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## Tree species and diversity effects on soil water seepage in a tropical plantation

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## ABSTRACT

Plant diversity has been shown to influence the water cycle of forest ecosystems by differences in water consumption and the associated effects on groundwater recharge. However, the effects of biodiversity on soil water fluxes remain poorly understood for native tree species plantations in the tropics. Therefore, we estimated soil water fluxes and assessed the effects of tree species and diversity on these fluxes in an experimental native tree species plantation in Sardinilla (Panama). The study was conducted during the wet season 2008 on plots of monocultures and mixtures of three or six tree species. Rainfall and soil water content were measured and evapotranspiration was estimated with the Penman-Monteith equation. Soil water fluxes were estimated using a simple soil water budget model considering water input, output, and soil water and groundwater storage changes and in addition, were simulated using the physically based one-dimensional water flow model Hydrus-1D.

In general, the Hydrus simulation did not reflect the observed pressure heads, in that modeled pressure heads were higher compared to measured ones. On the other hand, the results of the water balance equation (WBE) reproduced observed water use patterns well. In monocultures, the downward fluxes through the 200 cm-depth plane were highest below *Hura crepitans* (6.13 mm day<sup>-1</sup>) and lowest below *Luehea seemannii* (5.18 mm day<sup>-1</sup>). The average seepage rate in monocultures ( $\pm$ SE) was 5.66  $\pm$  0.18 mm day<sup>-1</sup>, and therefore, significantly higher than below six-species mixtures (5.49  $\pm$  0.04 mm day<sup>-1</sup>) according to overyielding analyses. The three-species mixtures had an average seepage rate of 5.63  $\pm$  0.12 mm day<sup>-1</sup> and their values did not differ significantly from the average values of the corresponding species in monocultures. Seepage rates were driven by the transpiration of the varying biomass among the plots ( $r = 0.61$ ,  $p = 0.017$ ). Thus, a mixture of trees with different growth rates resulted in moderate seepage rates compared to monocultures of either fast growing or slow growing tree species. Our results demonstrate that tree-species specific biomass production and tree diversity are important controls of seepage rates in the Sardinilla plantation during the wet season.

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## 1. Introduction

The area of planted forest increased globally by about 5 million ha per year between 2005 and 2010 and accounts for an estimated

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7% (264 million ha) of the total forested area today (FAO, 2010). In Panama, the area of planted forests in 2010 was 79,000 ha, six times larger than in 1990, with an annual growth of 5% over the last 5 years. Today, 44% of the land is still forested and the deforestation rate is low ( $-0.36\%$  yr<sup>-1</sup>) (FAO, 2010). It can be expected that with the expanding carbon markets (FAO, 2011) and increasing demands for bioenergy (UN Energy, 2007) the total area of forest plantation will further grow in the near future. Monocultures, for example, of the exotic hardwood tree *Tectona grandis* L.f. (teak tree) that accounted for 76% of plantations established in Panama between 1992 and 2000, may be very productive, but appear to have

drawbacks like promotion of soil erosion and reduction of soil quality (Wishnie et al., 2007). In general, the wide-spread monocultures of exotic species threaten the local biodiversity (Healey and Gara, 2003). Furthermore, it is increasingly reported that plant diversity is crucial for maintaining the function and stability of ecosystems and biogeochemical cycles calling for increased establishment of mixed-species plantations (Loreau et al., 2001).

Global analysis by Jackson et al. (2005) over 504 catchments showed that stream flow decreased dramatically within a few years after setting up plantations, which can impact the water cycle up to 20 years. In the watershed of the Panama Canal, reduction of the water supply due to enhanced evapotranspiration (ET) losses by large scale afforestation might cause limited trafficability of the canal, because the water budget for the canal is tight (Ibanez et al., 2002). However, forests are seen to secure the water supply of the canal by reducing sediment loads and ensuring sufficient dry season flow (Condit et al., 2001; Harmon, 2005).

Because of the growing concern that tree plantations might affect base flow conditions (Malmer et al., 2010; Scott and Prinsloo, 2008), the effect of mixed-species plantations as compared to the traditional monoculture plantations needs to be assessed thoroughly. Surveys over the last decade showed that tree diversity has an impact on ecosystem functioning such as the control of nutrient cycles in a mixed-species tree plantation in Panama (Oelmann et al., 2010; Potvin et al., 2011; Zeugin et al., 2010). From grassland experiments it is further known that plants in mixtures of species are often more productive and have greater water use than in monocultures, which might be related to complementary effects (Caldeira et al., 2001; Verheyen et al., 2008). Recently, Forrester et al. (2010) found higher transpiration rates in mixtures of *Eucalyptus globulus* Labill. and *Acacia mearnsii* De Wild, but the mixture also used the water more efficiently. In line with these findings, Kunert et al. (2012) showed for an experimental plantation in Panama that individual tree transpiration is enhanced in mixed-tree stands compared to monocultures, the water use efficiency of five-species mixtures being half that of either monocultures, two- or three-species mixtures. Consequently, mixed-tree stands might increase evaporative water losses following afforestation and thus, pose problems to water supply of the Panama Canal. Because of controversial results on water use of mixed-tree stands, it remains unclear whether tree diversity influences seepage rates during the wet season.

To answer this question, our objectives were to (1) calculate the seepage rates at plots of one, three, and six tree species with two approaches of different complexity and (2), to analyze the effect of the different species and the number of tree species on the seepage rates. Two approaches of water balance assessment were used to test if a simple water balance calculation can predict species specific water fluxes at a tropical plantation for the wet season in 2008 similarly well as a physically based soil water transport model (Hydrus-1D).

## 2. Materials and methods

### 2.1. Study site

The study site is located in Central Panama (9°19'30"N, 79°38'00"W) roughly 50 km north of Panama City close to the village of Sardinilla. The Smithsonian Tropical Research Institute (STRI) maintains a tree plantation for the "Sardinilla Project", with the goal to assess the influence of diversity on biogeochemical and water cycles. The site belongs to the Panama Canal catchment and has an altitude of about 70 m above sea level. The climate is

semi-humid tropical with a mean annual temperature of 25.2 °C, a mean annual precipitation of 2289 mm (2007–2009), and a pronounced dry season from January to April characterized by strong north-easterly trade winds (Wolf et al., 2011b).

The underlying sediments are tertiary limestones containing clayey schists and quartz sandstones (Wolf et al., 2011b). The soil type was classified according to IUSS Working Group (2006) as Vertic Luvisol shifting to a Gleyic Luvisol in depressions (Oelmann et al., 2010). Primary vegetation was a moist tropical forest (Potvin et al., 2004), which was cut down in 1952/1953 and converted to pasture afterwards (Scherer-Lorenzen et al., 2005). In July 2001, the experimental plantation of 9 ha was set up by planting six native tree species. The species, which are of local economic and ecological value, were chosen based on their range of relative growth rates (Delagrange et al., 2008): *Luehea seemannii* Triana & Planch (LS) and *Cordia alliodora* (Ruiz & Pavon) Oken (CA) are pioneers, *Anacardium excelsum* (Bert. & Balb. Ex Kunth) Skeels (AE) and *Hura crepitans* L. (HC) are light intermediate species and *Cedrela odorata* L. (CO) and *Tabebuia rosea* (Bertol.) DC. (TR) are classified as shade-intolerant non-pioneer species (Delagrange et al., 2008). Overall 24 diversity plots of 45 × 45 m were established with either one, three, or six tree species. Twelve plots (two for each species) are monocultures, six plots contain different combinations of three tree species (each triplet containing one species of the three categories of growth rates), and six plots contain all tree species (Scherer-Lorenzen et al., 2005). The plots are further divided into four 22.5 × 22.5 m subplots. The stem density in the plantation is 1111 ha<sup>-1</sup>, which is the commercially prevalent planting density in Central America (Scherer-Lorenzen et al., 2007). The moderately dense understory is removed three times per year (Potvin and Gotelli, 2008). In general, *C. alliodora* showed very high mortality, and therefore, monocultures of this species are not considered in this study.

### 2.2. Modeling

Seepage was either calculated with a soil water budget equation (WBE) incorporating water input, water output, and soil water storage changes, or modeled using the physically based soil water transport model Hydrus-1D (Šimůnek and Bradford, 2008; Šimůnek et al., 2009). In both cases any lateral flow such as surface-, inter-, or groundwater flow was assumed negligible, since the elevation differences between the plots were small (<5 m, see Appendix A) and the maximum saturated soil infiltration potential was estimated to be high (Wolf et al., 2011a). Therefore, only vertical water fluxes like infiltration, evapotranspiration, and flow into the groundwater were considered. The flow chart in Appendix B gives an overview of the processes involved in the two model approaches. In this study, we defined seepage as the downward fluxes through the –200 cm depth plane.

#### 2.2.1. Water budget equation

In general, the drainage to the groundwater ( $v_{Bot}$ ) (mm) can be calculated based on a simple approach (Eq. (1)), namely the water balance equation (WBE) by

$$v_{Bot} = \Delta S + P - AET \quad (1)$$

where  $\Delta S$  (mm) is the difference in water storage in the soil profile between two subsequent sampling dates ( $t_n - t_{n+1}$ ),  $P$  (mm) is the precipitation, and  $AET$  (mm) is the actual evapotranspiration.  $AET$ ,  $v_{Bot}$ , and capillary rise ( $CR$ ) (mm) were determined by the following relations:

$$\text{if } \Delta S + P < PET \text{ then} \\ AET = \Delta S + P \text{ and } v_{Bot} = 0 \quad (2)$$

$$\begin{aligned} \text{if } \Delta S + P > \text{PET then AET} &= \text{PET}, \\ \nu\text{Bot} &= \Delta S + P - \text{PET} \end{aligned} \quad (3)$$

$$\begin{aligned} \text{if } \Delta S < 0 \text{ and } |\Delta S| > P \text{ then} \\ \text{CR} &= \Delta S - P \text{ with AET} = 0 \text{ and } \nu\text{Bot} = 0 \end{aligned} \quad (4)$$

Hereby, the potential evapotranspiration (PET) was estimated using the Penman-Monteith equation as described by Allen et al. (1998) using standard meteorological data as input. The plot specific vegetation parameters for the aerodynamic and canopy resistance within the Penman-Monteith equation, namely tree height and leaf area index (LAI), were inferred from field surveys. Tree height was measured with hypsometers and the LAI was derived from hemispheric photos showing the surface cover fraction (SCF) using the following relation (Eq. (5)) as proposed by Šimůnek et al. (2009):

$$\text{LAI} = -2.16 \cdot \ln(1 - \text{SCF}) \quad (5)$$

The canopy interception  $I$  was modeled according to Šimůnek et al. (2009) as:

$$I = \text{alnterc} \cdot \text{LAI} \left( 1 - \left( 1 + \frac{\text{SCF} \cdot P}{\text{alnterc} \cdot \text{LAI}} \right)^{-1} \right), \quad (6)$$

where  $\text{alnterc}$  is an empirical constant, which was defined in a way to match modeled interception to observed interception (Schnee- beli et al., 2011). Due to a lack of species specific interception surveys,  $\text{alnterc}$  was defined equal for the entire plantation to be 1 mm. Since only weekly pressure head measurements were available, precipitation and evapotranspiration were also aggregated to weekly sums, and consequently weekly seepage sums were calculated using the WBE approach. To estimate subsurface water storage changes in the upper 200 cm of the soil profile, first soil water contents were derived from measured pressure heads using Eq. (8) according to the plot specific Mualem–van Genuchten parameters listed in Table 1. Then, the soil water contents were multiplied by the depth of the groundwater level below the surface to obtain changes of the stored water volume in the water-unsaturated (vadose) zone. Additionally, changes in the water-saturated zone were taken into account by multiplying the saturated water content with the groundwater level above the –200 cm depth plane. Finally, changes of the total storage in the unsaturated and saturated zone between two subsequent sampling dates represented  $\Delta S$ .

### 2.2.2. Hydrus modeling

For the one-dimensional simulation of the water flow, and root water uptake the Richards equation was solved using the finite

element code Hydrus-1D (Šimůnek and Bradford, 2008; Šimůnek et al., 2009).

For the parameterization of the retention ( $\theta(h)$ ) and unsaturated hydraulic conductivity function ( $K(h)$ ) the Mualem–van Genuchten approach (van Genuchten, 1980) was used, which requires the following soil hydraulic parameters:  $\theta_r$  ( $\text{cm}^3 \text{cm}^{-3}$ ) and  $\theta_s$  ( $\text{cm}^3 \text{cm}^{-3}$ ) as the residual and saturated volumetric water contents, respectively,  $\alpha$  ( $\text{cm}^{-1}$ ),  $n$  (–), and  $m$  (–) ( $m = 1 - 1/n$ ) as shape parameters, and  $K_s$  ( $\text{cm day}^{-1}$ ) as the saturated hydraulic conductivity. These required soil hydraulic parameters of the entire soil profile were determined by neural network predictions of ROSETTA (Schaap et al., 2001), based on textural information (sand, silt, and clay content) and bulk density ( $\text{g cm}^{-3}$ ).

The upper boundary was set to atmospheric conditions with precipitation and potential evapotranspiration and the lower boundary was described by variable pressure heads representing measured groundwater table depths. When the groundwater level dropped below the measurement limit of 65 cm below surface, the lower boundary was adapted in a way to improve the fit between observed and modeled pressure heads.

Root water uptake, represented by a sink term in the Richards equation, was simulated according to Feddes et al. (1978). The sink term is governed by a dimensionless root-water uptake water stress response function and the potential water uptake rate. The root-water uptake water stress response function, as defined by Feddes et al. (1978), assumes that water uptake of the trees will approach zero close to water saturation of the soil ( $h < P_0$ ) due to the lack of oxygen. On the other hand, at pressure heads below the permanent wilting point ( $h > P_3$ ) root water uptake will be reduced because smaller soil pressure heads exceed the highest possible suction of the plants. In between these pressure heads two additional points ( $P_{opt} < h < P_2$ ) delineate optimal root water uptake. Therefore, at pressure heads between  $P_0$  and  $P_{opt}$  and between  $P_2$  and  $P_3$ , the water stress response function decreases linearly. The Feddes parameters were chosen in that way to maximize the root-water uptake (PET = AET), since the wet season is the period of optimal environmental conditions for the trees at the plantation in Sardinilla (Kunert et al., 2010). Additionally, due to the fact that PET was again calculated using a simplified form of the Penman-Monteith equation, which takes only the mean height and the leaf area of a stand into consideration, the contribution of the root-water uptake to the AET was limited under the optimal conditions by these two parameters and not the root distribution, rooting depth, or the Feddes parameters. Rooting depth was set to be –140 cm because sparse point information about rooting depth indicates that this is the mean rooting depth at the plantation (Jef- ferson Hall, personal communication, unpublished data). The distribution of the roots was assumed to be decreasing linearly with soil depth. The resulting pressure heads from the simulation were

**Table 1**  
Soil physical properties for the stands as means across the entire soil profile of the different tree species and biodiversity levels with measured soil textural fractions (sand, silt, and clay content (wt.%)), bulk density (BD) ( $\text{g cm}^{-3}$ ), porosity (–) and ROSETTA (Schaap et al., 2001) based on estimations of the soil hydraulic properties  $\theta_r$  and  $\theta_s$  as the residual water content ( $\text{cm}^3 \text{cm}^{-3}$ ),  $\alpha$  ( $\text{cm}^{-1}$ ) and  $n$  as shape parameters as well as  $K_s$  as the saturated hydraulic conductivity ( $\text{cm day}^{-1}$ ). AE: *Anacardium excelsum*; CO: *Cedrela odorata*; HC: *Hura crepitans*; LS: *Luehea seemannii*; TR: *Tabebuia rosea*, Monocultures, three-species mixtures (three-species), six-species mixtures (six-species), and plantation: Average across all monoculture plots, all three-species plots, all six-species plots, and all plots at the plantation, respectively. All values as mean  $\pm$  standard error.

Species/diversity	Sand (%)	Silt (%)	Clay (%)	BD ( $\text{g cm}^{-3}$ )	Porosity (–)	$\theta_r$ ( $\text{cm}^3 \text{cm}^{-3}$ )	$\alpha$ ( $\text{cm}^{-1}$ )	$n$ (–)	$K_s$ ( $\text{cm d}^{-1}$ )
AE	1 $\pm$ 0	17 $\pm$ 5	82 $\pm$ 6	0.83 $\pm$ 0.04	0.69 $\pm$ 0.01	0.13 $\pm$ 0.00	0.045 $\pm$ 0.006	1.20 $\pm$ 0.01	60 $\pm$ 4
CO	3 $\pm$ 1	22 $\pm$ 9	75 $\pm$ 10	0.95 $\pm$ 0.05	0.64 $\pm$ 0.02	0.12 $\pm$ 0.01	0.033 $\pm$ 0.006	1.23 $\pm$ 0.02	47 $\pm$ 1
HC	1 $\pm$ 1	25 $\pm$ 8	74 $\pm$ 9	0.85 $\pm$ 0.02	0.68 $\pm$ 0.01	0.13 $\pm$ 0.00	0.039 $\pm$ 0.003	1.22 $\pm$ 0.01	79 $\pm$ 27
LS	1 $\pm$ 1	17 $\pm$ 5	82 $\pm$ 5	0.86 $\pm$ 0.02	0.68 $\pm$ 0.01	0.13 $\pm$ 0.00	0.042 $\pm$ 0.003	1.21 $\pm$ 0.01	56 $\pm$ 4
TR	1 $\pm$ 0	16 $\pm$ 1	83 $\pm$ 1	0.79 $\pm$ 0.00	0.70 $\pm$ 0.00	0.13 $\pm$ 0.00	0.048 $\pm$ 0.000	1.20 $\pm$ 0.00	67 $\pm$ 3
Monocultures	2 $\pm$ 0	19 $\pm$ 2	79 $\pm$ 3	0.86 $\pm$ 0.02	0.68 $\pm$ 0.01	0.13 $\pm$ 0.00	0.041 $\pm$ 0.002	1.21 $\pm$ 0.01	62 $\pm$ 5
Three-species	3 $\pm$ 1	29 $\pm$ 3	68 $\pm$ 4	0.84 $\pm$ 0.01	0.68 $\pm$ 0.00	0.12 $\pm$ 0.00	0.036 $\pm$ 0.002	1.23 $\pm$ 0.01	100 $\pm$ 14
Six-species	2 $\pm$ 0	21 $\pm$ 5	77 $\pm$ 5	0.81 $\pm$ 0.01	0.70 $\pm$ 0.00	0.13 $\pm$ 0.00	0.045 $\pm$ 0.002	1.21 $\pm$ 0.01	78 $\pm$ 11
Plantation	2 $\pm$ 0	22 $\pm$ 2	76 $\pm$ 2	0.84 $\pm$ 0.01	0.68 $\pm$ 0.00	0.13 $\pm$ 0.00	0.041 $\pm$ 0.001	1.21 $\pm$ 0.01	77 $\pm$ 6

compared to measured pressure heads. Finally, daily seepage was calculated for the 22 plots over the 151 day period from 6th of June 2008 (start of GWL measurements) to the 5th of December 2008 (end of wet season). The depth of the soil profile was set to be –200 cm. The profile bottom defines the horizontal depth at which seepage was calculated. The entire profile was initialized in pressure heads using measured data from pressure head sensors at –30 cm depth and the location of the groundwater table. For in between pressure heads we used linear interpolation. Since groundwater table depths were determined biweekly, linear interpolation was applied to get daily groundwater table depths. All other parameters required for the Hydrus-1D model runs are listed in Appendix C. To compare the results of the Hydrus model runs with the WBE approach, the daily seepage data were summed up again to weekly data.

### 2.3. Field surveys

For the determination of the physical parameters of the soils dry soil bulk density (BD) ( $\text{g cm}^{-3}$ ) and the soil texture were surveyed. BD was determined in April 2011 using undisturbed soil samples according to Blake and Hartge (1986). Cores were extracted on each subplot in both the top soil (5–15 cm) and subsoil (15–25 cm) in replication, resulting in 352 data points. Single BD values were averaged for each experimental plot afterwards. Soil texture was determined by wet sieving and the pipette method on bulked soil samples of eight subsoil samples for each plot separately.

The tensiometers (total length 40 cm, diameter 2 cm) had a mullite ceramic cup (ecotech, Bonn, Germany). In duplicate per plot, we drilled holes with a diameter of 2 cm and inserted the tensiometers for each of 16 plots at a depth of –30 cm in the last 2 weeks of March 2008. We used soil of the respective plot to fill the gap between the tensiometer tube and soil by sluicing with rain water and finally placed a collar around the tube to keep water from running down the tubes directly. After an equilibration time of one month, soil pressure heads were read weekly manually between the 5th of May 2008 and the 3rd of November 2008 directly in the field by means of a manual display unit (Infields 5, UMS, Germany). These measured pressure heads were transformed into soil moisture values via Eq. (8). In the water balance approach, the soil moistures represent the stored water volume in the unsaturated zone by multiplication with the depth of the groundwater level below surface.

The depths of the shallow groundwater table were also recorded biweekly for each subplot manually in piezometers from the 6th of June 2008 to the 27th of December 2008. The measurements were limited to –65 cm below surface, because the piezometers consist of PVC tubes reaching down to –65 cm soil depth with a notch at the bottom. The notch allowed water to infiltrate from the bottom, while PVC tubes were not perforated along the entire length.

Meteorological data were recorded in the Sardinilla plantation from February 2007 to July 2009 on a 15 m flux tower and comprised among others air temperature, relative humidity, net radiation, wind speed, and precipitation. Actual evapotranspiration (AET) was measured directly with the eddy covariance technique using an open-path infrared gas analyzer (Li-7500, LI-COR, Lincoln, USA) and a three-dimensional sonic anemometer (CSAT3, Campbell Scientific, Logan, USA). A full description of the setup and data processing is given by Wolf et al. (2011a).

Tree height was recorded annually around the end of the year using hypsometers. To get information about tree heights in the wet season 2008, mean values of the surveys in winter 2007/08 and winter 2008/09 were calculated. Additionally, above-ground biomass for each plot was computed annually in January by spe-

cies-specific least square linear regression between tree biomass and basal diameter, tree height, and the sum of the diameter at breast height of all stems (Oelmann et al., 2010; Potvin et al., 2011). Furthermore, hemispheric photos taken on the 20th of July 2007 were used to determine the canopy openness, which was used to calculate the surface cover fraction by  $1 - \text{canopy openness}$ .

### 2.4. Statistical analyses

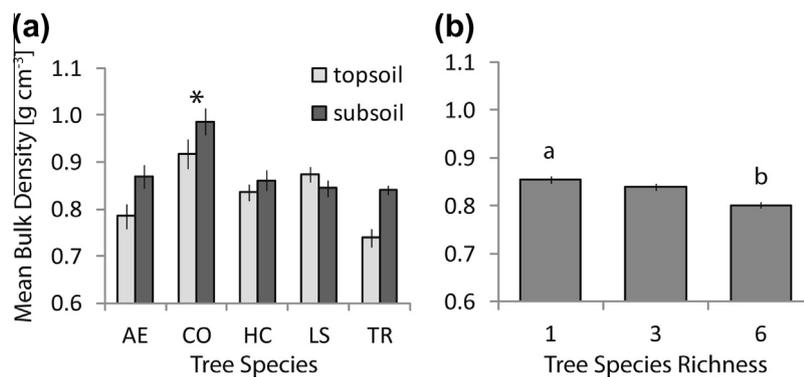
All statistical analyses were performed using SPSS statistics version 19 (SPSS Inc., Chicago, USA), whereby the significance level was set to be  $p < 0.05$  for all tests. Analysis of variance (ANOVA) were carried out as type I sums of squares followed by a post hoc Tukey HSD (Honestly Significant Difference) test to assess differences of the bulk density and seepage rates among plots of different tree species and tree diversity levels. The paired Student's *t*-test was used to determine differences of BD with regard to soil depth. The Kruskal-Wallis one way analysis of variance on ranks was used to compare groundwater table depth at the different diversity levels, which were not normally distributed. In accordance with Hector et al. (2002) a proportional deviation index was calculated to compare observed and expected seepage rates of a mixture with  $D_{mean} = (O - E_{mean})/E_{mean}$ , where *O* is the simulated seepage rate at a mixture plot and  $E_{mean}$  is the average of the corresponding tree species in monoculture plots (termed non-transgressive overyielding). Hence, for  $D_{mean} < 0$ , the seepage rate in the mixture is lower than the average of the corresponding tree species. We tested if these deviation indices were significantly different from null with a Mann-Whitney-*U* test. Pearson's correlation analyses were performed to detect relationships between parameters such as tree height, canopy openness, and biomass or biomass and GWL, or modeled seepage rates, respectively. Finally, linear regressions were used to compare modeled and measured data as well as to assess the two model approaches. The goodness of the fit between observed and simulated pressure heads or evapotranspiration was furthermore described by the root mean square error (RMSE) as defined by Šimůnek and Hopmans (2002). If not stated otherwise, all reported values are given as arithmetic mean  $\pm$  standard error. Note that negative water fluxes indicate downward movement (e.g. seepage or infiltration) and positive fluxes moved upwards (e.g. capillary rise, evapotranspiration).

## 3. Results and discussion

### 3.1. Seepage calculation approaches

#### 3.1.1. Parameter evaluation

The measured bulk density (BD) of the different plots ranged between  $0.79 \pm 0.01$  and  $0.95 \pm 0.02 \text{ g cm}^{-3}$ , and the mean BD over the entire plantation was  $0.84 \pm 0.01 \text{ g cm}^{-3}$ . In general, the soils of the plots of *C. odorata* (CO in Fig. 1) stands showed significantly higher BD compared to the other species. BD differed significantly over soil depth with higher values in the subsoil compared to the topsoil ( $T_{355} = 2.742$ ,  $p = 0.006$ ). Exceptions were the two monocultures of *L. seemannii* (LS in Fig. 1) which do not show any significant difference between soil depths. Among the diversity levels an effect on the composite BD was also observed with significantly higher BD of  $0.86 \pm 0.01 \text{ g cm}^{-3}$  for soils under monocultures compared to a BD of  $0.81 \pm 0.01 \text{ g cm}^{-3}$  for the soils under mixed stands with six species. No coarse material ( $>2 \text{ mm}$ ) was found at any of the soil sample locations in the plantation. On the other hand, the soil was heavy clayey with mean clay amount of  $75.5 \pm 2.2 \text{ wt.}\%$ , and therefore, has to be classified as clay soils according to the USDA classification. The mean sand and silt fraction were only  $1.4 \pm 0.3\%$  and  $22.4 \pm 2.0 \text{ wt.}\%$ , respectively.

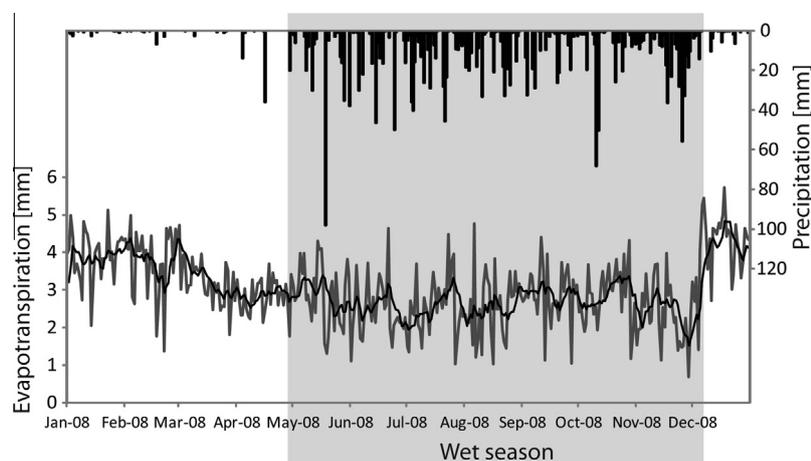


**Fig. 1.** Mean bulk density ( $\text{g cm}^{-3}$ ) (a) at the different tree species mixtures in the topsoil (light gray) and subsoil (dark gray) and (b) at the different diversity plots not distinguished between top- and subsoil. Error bars indicate standard error and \* letters indicate significant differences among species and diversity levels, respectively. AE: *Anacardium excelsum*; CO: *Cedrela odorata*; HC: *Hura crepitans*; LS: *Luehea seemannii*; and TR: *Tabebuia rosea*.

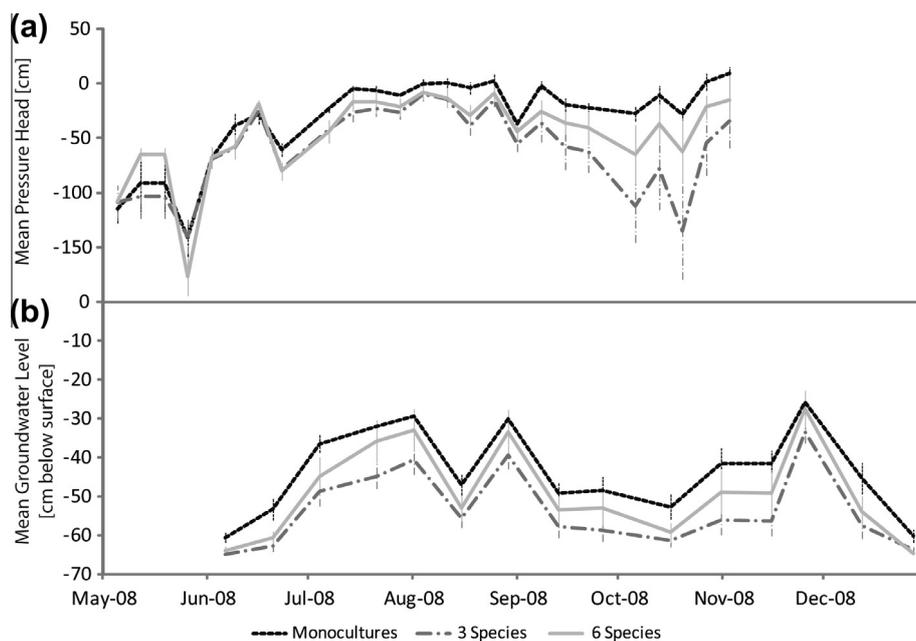
To estimate the Mualem–van Genuchten (MVG) parameters for each single plot the textural as well as the bulk density information were used and the parameters were predicted by the ROSETTA pedo-transfer function (Schaap et al., 2001). As expected, hydraulic properties did not differ significantly among plots at the plantation due to the relatively homogeneous soil texture and bulk density. Saturated and residual water content ranged between  $0.64$  and  $0.70 \text{ cm}^3 \text{ cm}^{-3}$  and  $0.12$  and  $0.13 \text{ cm}^3 \text{ cm}^{-3}$ , respectively. The relatively large saturated water contents are in good agreement with the bulk densities and porosities measured independently from undisturbed soil columns. The MVG shape parameters  $\alpha$  and  $n$ , ranged between  $0.036$  and  $0.048 \text{ cm}^{-1}$  and  $1.20$  and  $1.28$ , respectively. The saturated hydraulic conductivity ( $K_s$ ) estimated with ROSETTA was between  $47$  and  $100 \text{ cm day}^{-1}$ . All soil characteristics are listed in Table 1.

In 2008, the dry season, defined as the time span during which it never rained more than four consecutive days, lasted 77 days from the 18th of January to the 3rd of April and the wet season, defined as the contrary of the dry season, started on the 29th of April and ended the 5th of December (221 days; Fig. 2). Around 95% of the precipitation was recorded during the wet season. Differences between the seasons in mean maximum air temperature were negligible, but minimum temperatures were slightly lower and varied less during the dry season than during the wet season. Net radiation was about 30% and wind speed was more than 50% lower in the wet season than in the dry season. Eddy covariance measured daily evapotranspiration (ET) rates in the wet season were 25% lower compared to the dry season in 2008 (Appendix D).

Over the dry season the groundwater level (GWL) dropped mainly below  $-65 \text{ cm}$  (max. installation depth of the piezometers), and therefore, no exact measurements were possible. After the first 3 weeks of the wet season in 2008, the groundwater level rose above the  $-65 \text{ cm}$  as a response to the heavy rainfall and mean GWL at the plantation reached  $-30 \text{ cm}$  (Fig. 3b). Additionally, GWL never dropped below  $-65 \text{ cm}$  between July and December (end of the wet season). Variations among the plots, indicated by the error bars in Fig. 3b, were highest in times of high GWLs. The highest groundwater tables occurred under the *A. excelsum* stands and lowest GWLs were found in the three-species mixtures (Table 2). Because GWLs directly influence the pressure head characteristics in the soil during the wet season, which is mainly dominated by downward movement of the water, mean soil pressure heads also increased after the first precipitation events of the wet season in 2008. The highest mean pressure heads at the plantation was recorded in August 2008, where the soil was almost saturated at  $-30 \text{ cm}$  depth with a pressure heads of  $-6 \text{ cm}$ . Standard errors, shown as error bars in Fig. 3a, indicate that the variance of pressure heads among the plots was largest in periods of lower pressure heads (September and October), which is contrary to the general findings that the variance of pressure heads or water contents decreases for medium water contents (or pressure heads) as shown by Vereecken et al. (2007) and Jonard et al. (submitted for publication). The reasons for this behavior are either based on differences in the groundwater level, which were not observed as shown above, or local changes of the water content within the



**Fig. 2.** Time series of measured open field precipitation (black columns) (mm) and evapotranspiration (gray curve) (mm) in 2008. Period of wet season shaded gray. Black curve indicates 7 days running mean.



**Fig. 3.** Time series of (a) pressure heads (cm) in –30 cm soil depth and (b) groundwater table (cm below surface) in 2008 averaged for each tree diversity. Error bars indicate standard error.

**Table 2**

Species and diversity specific data of mean groundwater level (GWL) and mean pressure head (cm) at –30 cm soil depth for the wet season in 2008. Mean tree height (cm) and biomass ( $\text{Mg ha}^{-1}$ ) recorded in January 2008. Canopy openness (%) recorded in July 2007. Abbreviations and descriptions of species and diversity like in Table 1. All values as mean  $\pm$  standard error.

Species/diversity	GWL (cm below soil surface)	Pressure head (cm)	Tree height (cm)	Biomass ( $\text{Mg ha}^{-1}$ )	Canopy openness (%)
AE	35 $\pm$ 2	–23 $\pm$ 6	588 $\pm$ 8	10.8 $\pm$ 1.5	43 $\pm$ 4
CO	42 $\pm$ 2	–22 $\pm$ 8	840 $\pm$ 11	14.6 $\pm$ 2.0	47 $\pm$ 2
HC	40 $\pm$ 2	–42 $\pm$ 8	422 $\pm$ 42	8.9 $\pm$ 2.2	51 $\pm$ 3
LS	45 $\pm$ 3	–32 $\pm$ 7	794 $\pm$ 181	30.4 $\pm$ 8.1	27 $\pm$ 4
TR	50 $\pm$ 3	–33 $\pm$ 9	674 $\pm$ 1	31.0 $\pm$ 2.7	30 $\pm$ 3
Monocultures	43 $\pm$ 1	–32 $\pm$ 6	628 $\pm$ 53	19.1 $\pm$ 2.3	40 $\pm$ 2
Three-species	53 $\pm$ 1	–60 $\pm$ 9	733 $\pm$ 55	24.0 $\pm$ 3.1	32 $\pm$ 3
Six-species	48 $\pm$ 2	–46 $\pm$ 8	712 $\pm$ 50	22.2 $\pm$ 2.2	33 $\pm$ 3
Plantation	47 $\pm$ 1	–46 $\pm$ 5	680 $\pm$ 32	21.3 $\pm$ 1.5	36 $\pm$ 2

unsaturated zone due to local root water uptake. This unexpected behavior is also reflected by the weak correlation between plot specific mean pressure heads and groundwater levels for the wet season 2008. The dramatic changes of water stored in the soil at the plantation can be supported by Fe(III) oxides embedded in a reduced soil matrix (reddish mottles), found in soil horizons at a depth below 20 cm soil depth. Mean pressure heads are also listed in Table 2. There was a significant difference in GWL depth among the different diversity plots within the wet season. On average, GWL was –43 cm at monocultures and –53 cm at the three-species mixtures. Similarly, the pressure heads were significantly different among the three diversity levels. Again, the difference between monocultures (–32 cm, averaged across the wet season) and three-species mixtures (–60 cm) was significant. The consistent ranking over time among the monocultures, three-species mixtures, and six-species mixtures in pressure head and groundwater level suggest that the water use among the diversity levels is different. Apparently, the differences seem to be greater in periods of lower pressure heads (September and October) than during times of higher pressure heads.

The mean tree height for the entire plantation was 680 cm in summer 2008, whereby tallest trees grew on average in monocultures of *C. odorata* (840 cm). *Hurea crepitans* monocultures showed smallest average tree height with 422 cm, the most open canopy

(51%), and the lowest biomass ( $9.8 \text{ Mg ha}^{-1}$ ). In contrast, monocultures of *L. seemannii* and *T. rosea* showed the lowest canopy openness and the highest biomass (Table 2). The mean biomass per plot was  $23.5 \text{ Mg ha}^{-1}$  in 2008. The high rates of growth of *T. rosea* and *C. odorata* monocultures is consistent with the grouping of the species according to growth rates (Potvin et al., 2011). There was a significant negative correlation between canopy openness and both tree height ( $r = -0.64$ ) and biomass ( $r = -0.82$ ). Also, tree height and biomass correlated significantly with an  $r = 0.75$ . Tree height, biomass, and canopy openness are listed in Table 2. Leaf shedding of the tree species in Sardinilla mainly occurs during the dry seasons (Kunert et al., 2010), and hence, changes in canopy openness due to changes in foliage were negligible for the wet season.

To avoid misinterpretations about the plants and their feedback on water fluxes a correlation between the elevation of plots, with a maximum difference among the plots of 5 m (Appendix A), and the mean GWL of the wet seasons in 2007 and 2008 was calculated. The results clearly indicated that there is no significant correlation between elevation and GWL ( $r = -0.32$ ), which leads to the assumption that seepage and GWL are mainly influenced by the vegetation on the plots. This assumption was confirmed by the significant correlations between the mean GWLs and both tree height and canopy openness (Fig. 4). The correlation of GWLs with tree height and canopy openness indicate that trees either grow faster

on plots with low groundwater levels or that large trees with low canopy openness lower the GWLs due to their higher water demand.

Hence, the trees affect the groundwater through evaporation, root water uptake, and interception according to their height, canopy openness, and biomass. This is in line with findings of Dierick et al. (2010) who reported for the tree plantation in Sardinilla, as well as for plantations in the Philippines and Indonesia, a strong positive correlation between maximum daily water use (determined by sap flow measurements) of individual trees and tree diameter. Kunert et al. (2010) found with sap flow measurements that the correlation between tree size and water use is especially strong at the plantation in Sardinilla during the wet season, when optimal environmental conditions for growth prevail.

### 3.1.2. Evapotranspiration

During the wet season, PET equals AET and is on average 422 mm based on the Penman-Monteith equation, which represents one-third of the rainfall in the simulation period (1243 mm). Averaged daily AET during the wet season 2008 was 2.8 mm (Table 3), which is in line with eddy covariance measurements (2.7 mm day<sup>-1</sup>, Appendix D). A root mean squared error (RMSE) of 0.41 mm day<sup>-1</sup> indicates that also the variation over the simulation period of the calculated daily evapotranspiration match well with the field observations. Bigelow (2001) modeled AET to be 41–47% of annual precipitation (depending on species) at a Costa Rican plantation with tree heights of 10 m, 4 years after planting. These percentage losses agree with the measurements by Wolf et al. (2011a) and modeled AET of 54%. Also evapotranspiration analysis in the tropical Reserve Ducke Forest in Amazonia, Brazil by Shuttleworth (1988) resulted in losses of 54% of the annual precipitation due to AET. For the plantation in Costa Rica, median AET almost equals PET (AET/PET = 0.97) according to Bigelow et al. (2004), which is in line with the results of the calculations for the plantation in Sardinilla in 2008.

The range and mean of modeled daily ET are consistent with the measured values by Wolf et al. (2011a) of 0.6–6 mm day<sup>-1</sup> and 3 mm day<sup>-1</sup>, respectively. Hydrus-1D modeled mean root-water uptake at the plantation was 0.9 mm day<sup>-1</sup> which is only half of the values reported by Kunert et al. (2010) for the plantation in Sardinilla and a plantation in the Parque Metropolitan, Panama (2 mm day<sup>-1</sup>) as reported by Phillips et al. (1999). Because of the varying tree species, tree biomass and height, differences in AET sums were detectable among the plots for the wet season. Lowest and highest AET in monocultures were simulated for *C. odorata* and *L. seemannii* plots with 385 mm and 443 mm, respectively. A higher ET in trees of low canopy openness might result from structural characteristics of the canopy architecture, as suggested by Bauhus

et al. (2004), who found that the productivity gains in tree mixtures may be partially attributable to aboveground niche separation among species. With regard to root water uptake, competitive and complementary interactions might be the driver for intensified transpiration in mixed stands (Jose et al., 2006).

The modeled interception at the plantation ranged between 3% and 62% of rain water depending on the rain intensities with a mean amount of 10%. This range is supported by field surveys done by Schneebeil et al. (2011) in Sardinilla and Phillips et al. (1999) in the Parque Metropolitan, Panama.

### 3.1.3. Seepage

Calculation of seepage with the water balance equation (WBE) was limited to the 16 plots where soil pressure head and groundwater level were measured at the same time (151 days, from 9th of June 2008 to 3rd of November 2008). The lowest seepage rate was calculated for the *L. seemannii* plot with 5.18 mm day<sup>-1</sup> (Table 3) and the highest for the *H. crepitans* plot with 6.13 mm day<sup>-1</sup>.

The results from the Hydrus-1D simulations averaged over the entire plantation suggested that there was no seepage, but capillary rise, in the dry season of 2008, when the capillary rise decreased after the first precipitation events during the transition period, indicating downward movement of the soil water. After 1st days of more intensive rainfall at the beginning of May seepage started with a certain lag time, indicating a change in water storage within the profile (Fig. 5). With progressively more rainfall in July, higher proportions of water percolated into the groundwater. Nevertheless, capillary rise is still detectable during periods of the wet seasons where little or no precipitation occurred (see Fig. 5). In general, seepage was highest after several consecutive days of high precipitation as recorded end of November. Seepage rates simulated with Hydrus for the wet season were averaged for the duplicate monoculture plots and for the diversity levels. The highest and lowest seepage rates were found under *C. odorata* with 6.00 mm day<sup>-1</sup> and *L. seemannii* with 5.25 mm day<sup>-1</sup> (Table 3). In general, minor differences in mean seepage rates were detectable among the monocultures, three- and the six-species mixtures with 5.61, 5.57 and 5.58 mm day<sup>-1</sup>, respectively.

Modeled soil pressure heads at -30 cm as depicted in Fig. 6 did not match well with the measured pressure heads. In general, modeled pressure heads showed less dynamics compared to measured ones, nevertheless, the measured and modeled pressure heads correlate significantly ( $r = 0.496$ ,  $p < 0.001$ ). Especially, during the drier period in October and November a larger mismatch was detectable, whereby the Hydrus simulations indicate wetter conditions compared to the measurements. The RMSE between measured and simulated pressure heads ranged between 16 and 116 cm. The reasons for this mismatch are manifold. On the one

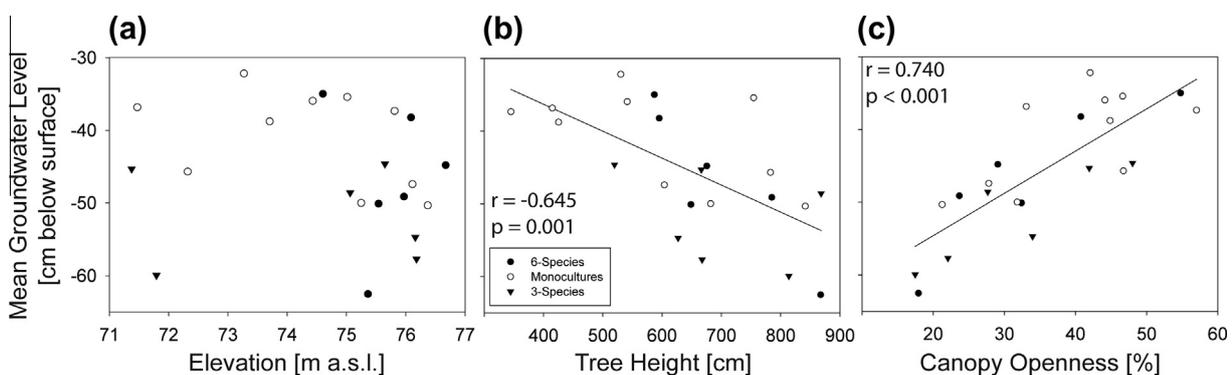


Fig. 4. Mean groundwater level of the plots as a function of (a) mean elevation of the corresponding plot, (b) surveyed mean tree height, and (c) surveyed canopy openness at corresponding plot. Black circles indicate six-species mixtures, black triangles three-species mixtures and white circles monocultures.

**Table 3**

Species and diversity specific data of potential evapotranspiration (PET) (mm), actual daily evapotranspiration rate (mm day<sup>-1</sup>), actual daily evaporation rate (mm day<sup>-1</sup>), actual root water uptake (mm day<sup>-1</sup>), and actual interception rate (mm day<sup>-1</sup>) (all three simulated with Hydrus-1D), as well as seepage rates (mm day<sup>-1</sup>) calculated with the water balance equation (WBE) and simulated with Hydrus-1D (Hydrus) for the wet season 2008. Abbreviations and descriptions of species and diversity like in Table 1.

Species/ diversity	PET (=AET) (mm)	Evapotranspiration (mm day <sup>-1</sup> )	Evaporation (mm day <sup>-1</sup> )	Root-water uptake (mm day <sup>-1</sup> )	Interception (mm day <sup>-1</sup> )	Seepage WBE (mm day <sup>-1</sup> )	Seepage Hydrus (mm day <sup>-1</sup> )
AE	408	2.70	1.16	0.81	0.73	-5.67	-5.71
CO	385	2.55	1.19	0.70	0.66	-5.98	-6.00
HC	398	2.63	1.34	0.69	0.60	-6.13	-5.70
LS	443	2.93	0.79	1.08	1.06	-5.18	-5.25
TR	437	2.89	0.86	1.04	0.99	-5.37	-5.40
Monocultures	414	2.74	1.07	0.86	0.81	-5.66	-5.61
Three-species	430	2.85	0.89	0.98	0.97	-5.63	-5.57
Six-species	427	2.83	0.91	0.97	0.95	-5.49	-5.58
Plantation	422	2.79	0.98	0.92	0.89	-5.60	-5.59

hand, they might be associated with the field measurements: (i) tensiometer readings are only point information reflecting the pressure head information only at one point within a non-homogeneous soil profile, (ii) local root water uptake might influence the lateral water distribution, and therefore, tensiometers might show different values, and (iii) the Hydrus simulations treat the soil profile as uniform, and therefore, lateral heterogeneity and preferential flow are not reflected by the model. On the other hand, the Hydrus model was incapable of simulating dry conditions because of the lower boundary that was defined by groundwater level measurements, which were limited to a soil depth of -65 cm. Therefore, in dry piezometers a GWL of 65 cm below the surface had to be assumed. This resulted in an overestimation of the GWL if one of the four piezometers in each plot was dry. This is the main reason for the overestimation of the pressure heads mainly during drier periods when low pressure heads were observed (Fig. 6). Nevertheless, the overall range of the measured data is captured by the model.

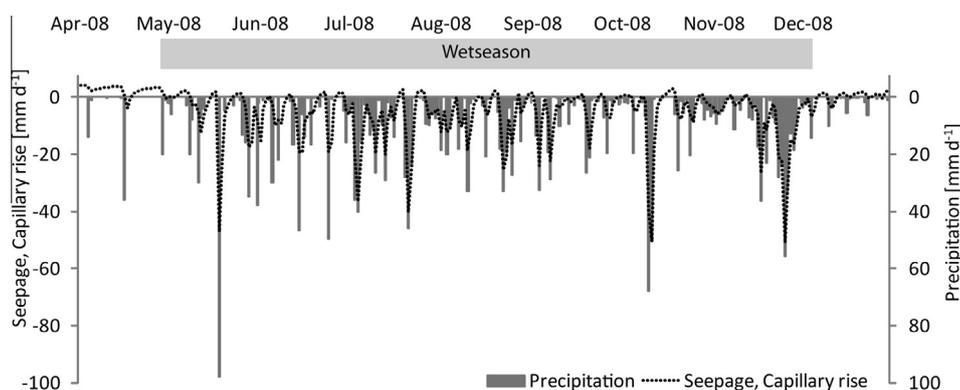
A major drawback of the water balance calculation is the low temporal resolution, which is given in this study by the manual weekly pressure head measurements. In contrast, the Hydrus model approach allows simulating flow processes in higher resolution as shown in Fig. 5. Comparing simulated weekly seepage sums obtained from both models shows that they provide similar results (Fig. 7) and neither of the models generally over- or underestimate seepage. Hence, the seepage simulations of both models seem to be of equal quality. Because of the poor representation of the observed pressure heads in the Hydrus simulation under the present conditions of data availability, only seepage rates resulting from the WBE approach will be further discussed.

### 3.2. Tree species identity and diversity effects on seepage

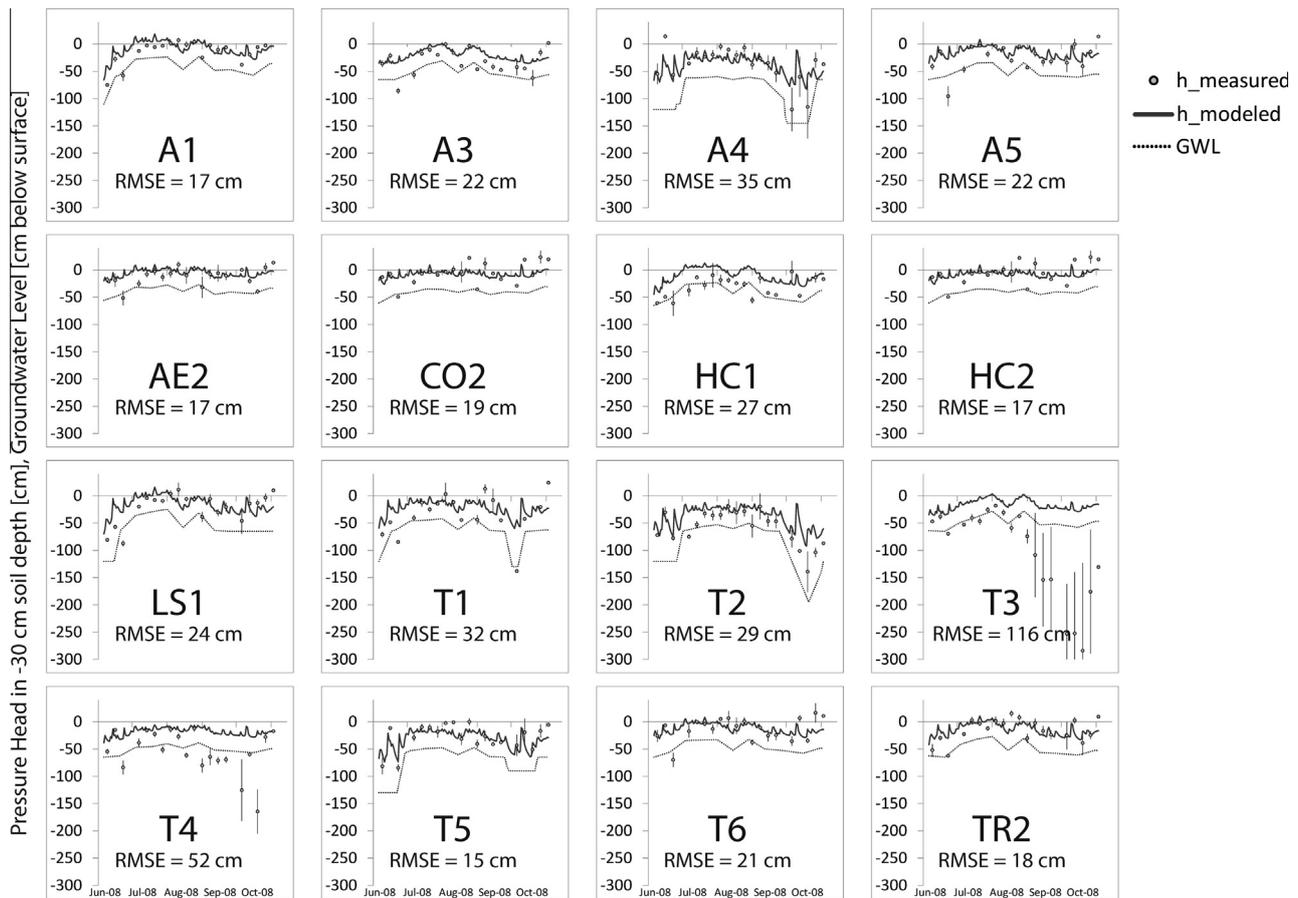
Seepage rates calculated with the WBE approach were driven by differences in biomass among the plots ( $r = 0.61$ ,  $p = 0.017$ ) representing the transpiration of the trees. While under monoculture plots of high stand biomass lower seepage rates occurred than under monocultures of low biomass, the differences among the three- and six-species mixtures in seepage rates and biomass are minor (Fig. 8). One exception is the three-species plot T3, where pressure heads dropped sharply in October leading to very high seepage losses based on the WBE approach.

All other tree mixtures showed an intermediate seepage flux compared to the higher flux rates under *H. crepitans* and *C. odorata* and lower flux rates under *L. seemanii* and *A. excelsum*. Seepage rates under *T. rosea* were similar to those under the mixed plots. It has to be mentioned that the sample size of the experimental repetitions in WBE approach ( $n = 1$  per tree species for the monocultures) was too low for analysis of variance and a significance test on the species level. On the diversity level, an ANOVA was performed but no significant influence of tree diversity on seepage was found. While in an ANOVA species-specific differences might counterbalance each other, overyielding calculation accounts for species-specific responses by comparing mixture to monoculture performance. Our overyielding analyses showed that the seepage rates below six-species mixtures were significantly lower than below the average monoculture plot.

The lower seepage rates in mixed trees stands agree with high transpiration rates, which were found with sap flow measurements of individual trees by Kunert et al. (2012). Also the rank orders of



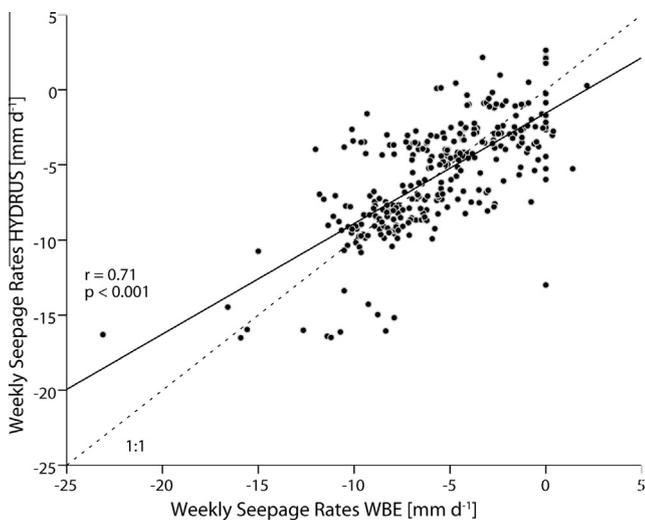
**Fig. 5.** Mean daily seepage rate (negative values) and capillary rise (positive values) of all plots (dotted line) and daily precipitation (gray columns) from April to December 2008.



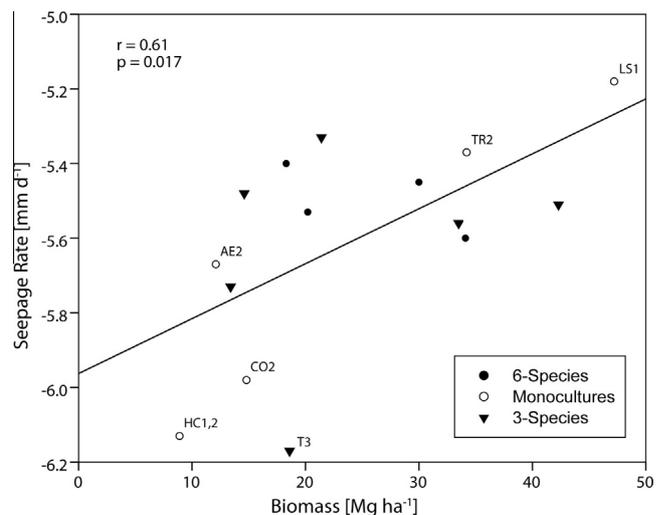
**Fig. 6.** Modeled (solid line) and measured (points) pressure heads (cm) in  $-30$  cm soil depth during the simulation period in 2008 as well as groundwater level (cm below the surface) (dotted line). A1, 3, 4, 5: six-species plots, T, 1, 2, 3, 4, 5, 6: three-species plots, AE2: *Anacardium excelsum*; CO2: *Cedrela odorata*; HC1, 2: *Hura crepitans*; LS1: *Luehea seemannii*; TR2: *Tabebuia rosea*.

the calculated seepage rates under monoculture plots are in line with rank orders of the measured transpiration rates by Kunert et al. (2012). Although our results indicate a significant increase in water use of the mixed tree plantation like it was also suggested by Kunert et al. (2012) who used another method, we only find a small increase in the actual evapotranspiration rate of the mixed

tree stands compared with monocultures (i.e. 3% of incident precipitation) which has a small effect on the overall water budget of the forest stands.



**Fig. 7.** Comparison of the weekly seepage rates ( $\text{mm day}^{-1}$ ) modeled with WBE and Hydrus-1D; the dotted line indicates the 1:1 line.



**Fig. 8.** Regression between seepage rates calculated with the WBE approach ( $\text{mm day}^{-1}$ ) and the stand biomass ( $\text{Mg ha}^{-1}$ ). Black circles indicate six-species mixtures, black triangles three-species mixtures and white circles monocultures. Results for the monoculture plots are labeled as follows: AE: *Anacardium excelsum*; CO: *Cedrela odorata*; HC: *Hura crepitans*; LS: *Luehea seemannii*; and TR: *Tabebuia rosea*.

The results showed that between 63% and 74% of the precipitation leaked into the subsoil deeper than –200 cm during the simulation period. Bigelow et al. (2004) found with 55–77% of annual precipitation a very similar proportion of seepage at a tropical plantation in Costa Rica and they agree with the present study, that most of the drainage occurred during the wet season, while almost no drainage occurred in the dry season.

Parallel to the seepage losses, eddy covariance measurements showed that 54% of annual rainfall was lost due to evapotranspiration over the year at the plantation in Sardinilla (Wolf et al., 2011a). Hence, the groundwater storage got filled during the wet season and depleted by capillary rise and root water uptake during the dry season. This idea is supported by other studies reporting field measurements. Meinzer et al. (1999) found with analysis of the stable hydrogen isotope composition ( $\delta D$ ) of xylem and soil water on Barro Colorado Island that *L. seemannii* took up water mainly from a depth of greater than –100 cm in the dry season. According to results from Sardinilla, *H. crepitans* and *C. odorata* primarily obtained water from the upper 30 cm, whereas *T. rosea*, *A. excelsum*, and *L. seemannii* took up most of its water from soil depths below 30 cm (L. Schwendenmann and R. Sánchez-Bragado, cited in Kunert et al., 2012). It is remarkable that at the plots of the tree species that relied on water from deep soil horizons (*T. rosea* and *L. seemannii*), the GWLs and seepage rates were lowest. Furthermore, it is noteworthy that highest calculated seepage occurred at the plots where trees obtain water from the upper soil horizons (*H. crepitans* and *C. odorata*).

#### 4. Conclusion

The presented study showed that the water balance equation (WBE) was superior to the mechanistic water transport model Hydrus-1D for the available data at the Sardinilla site. While the Hydrus model could not reconcile observations of the soils pressure heads, the WBE approach succeeded in reproducing the relative differences in observed transpiration rates of the tree species and the diversity levels. The seepage below six-species mixtures was lower than under the average monoculture based on overyielding analyses. Our findings suggest that planting mixtures of pioneers and shade tolerant tree species leads to moderate seepage rates, since tree heights and canopy openness are leveled out compared to monocultures of either fast or slow growing tree species. Therefore, afforestations of mixtures can even out the tradeoff between the need of the water supply of the Panama Canal on the one hand and the prevention of increased leaching of nutrients on the other hand. To better understand and simulate the processes of flow and transport in the different hydrological compartments at the plot scale, field surveys including extended investigation of the soil profile, depths, and distribution of the roots, the isotopic composition of the rain water, groundwater, soil water, and in the xylem in combination with high temporal and spatial observations of pressure head across the soil profiles, groundwater levels, and sap flow seem to be promising. Such information could be used to improve our knowledge about the interactions among percolation, evaporation, and root water uptake influencing the seepage rates of different tree species and tree diversity.

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#### Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version, at <http://dx.doi.org/10.1016/j.foreco.2013.03.022>.

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