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Daily and seasonal courses of gas exchange and niche partitioning among coexisting tree species in a tropical montane forest

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ABSTRACT

We investigated the seasonal gas exchange patterns of three different functional types of tropical afromontane trees, namely *Podocarpus falcatus* (Thunb.) Mirb. (evergreen gymnosperm), *Prunus africana* (Hook. f.) Kalkm. (broad-leaf evergreen), and *Croton macrostachyus* Hochst. ex Del. (broad-leaf deciduous) which grow side-by-side in the Munessa forest, southern Central Ethiopia. The hypothesis is that the trees can make different use of the environmental conditions which change seasonally and also from year to year. These changes can be understood as fluctuating niches, the utilization of which allows coexistence through balanced carbon gain. In this study, light and moisture were considered the two main fluctuating niches. Porometry was used to measure the daily and seasonal responses of the leaves to environmental variables under dry and wet season conditions in the course of the climatically differing years 2009 and 2010. Correlations of the patterns of these responses were analyzed by regression analysis. From daily integrated rates of irradiation, photosynthesis and transpiration, light and water use efficiencies of photosynthetic carbon gain and their mutual interdependences were determined. Except an extended dry season in 2009 when *C. macrostachyus* had shed its foliage, all three species continued photosynthetic net CO_2 uptake concomitant with transpiration at all seasons, although at varying rates. Ecophysiological performance of *P. falcatus* leaves is mainly light-driven and responds relatively little to a change in moisture conditions. Its carbon and water relations are striving for stability rather than flexibility. As of a typically subdominant species of the forest, *P. africana* leaves can efficiently use low light intensities but suffer from photoinhibition at full light. Their performance, showing more dynamic response to the environment than *P. falcatus*, *P. africana* appears driven more by moisture than by light. Compared to the two evergreens *C. macrostachyus* exhibited the highest flexibility in its leaves' physiological responses to environmental conditions, in particular to the light climate which is additionally potentiated by the fast turnover of its foliage. This species optimizes its carbon gain during the wet season and during the early dry period when cloud cover is minimal. Our findings thus reveal that elasticity of the response to fluctuating environmental conditions is an additional aspect in the assessment of the utilization of temporally fluctuating niches by adult tree individuals.

Introduction

Environmental factors that fluctuate temporarily (and spatially) in a forest affect the performance, in particular photosynthetic carbon acquisition and growth of the trees. Diurnal and seasonal gas exchange of the leaves respond to a variety of abiotic environmental factors such as light, temperature, leaf to air vapor pressure difference, and soil moisture (Eamus et al., 1999; Markesteijn et al., 2011; Tucci et al., 2010). In mixed stands which are typical of tropical forests, tree species of different functional types (Han et al., 2010), even when growing at the same site may show different responses to such environmental conditions. Species-specific responses can also be expected from differences in leaf traits, wood anatomy and hydraulic properties, growth rates, and phenological phenomena (Borchert, 1994; Brodribb et al., 2002; Han et al., 2010; Markesteijn et al., 2011). Such differences in functional traits may be fundamental for the successful interspecies competition for limited resources and coexistence of many woody species.

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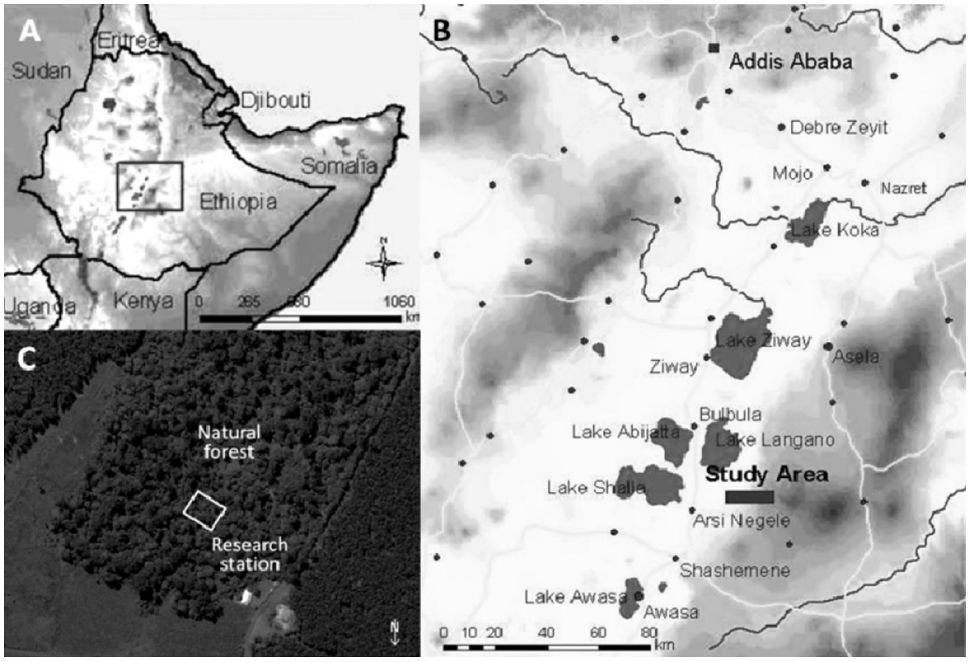

Fig. 1. Map of Ethiopia (A), Central Ethiopian rift valley (Arsi region), the study area marked by a black rectangle (source: Ormsby (2001), modified by Rückamp (2010)) (B), satellite image of the research area "Kuke" in the Munessa-Shashamene Forest, with the research plot marked by a white rectangle in the natural forest (C) (Google Earth).

The Janzen-Connell hypothesis explains diversity of tree species in a tropical forest by increase of seedling mortality around and under the parental tree which renders juveniles of other tree species a better chance of survival. While such effects are unquestioned, e.g. Hubbell (1979), Connell et al. (1984), Harms et al. (2000), and Wright (2002) stated that their "implications for species coexistence and plant diversity remain conjectural" (l.c., p. 10). In line with this statement is the idea that not only recruitment of juveniles but also the performance of the adults is determinant for coexistence of different tree life-forms in a forest. Ecological theories suggest that multi-species coexistence requires a variation of resources through space at any point in time or through time at any point in space (Wright, 2002). Resource partitioning by exploiting differing niches stabilizes coexistence by causing species to limit their growth and propagation more than they limit that of their competitors (Chesson, 2000). By occupying temporally available niches species may experience a period of time where environmental factors are more favorable for growth and propagation than they are for competing species (Lovelock and Feller, 2003). This idea is picked up by the fluctuation niche hypothesis which predicts that recurrent temporal fluctuation of environmental conditions allows the coexistence of species by tolerating inter-pulse periods through fine-tuned life-cycle or eco-physiological mechanisms (Terradas et al., 2009).

The Munessa forest in the central Ethiopia is an anthropogenically degraded tropical mountain forest where two deciduous tree species coexist with many evergreen taxa (Müller-Hohenstein and Abate, 2004). Several aspects of this forest have already been studied, e.g. the propagation of the dominant tree species (Teketay, 2005; Tesfaye et al., 2010), seedling recruitment under different shelter canopies (Fetene and Feleke, 2001; Strobl et al., 2011) phenology of flowering and fruiting (Tesfaye et al., 2011) and the potential contributions of arbuscular mycorrhizas for restoration of the indigenous flora (Wubet et al., 2003). Addressing the idea of multi-species coexistence, an extensive study of the foliage dynamics of three dominant tree species has recently been communicated (Seyoum et al., 2012). Here, we examined the hypothesis that the utilization of fluctuating niches can stabilize the coexistence of different functional types of trees by balancing photosynthetic carbon gain and water relations over a sequence of dry and wet months in the course of the year. To that end, we investigated the daily courses of CO_2 uptake and stomatal responses with respect to light and moisture conditions and the seasonal patterns of light and water use efficiency of three coexisting functional tree types of this forest. As the study extended over two successive years (2009 and 2010) it could also benefit from substantial differences in the seasonality of rainfall, thus demonstrating the importance of flexibility in the utilization of temporal niches. As basis for interpretation of the data, the species specific variation in light response of CO_2 net uptake and stomatal conductance was also investigated.

Material and methods

The study area

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 Ethiopia's capital Addis Ababa on a large topographic flattening at 2300 m altitude that is locally known as "Kuke". In this forest, large plantations of exotic trees alternate with patches of the natural forest (Fig. 1). The vegetation, characterized as semi-moist evergreen montane forest (Abate, 2004) is dominated by canopy and subcanopy species such as *Podocapus falcatus* (Thunb.) Mirb, *Croton macrostachyus* Hochst. ex Del., *Olea europaea* ssp. *cuspidata* (Wall. Ex. DE) Cifferri, *Schefflera abyssinica* Harms, *Prunus africana* (Hook.f.) Kalkm. and *Allophyllus abyssinica* (Hochst.) Radlkofer. Fritzsche et al. (2007) have characterized the soil of the study area as Mollic Nitisol which is rich in most of the nutrients, except phosphate (Lemenih et al., 2004). Further details of the study area are described by Abate (2004).

Climate

Rainfall, relative humidity, and temperature data were collected as hourly means from the research station's climate station (Pessl Instruments, Weiz, Austria), located at 200 m distance from the