

Higher tree transpiration due to road-associated edge effects in a tropical moist lowland forest



Norbert Kunert^{a,b,*}, Luiza Maria Teóphilo Aparecido^{b,1}, Niro Higuchi^b,
Joaquim dos Santos^b, Susan Trumbore^a

^a Department of Biogeochemical Processes, Max-Planck-Institute for Biogeochemistry, Jena, Germany

^b Laboratory of Forest Management, Brazilian National Institute for Research in the Amazon, Manaus, Brazil

ARTICLE INFO

Article history:

Received 11 March 2015

Received in revised form 15 June 2015

Accepted 21 June 2015

Keywords:

Sap flux

Forest edge

Amazon

Terra firme

ABSTRACT

Newly created forest edges have significant ecophysiological effects on bordering trees. We studied edge effects on microclimate and tree transpiration rates during wet and dry seasons along a 250 m transect spanning the edge of an unpaved road into an old growth tropical lowland forest in the Central Brazilian Amazon. Canopy openness decreased only minimal from the road (3.68%) towards the forest interior (1.69%). Vapor pressure deficit (measured at 2.2 m height above ground) was lower in the forest interior. The edge effect on microclimate penetrated deeper into the forest (>100 m) during the dry season compared to the wet season (<100 m). Overall, sap flux, and therefore transpiration rate, was 54% higher in trees adjacent to the road compared to forest interior trees. Higher transpiration rates at the forest edge can be explained by higher turbulences and energy exchange of the canopy boundary layer and by a shift in species composition to high water using secondary forest species 25 years after the road construction. Similar changes might be expected for other disturbances affecting local relative humidity and in situations that favor plants with water use traits differing from those found in the forest interior.

© 2015 Elsevier B.V. All rights reserved.

1. Introduction

Tropical forests play a key role in the global climate system (Laurance, 1999) and are among the world's hotspots in sustaining biodiversity (Lowman et al., 2006). Despite the manifold environmental services that tropical forest provide, the rate at which remaining pristine forest is lost remains high and worldwide, tropical landscapes become increasingly fragmented (Laurance et al., 2006). In many cases the construction of roads plays a key role in deforestation (Laurance et al., 2001b), since roads provide access for logging or conversion of forest to other land uses. Even if land conversion around the road is minimal, certain road-associated physical and ecological edge effects on the adjacent forest can be expected (Forman and Alexander, 1998; Laurance et al., 2009). Roads are effectively narrow but very long forest gaps creating contrasting meso- and micro-climatic conditions compared to the

neighboring forest (Laurance et al., 2009). Better understanding the edge effects caused by roads might help to reduce the negative effects of road networks on already stressed ecosystems (Delgado et al., 2007).

The creation of forest edges, of which roads are a subset, has numerous abiotic and biotic effects on the remaining forest (Harper et al., 2005; Laurance et al., 2002). These sharp boundaries alter the forest climate locally, with increased diurnal amplitude for temperature, humidity, radiation, wind speed close to the forest edge and advection energy (Ewers and Banks-Leite, 2013; Roberts and Rosier, 2005; Turton and Freiburger, 1997). This exposure and change in microclimate conditions results inevitably in an alteration of many tree physiological processes and forest structure in the short term, and forest species composition in the long term (Laurance et al., 2002; Ramos et al., 2013). The intensity of those effects depends on the physical contrast with the adjacent habitat and how the forest edge is structured (Didham and Lawton, 1999). Furthermore, the intensity of effects is expected to decrease over time as forest edge structure changes and some regrowth occurs in cleared areas (Ewers and Banks-Leite, 2013).

Most studies to date have focused on edge effects associated with large deforested blocks where forest vegetation may

* Corresponding author at: Department of Biogeochemical Processes, Max-Planck-Institute for Biogeochemistry, Jena, Germany. Fax: +49 3641 577102.

E-mail address: nkunert@bgc-jena.mpg.de (N. Kunert).

¹ Present address: Laboratory of Ecohydrology, College of Agriculture and Life Sciences, Texas A&M University, USA.

Table 1
Summary of species names and characteristics of study trees.

Species	Family	Subplot	DBH (cm)	Ac (m ²)	Height (m)	Successional state
<i>Licania</i> sp.	Chrysobalanaceae	10 m	27.6	159	22	late secondary ^a
<i>Pourouma bicolor</i> Mart.	Moraceae	10 m	24.5	53	21	pioneer ^b
<i>Micropholis guyanensis duckeana</i> (Bahni) T.D. Penn.	Sapotaceae	10 m	22.0	87	17	late secondary ^a
<i>Caryocar glabrum</i> (Aubl.) Pers.	Caryocaraceae	10 m	19.5	32	13	late secondary ^a
<i>Protium apiculatum</i> Swart	Burseraceae	10 m	17.6	27	18	late secondary ^a
<i>Pouteria cladantha</i> Sandwith	Sapotaceae	10 m	22.8	31	22	late secondary ^a
<i>Eschweilera wachenheimii</i> (Benoist) Sandwith	Lecythidaceae	50 m	23	84	19	climax ^c
<i>Euphorbiaceae</i> sp.	Euphorbiaceae	50 m	17.2	Tree crown broke during the study		
<i>Jacaranda copaia</i> (Aubl.) D. Don.	Bignoniaceae	50 m	25.7	68	24	pioneer ^a
<i>Protium pallidum</i> Cuatrec.	Burseraceae	50 m	20.8	101	21	late secondary ^a
<i>Eschweilera wachenheimii</i> (Benoist) Sandwith	Lecythidaceae	50 m	17.5	40	20	late ^e
<i>Eschweilera truncata</i> A.C.Sm.	Lecythidaceae	50 m	17	34	18	late ^e
<i>Tachigali paniculata</i> Aubl.	Fabaceae	100 m	34.2	138	27	late secondary ^d
<i>Tachigali paniculata</i> Aubl.	Fabaceae	100 m	23.8	93	24	late secondary ^d
<i>Eschweilera wachenheimii</i> (Benoist) Sandwith	Lecythidaceae	100 m	21.3	41	20	climax ^c
<i>Protium hebetatum</i> D.C. Daly	Burseraceae	100 m	23.9	92	22	late secondary ^e
<i>Minuartia macrophylla</i> Ducke	Olacaceae	100 m	25.9	93	25	climax ^c
<i>Virola calo phylla</i> (Spruce) Warb.	Myristicaceae	100 m	19.7	47	23	late secondary ^f
<i>Licaria crassifolia</i> (Pior.) P.L.R. Morales	Lauraceae	250 m	26.5	75	26	late ^e
<i>Virola calophylla</i> (Spruce) Warb.	Myristicaceae	250 m	18.6	30	23	late secondary ^f
<i>Corythophora alta</i> R.Knuth	Lecythidaceae	250 m	44.0	259	28	late ^f
<i>Pouteria retinervis</i> T.D.Penn.	Sapotaceae	250 m	21.3	37	25	late secondary ^e
<i>Pouteria erythrochrysa</i> T.D.Penn.	Sapotaceae	250 m	19.7	57	26	late secondary ^e
<i>Plethogyne catingae</i> Duke	Fabaceae	250 m	48.5	242	26	late ^f

^a Amaral et al. (2009).

^b Basset (2001).

^c genus classified in Swaine and Whitmore (1988).

^d genus classified in Peña-Claros (2003).

^e genus classified in Marra et al. (2014).

^f classified by our field botanist following the criteria of Kammesheidt (2000).

be replaced with other kinds of plants (e.g. pasture grasses), but the area is still vegetated (Chen et al., 1995; Giambelluca et al., 2003; Laurance et al., 2002). Road-associated edge effects are much less explored (Dambros et al., 2013), and differ in several ways, including the lateral extent of the clearing which is smaller but permanent, and the fact that roads remain unvegetated. In general, forest edges situated downwind of a contrasting habitat are expected to show higher evapotranspiration rates (Giambelluca et al., 2003). Most evidence to date is derived from indirect measurements such as soil water content (Kapos, 1989) and show edge-related influence on microclimate and soil moisture extending 20 up to 100 m into the remnant forest (Davies-Colley et al., 2000; Ewers and Banks-Leite, 2013; Laurance et al., 2002). Differences in the area influenced by edge effects have been related to the degree of contrast between the adjacent habitat, the size of the forest patch and the time elapsed since the change in forest structure (Harper et al., 2005).

Although large-scale edge effects of >1 km appear to have been detected with remote sensing technology along the eastern Amazon deforestation frontier (Briant et al., 2010), effects of edges on tree transpiration rates remain largely unexplored, especially next to roads. However, the few existing ecophysiological studies on edge effects reveal a significant enhancement of tree water use due to the forest edge (Giambelluca et al., 2003; Herbst et al., 2007; Ringgaard et al., 2012; Wright et al., 2012). To our knowledge no previous study exists evaluating the ecophysiological response of trees growing next to a road in the tropics. Here, we explore road-associated edge effects on spatial variations in microclimate and tree transpiration rates in a tropical lowland forest close to Manaus in the Central Amazon. Our objectives were to determine (1) the effects of a road on the microclimate within an adjacent old growth forest, (2) how tree transpiration rates differ with distance to the road, and (3) if there are variations in the intensity of edge effects between the dry and wet seasons.

2. Material and methods

2.1. Study site

The study area is located approximately 60 km to the north west of Manaus, Brazil (02°38'22.54"S 60°09'51.34"W). A climate station located 25 km from the study sites shows that average rainfall in the area averages 2550 mm y⁻¹. There is a short dry season (defined as consecutive months with <100 mm rainfall) of one month in August, though monthly rainfall can also be below 100 mm in months between June and October. Average annual air temperature is 25.8 °C and varies little between months. The terrain in the study area has an undulating topography, with high-clay Oxisols dominating on plateaus, whereas in the riverbeds a sand rich Spodosols are the dominant soil type. The natural vegetation on plateau areas is well-drained species-rich evergreen tropical moist forest (*terra firme*) with usually over 250 tree species per hectare (trees ≥ 10 cm in diameter) and seasonally inundated tropical moist forest (*igapó*) with lower species richness in the valley streams.

The study site is along the access road to the field station for forestry management of the Brazilian National Institute for Research in the Amazon (INPA) at the kilometer mark 18. The access road is ~6 m wide and was built in the 1980s and is maintained yearly, including an approximately 9 m wide buffer zone to avoid blocking of access by falling trees. The total distance from forest edge to forest edge measures approximately 24 m. Average canopy height in the area is 28 m, however canopy trees growing next to the road were not as tall as in the forest interior (compare Table 1). At the study site, the road trends from East-northeast to West-southwest and transects a large plateau of approximately 1.4 × 1.0 km area. A transect was marked perpendicular to the road and extending 250 m south-southeast into the forest, starting at the forest edge and ending in the middle of a one hectare monitoring plot (Fig. 1). Subplots of 20 × 50 m were established along the transect between 0 and 20 m, 40 and 60 m, 90 and 100 m and 240

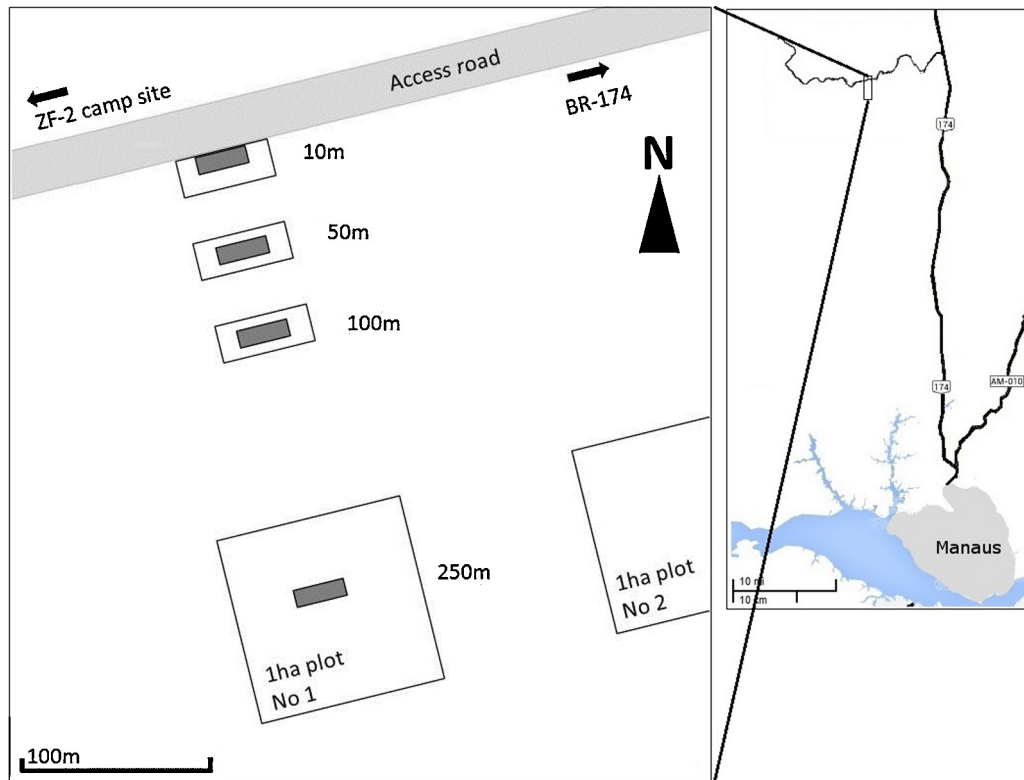


Fig. 1. Map of the plot layout within the transect and with subplots where selected trees were located highlighted in dark gray and location of the study area.

and 260 m from the road edge; these are referred to as 10 m, 50 m, 100 m and 250 m distances, respectively.

2.2. Meteorological measurements

Air temperature, relative humidity and precipitation were recorded at half hourly intervals on the road border, approximately 7 m outside of the forest and 2.2 m above the ground using a professional weather station (PCE-FWS 20, PCE Inst., Meschede, Germany). An additional weather station also operated in open terrain adjacent to the field camp, located approximately 4 km away from the study site. A Quantum Sensor (LI-190A, Licor Inc., Lincoln, USA) set up at the same height was used to record Photosynthetic Photon Flux Density (PPFD, $\mu\text{mol s}^{-1} \text{m}^{-2}$) in the open terrain. Within each subplot along the transect, we set up an automatic thermohygrometer (Votcraft DL121TH, Conrad Electronic Ltd., Barking, UK) to record air temperature and humidity at half hourly intervals at 2.2 m height. Correct recording of the different thermohygrometers was tested in a controlled lab environment

for eventual variation before deployed in the field. Variation between thermohygrometers was lower than the accuracy of the instruments given by the manufacturer ($T \pm 1 \text{ }^\circ\text{C}$ and $\text{Rh} \pm 3\%$). Thermohygrometers were deployed from late February 2013 to the end of December 2013.

2.3. Sap flux measurements, tree water use and tree transpiration rates

Sap flux density was measured in six trees of similar diameter, that were selected from each of the plots at 10 m, 50 m, 100 m and 250 m plot (Table 2). All of these trees reached the upper canopy and were not shaded by other trees. We focused on canopy trees in this study as understory and sub-canopy trees usually only make minor contribution (<10%) to the overall stand transpiration rate in a tropical old growth forest (Horna et al., 2011). Sap flux density (J_s , $\text{g cm}^{-2} \text{h}^{-1}$) was measured continuously in the 10 m, 50 and 100 m plot from 4th of March 2013 until 31st of December 2013 and in the 250 m plot from 1st of January 2013 until 31st of December

Table 2

Structural characteristics of the transect plots such as stem density, basal area (trees $\text{DBH} \geq 5 \text{ cm}$) and mean diameter at breast height (DBH), mean maximum sap flux densities ($J_{s\text{max}}$) and tree transpiration rates for the dry and wet season (E_t). Upper case letters indicate significant differences of $J_{s\text{max}}$ between subplots (ANOVA followed by a post hoc Tukey HSD test) and lower case letters indicate significant differences in tree transpiration rates among seasons for a given plot (paired Student's *t*-test).

Plot	Stem density ^a (Stems ha ⁻¹)	Basal area ^a (m ² h ⁻¹)	DBH ^a		Canopy openness		Leaf area		$J_{s\text{max}}$		E_t			
			(cm)		(%)		(m ² m ⁻²)		(g cm ⁻² h ⁻¹)		(mm)		(mm)	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
			Wet		Dry		Wet		Dry		Wet		Dry	
10 m	720	23.0	8.6	12.3	3.68	0.80	4.08	0.33	16.7 ^A	7.9	3.42 ^a	1.30	4.03 ^b	0.91
50 m	980	21.6	13.7	9.7	3.47	0.94	4.52	0.51	16.4 ^A	6.4	2.82 ^a	0.99	3.28 ^b	0.67
100 m	760	19.0	13.9	13.9	1.98	0.83	4.99	0.58	11.1 ^B	3.9	2.07 ^a	0.93	2.50 ^b	0.70
250 m	830	24.2	14.6	12.8	1.69	0.56	5.09	0.54	9.9 ^B	3.8	2.23 ^a	0.65	2.51 ^a	0.41

^a (trees $\text{DBH} \geq 5 \text{ cm}$).

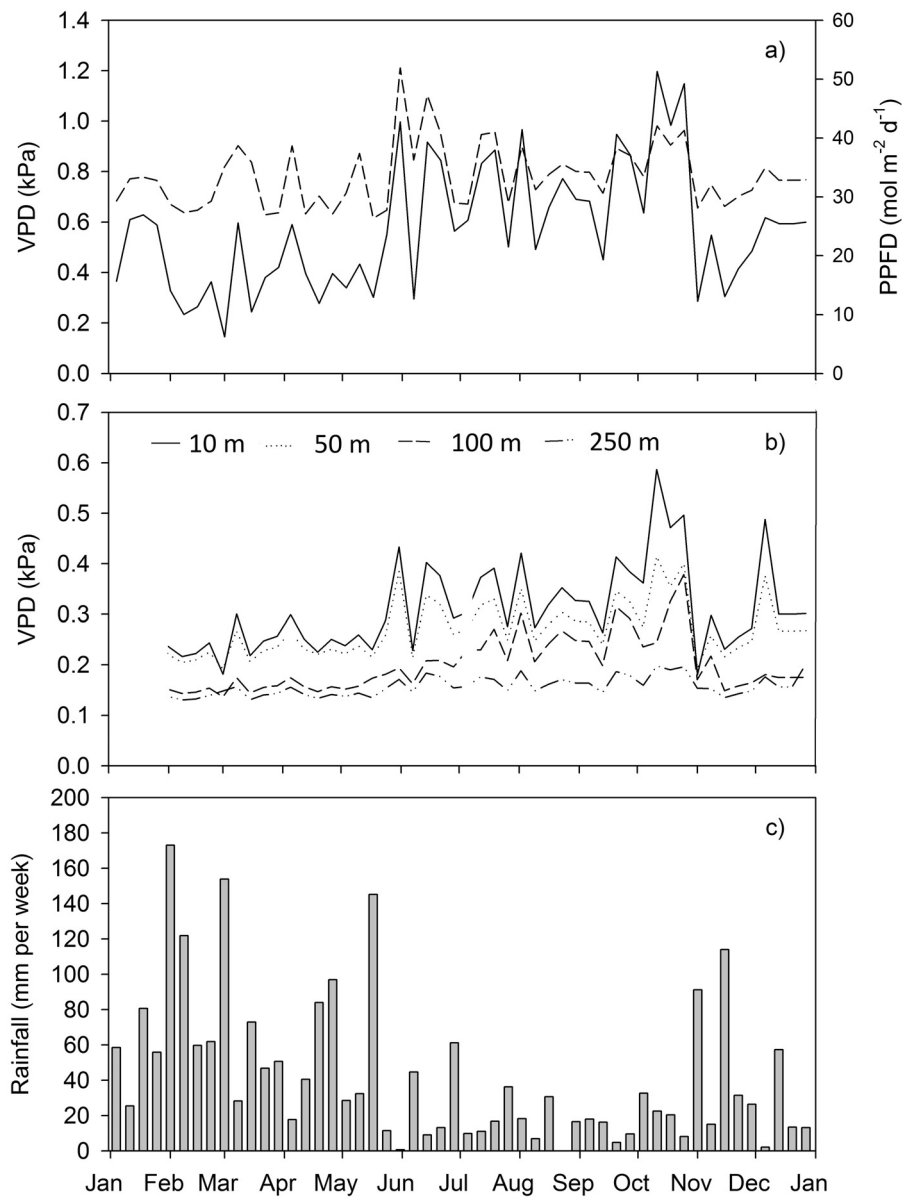


Fig. 2. Annual course of (a) vapor pressure deficit (VPD, solid line) and photosynthetic photon flux density (PPFD, dashed line) measured outside of the forests, (b) VPD measured at different distances from the forest edge, and (c) weekly rainfall.

2013. Each tree was equipped with two 2 cm long Granier type thermal dissipation probes at breast height (1.30 m) per tree (Granier, 1987). According to our staining experiment, the sap wood of all trees was deeper than 2 cm (Aparecido et al., 2015). One sensor was installed on the northern side and the other on the southern side of the stem. Sensors were protected with aluminium shielded insulation and then covered with plastic foil which was sealed with silicon to the stem above the sensor set up (Dierick et al., 2010). The heating elements of all sensors were constantly supplied with 0.2 W. The voltage output from the thermocouples was measured every 30 s and 15 min averages were stored on a data logger (CR800 and CR10x; AM16/32a multiplexer, Campbell Scientific Inc., Logan, UT, USA). We calculated individual tree water use (Q , kg h⁻¹) by relating the measured sap flux densities to the total conductive xylem area (A_x , m²) of a given tree:

$$Q = J_s \times A_x \quad (1)$$

The A_x of the trees was determined using an interspecific general allometric equation established for the study area (Aparecido

et al., 2015). Briefly, 34 trees with a diameter at breast height (DBH) of 10–40 cm were harvested and 30–40 cm long stem segments were cut and placed immediately upright into a solution of indigo carmine. Blue stains appeared within a short time on top of the stem segments. Coloured cross section was assumed to be the conductive xylem area. The 34 harvested trees belonged to 27 different species, but we had a certain overlap in species pool with trees chosen for the sap flux study. An allometric relationship was established between measured conductive area and DBH ($A_x = 15.4138 \times 1.1198^{DBH}$; R^2_{adj}). We used this relatively destructive method to estimate the conductive sap wood area, as the commonly applied injection of indigo carmine into the standing tree and the extraction of wood cores (Meinzer et al., 2001) did not bring any satisfying results. We estimated the tree transpiration rate (E_t , mm day⁻¹) as

$$E_t = \frac{Q}{A_c} \quad (2)$$

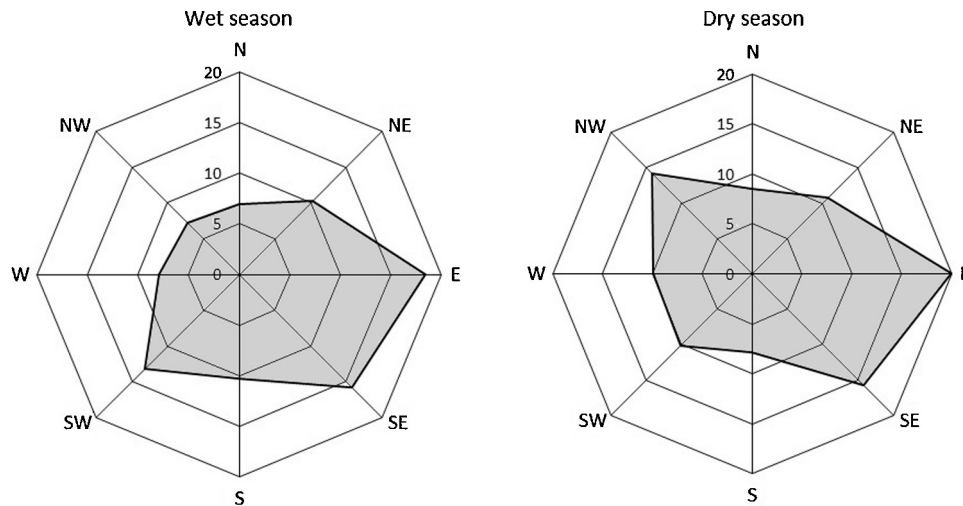


Fig. 3. Wind direction frequency (%) during the wet and dry season.

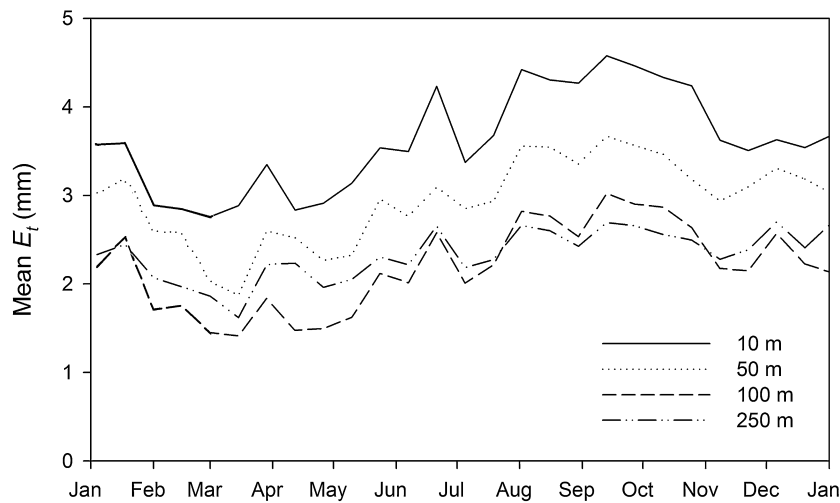


Fig. 4. Mean tree transpiration rates (E_t) estimated for the trees growing in different distances to the road ($n=6$ trees per subplot) over the course of the study period. Gap filling was performed for missing data points; modelled E_t is underlined in grey.

where A_c is the crown projection area (m^2) of a given tree (Kunert et al., 2013).

2.4. Tree characteristics, stand structure and leaf area

We measured diameter at breast height, tree height and crown projection area for each tree equipped with sap flux sensors (Table 1). Tree diameter was measured with a girth tap and a Baltimore stick was used to estimate the tree heights (Anon., 1998). Crown projection areas for each of the trees were calculated as the sum of eight pitch circles derived from eight cardinal measurements of the crown extension of a given tree (Röhle, 1986). Further, we conducted a forest inventory in all subplots. The inventory was done assessing all trees >5 cm (DBH) in the subplots. Six digital hemispherical photographs per subplot were taken on monthly basis (Minolta Dimage Xt, Chuo-Ku, Osaka, Japan; equipped with a 185-fish-eye lens and leveling device from Regent Instruments, Sainte-Foy, Quebec, Canada). Additional photographs were taken when we observed major changes in foliage cover. Leaf area and canopy openness were calculated by analyzing the hemispherical pictures with Gap Light Analyzer Version 2.0 (GLA, Simon Fraser University, Burnaby, BC, Canada). Stem density, at 980 stems ha^{-1} , was highest in the subplot 50 m away from the road and low-

est (720 stems ha^{-1}) in the subplot adjacent to the road (Table 2). Basal area ranged between 19.0 m^2 ha^{-1} and 24.2 m^2 ha^{-1} ; lowest basal areas were found in the subplots at 100 m and highest at 250 m from the forest edge, respectively. Maximum tree height of emerged trees was higher in the forest interior than at the forest edge (18.8 ± 3.5 m, 20.4 ± 2.3 m, 23.5 ± 2.4 m and 25.7 ± 1.6 m in the 10 m, 50 m, 100 m and 250 m subplot, respectively). Leaf area index increased with distance from the forest edge from 4.08 m^2 m^{-2} to 5.09 m^2 m^{-2} in the forest interior at 250 m. Leaf area did not vary significantly between seasons. However, canopy closure was not significantly affected by the edge and was 96% at the forest edge and 98% in the forest interior.

2.5. Data analysis

Maximum sap flux density was defined as the daily maximum observed value lasting for at least 45 min and having a maximum variation of 5% (Kunert et al., 2010). For those subplots where only 9 months of measured sap flux data were available, we estimated the values for the remaining three months by fitting the relationships between tree transpiration rates (E_t) and vapor pressure deficit (VPD) for each tree during the wet season. For the comparison of the species-specific responses to environmental factors, we assumed

that the VPD measured outside the forest corresponded to the VPD above the forest canopy. Using a definition of dry season months as those with less than 100 mm rainfall (Dietrich et al., 1996), the dry season lasted from June until September (July had 117.9 mm of rainfall due to a single heavy rain event) and the wet season months included January to May and October to December (Fig. 2). We defined months with a potential soil water deficit as months with higher mean monthly tree transpiration rates than monthly precipitation rates. The water deficit is thus expressed as that month's precipitation minus the mean monthly tree transpiration rate for a given subplot. Differences in tree transpiration rates between subplots and seasons were determined with a paired Student's *t*-test. Statistical analyses were performed with SPSS 16.0 (SPSS Inc., Chicago, USA).

3. Results

3.1. Meteorological conditions

The total amount of precipitation at the transect was 2300 mm in 2013. Rainfall averaged 248 mm per month during the wet and 80 mm per month in the dry season (Fig. 2). Mean values of PPFD and VPD measured at our reference station outside the forest were substantially lower during wet months ($31.4 \pm 6.9 \text{ mol m}^{-2} \text{ day}^{-1}$ and $0.21 \pm 0.14 \text{ kPa}$, respectively) than during the dryer months ($38.0 \pm 8.6 \text{ mol m}^{-2} \text{ day}^{-1}$ and $0.65 \pm 0.19 \text{ kPa}$, respectively) (Fig. 2). Relative air humidity had distinct daily courses and was in general higher inside the forest than outside and increased with distance from the edge. Daily minimum values of relative humidity were higher in the forest interior than at the forest edge. The relative humidity never dropped below 89% at a distance of 250 m inside the forest during the wet season, but a minimum of 56% was recorded outside the forest beside the road on the same day. During the wet season there was no significant change in humidity between 100 m and 250 m from the edge. However, during the dry season a significant further increase in relative humidity could be observed between 100 and 250 m. Air temperature was significantly lower inside the forest than outside. Air temperatures reached higher maxima and lower minima during the dry season, but temperatures at 2.2 m height did not vary with distance from the edge of the forest to the interior. Water vapor pressure deficit at 2.2 m height inside the forest declined rapidly with distance from the edge and reached its minimum at 100 m from the edge with no further significant decline toward the forest interior (250 m, see Fig. 2). VPD showed the same seasonal behavior as observed for relative humidity. Main wind direction during the wet months was from the East (Fig. 3, left hand side), whereas during the dry months the wind was increasingly blowing from Northwest (Fig. 3, right hand side).

3.2. Sap flux density and tree transpiration rates

The highest maximum sap flux densities (on average $16.7 \pm 7.9 \text{ g cm}^{-2} \text{ h}^{-1}$) were found at the forest edge and declined with distance from the edge (on average $9.9 \pm 3.8 \text{ g cm}^{-2} \text{ h}^{-1}$) in the forest interior at 250 m (compare Table 2 and Fig. 5). Higher sap flux densities were also present in typical pioneer species such as *Pourouma bicolor* or early successional species as *Jacaranda copaia* that reached maxima of up to $26.8 \text{ g cm}^{-2} \text{ h}^{-1}$ and $23.2 \text{ g cm}^{-2} \text{ h}^{-1}$, respectively. The maximum sap flux densities for typical late successional species such as different *Eschweilera* sp. or *Minquartia macrophylla* were lower, ranging from 10 to $16 \text{ g cm}^{-2} \text{ h}^{-1}$ (for more details on successional state of species see Table 1). Accordingly, sap flux densities of trees growing next to forest edge responded differently to the above canopy VPD compared to trees growing in the forest interior, reaching higher maximum values

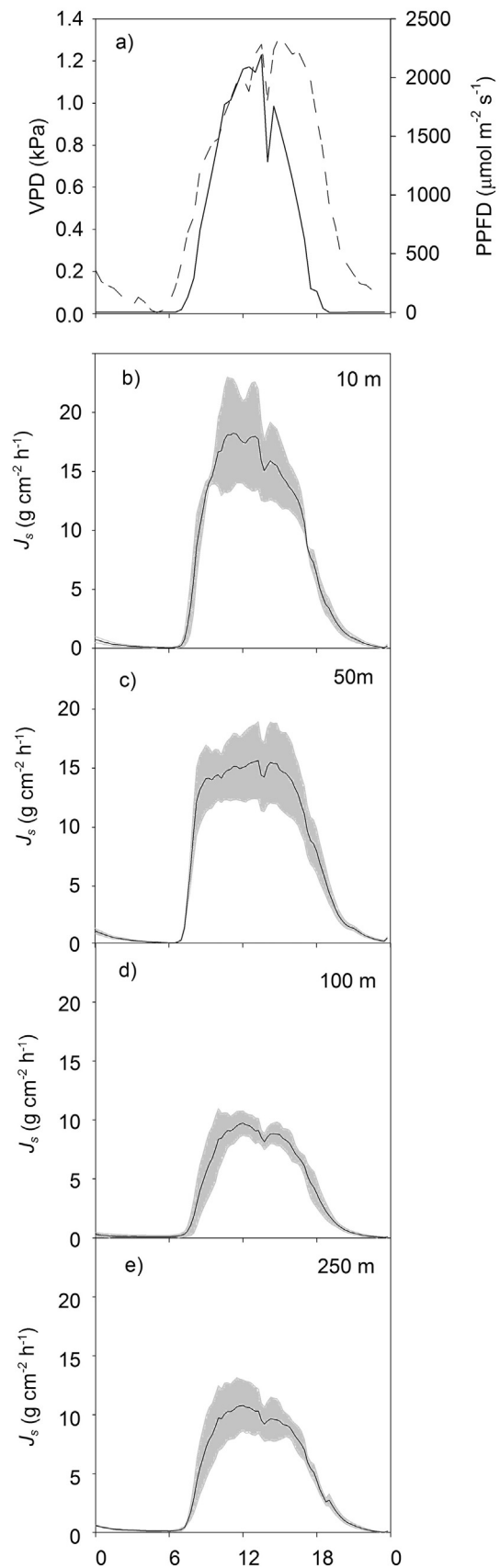


Fig. 5. Diurnal course of (a) photosynthetic photon flux density (PPFD, solid line) and vapour pressure deficit (VPD, dashed line) and (b–e) mean sap flux density (J_s) in the trees at the different distances from the edge ($n=6$ trees per distance from edge, means and standard deviation as shaded area) on a bright sunny day during the dryer months.

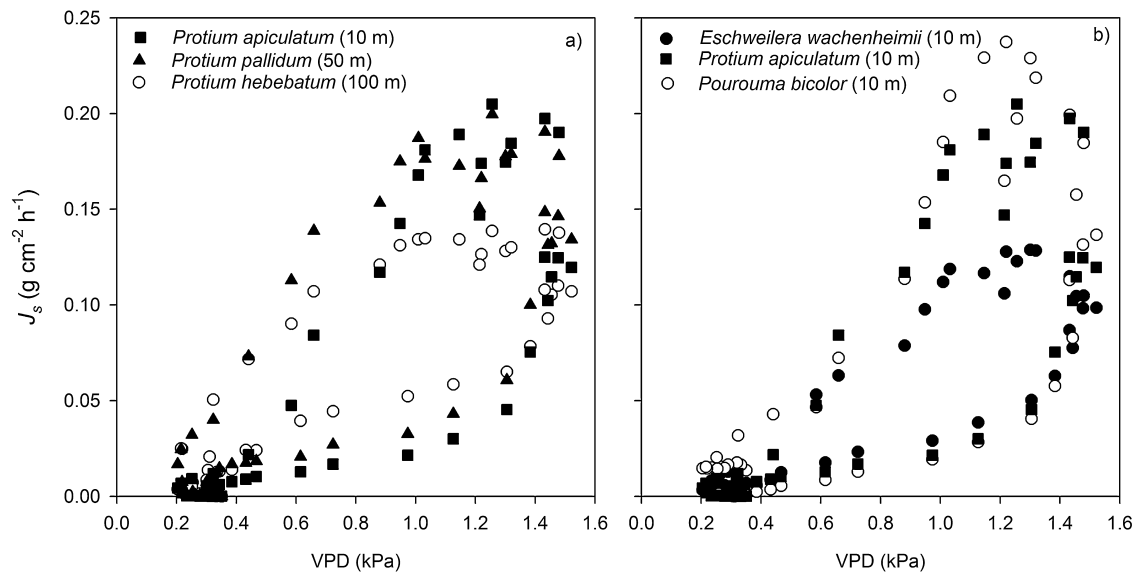


Fig. 6. Sap flux density (J_s) versus above canopy vapor pressure deficit (VPD) for (a) three tree individuals from the genus *Protium* growing at different distances from the forest edge and (b) one pioneer, one late successional and one climax tree species (*Pourouma bicolor*, *Protium apiculatum*, *Eschweilera wachenheimii*, respectively) growing 10 m from the edge. We considered vapor pressure deficit measured outside of the forest to correspond to the actual vapor pressure deficit above the canopy boundary layer and to be the same for all trees. Different responses of sap flux densities to above canopy VPD should result out of spatially varying microclimate within the boundary layer or should be due to species specific sap flux characteristics.

at the same level of above canopy VPD (Fig. 6a). Further, early successional species showed higher sap flux densities than late successional/climax species, at the same level of above canopy VPD (Fig. 6b).

The highest and lowest maximum tree transpiration rates were measured for the pioneer species *Pourouma bicolor* (4.74 mm day^{-1}) and for a typical species of the climax forest *Eschweilera wachenheimii* (0.29 mm day^{-1}), respectively. Sap flux density of tree individuals from the genus *Protium* reached higher maximum values in trees closer to the edge (10 and 50 m) than in the forest interior (100 m) when experiencing the same above canopy vapor pressure deficit (Fig. 6b). Mean annual transpiration rates totaled $1319 \text{ mm year}^{-1}$, $1083 \text{ mm year}^{-1}$, 805 and 845 mm year^{-1} for the subplots at 10 m, 50 m, 100 m and 250 m, respectively. Tree transpiration rates were significantly higher in the subplots 10, 50 and 100 m away from the road in the dry seasons (18 %, 16 % and 21 %, compare Table 2 and Fig. 4). The mean tree transpiration rate was 12 % higher in the subplot 250 m away from the road during the dry season but this difference was not statistically significant. The annual mean tree transpiration rate was on average 61 % and 53 % higher at the forest edge (10 m) compared to the forest interior (250 m) during the dry and wet season, respectively. A positive ecosystem water balance and thus a higher input via precipitation than output via transpiration could be observed during the wet season. However, in the undisturbed forest interior the subplots (100 m and 250 m) had a negative water balance for two months (Fig. 7). Monthly transpiration rates exceeded the ecosystem water input via precipitation for five months in the transect plot 10 m next to the road but for only three months in the plot 50 m away from the forest edge (Fig. 7).

4. Discussion

4.1. Edge effects on tree transpiration rate

Our intense long-term study of sap flux density in 24 trees over one entire year suggests that the forest edge caused a sharp and significant enhancement of in tree transpiration rates. The most plausible explanation for this pattern is that the observed much

greater transpiration rates at the forest edge could result from: (1) different species composition; (2) different forest structure, or (3) higher VPD closer to the forest edge. Leopoldo et al. (1995) and da Rocha et al. (2004) reported eddy-covariance based estimates of annual evapotranspiration rates of 1240 mm and 1300 for undisturbed terra firme forests at Reserva Ducke (70 km from our site) and the eastern Amazon. If we subtract 20–25% from those estimates of the annual evapotranspiration rate for evaporative loss from canopy interception (Shuttleworth, 1988) and account the other 10% for other evaporation or transpiration by understory vegetation (Horna et al., 2011), then our estimates of the annual transpiration rate by the canopy trees of 845 mm in the undisturbed forest interior fit very well into an overall water budget. However, our estimates for the annual transpiration rate of 1319 mm at the forest edge accounts already for 100% of the expected annual evapotranspiration rate.

The subplots 10 and 50 m from the road had higher abundances of pioneer and early successional species, characterized by low wood density and fast growth rates, than subplots in the forest interior (Table 1). Further, the canopy closure might not have been different, but emergent canopy trees were on average 5.9 and 5.3 m taller in the forest interior at 250 m than 10 m and 50 m from the forest edge. Changes in species composition and forest structure have been commonly observed near to new forest edges and explained by increasing tree mortality and a colonization of the gaps with fast growing early successional forest species (Murcia, 1995). The edge at our study site was created 25 years ago, allowing early succession species enough time to establish and dominate leaf area within the canopy. Typical pioneer tree species have a higher tendency of excessive water use rates (Nogueira et al., 2004). This was confirmed with our measurements e.g. the pioneer species *Pourouma bicolor* was characterized by an on average more than two fold higher maximum sap flux density than the climax species *Eschweilera wachenheimii*, when both were growing adjacent to the forest edge (Fig. 6b, note shown values are absolute values and not mean values). While we were unable to find the same species to measure across the whole 250 m transect to test for effects of microclimate on tree transpiration alone, individuals from the same genus (*Protium*), growing at distances up to 50 m from the road, had up to 30%

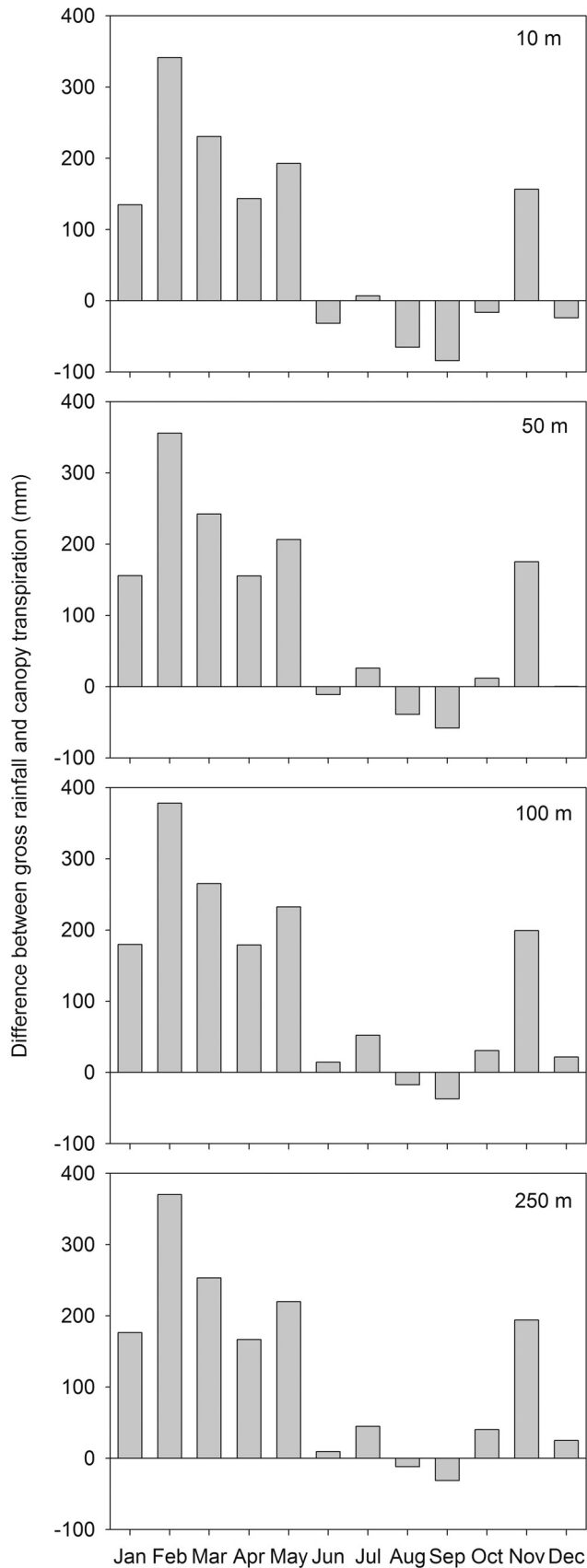


Fig. 7. Difference between gross rainfall and canopy transpiration given as the fraction of total monthly precipitation minus mean monthly tree transpiration rate.

lower maximum sap flux densities on days with high evaporative demand compared to a *Protium* tree located 100 m from the forest edge. Despite their diverse functionality, all species and individuals showed the often described hysteresis between VPD and sap density flux (Fig. 6). The hysteresis is supposed to be due to the lack time between the onset of canopy transpiration and the sap flux response at the base of the tree and/or refilling processes at night time (O'Brien et al., 2004).

On average sap flux densities were up to 54% higher adjacent to the road than in the forest interior (Fig. 5). Similar results and effects were reported by a study conducted in a Norway spruce plantation in Denmark where sap flux densities were significantly influenced by forest edges (Ringgaard et al., 2012). Trees adjacent to an edge with minimal contrast in vegetation had up to twofold higher maximum transpiration rates on days with high evaporative demand, but edges where the contrast was higher enhanced tree transpiration rates up to 2.5 fold compared to forest interior trees (Ringgaard et al., 2012). Similar results were presented in a study from Vietnam where trees from the same tree species growing to an adjacent swidden were showing about two times higher sap flux derived transpiration rates than trees in the interior of the forest (Giambelluca et al., 2003). Even where the species remain the same, changes in the canopy roughness length might have strong effects on tree water loss at the edges. Forest disturbance means a less dense forest canopy. Lesser canopy density induces a higher canopy roughness and with this increased sub-canopy turbulences leading to stronger mixing effects between air masses (Poggi et al., 2004). The mixing of dryer air masses with the bulk air at the canopy will increase the boundary layer conductivity and consequently enhance tree transpiration rate. Thus, according to our results, both species and microclimate effects created by the edge are influencing the higher losses of water by transpiration at the road edge in our study.

4.2. Edge effects on microclimate

Edge effects on the microclimate of forests are well documented in the literature for almost all forest ecosystems, with significant increases observed in light availability, air and soil temperature, lower relative humidity and lower soil moisture at the forest edge (Brothers, 1993; Chen et al., 1995; Matlack, 1993; Young and Mitchell, 1994). Further, the intensity of edge effects on the microclimate might depend largely on the cardinal direction in which the edge is facing (Radler et al., 2010). Nevertheless, the solar angle in the tropics is different to the study of Radler et al. (2010), so that we assume that edges are affected equally and independently from their cardinal direction. However, we could confirm with the results from our study that there are significant edge effects on relative humidity; but air temperature inside the forest was not significantly affected by the edge. Delgado et al. (2007) also found only minimal temperature variations in forest further than 6–10 m from an adjacent road edge in Tenerifian pine and laurel forest. The small temperature variations are probably due to similar canopy structure at the edge compared to the forest interior (Delgado et al., 2007). The canopy structure at our study site was also relatively similar at edge and the interior as the variation of the canopy closure between the edge and the interior was only 2% (Table 2).

The edge effect observed for relative humidity extended about 100 m into the forest and is consistent with the edge effects reported in other microclimate studies (Cadenasso et al., 1997; Chen et al., 1995; Davies-Colley et al., 2000; Didham and Lawton, 1999; Williams-Linera et al., 1998). The stronger edge effect on humidity during the dry season in August–September has two likely causes. First, there was a higher frequency of wind coming from the Northwest during the dryer months (Fig. 3), hence dryer air could more easily enter into the forest stand and reach further into the

forest interior along our transect during dry season months. Second, the dryer months have a higher contrast between day and night time temperatures, inducing high vapor pressure deficits during the day. A steeper gradient in microclimate is known to facilitate lateral exchange between wet forest air and dry air in the adjacent open area (Chen et al., 1995). From the second fact we can also assume that in drier tropical climates with a more extreme day and night cycle edge effects might even be more pronounced and microclimate effects might extend further into forest interiors than in our study.

In our study, the strong influence of the road on the microclimate in adjacent forest confirms our initial hypothesis that roads form strong contrasting edges. Edge effects are expected to be stronger with more extreme contrasts between the two habitats (Harper et al., 2005). The road was in total only 24 m wide and surrounded by uninterrupted tropical forest; however it had created a strong contrast in microclimate because all vegetation was removed exposing the mineral top soil layer. Despite this high contrast, we might have expected a smaller edge effect. First, the road was built over 25 years ago, allowing the forest structure to have high canopy closure even up to the edge, thus buffering the influence from the more extreme macroclimate outside of the forest (Ewers and Banks-Leite, 2013). Second, the contrasting habitats were downwind from the main wind direction for most of the year. Nonetheless we observed higher evaporative demand at the forest edge, indicating that even small (in terms of lateral extent) disturbances like roads can affect the moisture regime of the remaining forest through alteration of local microclimate. Hence, road construction will always affect the forest structure. The construction of small roads will induce significant edge effect on the stand microclimate even if the logging of big trees is avoided. The mechanical damage to trees caused by heavy machinery will result in tree mortality and open up the closed canopy along the road. In general we assume that edge effects on the stand microclimate will increase with road width.

4.3. Seasonal differences in edge effects

Climates characterized by high cloudiness and/or high precipitation rates are commonly assumed to have a reduced energy exchange between open areas and forest and thus show less intense edge effects (Harper et al., 2005). Further, in seasonally wet and/or dry climates edge effects are of seasonally altering intensity due to changes in climate conditions. We found distinct seasonal differences in the climate conditions between the wet months and the dryer months and accordingly differences in the intensity of the edge effects. For example, VPD measured outside of the forest was almost two times greater during the dry season compared to the wet season months (Fig. 2). This is very typical for the humid tropics mostly due to higher monthly radiation compared to wet and overcast months. Nevertheless, we recorded only 15% higher monthly radiation during the dry months between June and September (Fig. 2), whereas an increase for up to 50% due to cloud free sky is reported in the literature (Kunert et al., 2010). However, atmospheric evaporative demand was significantly higher during dryer months and hence the edge effect on microclimate extended further into the forest. This confirms the earlier finding from Giambelluca et al. (2003), who observed a parallel increase in the latent heat of vaporization over an adjacent open area and the forest interior which suggests stronger edge effects when the forest canopy is dry. Nevertheless, the forest edge adjacent to the open area was affected more than the interior (Giambelluca et al., 2003).

We found significant seasonal changes in the transpiration rates with higher rates during the dry season. This was true in all sub plots (Fig. 4). Despite the high water use rate during the driest month

(September with less than 50 mm of rainfall), we could not find any evidence of soil water limitation, e.g., reduced transpiration rates with high radiation availability (Kunert et al., 2010). Additionally, we did not observe a significant reduction in leaf area during the dryer months compared to wet months. The studied trees maintained their leaves and did not shed them to avoid water stress. In addition, eddy covariance measurements confirm that trees do not suffer from essential water limitation during a regular dry season in the *terra firme* forest (da Rocha et al., 2004). Ample soil water conditions in deeper soil layers and the ability of trees to access those resources with deep roots are usually considered responsible for the lack of seasonal effects in transpiration rates for individual tropical forests canopy trees (Meinzer et al., 1999; Nepstad et al., 1994; Schwendenmann et al., 2015). Canopy trees in the *terra firme* forests are known to have deep roots and to experience nighttime redistribution of soil water (da Rocha et al., 2004).

Nevertheless, da Rocha et al. (2004) pointed out, that the ecosystem input in the Eastern Amazon by precipitation with 2200 mm was only 40% higher than evaporative water loss in 2001 and hence the forest might be susceptible to water stress in years with less precipitation. In our study and not accounting for evaporation, tree transpiration rate of canopy trees already accounted for 36% of the annual water loss to the atmosphere in the undisturbed forest interior. With increasing edge-related disturbance canopy trees were consuming even up to 64% of the annual gross precipitation. Our study also shows that on a monthly basis, the difference between gross ecosystem input by precipitation and water loss via transpiration was negative for a longer time period at the forest edge which means that water consumption by trees exceeded soil water recharge rates. This excessive water use of trees growing at forest edges could help explain the much higher mortality rates at forest edges found after the El Niño year in 1997 and described by Laurance et al. (2001a). Hence, the commonly higher tree mortality found next to forest edges could be partly due to higher susceptibility of trees to water stress (Laurance et al., 2002).

5. Conclusion

We found the edge effect created by the presence of a road had a strong influence on the overall water use in a tropical forest stand. The effect was caused both by strong direct edge effects related to forest structure and species composition as well as (often partly related) changes in the microclimate. At our site, road construction 25 years ago induced higher tree mortality at the forest edge due to mechanical damage and climax forest species were replaced by more early-successional tree species with higher water use. This change of tree species composition and the new physical setting both contribute to higher water use rates and higher potential drought stress susceptibility of trees growing adjacent to the road. Thus, the initial disturbance has a positive feedback as increased transpiration rates caused by disturbances enhance drought related tree mortality, which further alters the microclimate and increases forest fragmentation. Furthermore, we assume that similar feedbacks might be expected for other anthropogenic or natural disturbances affecting local relative humidity, since alterations in water relations affect the long-term trajectory of forest vegetation composition.

Acknowledgements

We want to thank Tatiana Gaudi for identifying the trees species and classifying successional states of trees with existing records from the herbarium at INPA. Many thanks to Alida Mercado Cárdenas and Susan G. Laurance for useful comments on an earlier version of this manuscript. We also would like to thank four anonymous

reviewers for valuable suggestions. Special thanks to LBA-project for providing climate data for the study site over the last 12 years.

References

- Amaral, D., et al., 2009. Checklist of remnant forest fragments of the metropolitan area of Belém and historical value of the fragments. *State of Pará, Brazil. Boletim Museo Para Emilio Goeldi Ciencia Natura* 4 (3), 231–289.
- Anon., 1998. How Much Lumber in That Tree? In: U.P.F.E. office (Editor), Extension Bulletin. Michigan State University Michigan.
- Aparecido, L.M.T., dos Santos, J., Higuchi, N., Kunert, N., 2015. Ecological applications of differences in the hydraulic efficiency of palms and broad-leaved trees. *Trees*, 1–15.
- Basset, Y., 2001. Communities of insect herbivores foraging on saplings versus mature trees of *Pourouma bicolor* (Cecropiaceae) in Panama. *Oecologia* 129 (2), 253–260.
- Briant, G., Gond, V., Laurance, S.G.W., 2010. Habitat fragmentation and the desiccation of forest canopies: a case study from eastern Amazonia. *Biol. Conserv.* 143 (11), 2763–2769.
- Brothers, T., 1993. Fragmentation and edge effects in central Indiana old-growth forests. *Nat. Areas J.* 13, 268–275.
- Cadenasso, M.L., Traynor, M.M., Pickett, S.T., 1997. Functional location of forest edges: gradients of multiple physical factors. *Can. J. For. Res.* 27 (5), 774–782.
- Chen, J., Franklin, J.F., Spies, T.A., 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecol. Appl.* 5 (1), 74–86.
- da Rocha, H.R., et al., 2004. Seasonality of water and heat fluxes over a tropical forest in Eastern Amazonia. *Ecol. Appl.* 14 (sp4), 22–32.
- Dambros, C.d.S., da Silva, V.N.V., Azevedo, R., de Morais, J.W., 2013. Road-associated edge effects in Amazonia change termite community composition by modifying environmental conditions. *J. Nat. Conserv.* 21 (5), 279–285.
- Davies-Colley, R., Payne, G., van Elswijk, M., 2000. Microclimate gradients across a forest edge. *New Zealand J. Ecol.* 24, 111–121.
- Delgado, J.D., Arroyo, N.L., Arévalo, J.R., Fernández-Palacios, J.M., 2007. Edge effects of roads on temperature, light, canopy cover, and canopy height in laurel and pine forests (Tenerife, Canary Islands). *Landsc. Urban Plann.* 81 (4), 328–340.
- Didham, R.K., Lawton, J.H., 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31 (1), 17–30.
- Dierick, D., Kunert, N., Köhler, M., Schwendenmann, L., Hölscher, D., 2010. Comparison of tree water use characteristics in reforestation and agroforestry stands across the tropics. In: Tscharnkte, T., et al. (Eds.), *Tropical Rainforests and Agroforests under Global Change*. Springer, Berlin, pp. 293–308.
- Dietrich, W., Windsor, M., Dunne, T., 1996. Geology, climate and hydrology of Barro Colorado Island. In: Leigh, J.E., Rand, A., WDM (Eds.), *The Ecology of a Tropical Forest. Seasonal Rhythms and Annual Changes*. Smithsonian Institution Press, Washington, DC, pp. 21–46.
- Ewers, R.M., Banks-Leite, C., 2013. Fragmentation impairs the microclimate buffering effect of tropical forests. *PLoS One* 8 (3), e8093.
- Forman, R.T.T., Alexander, L.E., 1998. Roads and their major ecological effects. *Annu. Rev. Ecol. Syst.* 29 (1), 207–231.
- Giambelluca, T.W., Ziegler, A.D., Nullet, M.A., Truong, D.M., Tran, L.T., 2003. Transpiration in a small tropical forest patch. *Agric. For. Meteorol.* 117 (1–2), 1–22.
- Granier, A., 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiol.* 3 (4), 309–320.
- Harper, K.A., et al., 2005. Edge Influence on Forest Structure and Composition in Fragmented Landscapes. *Influencia del Borde sobre la Composición y Estructura de Bosques en Paisajes Fragmentados. Conserv. Biol.* 19 (3), 768–782.
- Herbst, M., Roberts, J.M., Rosier, P.T.W., Taylor, M.E., Wowing, D.J., 2007. Edge effects and forest water use: a field study in a mixed deciduous woodland. *For. Ecol. Manage.* 250 (3), 176–186.
- Horna, V., Schuldt, B., Brix, S., Leuschner, C., 2011. Environment and tree size controlling stem sap flux in a perhumid tropical forest of Central Sulawesi, Indonesia. *Ann. For. Sci.* 68, 1027–1038.
- Kammesheidt, L., 2000. Some autecological characteristics of early to late successional tree species in Venezuela. *Acta Oecol.* 21 (1), 37–48.
- Kapos, V., 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *J. Trop. Ecol.* 5, 173–185, 2).
- Kunert, N., Barros, P., Higuchi, N., 2013. Do palm water use characteristics explain the spatial distribution of palms in the Central Amazon? *Acta Hort.* 991, 197–204.
- Kunert, N., Schwendenmann, L., Hölscher, D., 2010. Seasonal dynamics of tree sap flux and water use in nine species in Panamanian forest plantations. *Agric. For. Meteorol.* 150 (3), 411–419.
- Laurance, W., et al., 2001a. Effects of a strong drought on Amazonian forest fragments and edges. *J. Trop. Ecol.* 17 (06), 771–785.
- Laurance, W.F., 1999. Reflections on the tropical deforestation crisis. *Biol. Conserv.* 91 (2–3), 109–117.
- Laurance, W.F., et al., 2001b. The Future of the Brazilian Amazon. *Science* 291 (5503), 438–439.
- Laurance, W.F., Goosem, M., Laurance, S.G.W., 2009. Impacts of roads and linear clearings on tropical forests. *Trends Ecol. Evol.* 24 (12), 659–669.
- Laurance, W.F., et al., 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conserv. Biol.* 16 (3), 605–618.
- Laurance, W.F., et al., 2006. Rapid decay of tree-community composition in Amazonian forest fragments. *Proc. Natl. Acad. Sci.* 103 (50), 19010–19014.
- Leopoldo, P.R., Franken, W.K., Villa Nova, N.A., 1995. Real evapotranspiration and transpiration through a tropical rain forest in central Amazonia as estimated by the water balance method. *For. Ecol. Manage.* 73 (1–3), 185–195.
- Lowman, M.D., Burgess, J., Burgess, E., 2006. It's a jungle out there—more tales from the treetops. Yale University Press, New Haven.
- Marra, D.M., et al., 2014. Large-scale wind disturbances promote tree diversity in a central Amazon Forest. *PLoS ONE* 9 (8), e103711.
- Matlack, G.R., 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biol. Conserv.* 66 (3), 185–194.
- Meinzer, F., et al., 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia* 21, 293–301.
- Meinzer, F.C., Goldstein, G., Andrade, J.L., 2001. Regulation of water flux through tropical forest canopy trees: do universal rules apply? *Tree Physiol.* 21 (1), 19–26.
- Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. *Trends Ecol. Evol.* 10 (2), 58–62.
- Nepstad, D.C., et al., 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* 372 (6507), 666–669.
- Nogueira, A., Martinez, C., Ferreira, L., Prado, C., 2004. Photosynthesis and water use efficiency in twenty tropical tree species of differing succession status in a Brazilian reforestation. *Photosynthetica* 42 (3), 351–356.
- O'Brien, J.J., Oberbauer, S.F., Clark, D.B., 2004. Whole tree xylem sap flow responses to multiple environmental variables in a wet tropical forest. *Plant Cell Environ.* 27 (5), 551–567.
- Peña-Claros, M., 2003. Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon. *Biotropica* 35 (4), 450–461.
- Poggi, D., Porporato, A., Ridolfi, J., Albertson, J., Katul, G., 2004. The effect of vegetation density on canopy sub-layer turbulence. *Boundary Layer Meteorol.* 111, 565–587.
- Radler, K., Oltchev, A., Panferov, O., Klinck, U., Gravenhorst, G., 2010. Radiation and temperature responses to a small clear-cut in a spruce forest. *Open Geogr. J.* 3, 103–114.
- Ramos, C., Buitrago, S., Pulido, K., Vanegas, L., 2013. Variabilidad ambiental y respuestas fisiológicas de *Polylepis cuadriflora* (Rosaceae) en un ambiente fragmentado en el Páramo de la Rusia (Colombia). *Revista de Biología Tropical* 61 (1), 351–361.
- Ringgaard, R., Herbst, M., Friborg, T., 2012. Partitioning of forest evapotranspiration: the impact of edge effects and canopy structure. *Agric. For. Meteorol.* 166–167, 86–97.
- Roberts, J., Rosier, P., 2005. The impact of broadleaved woodland on water resources in lowland UK: III. The results from Black Wood and Bridgets Farm compared with those from other woodland and grassland sites. *Hydro. Earth Syst. Sci.* 9 (6), 614–620.
- Röhle, H., 1986. Vergleichende Untersuchungen zur Ermittlung der Genauigkeit bei der Abtrotung von Kronenradien mit dem Dachlot und durch senkrechtes Anvisieren des Kronenrandes. *Forsta* 57, 67–71.
- Schwendenmann, L., Pendall, E., Sanchez-Bragado, R., Kunert, N., Hölscher, D., 2015. Tree water uptake in a tropical plantation varying in tree diversity: interspecific differences, seasonal shifts and complementarity. *Ecohydrology* 8 (1), 1–12.
- Shuttleworth, W.J., 1988. Evaporation from Amazonian Rainforest. *Proc. R. Soc. Lond. B.* 233, 321–346.
- Swaine, M.D., Whitmore, T.C., 1988. On the definition of ecological species groups in tropical rain forests. *Vegetation* 75 (1–2), 81–86.
- Turton, S., Freiburger, H., 1997. Edge and aspect effects on the microclimate of a small tropical forest remnant on the Atherton Tableland, northeastern Australia. In: Laurance, W., Bierregaard, R.J. (Eds.), *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago, pp. 45–54.
- Williams-Linera, G., Domínguez-Gastélú, V., García-Zurita, M.E., 1998. Microenvironment and floristics of different edges in a fragmented tropical rainforest. *Conserv. Biol.* 12 (5), 1091–1102.
- Wright, T.E., et al., 2012. Edge type affects leaf-level water relations and estimated transpiration of *Eucalyptus arenacea*. *Tree Physiol.* 32 (3), 280–293.
- Young, A., Mitchell, N., 1994. Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. *Biol. Conserv.* 67 (1), 63–72.