Ecological Indicators 83 (2017) 550–558

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Original Articles

Water relations and photosynthetic water use efficiency as indicators of slow climate change effects on trees in a tropical mountain forest in South Ecuador

Simone Strobl[a,*], Eduardo Cueva[b], Brenner Silva[c], Johannes Knuesting[d], Michael Schorsch[d], Renate Scheibe[d], Jörg Bendix[c], Erwin Beck[a]

[a] University of Bayreuth, 95440 Bayreuth, Germany
[b] Naturaleza y Cultura Internacional, Loja, Ecuador
[c] Philipps University Marburg, 35032 Marburg, Germany
[d] University of Osnabrueck, 49076 Osnabrueck, Germany

ARTICLE INFO

Article history:
Received 30 May 2016
Received in revised form
11 November 2016
Accepted 9 December 2016
Available online 21 December 2016

The authors dedicate this publication to Prof. Dr. Ulrich Lüttge on the occasion of his 80th birthday.

Keywords:
Physiological indicators
Tropical trees
Water and carbon relations
Water use efficiency
Long- and short-term monitoring

ABSTRACT

The effects of an increasing moisture on trees of the tropical species-rich mountain rain forest in the South Ecuadorian Andes was investigated, using the daily total water consumption (TWC) and the instantaneous water use efficiency (WUE, ratio of photosynthetic CO_2 uptake per water loss by transpiration) as eco-physiological indicators. Two canopy and one sub-canopy tree species, (*Vismia tomentosa*, Clusiaceae, an as of yet unknown Lauracee, and *Spirotheca rosea*, Bombacaceae) were the experimental objects. Seasonal changes as well as a long-term (18 months) trend of increasing precipitation caused an inverse reaction of the TWC of the trees. Because of a rather unlimited water supply to the trees from a permanently high water content of the soil, transpiration followed mainly the atmospheric demand of water vapor, and increasing moisture hence reduced water loss by transpiration. It was hypothesized that in spite of the reduction in transpiratory water loss photosynthetic carbon acquisition would be not or less affected due to an increase in water use efficiency. Concomitant measurements of photosynthetic net CO_2 uptake showed the expected increase of WUE in *V. tomentosa* and *S.* rosea, but no clear reaction of the Lauracee. Accompanying measurements of stem extension growth confirmed an undiminished growth of *V. tomentosa* and *S. rosea* but showed also suspended growth of the Lauracee during the wettest months. While TWC can be continuously monitored with the heat dissipation technique, WUE is determined by leaf porometry in campaigns for which access to the canopy is required. Simultaneous recordings of the gas exchange of leaves at 4 different positions in the crown of one of the experimental trees (*V. tomentosa*) showed the usability of the trait WUE in combination with the total daily water consumption as indicator set for assessing the response of trees to a subtly changing climate. However, not all tree species appear as likewise useful indicator trees.

1. Introduction

The responses of trees (and tree assemblages) to environmental changes can be considered bottom-up, starting with immediate physiological responses, such as water consumption and carbon gain, followed by functional responses, *e.g.* growth and reproduction, which in the long run could end in an altered species composition of the forest. With trees as long-lived organisms, such changes become obvious at different time-scales and therefore require different monitoring periods to establish the effects in a reliable way. When monitoring water and carbon relations the effects of longer lasting trends must be differentiated from transitory changes, which may be compensated as the year advances. Physiological responses of trees may be small, however we assume that a detection of a climatically caused change in the tree's performance is possible already after two consecutive years, a time-span after which a change in reproduction can never be established, not to mention changes of species composition which may come up in decades or even centuries.

Here we report about monitoring of basic physiological processes of tropical trees as indicators of potential environmental changes: Water relations, carbon uptake and as a medium-term

* Corresponding author.
E-mail address: simone.strobl@uni-bayreuth.de (S. Strobl).

http://dx.doi.org/10.1016/j.ecolind.2016.12.021

reaction: extension growth. Tree water consumption and extension growth can be recorded continuously, while transpiration and carbon relations have to be measured in campaigns since leaves cannot be clamped in a cuvette for many days. The continuous recording allows the differentiation between the effects of recurrent events, such as seasons from those of longer lasting trends which overlie the periodical changes. The combination of the continuous with the campaign measurements is necessary for an understanding of the indicators' message: A reduced daily water consumption can result from stomata closure due to a high evaporative demand of the air at a limited water supply from the soil, or in contrast because a high moisture of the air decreases the release of water vapor from the leaves. In the first case, photosynthetic CO_2 net uptake will also decrease while it could even increase in the latter case, given a sufficient light intensity. Both ecophysiological responses transpiration and CO_2 net uptake can be combined in the trait "water use efficiency" (WUE). It is species-specific (Cernusak et al., 2007) and can be used for the identification of suitable indicator trees: Reactions to an environmental change of trees with a high WUE will be more subtle than of those with a low WUE resulting from a high water consumption that responds more directly to the environment. WUE can be determined on different scales: On the plot, on the whole-plant and on the leaf level (Medrano et al., 2015). In physiological research WUE on the leaf level is mostly employed. It has been termed instantaneous WUE (Farquhar et al., 1989), and is expressed as assimilatory net CO_2 uptake (A_N) related to transpiratory water loss (E): A_N/E [mmol CO_2/mol H_2O]. It changes in the course of the day, due to changing conditions of the microclimate and the illumination. For monitoring purposes a meaningful value is the integral over entire days. We hypothesize that a sustained change of WUE is most likely a manifestation of the fastest response of trees to a changing environment. Employing instantaneous WUE as an indicator of plant responses to environmental change requires some additional measurements. In particular climate variables must be co-monitored since the entire region is subjected to the El Nino Southern Oscillation Phenomenon.

2. Material and methods

2.1. Study site

The study site (3°58′26″ S, 79°4′32″ W, 1970 m a.s.l.) is located on a north-facing slope of the eastern range of the South Ecuadorian Andes which is covered by an extremely species-rich rain forest (Fig. 1). A detailed description of the area (the Reserva Biológica San Francisco, RBSF) has been presented by Bendix and Beck (2016). The forest has been classified as a subtype of a tropical evergreen lower montane forest with tree heights up to 18 m and a high presence of representatives of Lauraceae and Melastomataceae (Homeier et al., 2008). Mean temperature in the RBSF forest is 15.5 °C with a mean annual precipitation of 2000 mm (up to 2100 mm per year) (Volland et al., 2016). The amount of precipitation is higher from April to July, October to January are a little less wet (Beck et al., 2008). At the elevation of the research plot the soil has been characterized as humic cambisol which is covered by a thick raw humus layer, on average 16 cm thick but reaching depths of up to 35 cm (Wilcke et al., 2008). Due to a high percentage of rainy days in the course of the year (*e.g.* 324 days with rain in 2014) the soil is permanently wet and almost water saturated (Kreutzer and Martini 2002).

2.2. Research plot and study trees

On the research plot, in a horizontal distance of approx. 100 m, two observation towers, 30 and 36 m high, respectively, overtop the forest. They are equipped with two platforms at 11 and 15 m from which the canopy of neighbouring trees can be reached. Gas exchange measurements were performed on leaves of the lower and upper crowns of *Vismia tomentosa* (Clusiaceae), of a yet unknown Lauracee, and of *Spirotheca rosea* (Bombacaceae). *V. tomentosa* and the Lauracee are evergreen, while *S. rosea* is facultatively deciduous. During the investigation period, however, *S. rosea* maintained at least major parts of its foliage. *V. tomentosa* and the Lauracee are canopy trees with open crowns while *S. rosea* is a subcanopy species. The investigated trees are characterized in Table 1.

Table 1
Traits (height, diameter at breast height (dbh), sap wood area, specific leaf area (SLA), projected crown area and life form) of the investigated trees *V. tomentosa*, Lauracee and *S. rosea*. $^{+}/^{++}$ indicate leaves of the upper ($^{+}$) and of the lower crown ($^{++}$) of *V. tomentosa*. SLA was calculated from a mixed sample of 35 leaves.

	V. tomentosa	Lauracee	*S. rosea*
Height [m]	17	10	12
Dbh [cm]	22.3	11.0	14.8
Sap wood area [cm^2]	180.2	67.0	160.7
SLA [$cm\,g^{-1}$]	$50.0^{+}/70.0^{++}$	79.4^{+}	83.3^{++}
Projected crown area [m^2]	18.4	11.0	5.3
Life form	evergreen tree	evergreen tree	deciduous tree

Table 2
Correlation factors (r^2) between sap flow and leaf transpiration of the investigated trees in 2014 and 2015. *P*-values for all combinations were $p < 0.001$.

	V. tomentosa	Lauracee	*S. rosea*
2014	$r^2 = 0.61$	$r^2 = 0.82$	$r^2 = 0.44$
2015	$r^2 = 0.82$	$r^2 = 0.83$	$r^2 = 0.37$

The towers were also used for climate measurements, including a tipping bucket rain gauge (52203, RM Young Inc; RM Young, USA). Rel. humidity and air temperature was measured with a shield protected thermometer and hygrometer (HC2S3; Campbell Sci. Inc., USA). Net radiation sensors (8111; Schenk GmbH, Austria; and CNR01; Kipp & Zonen, Netherlands) and wind speed (W200P; Vector Instruments, Ltd., UK) were installed 5 m above the canopy.

2.3. Leaf gas exchange

Leaf gas exchange was recorded by porometry using a LICOR portable photosynthesis system (LI6400 XT, Li-COR Biosciences GmbH, Bad Homburg, Germany). Fully expanded, intact leaves were clamped in the sensor cuvette, maintaining their natural position. The leaves were flushed with ambient air (flow rate 500 μmol $m^{-2}\,s^{-1}$), of which temperature and relative humidity were simultaneously recorded. PPFD was recorded with an external quantum sensor and a GaAsP sensor in the chamber. Water vapour release (E), CO_2 net uptake (A_n), light intensity (PPFD) and the microclimate were recorded in intervals of 5 min. A leaf was kept in the cuvette for a maximum of 48 h after which E and A_N started to decline. Due to technical constraints porometry can only be employed when there is no or only very little precipitation and the leaf surface is not wet. Therefore recording leaf gas exchange in campaigns during favourable weather conditions has also a technical reason.

For light response curve measurements, the cuvette chamber was equipped with an external light source (6400-02B LED light source, LiCor Inc., Lincoln, NE, USA). Measurements were taken when CO_2 uptake was stable after adaptation to the new light intensity. Light response curves were produced at 20 °C and 60% relative humidity. At each light level, 3 measurements were run and the means are shown in Fig. 4 .