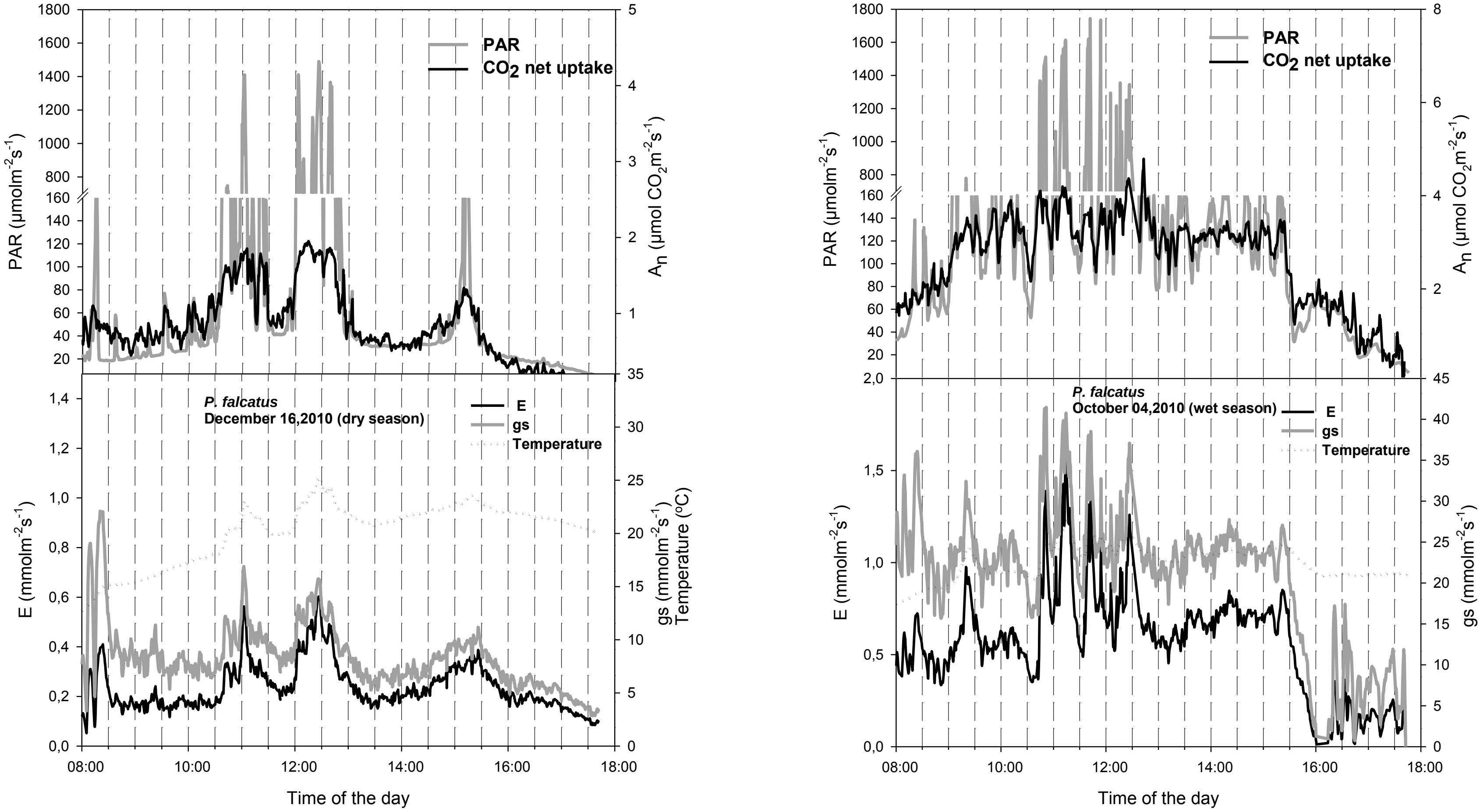


Fig 3.3.1-A. Daily courses of PAR (Photosynthetically active radiation), A_n (net assimilation rate), E (respiration), gs (stomatal conductance) and temperature during dry and wet days of the two investigation years for *P. falcatus.*

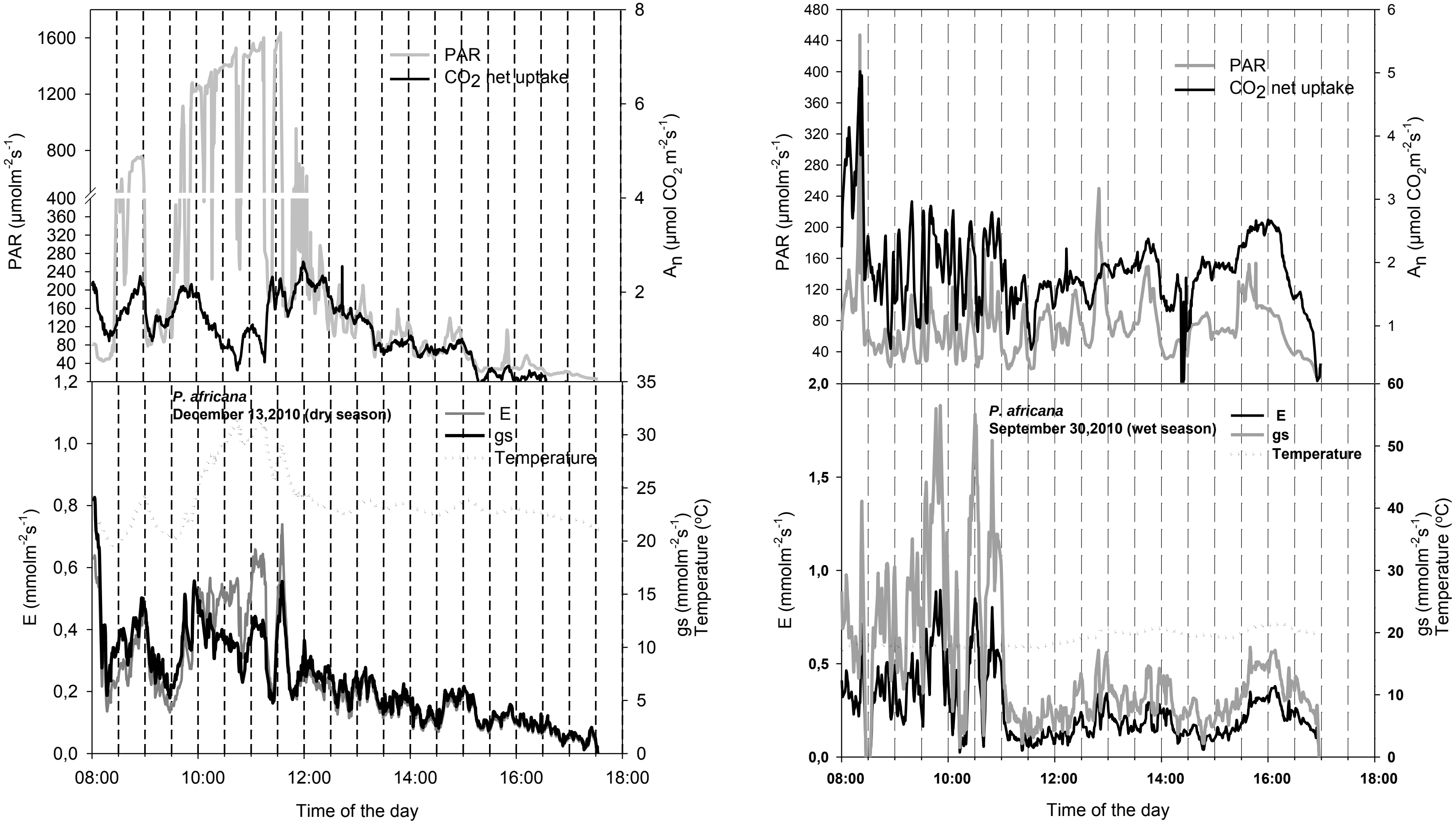


Fig 3.3.1-B. Daily courses of PAR (photosynthetically active radiation), A_n (net assimilation rate), E (respiration), gs (stomatal conductance) and temperature during dry and wet days of the two investigation years for *P. africana*.

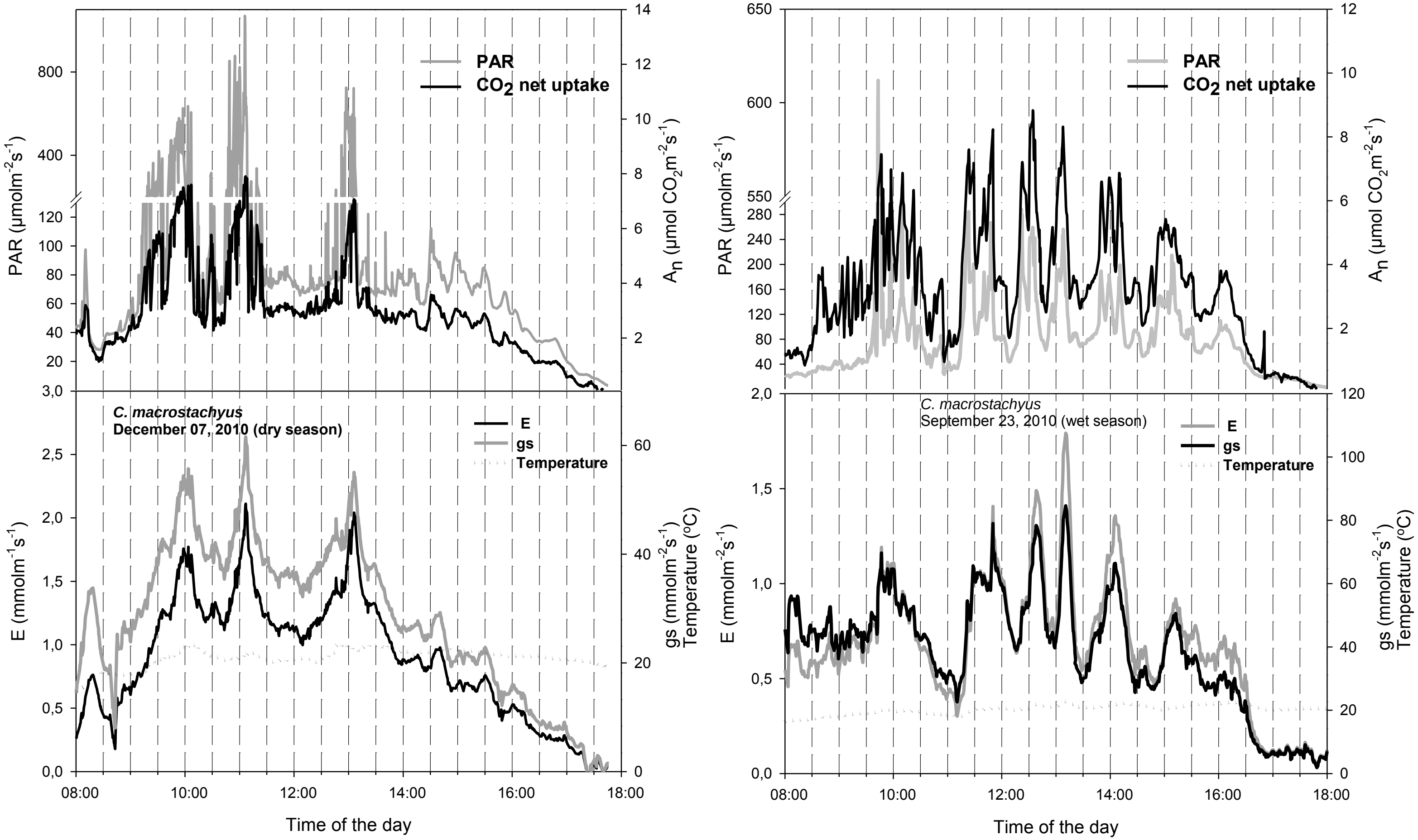
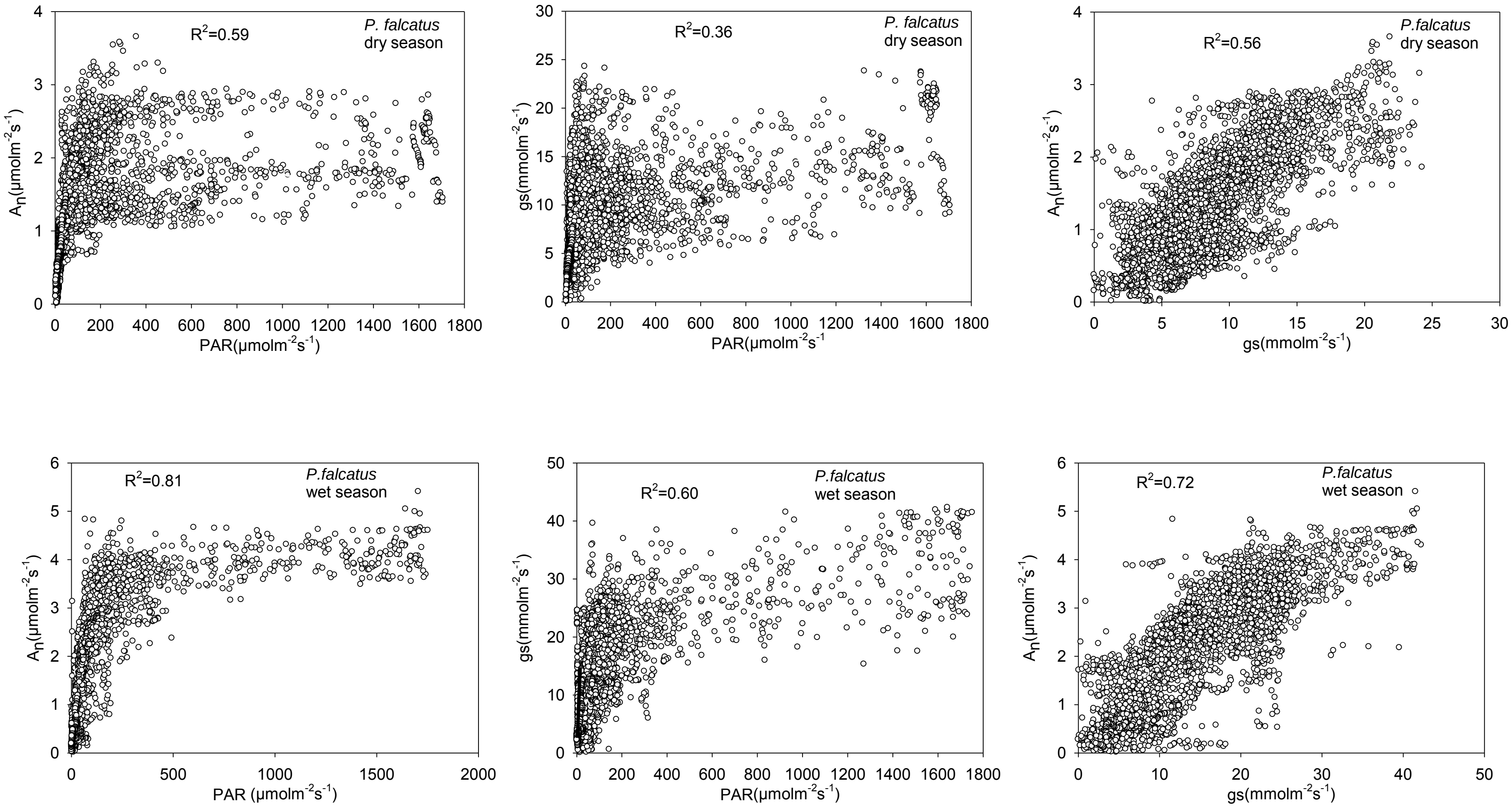


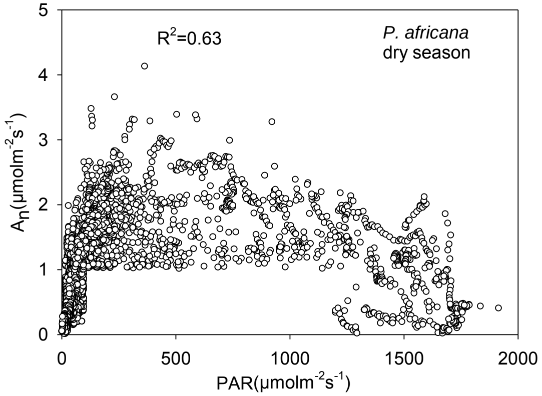
Fig 3.3.1-C. Daily courses of PAR (Photosynthetically active radiation), A_n (net assimilation rate), E (respiration), gs (stomatal conductance) and temperature during dry and wet days of the two investigation years for *C. macrostachyus*.

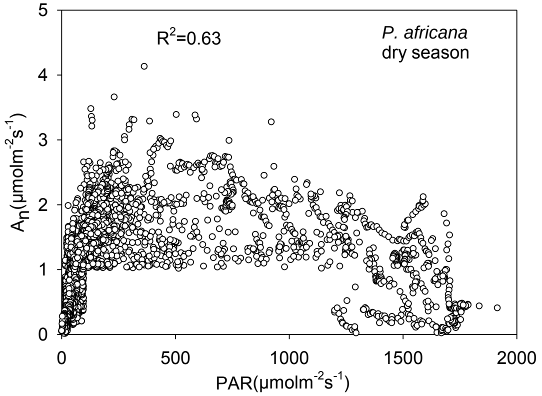
3.3.4 P. africana

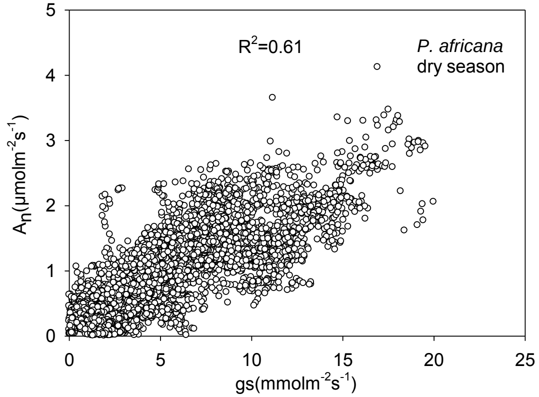
During days of the wet season the daily curves closely followed the patterns of PAR. These patterns were also reflected in the scatter plots. The regression coefficient in the scatter plots showed stronger influence of PAR (being a surrogate estimate of light) on A_n than its influence on gs (Fig 3.3.2).

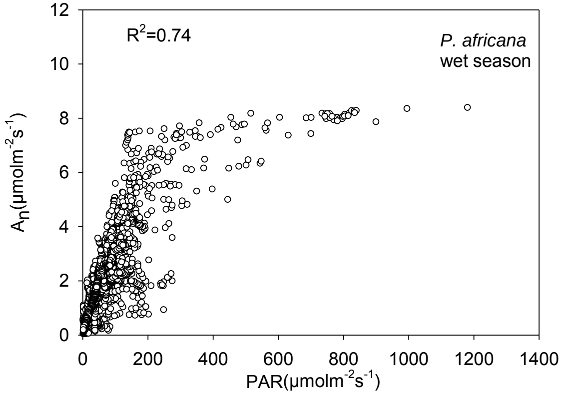
As observed in the plots of PAR versus gs, slight positive response of stomata to increasing PAR was also reflected in the light response plot of gs to PAR (Fig 3.3.4) in the wet season of 2010. Similar as *P. falcatus*, gs and A_n showed linear relationship during days of both seasons but gs was lower during days of the dry season implying more frequent stomatal closure. In contrast to days of the wet season, the significance of irradiance in influencing stomatal aperture and reducing A_n was apparent during days of the dry season that increased irradiance has almost led to complete stomatal closure and cessation of A_n (protective photoinhibition), which is a physiological response to excess light (Fig 3.3.2). The daily course of PAR and A_n during the day of the dry season showed not only overlapping pattern of the peaks but also the incidence that peaks of extremely high irradiance were shortly followed by a sharp fall of A_n and gs as observed on December 13, 2010 (Fig 3.3.1). Except a decline in the mean gs during the dry season days of 2010, all other accumulated values for the wet and dry season days were not significantly different (Fig 3.3.3).

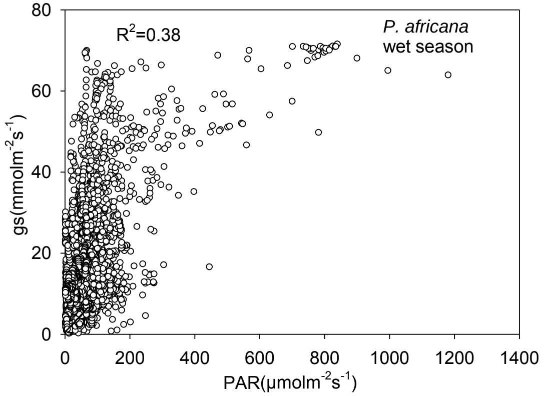

R^2=0.59
P. falcatus
dry season
A_n(µmolm^{-2}s^{-1})
PAR(µmolm^{-2}s^{-1})
0
1
2
3
4
0
200
400
600
800
1000
1200
1400
1600
1800
R^2=0.36
P. falcatus
dry season
gs(mmolm^{-2}s^{-1})
PAR(µmolm^{-2}s^{-1}
0
5
10
15
20
25
30
R^2=0.56
P.falcatus
dry season
A_n(µmolm^{-2}s^{-1})
gs(mmolm^{-2}s^{-1})
0
5
10
15
20
25
30
R^2=0.81
P.falcatus
wet season
A_n(µmolm^{-2}s^{-1})
PAR (µmolm^{-2}s^{-1})
0
1
2
3
4
5
6
0
500
1000
1500
2000
R^2=0.60
P.falcatus
wet season
gs(mmolm^{-2}s^{-1})
PAR(µmolm^{-2}s^{-1})
0
10
20
30
40
50
R^2=0.72
P.falcatus
wet season
A_n(µmolm^{-2}s^{-1})
gs(mmolm^{-2}s^{-1})

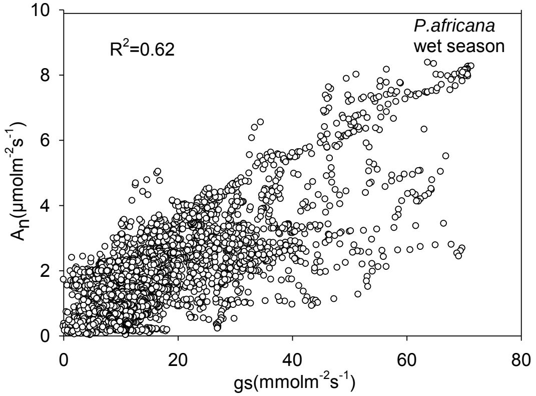

R^2=0.63
P. africana
dry season
A$_n$(µmolm^{-2}s^{-1})
PAR(µmolm^{-2}s^{-1})
0
1
2
3
4
5
0
500
1000
1500
2000


R^2=0.63
P. africana
dry season
A$_n$(µmolm^{-2}s^{-1})
PAR(µmolm^{-2}s^{-1})
0
1
2
3
4
5
0
500
1000
1500
2000


R^2=0.61
P. africana
dry season
A$_n$(µmolm^{-2}s^{-1})
gs(mmolm^{-2}s^{-1})
0
1
2
3
4
5
0
5
10
15
20
25


R^2=0.74
P. africana
wet season
A$_n$(µmolm^{-2}s^{-1})
PAR(µmolm^{-2}s^{-1})
0
2
4
6
8
10
12
0
200
400
600
800
1000
1200
1400


R^2=0.38
P. africana
wet season
gs(mmolm^{-2}s^{-1})
PAR(µmolm^{-2}s^{-1})
0
20
40
60
80
0
200
400
600
800
1000
1200
1400


R^2=0.62
P.africana
wet season
A$_n$(µmolm^{-2}s^{-1})
gs(mmolm^{-2}s^{-1})
0
2
4
6
8
10
0
20
40
60
80

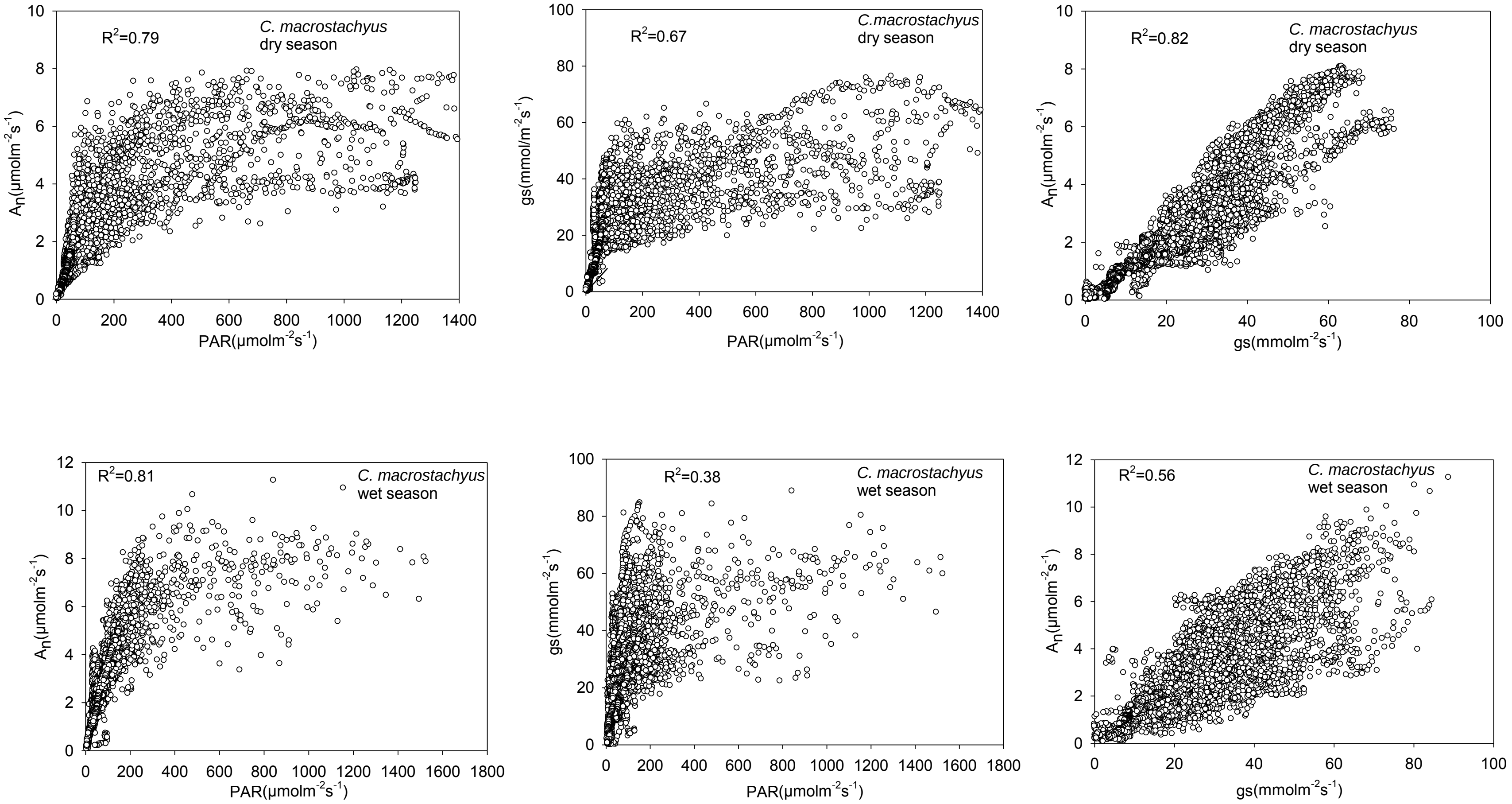


Fig 3.3.2 Scatter plots of net assimilation rate (A_n), stomatal conductance (gs) and photosynthetically active radiation (PAR) during wet and dry days of the two investigation years. Each plot is determined from 6 daily curves of each species (*P. falcatus, P. africana*, and *C. macrostachyus)*.

3.3.5 C. macrostachyus

As compared to the other two species, there was less A_n and gs variation between the dry and wet season days. Logarithmic functions fitted to the relationships of PAR with both A_n and gs, confirmed the strong interdependencies of these traits (Fig 3.3.2). The daily courses and the scatter plots revealed that both A_n and gs increased with PAR. The degree of correlation between PAR and A_n was almost similar over the two seasons. Nevertheless, the correlation of PAR with gs was less strong during the wet season partly because of much concentration of PAR in the lower range (<400 µmol $m^{-2}s^{-1}$) (Fig 3.3.1, 3.3.2). In contrast to the other two species, gs was not considerably lower during days of the dry than days of the wet season (Fig 3.3.2, 3.3.3). Rather there was significantly higher mean gs during days of the dry than days of the wet season of 2009. Limitation by PAR was reflected by comparatively lower R^2 between gs and A_n as well as by the flatter slope of the scatter plot during days of the wet season (Fig 3.3.2). The light response experiment also showed the sensitivity of stomata to the light environment, gs decreasing with decreasing PAR (Fig 3.3.4).

For this broadleaved facultative deciduous tree the daily cumulated A_n was not significantly different between the wet and dry season days of 2010. But in 2009, cumulated A_n was significantly higher during days of the dry than the wet season. High A_n during days of the dry season of 2009 was complemented by significantly higher gs and PAR. Likewise, lack of such variation in 2010, was consistent with the seasonal pattern of PAR and gs which were not significantly different between dry and wet season days (Fig 3.3.3).

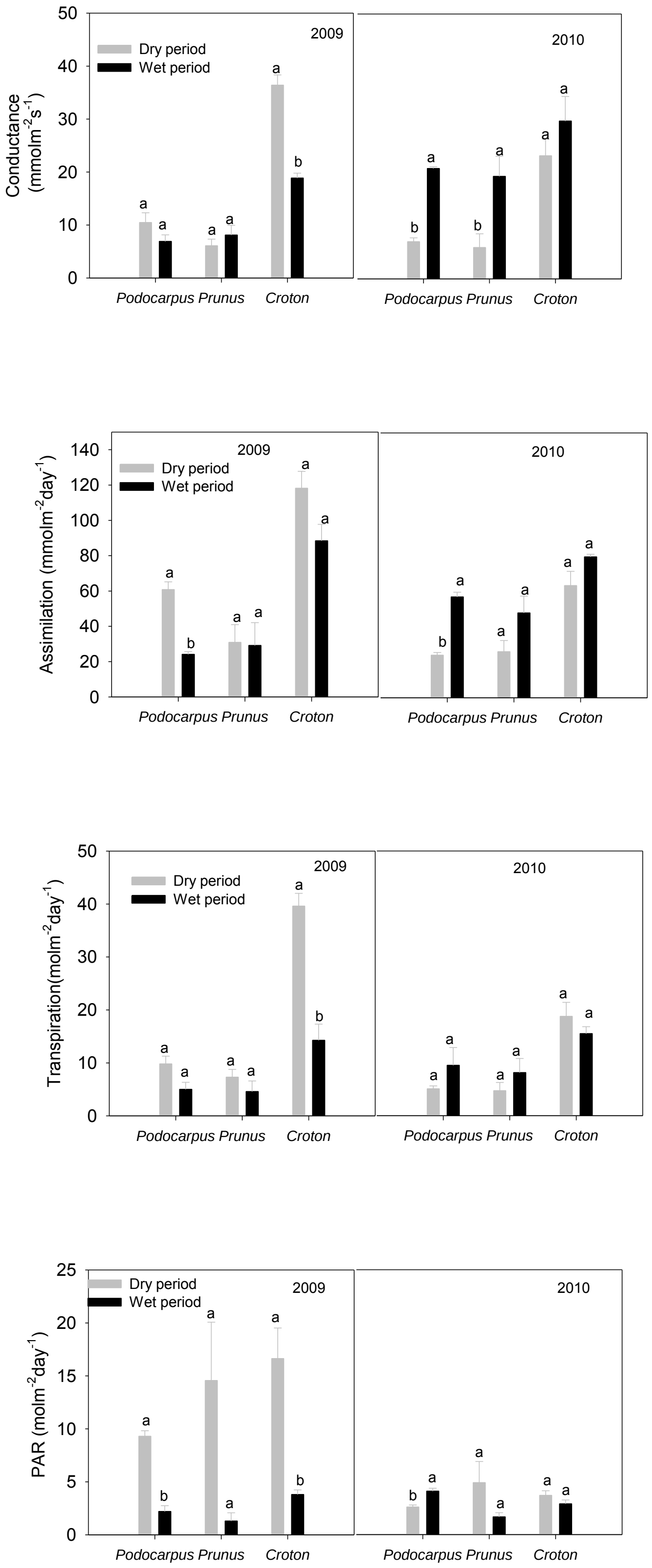
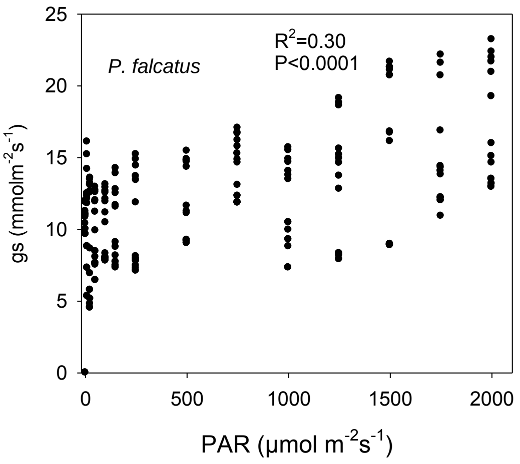
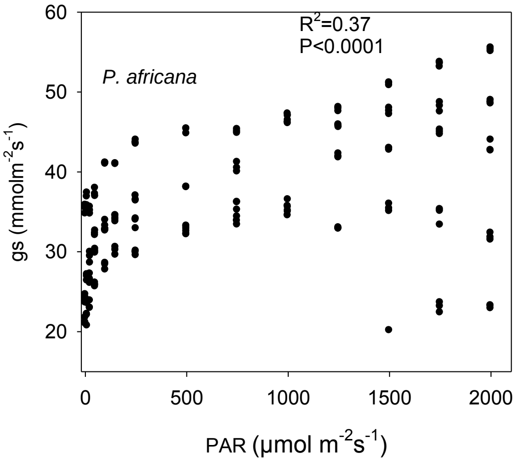


Fig 3.3.3 Mean stomatal conductance, daily integrated transpiration, assimilation and photosynthetically active radiation (PAR) of the three functional types (*P. falcatus, P. africana*, and *C. macrostachyus*) during dry and wet days of the two investigation years.

3.3.6 Light response of photosynthesis

Photosynthetic rate of *P. falcatus* and *P. africana* saturated at PAR of about 700 and 750 µmol $m^{-2}s^{-1}$ (Fig 3.3.5) attaining assimilation rate of 4 and 5.34 µmol $m^{-2}s^{-1}$, respectively. Photosynthetic rate of the broad leafed *C. macrostachyus* was saturated at PAR of 1750 µmol m^{-2}s reaching about 9.5 µmol $m^{-2}s^{-1}$. Comparison of the light saturated maximum photosynthesis (A_{nmax}) and stomatal conductance (gs_{max}) among functional types showed that *C. macrostachyus* had significantly higher A_{nmax} and gs_{max} during days of the wet season. During days of extended dry season *P. africana* had significantly ($P<0.05$) higher A_{nmax} (Fig 3.3.6). During the same season *P. falcatus* showed significantly ($P<0.05$) lower gs_{max}. The apparent A_{nmax} decline from wet to dry season was 34%, 25% and 70% in *P. falcatus*, *P. africana* and *C. macrostachyus*, respectively. Likewise, gs_{max} declined by 28%, 64% and 70% in *P. falcatus*, *P. africana* and *C. macrostachyus*, respectively. For all investigated tree species, wet to dry season variations in A_{nmax} and gs_{max} were statistically significant ($P<0.05$) (Table 3.3.2).





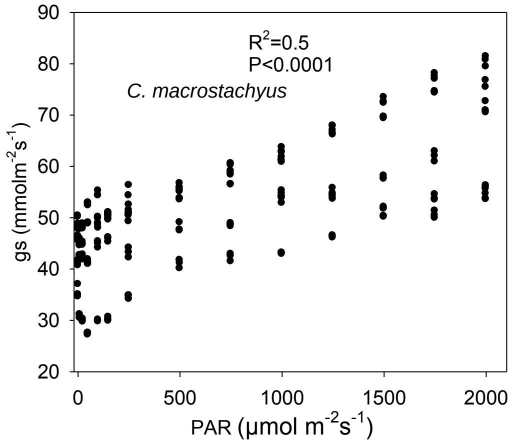


Fig 3.3.4 Regression of PAR with stomatal conductance (gs) of the three functional types of trees (*P. falcatus, P. africana*, and *C. macrostachyus*) during the wet season of 2010.

3.3.7 Water use efficiency

WUE determined as the ratio of daily accumulated A_n and E during representative dry and wet periods can be inferred to understand seasonal water utilization pattern of functional types of trees. In the present investigation the deciduous broad-leaf *C. macrostachyus*, in contrast to the two evergreens, showed significantly higher WUE during days of the wet than of the dry season of both years (Fig 3.3.7). An increase in leaf gs and E during days of the dry season in *C. macrostachyus* leaves were not accompanied by a proportional increase in A_n. In the case of the two evergreens, *P. africana* and *P. falcatus,* E was less seasonal and only slightly affected the seasonal pattern of WUE. Examination of WUE during days of the dry season revealed that functional types of trees considerably vary with respect to the rate of CO_2 uptake per water lost but the variation was not statistically significant ($P=0.08$) (Fig 3.3.8). However, this variation did not prevail during the wet season.

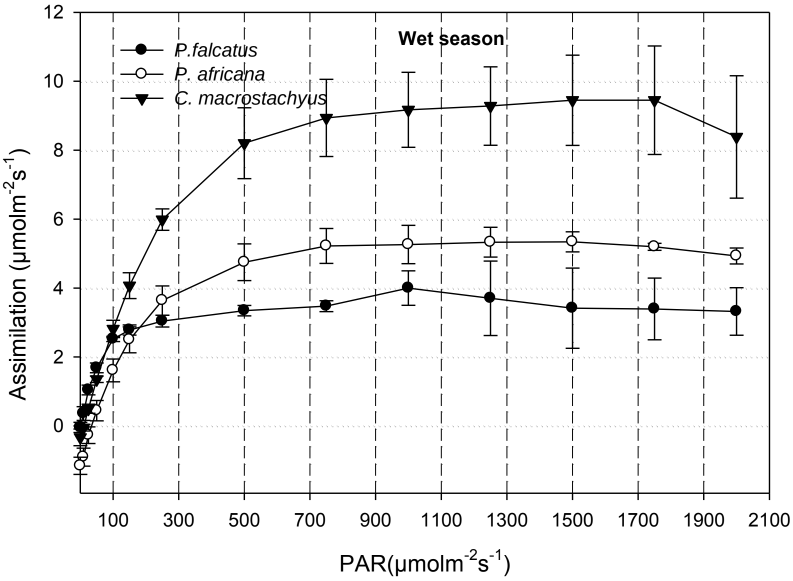


Fig 3.3.5 Light response of assimilation for the three functional types of trees (*P. falcatus, P. africana*, and *C. macrostachyus*) during the wet season of 2010.

Table 3.3.2 T-test comparison of light saturated assimilation rate (A_{max}, μmolm^{-2}s^{-1}) and stomatal conductance (g_s, mmol m^{-2}s^{-1}) between dry and wet season.

Species	A_{max}		g_s	
	Dry	Wet	Dry	Wet
P. falcatus	2.63(0.24)B	4(0.20)A	10.55(1.26)B	14.70(0.34)A
P. africana	3.99(0.2)B	5.34(0.16)A	16.84(2.33)B	47.13(1.18)A
C. macrostachyus	2.84(0.13)B	9.44(0.33)A	17.87(1.4)B	58.43(3)A

Mean values (n=12) within the same species that are followed by different uppercase letters are significantly different at P≤0.05. Numbers in parenthesis represent ±S.E.

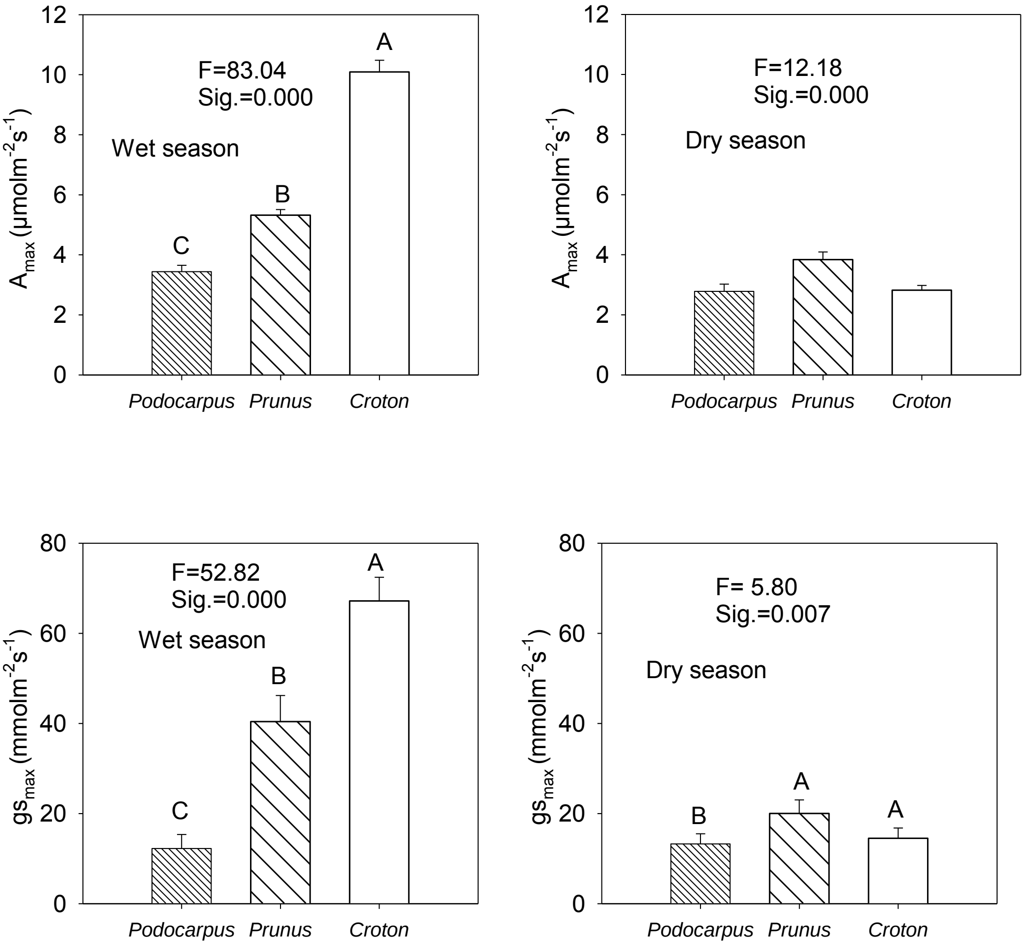


Fig 3.3.6 Anlysis of variance for seasonal maximum assimilation rate (A_{nmax}) and stomatal conductance (g_{smax}) of three coexisting functional types of trees (*P. falcatus, P. africana*, and *C. macrostachyus*) of Munessa. Bars denoted with similar letters are not significantly different among species at $P \leq 0.05$. Error bars represent ± S.E.

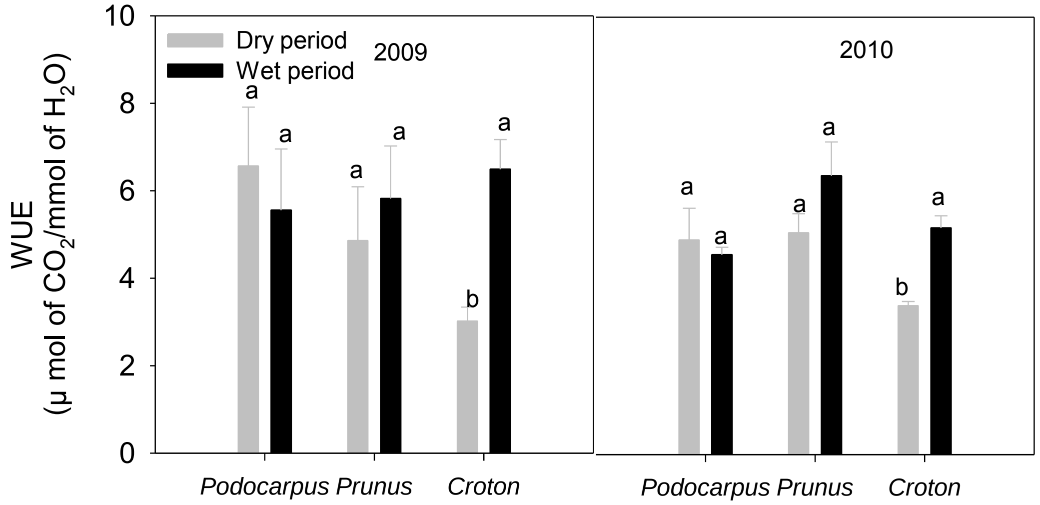


Fig 3.3.7 Water use efficiency (WUE) of the three functional types (*P. falcatus, P. africana*, and *C. macrostachyus*) during dry and wet season in Munessa Forest. Within species bars denoted with similar letters are not significantly different at P≤0.05. Error bars represent ± S.E.

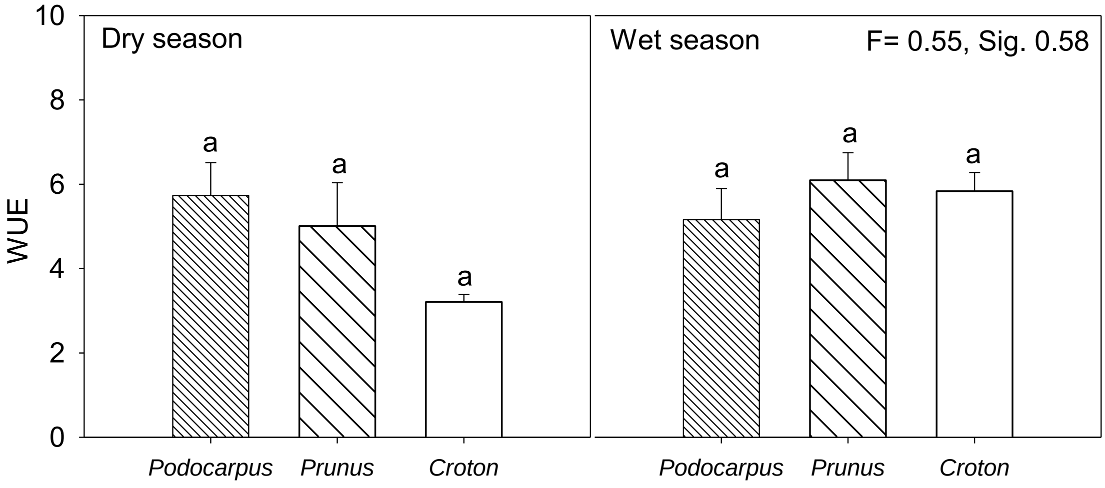


Fig 3.3.8 Analysis of variance for water use efficiency (WUE) of the three functional types of trees (*P. falcatus, P. africana*, and *C. macrostachyus*) during dry and wet season of 2009 and 2010 in Munessa Forest. Bars denoted with similar letters are not significantly different among species (at P≤0.05, N (days) =6). Error bars represent ± S.E.

4 Discussions

4.1 Foliage turnover, leaf traits and growth

4.1.1 Leaf development and canopy foliage dynamics: What controls foliage dynamics in an evergreen tropical montane forest?

The ecophysiological differences of the studied functional types of trees were substantiated by the life-spans of their leaves which were >2 years, 6 months and 3 months for *P. falcatus*, *P. africana* and *C. macrostachyus,* respectively and the metabolic activities which were inversely correlated with the life-spans. From such fundamental differences considerable effects on the dynamics of the foliage could be expected.

Patterns of phenophases of tropical trees are known to respond to changes in various environmental conditions such as first rainfall after drought (Ragusa and Silva, 2007; Williams *et al.*, 2008; Yadav and Yadav, 2008), changes in temperature and photoperiod (Rivera *et al.*, 2002; Singh and Kushwaha, 2005; Elliott *et al.*, 2006; Yadav and Yadav, 2008; Getachew Tesfaye *et al.*, 2011) and also in cloudiness and irradiance (Bendix *et al.*, 2006). Most of the phenological studies with tropical trees have focused on the seasonal timing of flowering (for recent review see Lüttge and Hertel, 2009). Phenology of the foliage of tropical trees has also been addressed, however preferentially with deciduous species in dry or semi-dry forests (Reich and Borchert, 1982; Rivera *et al.,* 2002) where the leafless status of the trees has ecophysiological significance for overcoming rainless periods. However, in evergreen tropical forests ecophysiological benefits of a synchronized leaf phenology are not very obvious. Considering such forests the question arises is that to which extent the foliages respond to external, mostly climatic or climate-induced factors and to which extent to intrinsic factors. Quantification of inter-species phenophase synchrony has been proven useful in assessing the impact of environmental factors on the phenology of functional types of tropical trees (Aide, 1993; Rivera *et al.*, 2002; Singh and Kushwaha, 2005).

Tropical trees may show interspecific (different species), intra-specific (inter-individual) and intra-individual (sections of a tree-crown) phenophase synchronization ranging from complete synchrony to complete asynchrony (Van Schaik *et al.*, 1993). In *P. falcatus* inter-individual synchronization was strong while intra-individual control of foliage phenophases was rather weak. The strong inter-individual synchronization of leaf production and the significant contribution of soil moisture as revealed by the best model for predicting leaf flush (in 2009 but not in the humid year 2010) suggest that a substantial change in moisture, i.e. from dry to wet conditions could be the crucial environmental trigger. As the model explains not more than 55% of the synchronization, other factors than those recorded in this work must have also substantially contributed. Leaf fall was interpreted differently for the two investigation years by the models based on soil moisture, total radiation and temperature. Negative correlation with soil moisture and positive correlation with total radiation suggest the short dry season from November 2009 to January 2010 as trigger of shedding senesced leaves. In 2010 soil moisture was high from February to October and thus the dry season had no impact on leaf fall. Air temperature and total radiation contributed positively to that phenophase, the former likely representing a proxy for another yet unknown factor. Since the degree of intra-individual synchronization of the *P. falcatus* trees was rather low, correlations of the dynamics of twig leafiness with climate variables, such as temperature are not very relevant. As indicated by comparatively low R^2 resulting from the best models in both years, soil moisture, temperature and total radiation had at best minor effects on the leafiness of the twigs. However, the effects of climate might have been blurred by the wide-spread precocious senescence and abscission of young leaves in 2010, the reason of which is still unknown.

Of the three studied functional types inter-individual synchronizations of both leaf sprouting and fall were weakest in *P. africana*. High asynchrony in plant phenophases has been interpreted to indicate high species plasticity (Devineau, 1999). This might apply to *P. africana* which in the Munessa Forest is not only subjected to the change of climate factors but also to biotic stress. Intra-individual synchronizations of the peaks of leaf production and leaf senescence were low, too, and occurred at most sporadically on some of the trees. Despite a low degree of synchronization, considerable influence of total radiation and temperature on the dynamics of the foliage of *P. africana* appeared from autoregression analysis (Table 3.1.5). This was of relevance to leaf flush in 2010 and to leaf fall in 2009. Synchronizing effects of the climate on leaf fall were clearly overridden by the effects of a heavy fungal infestation whose strength, in turn, might respond to environmental factors. As reported from Kenya, *P. africana* leaves were heavily attacked by the so-called shoothole disease, caused by *Colletotrichum gloeosporioides* (Penz.), which resulted in a precocious abscission of seriously damaged leaves (Mwanza and Waithaka, 1998) (Fig 3.1.4). High long lasting moisture as in 2010 could have favored spreading of that phytopathogen. An almost leafless stage of 3 seriously infested individuals of the investigated *P. africana* trees was observed during September 2010. Subsequent regrowth of the foliage, starting in October and lasting for 2 months must have resulted in some intra-individual foliage synchronization of the attacked individuals.

In contrast to the evergreens a high degree of synchronization by climate factors could be expected in the case of the deciduous *C. macrostachyus* by the change of dry and wet seasons. Depending on the intensity and duration of the dry season, leafless *C. macrostachyus* trees can be encountered in the investigated forest. However, the opposite, foliated *C. macrostachyus* all year round, is also not uncommon. The fast adaptation to the climatic conditions and the concomitant inter-annual variability can be explained by the relatively short life-span of three months of the leaves. The dry season did not curtail the life-time of the leaves, but during that season new leaves did not emerge (Fig 3.1.2). At the end of the pronounced dry season 2008/2009 all investigated *C. macrostachyus* trees were almost leafless and new foliage was produced synchronously after the onset of the rains. Whereas inter-individual synchronization of leaf phenophases was high in 2009 and 2010, intra-individual synchronization of the peaks of leaf flush and leaf fall was weak. After induction of leaf bud break in April 2009 development of the entire foliage took about 4 months with a peak by end of June. At that time, the first leaves had already started to senesce.

Soil moisture was the factor contributing most to leaf flush in 2009 while due to an only very short dry period at the end of this year no environmental factor for that phenophase could be identified for the following 2010. Thus, 2010 started with still partially foliated though partly senescing *C. macrostachyus* crowns. The poorly synchronized peak of leaf flush was mirrored in the dynamics of the leafiness of the twigs in 2010 (Fig 3.1.2). Autoregression analysis of the leaf fall data from 2010 revealed its weak association with total radiation as the dry season at the end of the year approached and young leaves were not produced anymore. Bearing in mind, that for the correlations of phenophases, a head start of the climate of one month was assumed, leaf production was not observed during the pronounced dry seasons at the turn of the years 2008/2009 and 2010/2011. Even during the very short dry period at the turn of the year 2009/2010, new leaves were not produced. Thus, synchronization of the foliage dynamics of *C. macrostachyus* is by the onset of the rainy and not by the dry season. In years of rainy months as 2010, *C. macrostachyus,* due to an ongoing foliage turnover maintained a high percentage of its foliage and thus adopts traits of an evergreen tree, with short phases of foliage rejuvenation. An extended rainy season, as in that year could have allowed some of the trees an even threefold replacement of their foliage. In summary, it is conclude that in *C. macrostachyus* endogenous factors controlling the life-span of the leaves are effecting the dynamics of the foliage while some synchronization was induced by the triggering of leaf flushing by the first rains after the dry months.

Master regulatory effects of the environment on the dynamics of the foliage of the three coexisting tree life forms might also be detected by inter-specific coincidence of phenophases. To that end, utilization of the data of the first, less humid year 2009 should give clearer results while during the more humid year 2010 intrinsic control factors may become apparent. For *C. macrostachyus* and *P. falcatus*, onset of the rains was correlated with sprouting of new leaves, but for *P. africana* such trigger could not be observed, and no evidence at all was found for inter-specific synchronization of leaf fall. Although other environmental factors, e.g. temperature or relative humidity cannot be completely ruled out as seasonally recurrent triggers, the present data do not present any clue in that respect. In particular, it is not the dry season that had a synchronizing effect on the dynamics of the foliage but rather the onset of the rains. Obviously the trees had sufficient accessibility to moisture or water reserves to maintain their leaves until the natural end of their life-spans (Borchert, 1994).

In the course of the past years during which the climate of the specific area was recorded the short dry season disappeared more and more and the long rains extended over up to 9 months (Strobl *et al*., 2011). Such years, as 2010 with only 1 dry season had consequently only 1 moisture-triggered synchronizing event at the beginning of the rainy season. As a consequence, also the facultative deciduous *C. macrostachyus* maintained a foliated crown during that entire year.

4.1.2 Leaf life-spans and functional traits

The ecophysiological traits of the investigated leaves correlate very well with those reported for tropical evergreen and deciduous trees, respectively (Reich *et al.*, 1992; Feng *et al*., 2004; Poorter and Bongers, 2006). Leaves of deciduous species have high rates of photosynthesis, which decline very rapidly upon onset of senescence, they have a high nitrogen content (not measured in this work, but commonly interpreted as indicator of the metabolic activity which was measured Table 3.1.9 and Fig 3.1.5) and a high specific leaf area indicating low construction costs, whereas evergreen species have low rates of photosynthesis which decrease slowly when senescence commences. They show a low metabolic rate (N-content, Villar and Merino, 2001) and a small specific leaf area, typical of high construction costs. Growth rates of leaves from deciduous trees are high but LLSs are usually short in contrast to the longevity of leaves of evergreen trees (Ackerly, 2004) which are considered to balance the much lower photosynthetic rates. Long LLS of *P. falcatus* is in agreement with reports on other evergreen tropical gymnosperms. In Jamaica, *Podocarpus urbanii* leaves have been observed to live 29 months (Aylett, 1985 quoted in Williams-Linera, 2000). This may also hold true for *P. falcatus*. On the other hand, the short LLS of *C. macrostachyus* is in agreement with the mean LLS of other tropical deciduous tree species which has been estimated between 2 and 4 months (Ackerly, 2004). *P.*

africana represents an interesting case of an evergreen tree with relatively short LLS of about 6 months. A similar case has been reported for a broad leaf evergreen representative of the Chloranthaceae, *Hedyosmum mexicanum,* whose LLS is between 6.4-7.8 months (Williams-Linera, 2000). As an evergreen species with a final SLA identical to that of a *P. falcatus* leaf the *P. africana* leaf combines high construction costs with a short leaf longevity which may be less than one fourth of the former and only two times that of a *C. macrostachyus* leaf. The high turnover in the foliage of *P. africana* is enabled by a comparatively high payback, as the (maximum) photosynthetic rate is twice as high as that of a *P. falcatus* leaf while dark respiration is about the same (Fig 3.1.5). Moreover, ^{18}O signature analysis revealed that *P. africana* mainly extracts water from the soil layer below 1m implying the competitive advantage of this broad leaf evergreen species in persisting assimilation during the dry season. Considering the high susceptibility of the *P. africana* leaves to pathogens, a genetically defined twofold foliage turnover per year appears favorable.

Functionality of LLS of tropical trees has been addressed mainly with respect to the reaction of the foliage to the pronounced change of dry and wet seasons (De Bie *et al.*, 1998; Reich and Borchert, 1982; Ackerly, 2004). The question arises whether intrinsic factors such as genetically fixed LLS can override external factors or vice versa. Among many others, Borchert *et al.* (2002) and Myers *et al.* (1998) have investigated the interaction between the water status and the response of the foliage, and drought-induced water stress has been considered as a major cause for leaf shedding. In the quoted studies the question has been addressed whether water stress or high humidity can shorten or expand the longevity of leaves in tropical dry forests. But only in the work of Myers *et al.* (1998) leaves have been tagged and their physiological status and longevity have been recorded individually. This is an important point as the phenophases of the crowns may not necessarily reflect the dynamics of the individual leaves. In the study of Myers *et al.* (1998), irrigation during the dry season had relatively little effect on the longevity of the leaves of both deciduous and evergreen trees. In contrast, Borchert *et al.* (2002) reported, (although on the basis of total foliage observation) that severe drought could shorten the life-span of young leaves and accelerate shedding of old leaves whose stomatal control was declining. Here, a facultative deciduous tree species (*C. macrostachyus*) in a tropical evergreen montane forest was investigated and compared with two of the evergreen species. Although a synchronizing effect of the onset of the rains after the dry season on the phenophases of the foliage of *C. macrostachyus* was obvious, no cues could be detected for a general prevalence of (abiotic) environmental factors on the extension of the natural life-span of the leaves. Rather synchronization of the foliage resulted from the short LLS in combination with the suspended bud break in the course of the dry season.

4.1.3 Stem extension growth

The difference of relative growth rates between the “normal” year 2009 and the very humid year 2010 is astounding (Table 3.1.10). Several factors could have contributed to a higher growth rate during the second year, I) a higher rate of CO_2 uptake due to less limitation by stomatal conductance. For *P. falcatus* limitation of photosynthesis by stomatal conductance has been shown predominantly in the afternoons of dry season days (Strobl *et al.*, 2011), and similarly restricts gas exchange of the leaves of the other 2 species (Section 4.2). II) Although the observation data of the tree crowns are not sufficiently detailed to demonstrate a net increase of the foliage during the wet year 2010, examination of the leafiness of the selected individual twigs provides quantitative clues about a change of the size of a tree’s foliage. Surveying these data for the 2 years indeed showed significantly enlarged foliage of *P. falcatus* and *P.*

africana, for the second, moist year (Table 3.1.7), but not for *C. macrostachyus* . Thus, an enlargement of the foliage is another reason for a higher stem growth in 2010, at least for the evergreens. The differences in the annual growth rates (Table 3.1.10) between *P. falcatus* and *C. macrostachyus* show that in a normal year (2009) growth rate of *P. falcatus* is superior to that of *C. macrostachyus* , whereas in the humid year *C. macrostachyus* could catch up by a considerable temporal extension of the foliated state of the crown. *P. africana* is a slowly growing subdominant species which, however, also responded positively to the increase in moisture. High-resolution dendrometer study in the same site showed similar stem growth rates for *P. africana* for 2009 as reported here (Krepkowski *et al.*, 2011). These authors showed that cambial activities of evergreen trees started wood formation already during the short rainy season while growth of the deciduous tree was suspended until the long rainy season. Nevertheless, our rather summarizing data of stem growth suggest a kind of equilibrium between the different functional types of trees under changing environmental conditions.

In summary, because bud break and development of new leaves was suspended during the driest months the onset of the rainy season had a strong synchronizing effect on the development of the foliage of *P. falcatus* and *C. macrostachyus* but not of *P. africana*. However, the synchronizing effect, in contrast to the situation in temperate climates, did not cover all branches of the crowns to the same extent. Thus synchronization of leaf phenophases was stronger between individual trees than between the branches of an individual crown, at least for *P. falcatus* and *C. macrostachyus*, indicating the importance of intrinsic factors (longevity of the leaves) for the dynamics of the foliage. The study further showed that abiotic environmental factors did not reveal any cue for a significant modification of the life-span of the leaves. With respect to the overall performance of the studied functional types of trees a direct competitive advantage of one of the life forms with respect to growth could not be detected.

4.2 Water relations

4.2.1 Leaf water potential

The daily range of leaf water potential values exhibited differing seasonal response of the studied functional types of trees which could be illustrative of different strategies employed to cope up with a seasonal drought stress. The result shows a consistent difference between the mesic and short-lived *C. macrostachyus* leaves and the more coriaceous or even scleric leaves of the evergreen *P. africana* and *P. falcatus*. This difference is attributable to the only small or even lacking diurnal fluctuations of the leaf water potential of *C. macrostachyus* in contrast to the significant diurnal changes exhibited by the evergreens. Narrow diurnal ranges in dry season leaf water potentials of trees have been suggested to trigger leaf shedding and retarded growth (Kindeya Gebrehiwot *et al.,* 2005) and thus in turn indicating drought sensitivity of deciduous tree species. However, on the background of the foliage dynamics of *C. macrostachyus* and the life-span of its leaves which is unaffected by seasonal variation of the environmental conditions, such conclusion appear less convincing. It must be borne in mind that *C. macrostachyus* maintained still 50% of its foliage in January 2010 when the dry season water potential of its leaves was measured (Fig. 3.1.1). Wider daily fluctuations in leaf water potential could indicate over-night re-saturation and a higher drought tolerance of a tree species (Kindaya Gebrehiwot *et al.*, 2005, Aster Gebrekirstos *et al.*, 2006). In that case, the predawn water potential should be rather high (more positive), which is the case with *P. africana* and *P.*

falcatus, irrespective of years and seasons (Table 3.2.1). Therefore, if the evergreens are more drought resistant than *C. macrostachyus*, it is likely that this trait is linked to the water potentials of the leaves. Significantly higher diurnal fluctuations of the leaf water potential of the evergreens which were consistent over both study years could suggest re-saturation and capability of compensating for the daily plant water deficit (Bucci *et al.,* 2005). This is consistent with the observation of relatively less interrupted dry season CO_2 uptake of the evergreens (Section 4.3). The fact that none of the trees mainly depend on the soil water in the upper soil horizons, which is more conspicuous in *P. africana* (see section 3.2.4, Fig. 3.2.5 and Table 3.2.2) warrants water uptake over the whole year. On the other hand, dry season suspended new leaf production in *C. macrostachyus* may be associated with the lowest diurnal leaf water potential range that is a proxy to depleted tissue water status.

4.2.2 Stem water storage and whole tree water use

Stem water reservoirs buffer water potentials of stem xylem thereby mitigating the incidence of embolisms induced by a negative pressure in the xylem conduits (Tyree and Sperry, 1989 Williams *et al.*, 1996; Goldstein *et al.*, 1998). Evidences about the contribution of water from a water storing tissue in the stem (e.g. the pith, cortex or rays) to the transpirational water flux have been inferred through various observations, such as the incidence of night-time sap flux (Holbrook and Sinclair, 1992). The results of this study illustrate that dry season night time re-filling is the possible mechanism by which *P. falcatus* and to a lesser extent *P. africana* restore daily water deficits of the leaves in the canopy. The present observations in the extended night time sap flux of *P. falcatus* agrees with previous study conducted in the same site (Strobl, 2012). The trees investigated in the present study were selected for a round stem cross-section (necessary for sap flow measurements) and for accessibility of the crown (for porometry), but were by far not the biggest individuals of the respective species. Old *P. falcatus* trees may attain a DBH of up to 2 m and a height of up to 50 m but due to its irregular stem cross-section the Granier system cannot be used for measuring sap flow. Water transport in trees of this size may be restricted by increased frictional resistance and a high gravitational potential (Phillips *et al.*, 2003) and therefore a reservoir in the stem tissue acting as a buffer between transpiration and sap flow from the roots to the leaves appears beneficial. Presence of such a buffer could contribute to significantly higher daily water use of the trees particularly during the dry season as observed in *P. falcatus*. Frequent incidence of cavitations may considerably curtail hydraulic conductivity and in turn water flow in the xylem, as has been shown with western hemlock (*Tsuga heterophylla*, Kavanagh and Zaerr, 1997). Thus avoidance of cavitations and embolism by using water from an internal reservoir might be beneficial for the entire water relations of the trees.

Nocturnal sap flow was also observed in *P. africana*, but its extent was less obvious than in *P. falcatus*. Nevertheless water relations of this species, which can grow up to more than 30 m, could benefit from a dynamic water reservoir in the stem. *C. macrostachyus* trees are much smaller than *P. falcatus* and the benefits of a stem water reservoir are less obvious. However, since transpiration rates are at least twice as high as in *P. falcatus* and *P. africana* (Fig. 3.3.3), such a buffer should also be useful for mitigating cavitations in the xylem stream. Nocturnal sap flow, suggesting replenishment of the stem water reservoir was not observed in *C. macrostachyus*, although the step-by-step onset of sap flow in the branch and the stem indicated the presence and preferential utilization of such a reservoir. A hypothetical explanation for such seemingly inconsistent finding is that day-time sap flow in the stem was sufficient also to feed the reservoir, which at the end of the day was already charged.

Estimation of the size of the reservoirs in the stem tissues was not possible because only the stem and one of the major branches could be equipped with sap flow sensors. Thus, the extent of the contributions of the stem water reservoirs of the three investigated tree species to their water balances is difficult to assess, the more so, as sap flux density and not the real sap flux have been determined. .

The observed significant variation in whole tree water use of the studied functional types of trees as well as textbook knowledge suggest the dry season as the crucial phase for determining interspecies water use patterns. Similar sap flux densities measured in the investigated functional types of trees during the dry season imply that the difference in whole tree water use is attributable to differences in the sapwood areas. Also, foliage size correlates directly with whole tree water use because of a constant proportion maintained between foliage and sap wood area (Vertessy *et al.*, 1995; Calva-Alvarado *et al.,* 2008). Despite a twofold transpiration rate per unit leaf area of *C. macrostachyus* compared with that of *P. falcatus* (Fig 3.3.3), the whole tree water use was not significantly different between young trees of similar diameter size. Comparing the water relations of the two species, this observation demonstrates that a higher leaf-level transpiration rate as in the deciduous species can be "compensated" by the large foliage of the evergreen conifers. Of the total biomass produced, allocation to foliage is 60% more in *P. falcatus* than in *C. macrostachyus* (Strobl, unpublished).

For an assessment of the hydraulic traits of the investigated tree species, individuals of similar size must be considered. To that end young trees with a DBH of 14 cm were used (Fig. 3.2.2) whose water consumption was still low but nevertheless in a realistic range (Wullschleger *et al.*, 1998). In the present study, *P. falcatus* and *C. macrostachyus* showed considerably higher water consumption during the dry than the wet season, suggesting a higher sensitivity to environmental factors than *P. africana.* The seasonal pattern of the whole tree water use of *P. falcatus* is in agreement with the findings by Strobl (2012). Lower wet season whole tree water use of *P. falcatus* is consistent with its lower sap flux density which could be attributed to differential effect of these weather variables.

4.2.3 Partitioning of soil water and integrated water use efficiency

Comparing the ^{18}O signature of the xylem sap of the study trees with the ^{18}O content of soil water from various depths could provide information about the location of the major water sources in the soil. Such data allow conclusions whether there is competition for soil water or co-utilizes the hydrological niches exploited by the different functional types of trees. The present data show that *P. falcatus*[1] as well as *C. macrostachyus* are able to exploit soil water reservoirs of the top as well from deeper soil layers whereas *P. africana* apparently takes up water from more than 1m downwards. It must, however be mentioned, that the examination of the ^{18}O signatures were done in the exceptionally humid year 2010, when the dry season was short, drought was not observed and *C. macrostachyus* kept part of its foliage throughout the year. At least for that year association of deciduousness (of *C. macrostachyus*) with less use of soil moisture in the deeper soil layer (Jackson *et al.*, 1995, Meinzer *et al.*, 1999) cannot be confirmed. There are similar reports also showing deciduous trees extract soil water from deeper layers (Stratton *et al.,* 2000; Querejeta *et al.*, 2007).

As the ^{18}O signatures of soil water at least of the upper 50-100 cm changed with the seasons, such change could also be expected in the ^{18}O signature of the xylem fluid. However, a corresponding shift by 1.5 ‰ was only observed in the xylem fluid of *P.*

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[1] ^{18}O signatures for *P. falcatus* have been published (Fritzsche et al. 2006) which are, however with respect to the soil water profile less conclusive. The ranges of the xylem fluid signatures are in agreement with those presented in this thesis.

africana, whereas changes of the ^{18}O signatures of *P. falcatus* and *C. macrostachyus* were only by tendency. The δ^{18}O values of the xylem sap of the three study species were very similar, between 0 and 0.8‰ and only the value of *P. africana* from a rainy season day was slightly in the negative range (-0.8‰). Despite a clear indication that *P. africana* mainly exploiting water from the deeper soil layer (Table 3.2.2), lack of apparent variation in the twig ^{18}O samples constrains conclusive remarks on the water sources of the studied species. More specific conclusions would have been possible, if fine root and root hair assessments would have also been conducted along the soil profile. In such a case, layers of fine roots would be produced concomitantly with the shift. Fine root production, however, has been investigated only to a soil depth of 50 cm (Solomon Zewdie, unpublished) which expectedly responds to the seasonal changes of the soil moisture. Unfortunately, observations of the live fine root content of deeper soil layers are only available for *P. falcatus* with the highest biomass in the topsoil but also a more or less equal distribution down to 1 m (Fritzsche et al. 2006).

The question why *C. macrostachyus* shows a dry season switch to the upper layer deserves further investigation. Among others, it can be explained by the tendency of enhanced fine root development near the surface which can be an adaptive response of this species to utilize the first shower after the dry period. Such an adaptation could also be expected to facilitate a rapid uptake of soil moisture from small intermittent dry season rains. More uptakes from the topsoil during the dry than the wet season in *C. macrostachyus* has also been suggested from a comparison of root biomass over the upper 60 cm. About 65 % of the total fine roots of *C. macrostachyus* are located within the upper 10 cm (Hussien Indries, 2007). It is known that stress, e.g. drought stress can induce root formation, and slowly drying of the topsoil during the dry season of a "normal" year may result in enhanced formation of fine roots which was indeed observed with *C. macrostachyus* in the Munessa Forest (Zewdie, unpublished). In summary, though it is premature to quantify the soil water sources at this stage, the study clearly reveals the spatial and temporal sharing of water resources among the studied species.

^{13}C is a useful parameter that links plant water use with carbon gain and can be used to explore interspecific variation in long-term water use efficiency for carbon acquisition (Sobrado and Ehleringer, 1997; Querejeta *et al*., 2007) and thus can be used for assessing ecophysiological traits and for differentiating between functional types of plants (Bonal *et al.,* 2000; Leffler and Enquist, 2002). In tropical forests $\delta^{13}C$ values show strong variation because of higher plant biodiversity and spatial and temporal environmental changes that influence ^{13}C signature (Martinelli *et al*., 1998). In this study leaf $\delta^{13}C$-values of *C. macrostachyus* and *P. falcatus* were in agreement with values in previously published works from the same site (Lüttge *et al*., 2003; Strobl *et al*., 2011). Investigation of the leaves of the three study species during both major seasons were not indicative of frequent or prolonged restriction of gas exchange by an elevated stomatal resistance. The leaves of *P. africana* showed the least obstruction of gas exchange which in the light of the daily courses of stomatal conductance (Fig. 3.3.1) and the averaged values from the years 2009 and 2010 (Fig. 3.3.3) is surprising. Especially in 2010 the difference of dry season and wet season stomatal conductance is very pronounced.

The solution to this discrepancy may come from a consideration of the life-spans of the leaves and the time required for full expansion. Most of the carbon of a leaf is incorporated during unfolding and growth. In *P. africana* the average life-span of a leaf is half a year (Table 3.1.6) and unfolding and expansion growth takes about 1 month (Table 3.1.1). Thus harvesting a leaf at a given date will not necessarily reveal the actual seasonal δ^{13}C-value but a mixture of formerly incorporated (structural carbon) and lately incorporated (photosynthates such as starch and sucrose) carbon isotopes. Nevertheless, the high δ^{13}C-values of *P. africana* agree with its gas exchange characteristics of maintaining comparatively higher dry season assimilation rate (Table 3.3.2). Notwithstanding this finding, seasonal carbon isotope signatures of leaves with a long life-span are difficult to assess. This holds in particular for the leaves of *P. falcatus* with a life-span of more than 2 years and a growth period of at least 3 months. The situation is different with the short-lived leaves of *C. macrostachyus* whose δ^{13}C-values show a statistical significance between dry-season and wet-season leaves. As they need only 2 month for unfolding and expansion (Table 3.1.1) after which time-period their photosynthetic capacity already expires (Fig. 3.1.5) their δ^{13}C-values can be considered as good indicators of their reaction to environmental conditions such as soil moisture and humidity of the air. Thus it is not surprising that the δ^{13}C-values of *C. macrostachyus* correspond well with its seasonal values of stomatal conductance shown in Fig. 3.3.6 and Table 3.3.2.

In summary, the diurnal leaf water potential range showed positive dry season plant water status in the two evergreens, *P. africana* and *P. falcatus*. Such a dry season positive water balance is consistent with the use of the deeper soil water sources which was more evident in *P. africana*. In *P. africana* the use of deeper soil water was corroborated by high dry season intercellular CO_2 concentration and more negative δ^{13}C values. Dry season favorable plant water condition of *P. falcatus* could also be further attributed to stem water storage. Moreover, comparatively lower dry season intercellular CO_2 concentration of *P. falcatus* suggests stomatal control as an additional water loss regulation mechanism. The lowest diurnal range in leaf water potential of *C. macrostachyus* together with the phenological and gas exchange responses indicate less tolerance of prolonged drought. On the other hand, whole tree water use of trees of similar DBH (14 cm, with their full foliage) differed significantly among the studied species with *P. africana* showing the lowest values suggesting water resource requirements of the studied functional types are remarkably species specific.

4.3 Leaf gas exchange patterns of wet and dry days

4.3.1 The pattern of carbon gain along the seasonal moisture gradient

P. falcatus is known as a late successional shade tolerant species surviving under low light environment. The present findings on the seasonal as well as daily relationships between PAR and carbon gain imply that low light conditions could affect the total carbon gain of *P. falcatus*. Its tolerance and capability of assimilating under high irradiance as observed in the light response curves may explain how *P. falcatus* can acclimate to grow, survive in forest gaps where it is well represented (Demel Teketay, 1996). The light response characteristics of this species corroborates previous conclusion by Lüttge *et al.* (2003) who suggested that *P. falcatus* can be categorized in between shade tolerant and light demanding species. Our finding is also consistent with results of Getachew Tesfaye *et al.* (2011) who reported medium light requirement of seedlings at the same site in Munessa and with previous observations from an artificial shade seedling experiment (Masresha Fetene and Yonas Feleke, 2001) suggesting the wide range of irradiation intensities which *P. falcatus* leaves can utilize for photosynthesis or at least tolerate.

Parallel decline in gs_{max} and A_{nmax} of *P. falcatus* during days of the dry season shows CO_2 uptake limitation by a decrease of stomatal conductance. Irrespective of seasons, both A_{nmax} and gs_{max} of *P. falcatus* were the lowest of the studied trees and also in comparison with several other tropical tree species. Inherently low gas exchange characteristics are inversely proportional to leaf life spans (Mulkey *et al.,* 1993; Chabot and Hicks, 1982; Reich *et al*. 1992). Thus, low assimilation rates of *P. falcatus* leaves correspond with their long life spans (section 4.1).

In addition to seasonal changes of moisture and temperature, the gas exchange characteristics of *P. africana* leaves were further complicated by the wide amplitude of amount and intensity of irradiation to which they were exposed. With excessively high irradiance (leading to transient photoinhibition during midday) during the dry season and low light intensities during the wet season, both causing a decline in photosynthetic carbon gain, *P. africana* leaves were under greater influence of the light environment than its potential competitor *P. falcatus*. Despite its sensitivity to the light environment, daily carbon gain of *P. africana* leaves showed less sensitivity to seasonal changes in soil moisture. Dry period A_{nmax} rate of *P. africana* was the highest of all three investigated functional types of trees.

Protective photoinhibition, as observed in *P. africana*, and fine-tuned stomatal control during the peak dry season are known to form an adaptive mechanism to maintain high daily carbon gain (Mulkey *et al.*, 1996; Choat *et al.*, 2006). This observation contrasts with that of *C. macrostachyus* which showed a much stronger sensitivity of A_{nmax} to gs_{max}. The fact that the dry season maximum assimilation rates of *P. africana* leaves were relatively less affected by the decline in gs_{max} further explains less response of dry season carbon gain. Lower sensitivity of A_n to a decline in gs of *P. africana* may be attributed to less influence of drought induced stomatal closure on intercellular CO_2 concentration. This explanation is supported by the high Ci/Ca values determined from the leaf $\delta^{13}C$ signature (section 4.2). Stomatal closure can greatly influence A_n only below a threshold at which the gradient in CO_2

concentration between the ambient and the mesophyll substantially changes (Farquhar and Sharkey, 1982).

The observation in *C. macrostachyus* suggests an important role of irradiance in modulating dry and wet season patterns of CO_2 uptake. High rates of CO_2 uptake during the initial period of the dry season indicate that young leaves were physiologically active allowing the tree to extend its biochemical processes into the dry period when soil moisture already decreased. Continuous foliage turnover during the wet period (section 4.1) resulting in large proportion of young leaves at the end of the wet season allows *C. macrostachyus* to transiently maximize carbon gain during the early dry period. Some tropical trees are known to maximize carbon gain by producing more of highly assimilating young leaves during the early dry season when irradiance is less constrained by clouds (Mulkey *et al.*, 1996). Foliage dynamics of *C. macrostachyus* shows suspended leaf production but not premature leaf shedding during the dry season. The life span of *C. macrostachyus leaves* is 3 months and CO_2 uptake decreases dramatically above an age of 2 months (Table 3.1.6). Hence, carbon gain in the course of the dry period when soil moisture decreases is declining due to a high proportion of senescing leaves and significant proportion of leafless branches of *C. macrostachyus.* The effect of extended drought could be concluded from the low maximum rates of assimilation which were measured in January 2011 when about 50% of the leaves of *C. macrostachyus* were shed and most of the remaining leaves (>80%) were senescing.

The maximum photosynthetic rates of *P. africana* and *C. macrostachyus* leaves are in the ranges of other comparable tropical trees (Eschenbach *et al.,* 1998; Sobrado, 2003; Hölscher *et al*., 2006) but that of *P. falcatus* was substantially lower than reported in the literature (Reich *et al*., 1995; Mulkey *et al*., 1996; Masresha Fetene and Yonas

Feleke, 2001). On the other hand, maximum stomatal conductance measured for *C. macrostachyus* and *P. africana* agrees with previous reports (Nardini and Salleo, 2000; Jiregna Gindaba *et al.*, 2004; Motzer *et al.*, 2005) and that of *P. falcatus* complies with observations by Lüttge *et al.* (2003).

In summary, both the seasonal and daily carbon gain patterns showed the significance of irradiation on all functional types of trees especially during the wet period. However, under conditions of the dry period the physiological responses of the studied species were different. Stomatal control of CO_2-uptake was significant for carbon gain in the case of *P. falcatus,* whereas in *P. africana* relatively lower impact of stomatal control on carbon assimilation was accompanied by protective transient photoinhibition against excessively high irradiation. On the other hand, more sunny conditions during days of the early dry season when physiologically active leaves were still present contributed a major part to the annual carbon gain of the deciduous *C. macrostachyus* while an extended drought period resulted in senescence of the majority of the foliage and abolition of carbon uptake. Earlier dry season with high irradiance is the best period for maximum assimilation for *C. macrostachyus.* On the other hand, seasonal variations in soil moisture only partially reduced the rates of carbon gain by the evergreens. The strategies for coping with the combined stresses of high irradiation and scarcity in soil water during an extended dry season, when stomates close, appeared different for the three functional types but our study cannot explain the strategies of *P. falcatus* leaves.

4.3.2 Water use efficiency

WUE has been used as an index for comparing performance of plant species of differing hierarchical levels of a phytocenosis, and of seasonal patterns (Cienciala and

Lindroth, 1995). In the present study, interspecies comparison of WUE of the studied functional types of trees was season dependent. Interestingly, there was no significant WUE difference among functional types under wet season conditions while remarkable differences observed during the dry season implying differential gas exchange response of the species for seasonal variations. Furthermore, within species wet to dry season comparison showed that *C. macrostachyus* was the only species exhibiting a significant WUE decline during the dry season. Obviously this is an outcome of a weaker control of stomatal conductance in *C. macrostachyus* resulting in open stomates even when water supply to the leaves was low. High assimilation rates in pioneer species such as *C. macrostachyus have* been reported to be achieved at the expense of high water loss (Goldstein *et al.*, 1989; Sobrado, 1993; Eamus *et al.,* 1999). High water use efficiency of *P. falcatus* observed in the present study agrees well with low Ci/Ca values determined from the leaf $\delta^{13}C$ signature (section 4.2). Among others, effective water use strategy is a likely mechanism of the two evergreen functional types adapted to optimize their annual carbon gain in this seasonally dry ecosystem.

4.3.3 Niche partitioning

Segregation along an environmental resource axis, tradeoffs in performance as well as in traits are commonly used assays to prove whether niche partitioning is contributing to stable coexistence (Silvertown, 2004). The present study reveals that the mode of resource acquisition of the investigated functional types of trees is not random. The trees show different physiological and ecophysiological traits which may be instrumental in exploiting different niches thus stabilizing their coexistence (Chesson, 2000). The axis on which the niche fluctuates is composed of various combinations of light intensity, temperature, and water supply from the soil, which depending on the species, can be temporally used to acquire the amount of carbon which is necessary for annually balanced growth rates. Niche exploitation is thus reflected by the different strategies for carbon gain and water use. On one hand, the evergreen species maintain lower rates of assimilation also during dry periods benefiting from conservative water use. On the other hand, the deciduous *C. macrostachyus* maximizes assimilation with less control of water loss during times of high irradiance in particular during the early dry period when soil moisture is still sufficient. Under conditions of changing seasonal and inter-annual soil water availability the temporal physiological advantage of one species becomes balanced by the advantage of the other species at another time period (Penuelas *et al.*, 2011). Thus, a differential versatility of the gas exchange systems is important, that allows adaptation to fluctuations in inter-annual and seasonal variations of the abiotic variables (irradiance, temperature, and soil moisture).

The difference in strategies for carbon acquisition manifests in a tradeoff in WUE along soil moisture gradient. Long term studies of vegetation dynamics have provided increasing evidence that the tradeoffs which organisms faced in response to environmental constraints influence the general patterns of succession and the maintenance of diversity within communities (Rees *et al.,* 2001). The studied species showed differing WUEs signifying less conservative water use of the facultative deciduous *C. macrostachyus* (opportunistic strategy) and the reverse for the evergreens (conservative strategy). As predicted by the fluctuation niche hypothesis leaflessness is the likely physiological mechanism of *C. macrostachyus* to tolerate inter-pulse periods (i.e. drought periods) (Terradas *et al.* 2009) while the evergreens continue to assimilate at reduced rate. The differences in WUE along a moisture gradient demonstrate the dimension of the niche along which the investigated functional types of trees segregate. The measured variation in WUE conforms well to the hypothesis of Araya *et al.* (2011) who concluded that a systematic difference in WUE along a moisture gradient is required for species segregation along hydrological niches. Therefore, in addition to the regeneration niche that obviously allows a continuous segregation of the pioneer *C. macrostachyus (*Silvertown, 2004) with the late successional evergreens, the "*fluctuation niche*" may explain the ecophysiological basis of resource and niche partitioning modes that stabilized the coexistence of the studied functional types.

To summarize, the gas exchange study it reveals the significance of irradiance both on the seasonal and daily carbon gain patterns of all functional types of trees especially during the wet season. Dry season gas exchange responses differed among the studied tree species. Stomatal control and transient protective photoinhibition were peculiar dry season physiological characters of *P. falcatus* and *P. africana,* respectively. The study also shows that high WUE is the likely mechanism of the two evergreen tree types adapted to optimize their annual carbon gain. The study further implies that differing versatility of the gas exchange system of the studied functional types of trees is important in governing the carbon gain and adaptation to fluctuations in abiotic factors.

4.4 Conclusions and recommendations

This study for the first time documented the annual course of foliage dynamics as well as the proximate causes for three differing functional types of trees coexisting in Ethiopian Afromontane forests. It provides valuable information about the strategies that enable the coexistence of trees differing in ecophysiological traits. It addresses the hydraulic and carbon relations of functional types of trees and compiles information that can be used as essential input for developing sustainable management plan.

The findings of this study are summarized as:

1. Moisture regime induces significant control on leaf-bud sprouting of *P. falcatus* and *C. macrostachyus* but not on *P. africana.*
2. The course of foliage turnover in *P. falcatus* and *C. macrostachyus* is under the control of endogenous (leaf life span) rather than exogenous (weather) factors
3. Leaf life-span of the studied species (3, 6 and > 24 months for *C. macrostachyus, P. africana* and *P. falcatus*, respectively) is greatly independent of weather condition.
4. Diameter growth of all of the studied species reacts positively to moisture and there is no direct competitive advantage of one species over the others.
5. Whole tree water use is significantly different among functional types of trees during the dry period ranging between 4 and 10 kg of water per day for trees of 14 cm in DBH, *P. africana* exhibiting the lowest values during both seasons.
6. *P. falcatus* and also to some extent *P. africana* recharges their stem water reserve during night time. *C. macrostachyus* replenishes its stem water reserve during day time.
7. *P. africana* relies on the soil water in the deeper soil layer (deeper than 1m) while *P. falcatus* appeared to extract uniformly from all depths ≥ 20 cm. *C. macrostachyus* showed less consistent source for the dry and the wet periods.
8. Dry season gas exchange of *P. africana* appeared to be less obstructed by moisture deficit.

9. Seasonal variation in light intensity and soil moisture showed less control on carbon acquisition of the evergreens (*P. africana* and *P. falcatus*).
10. The studied species showed different performance along the gradients of soil moisture and light intensity. Sunny days when the tree is with physiologically active leaves provide an ideal condition for maximized carbon gain in *C. macrostachyus* while extended drought restricts the production of new leaves and decreases carbon gain. Under ideal conditions assimilation rate of *C. macrostachyus* leaves is 136% and 76% higher than that of *P. falcatus* and *P. africana*, respectively.
11. WUE (water lost per unit CO_2 fixed) of *C. macrostachyus* significantly differs between dry and wet seasons. WUE of the studied functional trees differ during the dry season but not during the wet season. Dry season high carbon gain of *C. macrostachyus* is at the expense of high water loss.

Based on these findings the formulated hypothesis is accepted and it is further concluded that:

1. The foliage dynamics of differing functional types of trees is controlled by several proximate factors. The impact of the onset of the rain in triggering leaf-bud break is not universal for all functional types of trees in the Munessa Forest. Though the onset of the rain appeared to trigger bud break on some species the overall foliage dynamics is rather under control of endogenous factors, controlling the life-spans of the leaves. Leaf life-span has an impact on several functional traits, such as leaf growth, photosynthetic capacity, and respiration. This observation implies its relevance in studying ecophysiological attributes and characterizing species in the studied community.

2. Differences in night and day time tissue re-charging, tissue water storage and whole tree water use are among the strategies that stablize the coexistence of the studied functional types of trees. Moreover, differing spatial and temporal use of water resources further contributes to the sustained coexistence of the species.
3. Balanced carbon gain of the investigated functional types of trees is maintained by exploiting various niches fluctuating along irradiance and soil moisture gradients. Thus, our finding emphasizes the importance of temporally changing patterns of these environmental factors for stabilizing the coexistence of adult individuals of different functional types, and in turn, plant diversity.

The present findings could provide useful information that can contribute to sustainable natural forest management as well as plantation programs involving indigenous tree species. Therefore, it is recommended that:

- The long term courses of irradiance and soil moisture condition could be used as a tool for modeling the impact of environmental changes on plant biodiversity and ecosystem services in the Munessa Forest. Likewise, predictions about the foliage dynamics of the forest in response to environmental changes should account endogenous controls such as leaf life span. These evidences are essential output of the present study providing useful information that assists the prediction of climate change consequences on vegetation dynamics.
- Enrichment planting to rehabilitate degraded dry forests should be carried out with species representing different functional types of trees so that the carbon and hydraulic budget of the overall ecosystem can be optimized. Thus, several

species of large number of functional types of trees should be preferred than several species of a few functional types of trees.

- Forest management activities should account the significance of the depth of soil water source of tree species in the ecosystem hydraulic cycle of seasonally dry forests.
- For a plantation program designed for high biomass production, broad leaf species can be selected to sites where moisture is not limiting and, high and persistent annual irradiance is prevailing.

Moreover, to generate useful ecophysiological information that can be utilized for sustainable management of the Munessa Forest future research interventions are recommended on:

- Ecosystem level carbon and hydraulic dynamics so that the studied processes can be further evaluated and quantified under different biophysical conditions
- The cause and extent of damage by precocious leaf abscission observed in *P. falcatus* and the shothole disease observed in *P. africana.*
- Possible interaction of foraging herbivores with phenological patterns of functional types of trees.
- Detailed study to investigate excess light tolerance strategies of *P. falcatus* leaves.

References:

Abdeal Gure, Wahlstrom, K., Stenlid, J. (2005). Pathogenicity of Seed-Associated Fungi to *P. falcatus* in Vitro. *Forest Pathology* **35**: 23-35.

Ackerly, D. (2004). Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecol Monogr* **74**: 25–44.

Aide, M. (1993). Patterns of leaf development and herbivory in a tropical understory community. *Ecology* **74**: 455-466.

Araya, Y.N., Silvertown, J., Gowing, D.J., McConway, K.J., Linder, H.P., Midgley, G. (2011). A fundamental, eco-hydrological basis for niche segregation in plant communities. *New Phytologist* **189**: 253–258.

Asferachew Abate (2004). Biomass and Nutrient Studies of Selected Tree Species of Natural and Plantation Forests: Implications for a Sustainable Management of the Munessa-Shashemene Forest, Ethiopia. Dissertation, University of Bayreuth, Bayreuth, Germany.

Aster Gebrekirstos, Demel Teketay, Masresha Fetene, Mitlohner, R. (2006). Adaptation of five co-occurring tree and shrub species to water stress and its implication in restoration of degraded lands. *Forest Ecology and Management* **229**:259-267.

Azene Bekele, Birnie, A., Tengnäs, B. (1993). Useful trees and shrubs for Ethiopia: Identification, propagation and management for agricultural and pastoral communities. Regional Soil Conservation Unit (RSCU), Swedish International Development Authority (SIDA), Addis Abeba, Nairobi.

Bartels, D. Hussain, S. (2011). Resurrection plants, physiology and molecular biology. In: Lüttge U, Beck E, Bartels D (ed) Plant desiccation tolerance, Berlin, Germany, pp 339-364.

Beck, E.H., Fetting, S., Knake, C., Hartig, K., Bhattarai, T. (2007). Specific and unspecific responses of plants to cold and drought stresses. *Journal of Biosciences* **32**:501-510.

Bendix, J., Homeier, J., Cuvea, O.E., Emck, P., Breckle, S.W., Richter, M., Beck, E. (2006). Seasonality of weather and tree phenology in a tropical evergreen mountain rain forest. *International journal of bimetreology* **50**:370–384.

Bonal, D., Barigah, T.S., Granier, A., Guehl, J.M. (2000). Late stage canopy tree species with extremely low $\delta^{13}C$ and high stomatal sensitivity to seasonal soil drought in the tropical rainforest of French Guiana. *Plant, Cell and Environment* **23**:445-459.

Borchert, R. (1994). Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* **75**: 1437-1449.

Borchert, R. (1998). Responses of tropical trees to rainfall seasonality and its long-term changes. *Climatic change* **39**:381-393.

Borchert, R., Rivera, G., Hagnauer, W. (2002). Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. *Biotropica* **34**:27–39.

Brodribb, T.J., Holbrook, N.M., Gutierrez, M.V. (2002). Hydraulic and photosynthetic co-ordination in seasonally dry tropical forest trees. *Plant, Cell and Environment* **25**:1435-1444.

Browse, J., Xin, Z. (2001). Temperate senescing and cold acclimation. *Current opinion in plant biology* **4**:241-246.

Bucci, S.J., Goldstein, G., Meinzer, F.C., Franco A.C., Campanello, P., Scholz, F.G. (2005). Mechanisms contributing to seasonal homeostasis of minimum leaf water potential and predawn disequilibrium between soil and plant water potential in Neotropical savanna trees. *Trees* **19**: 296-304.

Burkill, H.M. (1985). The Useful plants of West tropical Africa, Vol. 2. Royal Botanic Gardens, Kew. 636 pp.

Calva-Alvarado, J.C.C, Mcdowell, N.G., Waring, R. H. (2008). Allometric relationships predicting foliar biomass and leaf area: sapwood area ratio from tree height in five Costa Rican rain forest species. *Tree Physiology* **28:** 1601-1608.

Chabot, B.F, Hicks, D.J. (1982).The ecology of leaf life-spans. *Annual Review of Ecology and Systematics* **13**:229-59.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* **31**: 343-366.

Choat, B., Ball, M.C., Luly, J.G., Donnelly, C.F., Holtum, J.A.M. (2006). Seasonal patterns of leaf gas exchange and water relations in dry rain forest trees of contrasting leaf phenology. *Tree Physiology* **26**: 657-664.

Cienciala, E., Lindroth, A. (1995). Gas-exchange and sap flow measurements of *Salix viminalis* trees in short-rotation forest (II): Diurnal and seasonal variations of stomatal response and water use efficiency. *Trees* **9**:295-301.

Cueva, O. E., Homeier, J., Breckle, S.W., Bendix, J., Emck, P., Richter, M., Beck, E. (2006). Seasonality in an evergreen tropical mountain rainforest in Southern Ecuador, *Ecotropica* **12**: 69-85.

Cunninghum, A.B., Mbenkum F.T. (1993). Sustainability of harvesting *P. africana* bark in Cameroon, A medicinal plant in international trade, people and plants working paper 2, division of ecological sciences, UNESCO.

Dalitz, C.h., Dalitz, H., Musila, W., Masinde, S. (2011). Illustrated Field Guide to the Common Woody Plants of Kakamega Forest, 615 pp, Hohenheim.

Damesin, C., Rambal, S., Joffre, R. (1998). Seasonal and annual changes in leaf $\delta^{13}C$ in two co-occurring Mediterranean oaks: relations to leaf growth and drought progression, *Functional Ecology* **12**:778-785.

Dawson, T. E. (1996). Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: the roles of tree size and hydraulic lift. *Tree Physiology* **16**: 263-272.

De Bie, S., Ketner, P., Paasse, M., Geerling, C. (1998). Woody plant phenology in the West Africa savanna. *Journal of Biogeography* **25**: 883-900.

Demel Teketay (1996). Seed ecology and regeneration in dry afromontane forests of Ethiopia, Doctoral thesis, Swedish University of Agricultural Sciences, Silvestria 4. Umea.

Demel Teketay (2005). Seed and regeneration ecology in dry Afromontane forests of Ethiopia: Seed production - population structures. *Tropical Ecology* **46**: 29-44.

Devineau, J.L. (1999). Seasonal rhythms and phenological plasticity of savanna woody species in a fallow farming system (south-west Burkina Faso). *Journal of tropical ecology* **15**: 497-513.

Dharani, N. (2002). Field guide to common trees and shrubs of East Africa, Struik Publishers, South Africa.

Do, F.C., Venceslas, A.G., Olivier, G., Amadou, L.D., Mayecor, D., Alain, R., Leonard, E.A. (2005). Environmental influence on canopy phenology in the dry tropics. *Forest ecology and management* **215**: 319-328.

Eamus, D. (1999). Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. *Trees* **14**: 14-16.

Eamus, D., Myers, B., Duff, G., Williams, D. (1999). Seasonal changes in photosynthesis of eight savanna tree species. *Tree Physiology* **19**:665-671.

EFAP. (1994). Ethiopian Forestry Action Program. Volume I-Executive summary. Ministry of National Resources Development and Environmental Protection. Addis Abeba.

Ehleringer, J. R., Lin, Z. F., *et al.* (1987). Leaf carbon isotope ratios of plants from a subtropical monsoon forest. *Oecologia* **72**: 109-114.

Ehleringer, J.R., Dawson, T.E. (1992). Water uptake by plants: perspectives from stable isotope composition. *Plant, cell and environment* **15**:1073-1082.

Elliott, S., Baker, P.J., Borchert, R. (2006). Leaf flushing during the dry season: the paradox of Asian monsoon forests. *Global Ecology and Biogeography* **15**: 248-257.

Eschenbach, C., Glauner, R., Kleine, M., Kappen, L.(1998). Photosynthesis rates of selected tree species in lowland dipterocarp rainforest of Sabah, Malaysia. *Trees* **12**:356-365.

Eshetu Yirdaw (2002). Restoration of the native woody-species diversity, using plantation species as foster trees, in the degraded highlands of Ethiopia. Dissertation, Agriculture and Forestry of the University of Helsinki, Helsinki.

Espinosa, L.Y, Terrazas, T., Lauro, L.M. (2006). Integrated analysis of tropical trees Growth: A multivariate approach. *Annals of Botany* **98**: 637-645.

FAO. (2001). Global Forest Resources Assessment 2000. FAO Forestry Paper 140, FAO, Rome.

FAO. (2003): State of the World forest: The situation and developments in the forest sector, part one. FAO, Rome.

Farquhar, G.D., Ehleringer, J.R., Hubick, K.T.(1989). Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology* **40**: 503-537.

Farquhar, G.D., Sharkey, T.D. (1982). Stomatal conductance and photosynthesis, *Annual Review of Plant Physiology* **33**:317-345.

Feng, Y.L., Cao, K.F, Zhang, J.L. (2004). Photosynthetic characteristics, dark respiration, and leaf mass per unit area in seedlings of four tropical tree species grown under three irradiances. *Photosynthetica* **42**:431-437.

Friis, I.B. (1992). Forests and forest trees of Northeast tropical Africa. Kew Bulletin.

Fritzsche, F., Asferachew Abate, Masresha Fetene, Beck, E., Weise, S., Guggenberger, G. (2006). Soil-plant hydrology of indigenous and exotic trees in an Ethiopian montane forest. *Tree Physiology* **26**:1043-1054.

Fritzsche, F., Zech, W., Guggenberger, G. (2007). Soils of the main Ethiopian rift valley escarpment: a transect study. *Catena* **70**: 209-219.

Garten, C.T., Taylor, G.E. (1992). Foliar $\delta^{13}C$ within a temperate deciduous forest: spatial, temporal, and species sources of variation. *Oecologia* **90**:1-7.

Getachew Tesfaye, Demel Teketay, Masresha Fetene, Beck, E. (2010). Regeneration of seven indigenous tree species in a dry Afromontane forest, southern Ethiopia. *Flora* **205**:135-143.

Getachew Tesfaye, Demel Teketay, Masresha Fetene, Beck, E. (2011). Phenology of seven indigenous tree species in a dry Afromontane forest, southern Ethiopia. *Tropical Ecology* **52**:229-241.

Getachew Tesfaye, Demel Teketay, Masresha Fetene, Beck, E. (2011). Seedling growth and survival of indigenous tree species along a light gradient in a dry afromontane forest: In Forestry: Research, Ecology and Policies, ed: Diane A. B., Nova Science Publishers, Inc.

Getachew Tesfaye. (2007). Ecology of regeneration and phenology of seven indigenous tree species in a dry Afromontane forest of Ethiopia. Dissertation, Addis Ababa University, Ethiopia.

Givnish, T.J. (2002). Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. *Silva Fennica* **36**: 703-743.

Goldstein, G., Andrade, J. L., Meinzer, F. C., Holbrook, N. M., Cavelier, J., Jacksons, P., Celis, A. (1998). Stem water storage and diurnal patterns of water use in tropical forest canopy trees. *Plant, Cell and Environment* **21**: 397-406.

Goldstein, G., Rada, F., Rundel, P., Azocar, A., Orozco, A. (1989). Gas exchange and water relations of evergreen and deciduous tropical savanna trees. *Ann., Sci., For.* **46**:448-453.

Granier, A. (1987). Evaluation of transpiration in a *Douglas-fir* stand by means of sap flow measurements. *Tree Physiology*. **3**:309-320.

Graniet, A. (1985). Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. Ann. Sci. For. **42**:193-200.

Hall, J.B., O'Brien, E.M., Sinclair, F.L. (2000). *P. africana*. Dissertation, School of Agricultural and Forest Sciences, University of Wales.

Han, L., Xie, L.J., Dai, K.J., Yang, Q., Cai, Z.Q. (2010). Contrasting leaf characteristics of trees and lianas in secondary and mature forests in southwestern China, *Photosynthetica* **48**: 559-566.

Hasselquist, N. J., Allen, M. F., Santiago, L.S. (2010). Water relations of evergreen and drought-deciduous trees along a seasonally dry tropical forest chronosequence. *Oecologia*, **164**:881-890.

Hoelscher, D., Leuschner, C., Bohman, K., Hagemeier, M., Juhrbandt, J., Tjitrosemito, S. (2006). Leaf gas exchange of trees in old-growth and young secondary forest stands in Sulawesi, Indonesia. *Trees* **20**: 278-285.

Holbrook, N. M., Sinclair, T.R. (1992). Water balance in the arborescent palm, Sabal palmetto. II. Transpiration and stem water storage. *Plant, Cell and Environment* **15**: 401-409.

Hussien Indries (2007). Seasonal and depth related patterns of fine root mass in four indigenous tree species of a tropical dry afromontane forest in Ethiopia. Msc thesis, School of graduate studies, Addis Ababa University.

ICRAF. (2004). Agroforestry tree database, A tree species reference and selection guide.

IPCC (2000). Land use, land use change and forestry. Special report, Inter-governmental panel on climate change. Cambridge University Press, Cambridge, UK.

Jackson, P.C., Menzer, F.C., Bustamante et al. (1999). Partitioning of soil water among tree species in a Brazilian Cerrado Ecosystem. *Tree Physiology* **19**: 717-724.

Jackson, R. C., Cavelier, J., Goldstein, G., Meinzer, E. C., Holbrook, N. M. (1995). Partitioning of water resources among plants of a lowland tropical forest. *Oecologia* **101**: 197-203.

Jiregna Gindaba, Rozanov, A., Legesse Negash (2004). Response of seedlings of two Eucalyptus and three deciduous tree species from Ethiopia to severe water stress. *Forest Ecology and Management* **200**:119-129.

Kavanagh, K.L., Zaerr, J.B. (1997). Xylem cavitation and loss of hydraulic conductance in western hemlock following planting. Tree Physiol **17**: 59-63.

Kindeya Gebrehiwot, Muys, B., Mitiku Haile, Mitloehner, R. (2005). The use of plant water relations to characterize tree species and sites in the drylands of northern, Ethiopia. *Journal of Arid Environments* **60**:581-592.

Krepkowski, J., Brauning, A., Gebrekirstos, A., Strobl, S. (2011). Cambial growth dynamics and climatic control of different tree life forms in tropical mountain forest in Ethiopia. *Trees* **25**:59-70.

Larcher, W. (2003).Physiological Plant Ecology, Springer-Verlag, Berlin.

Leffler, A.J., Enquist, B. J. (2002). Carbon isotope composition of tree leaves from Guanacaste, Costa Rica: comparison across tropical forests and tree life history. *Journal of Tropical Ecology* **18**:151-159.

Legesse Negash (2010). A selection of Ethiopia’s indigenous trees, biology, uses and propagation techniques, Addis Ababa, University Press.

Legesse Negash, (1995). Indigenous trees of Ethiopia: Biology, uses and propagation techniques. SLU, Reprocentralen, Umea, Sweden.

Leicht, S.A., Silander Jr, J.A., Greenwood, K. (2005). Assessing the competitive ability of Japanese stilt grass, *Microstegium vimineum* (Trin.) A. Camus. *Journal of the Torrey Botanical Society* **132**:573-580.

Lieberman, D. (1982). Seasonality and phenology in a dry tropical forest in Ghana. *Journal of ecology* **70**: 791-806.

Lovelock, C.E., Feller, I.C. (2003). Photosynthetic performance and resource utilization of two mangrove species coexisting in a hypersaline scrub forest. *Oecologia* **134**:455-462.

Lüttge, U., Berg, A., Masresha Fetene, 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.

Lüttge, U., Hertel, B. (2009). Diurnal and annual rhythms in trees. *Trees* **23**:683-700.

Markesteijn, L., Poorter, L., Bongers, F., Paz, H., Sack, L. (2011). Hydraulics and life history of tropical dry forest tree species: coordination of species' drought and shade tolerance. *New Phytologist* **191**: 480-495.

Martinelli, L.A., Almeida, S., Brown, I.F., Moreira, M.Z., Victoria, R.L., Sternberg, L.S.L., Ferreira, C.A.C., Thomas, W.W. (1998). Stable carbon isotope ratio of tree leaves, boles and fine litter in a tropical forest in Rondonia, Brazil. *Oecologia* **114**:170-179.

Masresha Fetene, 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.

Masresha Fetene, Yonas Feleke (2001). Growth and photosynthesis of seedlings of four tree species from a dry tropical afromontane forest. *Journal of Tropical Ecology* **17**: 269-283.

McJannet, D.L., Vertessy, R.A., Clifton, C.A. (2000). Observations of evapotranspiration in a break of slope plantation susceptible to periodic drought stress. *Tree Physiology*. **20**:169-177.

Meinzer, F. C., Goldstein, G. and Andrade, J. L. (2001). Regulation of water flux through tropical forest canopy trees: Douniversal rules apply? *Tree Physiology* **21**: 19-26.

Meinzer, F.C., Andrade, J.L., Goldstein, G., Holbrook, M.N., Cavelier, J., Wright, S.J. (1999). Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia* **12:** 293-301.

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.

Melayah, A. and Bruckler, L. (1996). Modeling the transport of water stable isotopes in unsaturated soils under natural conditions, *Water resources research* **32:** 2047-2054.

Morellato, L.P.C, Talora, D.C., Takahasi, A., Bencke, C.C., Romera, E.C., Zipparro, V.B. (2000). Phenology of Atlantic rain forest trees: a comparative study. *Biotropica* **32**:811-823.

Motzer, T., Munz, N., Kuppers, 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.

Mulkey, S.S., Kitajima, K.S., Wright, S.J. (1996). Plant physiological ecology of tropical forest canopies. *TREE* **11**:408-412.

Mulkey, S.S., Wright, S.J., Smith, A.P. (1993). Comparative physiology and demography of three Neotropical forest shrubs: alternative shade-adaptive character syndromes. *Oecologia* **96**:526-536.

Mullugeta Lemenih, Olsson, M., Karltun, E. (2004). Comparison of soil attributes under *Cupressus lusitanica* and *Eucalyptus saligna* established on abandoned farmlands with continuously cropped farmlands and natural forest in Ethiopia. *Forest ecology and management* **195**: 57-67.

Murphy, P.G., Lugo, A.E. (1986). Ecology of tropical dry forest. *Annual review of ecological systems* **17**:67-88.

Mwanza, E.J.M., Waithaka, S.K. (1998). First Report of *Colletotrichum gloeosporioides* as a Foliar and Die-back Pathogen of *P. africana* in Kenya. *Plant Diseases* **83**:79.1-79.1.

Myers, B.A., Williams, R.J., Fordyce, I., Duff, G.A., Eamus, D. (1998). Does irrigation affect leaf phenology in deciduous and evergreen trees of the savannas of northern Australia, *Australian Journal of Ecology* **23**: 329-339.

Naeem, S., Wright, J. P. (2003). Disentangling biodiversity effects on ecosystem functioning: Deriving solutions to a seemingly insurmountable problem. *Ecological Letters* **6**: 567-579.

Nardini, A., Salleo, S. (2000). Limitation of stomatal conductance by hydraulic traits: sensing or preventing xylem cavitation? *Trees* **15**:14-24.

Noad, T.C., Birnie, A. (1989). Trees of Kenya, T.C Noad and A. Birnie, Nairobi, Kenya.

Orwa, C., Mutua, A., Kindt, R., Jamnadass, R., Simons, A. (2009). Agroforestry Database 4.0.

Penuelas, J., Terradas, J., Lloret, F. (2011). Solving the conundrum of plant species coexistence: water in space and time matters most. *New Phytologist* **189**: 5-8.

Phillips, D. L., Gregg, J.W. (2003). Source partitioning using stable isotopes: coping with too many sources. *Oecologia* **136**:261-269.

Phillips, N. G., Ryan, M. G., Bond B. J., Mcdowell, N. G., Hinckley, T. M., Èermak, J. (2003). Reliance on stored water increases with tree size in three species in the Pacific Northwest. *Tree Physiology* **23**: 237-245.

Pohjonen, V., Pukkala, T. (1990). *Eucalyptus globulus* in Ethiopian forestry. Forest *Ecology and Management* **36**: 19-31.

Poorter, L., Bongers, F. (2006). Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* **87**:1733-1743.

Querejeta, J. I., Estrada-Medina, H., Allen, M. F., Jimenez-Osornio, J.J. (2007). Water source partitioning among trees growing on shallow karst soils in a seasonally dry tropical climate. *Oecologia* **152**: 26-36.

Ragusa, N. J., Silva, R.R. (2007). Canopy phenology of a dry forest in western Brazil. *Brazilian journal of biol*ogy **67**: 569-575.

Rees, M., Condit, R., Crawley, M., Pacala, S., Tilman, D. (2001). Long-term studies of vegetation dynamics. *Science* **293**: 650-654.

Reich, P.B., Borchert, R. (1982). Phenology and ecophysiology of the tropical tree, *Tabebuia neochrysantha* (Bignoniaceae). *Ecology* **63**:294-299.

Reich, P.B., Kloeppel, B.D., Ellsworth, D.S., Waiters, M.B. (1995). Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. *Oecologia* **104**:24-30.

Reich, P.B., Waiters, M.B., Ellsworth, D.S. (1992). Leaf life-span in relation to leaf, plant and stand characteristics among diverse ecosystems. *Ecological monograph* **62**:365-392.

Rivera, G., Elliott, S., Caldas, L.S., Nicolossi, G., Coradin, V.T.R., Borchert, R. (2002). Increasing day-length induces spring flushing of tropical dry forest trees in the absence of rain. *Trees* **16**:445-456.

Rotter, J., Danish, K. (2000). Forest carbon and the kyoto protocol's clean development mechanism. *Journal of Forestry* **98**:38-47.

Sayer, A. J. Harcourt, S. C. and Collins, M. N. (1992). The conservation atlas of tropical forests Africa. IUCN, Cambridge, UK.

Scholander, P. F., Hammel, H.T., Bradstreet, E. D., Hemmingsen, E. A. (1965). Sap pressure in vascular plants. *Science* **148**:339-346.

Scrimgeour, C.M. (1995). Measurement of plant and soil water isotope composition by direct equilibration methods. *Journal of hydrology* **172**: 261-274.

Silvertown, J. (2004). Plant coexistence and the niche. *Trends in ecology and evolution* **19**: 605-611.

Singh, K.P., Kushwaha, C.P. (2005). Emerging paradigms of tree phenology in dry tropics. *Current science in India* **89**: 964-975.

Sobrado, M. A. (1993). Trade-off between water transport efficiency and leaf life-span in a tropical dry forest. *Oecologia* **96**: 19-23.

Sobrado, M. A. (2003). Hydraulic characteristics and leaf water use efficiency in trees from tropical montane habitats. *Trees* **17**: 400-406.

Sobrado, M.A. (1986). Aspects of tissue water relations and seasonal changes of leaf water potential components of evergreen and deciduous species coexisting in tropical dry forests. *Oecologia* **68**: 413-416.

Sobrado, M.A., Ehleringer, J.R. (1997). Leaf carbon isotope ratios from a tropical dry forest in Venezuela. *Flora* **192**:121-124.

Stewart, K.M. (2003). The African cherry (*P. africana*): Can lessons be learned from an over-exploited medicinal tree? Journal of Ethnopharmacology **89:** 3-13.

Stratton, L. C., Goldstein, G., Meinzer, F. C. (2000). Temporal and spatial partitioning of water resources among eight woody species in a Hawaiian dry forest. *Oecologia* **124**:309-317.

Strobl, S. (2012). Analysis of the "nurse-tree effect" of natural and exotic shelter trees on the growth of the indigenous *P. falcatus* in an Ethiopian montane forest. Dissertation, University of Bayreuth, Bayreuth, Germany.

Strobl, S., Masresha Fetene, Beck, E.H. (2011). Analysis of the ''shelter tree-effect'' of natural and exotic forest canopies on the growth of young *P. falcatus* trees in southern Ethiopia. *Trees* **25**:769-783.

Sucoff, E. (1971). Water potential in red pine: soil moisture evapotranspiration and crown position. *Ecology* **53**: 681-686.

Tamrat Bekele. (1993). Vegetation ecology of remnant Afromontane forests of the Central Plateau of Shewa, Ethiopia. *Acta Phytogeographica Suecica* **79**: 1-59.

Terradas, J., Penuelas, J., Lloret, F. (2009). The fluctuation niche in plants. *International Journal of Ecology* doi: 10.1155/2009/959702

Tesfaye Wubet, Kottke, I., Teketay, D., Oberwinkler, F. (2003). Mycorrhizal status of indigenous trees in dry Afromontane forests of Ethiopia. *Forest Ecology and Management* **179**: 387-399.

Thomas, D.S., Eamus, D., Bell, D. (1999). Optimization theory of stomatal behaviour - II. Stomatal responses of several tree species of north Australia to changes in light, soil and atmospheric water content and temperature. *Journal of Experimental Botany* **50**: 393-400.

Tsingalia, M.H. (1989). Variation in seedling predation and herbivory in *P. africana* in the Kakamega Forest, Kenya. African Journal of ecology **27**:207-217.

Tucci, M.L.S., Erismann, N.M., Machado, E.C., Ribeiro, R.V. (2010). Diurnal and seasonal variation in photosynthesis of peach palms grown under subtropical conditions. *Photosynthetica* **48**: 421-429.

Tyree, M.T., Sperry, J.S. (1989). Vulnerability of xylem to cavitation and embolism. *Annual review of plant physiology and plant molecular biolo* **40**:19-38.

Valdez-Hernández M, Andrade, JL, Jackson, PC, Rebolledo-Vieyra, M. (2010). Phenology of five tree species of a tropical dry forest in Yucatan, Mexico: effects of environmental and physiological factors. *Plant Soil* **329**: 155-171.

Van Oene, H., Berendse, F., Persson, T., Harrison, A.F., Schulze, E.-D., Anderson, B.R., Bauer, G.A., Dambrine, E., Högberg, P., Matteucci, G., Paces, T. (2000). Model analysis of carbon and nitrogen cycling in Picea and Fagus forests. *Ecological Studies* **142**: 419-467.

Van Schaik, C.P., Terborgh, J.W., Wright, S.J. (1993). The phenology of tropical forest: adaptative significance and consequences of consumers. *Annual review of ecological systems* **24**: 353-377.

Vertessy, R.A., Benyon, R.G., O'Sullivan, S.K., Gribben, P.R. (1995). Relationships between stem diameter, sapwood area, leaf area and transpiration in a young mountain ash forest. *Tree Physiol*ogy **15**:559-567.

Villar, R. Merino, J. (2001). Comparison of leaf construction costs in woody species with differing leaf life-spans in contrasting ecosystems. *New Phytologist* **151**: 213-226.

Von Breitenbach, F. (1962). National forestry development planning: A feasibility and priority study on the example of Ethiopia. Forestry Review No.3/4. MoA, Addis Ababa.

Walz, H.G. (2007). Portable Gas Exchange Fluorescence System GFS-3000, handbook of operation, Effeltrich, Germany.

Williams, L.E., Araujo, F.J. (2002). Correlations among predawn leaf, midday leaf, and midday stem water potential and their correlations with other measures of soil and plant water status in *Vitis vinifera. Journal of American society of horticultural science* **127:** 448-454.

Williams, L.J., Bunyavejchewin, S., Baker, P.J. (2008). Deciduousness in a seasonal tropical forest in western Thailand: interannual and intraspecific variation in timing, duration and environmental cues. *Oecologia* **155:** 571-582.

Williams, M., Rastetter, E.B., Fernandes, D.N., et al. (1996). Modelling the soil-plant-atmosphere continuum in a *Quercus-Acer* stand at Harvard Forest: the regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. *Plant Cell Environment* **19**: 911-927.

Williams-Linera, G. (2000). Leaf demography and leaf traits of temperate-deciduous and tropical evergreen-broadleaved trees in a Mexican montane cloud forest. *Plant Ecology* **149**: 233-244

Wright, S.J. (2002). Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* **130**: 1-14.

Wullschleger, S., Meinzer, F.C.,Vertessy, R.A. (1998). A review of whole-plant water use studies in trees. *Tree Physiology* **18**: 499-512.

Yadav, K., Yadav, A.S. (2008). Phenology of selected woody species in a tropical dry deciduous forest in Rajasthan, India. *Tropical Ecology* **49**: 25-34.

Yeshanew Ashagrie (2005). Effects of land-use changes on the properties of a Nitisol and hydrological and biogeochemical processes in different forest ecosystems at Munessa, south-eastern Ethiopia. Dissertation, University of Bayreuth, Bayreuth, Germany.

Yonas Yohannes, Shibistova, O. Asferachew Abate, Masresha Fetene, Guggenberger, G. (2011). Soil CO_2 efflux in an Afromontane forest of Ethiopia as driven by seasonality and tree species. *Forest ecology and managment* **261**:1090-1098.

Zar, J. H. (1996). Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, NJ.

Declaration

I, the undersigned, declare that this thesis is based on my original work and that it has not been presented for a degree in any other University. All sources of materials have been duly acknowledged.

Yigremachew Seyoum Signature ………………………………………..

This thesis has been submitted for examination with my approval as supervisor of the thesis.

Prof. Masresha Fetene Signature …………………………………..