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On the interrelations between topography, soil depth, soil moisture, transpiration rates and species distribution at the hillslope scale

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Abstract

Relations between the spatial patterns of soil moisture, soil depth, and transpiration and their influence on the hillslope water balance are not well understood. When determining a water balance for a hillslope, small scale variations in soil depth are often ignored. In this study we found that these variations in soil depth can lead to distinct patterns in transpiration rates across a hillslope. We measured soil moisture content at 0.05 and 0.10 m depth intervals between the soil surface and the soil–bedrock boundary on 64 locations across the trenched hillslope in the Panola Mountain Research Watershed, Georgia, USA. We related these soil moisture data to transpiration rates measured in 14 trees across the hillslope using 28 constant heat sapflow sensors. Results showed a lack of spatial structure in soil moisture across the hillslope and with depth when the hillslope was in either the wet or the dry state. However, during the short transition period between the wet and dry state, soil moisture did become spatially organized with depth and across the hillslope. Variations in soil depth and thus total soil water stored in the soil profile at the end of the wet season caused differences in soil moisture content and transpiration rates between upslope and midslope sections at the end of the summer. In the upslope section, which has shallower soils, transpiration became limited by soil moisture while in the midslope section with deeper soils, transpiration was not limited by soil moisture. These spatial differences in soil depth, total water available at the end of the wet season and soil moisture content during the summer appear responsible for the observed spatial differences in basal area and species distribution between the upslope and midslope sections of the hillslope.

Keywords: Soil moisture; Transpiration; Soil depth; Bedrock topography; Oak-hickory forest; Panola mountain research watershed

1. Introduction

Soil moisture, plants and their coupling are at the heart of ecohydrology and the soil water balance. On the one hand, climate and soil moisture control vegetation dynamics; on the other hand vegetation exerts important controls on the entire water balance and is responsible for many feedbacks to the atmosphere [28]. The spatial structure of soil moisture and its evolution in time is both cause and consequence of vegetation [32]. Despite recent calls for focused ecohydrological study [32,19,24], few investigations have examined systemically the interactions between physical, topographical and ecological form.

The hillslope scale is the basic building block for landscapes and the basic building block for catchment models [35]. Hillslope hydrologists have focused most of their process attention to date on rainfall events

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and the conversion from vertical to lateral water transfers under event driven conditions [3]. The studies that have examined the relations between topography and soil moisture have often been completed at the small catchment scale (e.g. [25,40]) or on transects (e.g. [8,23,44]). These studies have shown associations between shallow soil moisture and topography during wet periods, i.e. when potential evaporation is smaller than precipitation (e.g. [40]). Notwithstanding, these associations are weak or absent during dry periods, when potential evaporation is larger than precipitation. Whilst plant transpiration has been hinted at as a cause for the reduced importance of subsurface water redistribution and the elimination of topographic control on soil moisture patterns [40], this has not been examined in detail. To date, studies that have examined relations between soil moisture and topography have been restricted to the examination of shallow soil moisture within the upper 0.3 m or less of the soil profile (e.g. [1,23,25,40]). Tree water use is well beyond this exclusive shallow zone but studies have not examined how well these shallow soil moisture patterns represent soil moisture in the entire soil profile.

The influence of transpiration on soil moisture depletion and the influence of soil moisture on transpiration rates are both well known [2]. While modeling studies have examined the relations between climate, vegetation, and species (e.g. [20,21,31,33]), only few field studies have examined systematically how spatial patterns of soil moisture influence transpiration patterns (and vice versa) at the hillslope or plot scale. A notable exception is the work of Hupet and Vanclooster [15]. They showed that spatially variable vegetation growth within a flat 6300 m^2 corn field induced variable evapotranspiration rates and consequently variable root water uptake rates. This resulted in spatially variable shallow soil moisture. Schume et al. [34] showed that during a long drying cycle in spring, species-specific transpiration and rooting depth were the main source of variation in volumetric soil moisture content in a mixed Norway spruce (*Picea abies*) and European Beech (*Fagus sylvatica*) stand. While these studies have shown the influence of vegetation on soil moisture patterns, they have not shown how the spatial patterns in soil moisture, caused by the vegetation, in turn influenced transpiration or vegetation growth. Thus despite these recent field studies, the feedbacks between spatial and temporal soil moisture patterns and transpiration patterns at the hillslope or plot scale remain poorly understood.

This study examines the interrelations between topography, soil depth, soil moisture, transpiration rates and species distribution at a well instrumented 20 by 48 m study hillslope. We measured soil moisture in a 3-dimensional array from the soil surface to the soil–bedrock interface for a nine month period to address the following questions:

- How does soil moisture vary spatially and temporally at the hillslope scale?
- How does soil moisture vary with depth?
- How do vegetation and transpiration patterns affect soil moisture patterns in time and space at the hillslope scale?
- How do soil moisture patterns affect transpiration patterns in time and space at the hillslope scale?

We focus here on the hillslope scale because of the uniformity of atmospheric forcing factors and the uniform soil type. Because of the relatively small area, planar topography and uniform azimuth of the study hillslope we do not expect differences in incoming solar radiation, relative humidity, temperature, wind speed or other climatic variables across the hillslope. This allows us to reduce competing processes and to isolate the feedbacks between soil depth, soil moisture and transpiration patterns at this scale. We argue that if one were to look for these interactions at the catchment scale, the differences in climatic variables, soil type, soil depth, biogeochemistry and average soil moisture content between the hillslopes (without permanent groundwater) and the riparian zone (with permanent groundwater) could overwhelm the variations we might see at the hillslope scale and thus mask important patterns and relations at the hillslope scale.

2. Site description

The Panola Mountain Research Watershed (PMRW) is located within the Panola Mountain State Conservation Park in the southern Piedmont province southeast of Atlanta, Georgia (84°10′W, 33°37′N). The elevation of PMRW ranges from 222 to 279 m above sea level. Currently the watershed is 93% forested, consisting of hickory (*Carya* sp.), oak (*Quercus* sp.), tulip poplar (*Liriodendron tulipifera*), and loblolly pine (*Pinus taeda*) [6]. The remaining 7% of the watershed is comprised of bedrock outcrops with small vegetation islands, including a 3 ha outcrop in the southwestern corner of the watershed. The forest consists of predominantly even-aged deciduous or mixed deciduous and conifer stands and a smaller portion of predominantly coniferous stands. The forest composition and age structure at PMRW reflect historic land use and periods of agricultural abandonment typical for the Piedmont region in Georgia [17]. Historical records of regional land use and tree ring analysis at PMRW suggest that most of the timber was cut originally in ca. 1820 and that the land was farmed (cotton cultivation and pasture) until the early 1900s and has remained relatively undisturbed since [17]. Hickory (*Carya* sp.) is the dominant species on the study hillslope (54% of the total basal area of 24.8 m^2/ha). Oak (*Quercus* sp.) is the next dominant species on the study hillslope (25% of total basal area). Even though there are only two loblolly pine (*P. taeda*) trees on the study hillslope, they are the species with the third largest basal area on the study hillslope (13.5%). Mixed species stands dominated by oak (*Quercus* spp.) and hickory (*Carya* sp.) overstories are common throughout the southeastern US in areas that have been permitted to reach late successional stages of development.

The climate at PMRW is classified as humid, subtropical. The mean annual temperature is 16.3 °C and mean annual precipitation is 1240 mm. Rainfall tends to be of longer duration and lower intensity associated with the passage of fronts in the winter, and of shorter duration but higher intensity in the summer associated with thunderstorms. Streamflow at PMRW has a strong seasonal pattern, with the highest flow occurring in the November through March dormant season. Annual stream yield from the 41-ha catchment varies from 18% to 50% of precipitation (1989–2001). Subsurface stormflow measured at the study hillslope is short lived, less than a few days after then end of a storm, and also highly seasonal with average runoff ratios of 6, 10, 1 and less than 1% for the fall, winter, spring and summer respectively for the 1996–1998 period [37]. The dryness index (annual potential evaporation/annual precipitation) of the study site is 1.3, where potential evaporation is calculated using the Hargreaves equation [14]. The 2002 study period was drier than average (Fig. 1) mainly as a result of smaller storms (defined here as an event larger than 1 mm of precipitation separated by 24 h of no precipitation) (an average and median storm size of 16 mm and 11 mm respectively for the water year 2002 compared to an average and median storm size of 22 and 14 mm for the 1989–2001 period). For the water year 2002 there was on average one storm every 6.3 days while the 1989–2001 average was one storm every 6.1 days.

The study hillslope is located on a southeast facing slope and has a slope of 13°. The lower boundary of the study hillslope is located 30 m upslope from an ephemeral stream and is formed by a 20 m wide trench to bedrock. The upper boundary of the study hillslope is formed by a small bedrock outcrop. The surface topography of the study hillslope is relatively planar but has a small depression near the middle of the hillslope. The bedrock topography is highly irregular and is characterized by a dendritic shaped hollow (Fig. 2).

The 10-ha western upper catchment at Panola (within which the study hillslope is located) is underlain by the

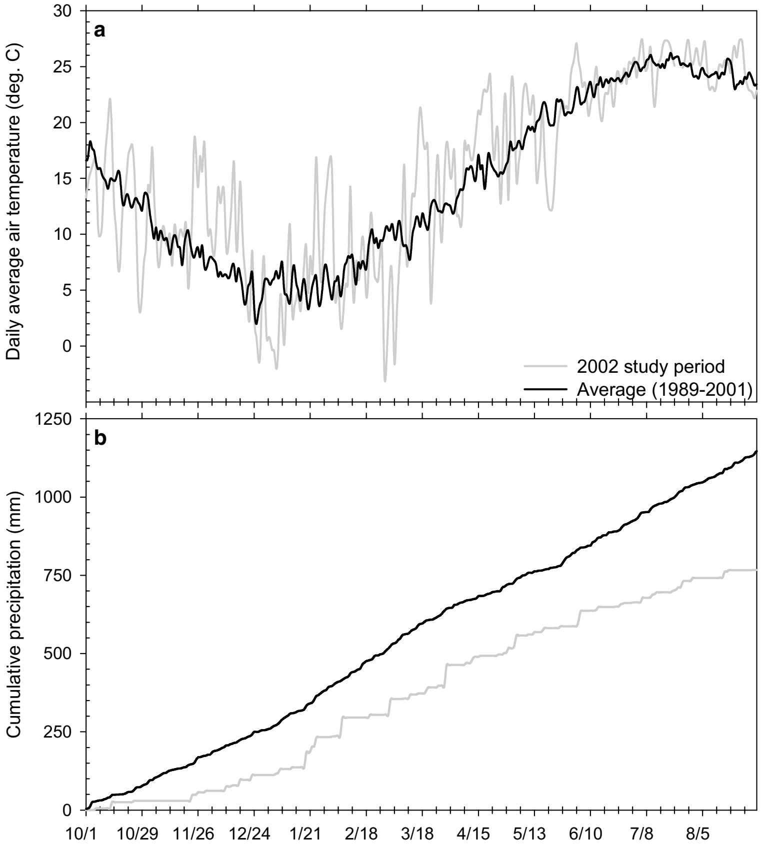

Fig. 1. Comparison of daily average temperature (a) and cumulative precipitation during the 2002 study period with the 12-year average (1989–2001) (b).

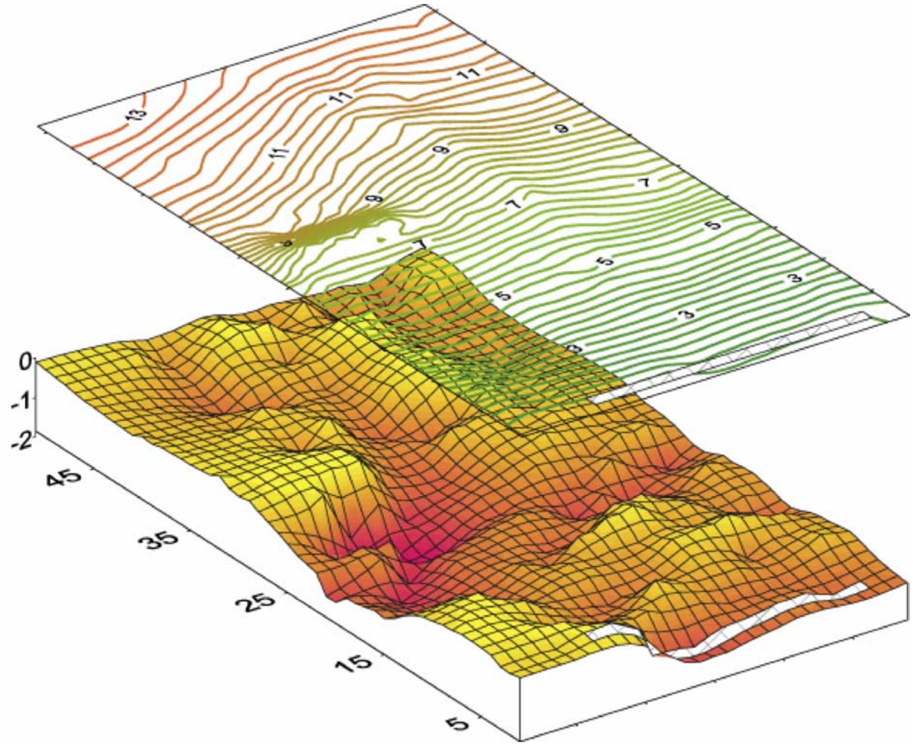

Fig. 2. The surface and bedrock topography and the dimensions of the study hillslope (in meters). The clear bar at the bottom of the hillslope represents the location of the trench.

Panola Granite, which is a biotite-oligoclase-quartz-microcline granodiorite [7]. The soil on the study hillslope is a light colored sandy loam without clear structuring or layering, except for a 0.15 m deep organic soil horizon. During augering for the installation of the soil moisture access tubes and wells no differences in soil type or soil texture were observed across the study hillslope. The average soil depth across the study hillslope is 0.63 m and ranges from 0 to 1.86 m. In general soils on the upslope part of the study hillslope were shallower than the soils on the midslope and lower slope.

3. Methods

3.1. Soil moisture measurements

Soil moisture was measured at 64 locations on 85 occasions between January 26 and August 26, 2002. Soil moisture was measured using the Aqua-pro sensor (Aqua-pro Sensors, Reno, NV) in polycarbonate access tubes that were installed to the soil–bedrock interface. The access tubes were located on a 4 by 4 m grid across the hillslope and on a 4 by 2 m grid on the lower 6 m of the hillslope. The Aqua-pro sensor is a capacitance (radio-frequency) sensor that measures soil moisture on a percent scale between 0 (in air or air dried soil) and 100 (in water or saturated soil). The relation between the Aqua-pro soil moisture values and gravimetrically determined volumetric soil moisture content is linear with a slope of approximately 1/(2.4) and an intercept that depends on soil type [J. Selker, Oregon State University, Personal Communication]:

$$\theta_{\mathrm{vol}} = \frac{A}{2.4} + b \qquad (1)$$

where θ_{vol} is the gravimetrically determined volumetric soil moisture content (%), A is the Aqua-pro measurement value (Aqua-pro %) and b is a constant that depends on the soil type. Unless explicitly mentioned in the text, all values reported in this paper are in Aqua-pro values (thus ranging between 0 and 100%). Repeated measurements were always within 2% (and usually within 1%) of each other.

Soil moisture was measured at 0.05 m increments to 0.3 m below the soil surface and at 0.10 m increments between 0.3 m and the soil–bedrock interface. The profile average soil moisture at a measurement location was calculated by multiplying the soil moisture values at the different measurement depths by the distance between the subsequent measurement depths and dividing this by the total soil depth at that measurement location. Hillslope average soil moisture was calculated by averaging the profile average soil moisture values for all measurement locations.

To obtain a measure of the '*total depth of water*' in the soil profile we multiplied the Aqua-pro soil moisture values at the different depths by the distance between the subsequent measurement depths and the 1/(2.4) factor from Eq. (1). Because we do not know the intercept of the relation between volumetric soil moisture and the Aqua-pro measurement value and thus omit the intercept (*b* in Eq. 1) in the calculation of the total depth of water in the soil profile, the calculated total depth of water is only a relative value.

Artificial water applications, which were a part of a related study on the role of flow through the bedrock, influenced soil moisture measurements at the lower 14-m of the hillslope during June 18–August 26, 2002. For these dates, soil moisture measurements on the lower 15 m of the hillslope that were influenced by the artificial water applications were excluded from the analyses. We observed no changes in soil moisture due to the artificial water applications at locations 16 m and further upslope from the trench.

3.2. Sapflow measurements

Transpiration was estimated from constant heat sapflow measurements using the thermal dissipation technique developed by Granier [12,13], generally following the procedures described by Phillips et al. [29]. Sapflow was measured at 15-min intervals in 14 trees using 28 constant heat sapflow sensors. All trees had two sensors inserted 0–20 mm in the sapwood on the east and west side of the tree trunk. Sapflow was averaged to hourly intervals using the average of the two sapflow sensors in each tree. Sapflow sensors were installed in Hickory trees (*Carya* sp.) in one of two diameter-at-breast-height (DBH) classes: 0.11–0.125 m (5 trees) and 0.175–0.215 m (9 trees). Hickory trees (*Carya* sp.) of these size classes were the dominant trees on the study hillslope. Eight of the trees with sapflow sensors were located on an upslope transect across the middle of the study hillslope while the other trees with sapflow sensors were distributed across the hillslope.

The DBH of all trees on or within approximately 5 m of the study hillslope was measured. We used the relations between DBH and sapwood area from Pataki and Oren [27, Table 2, p. 1273], at the Duke Forest in North Carolina to estimate our hillslope sapwood area. We used the relation between DBH and sapwood area for the hickory trees also for the species not listed by Pataki and Oren [27]. The estimated hillslope sapwood area was multiplied by the average sapflow flux from the 14 monitored trees, to obtain the estimated hillslope average transpiration rate. The Duke Forest is comparable to the forest in PMRW, not only in species composition but also in basal area and climate. The basal area in the Duke forest is 23.0 m^2/ha [26], while the average basal area of the Panola study hillslope is 24.8 m^2/ha. The climate in the Duke forest is slightly drier and colder than PMRW (15.5 °C and 1140 mm for the Duke Forest [26] vs. 16.5 °C and 1240 mm for PMRW). We acknowledge that even though the forests are similar, using the sapwood area-DBH relationship from the Duke forest rather than a relationship between sapwood area and DBH from PMRW (which is not available) will inhibit us from being able to calculate an absolute transpiration value with confidence. However, it does allow us to look at temporal and spatial patterns in transpiration and to estimate the hillslope average transpiration rate.

3.3. Air temperature, relative humidity and precipitation measurements

Air temperature and relative humidity were measured at 3 m above the ground surface on a tripod in a clearing approximately 200 m from the study hillslope using a Campbell Scientific Model CS500 probe (Campbell Scientific, Logan, Utah). Radiation was measured in the same clearing using an Eppley Model PSP pyranometer (Eppley Laboratory, Newport, Rhode Island). Precipitation was recorded each minute at three locations using tipping bucket rain gauges, continuously using a weighing bucket gauge in the clearing, and each week using several Tenite gauges. The tipping bucket rainfall data series were combined to yield one rainfall time series for the watershed. Throughfall was estimated from the rainfall measurements using a linear fit ($r^2 = 0.99$) to the measured throughfall and precipitation data from the deciduous forest site for 16 storms during the growing season at PMRW given by Cappellato et al. [5, Table 1, p. 135]:

$$T = 0.97P - 1.66 \qquad (2)$$

where T is the estimated total throughfall for the storm (in mm) and P is the measured total storm precipitation (mm).

3.4. Subsurface flow measurements

A 20-m long trench excavated down to bedrock normal to the fall line of the slope formed the lower boundary of the study hillslope. Total subsurface flow was measured by routing flow through tipping-bucket gages. The number of tips was recorded every minute. Additional details of the trench and the flow-collection system are described elsewhere [4,9,10,22].

3.5. Soil depth measurements

The hillslope was surveyed on a 2 m grid. Depth to bedrock was measured on the same survey grid network using a 25.4 mm soil corer forced down to refusal. A small hand auger was used when soil depth was greater than 1.25 m. The multidirectional flow algorithm of Quinn et al. [30] was used to calculate the drainage area for both the soil–bedrock interface and the soil surface. The topographic index ($\ln[a/\tan\beta]$, where a is the accumulated area and β is the local slope) [18] was calculated for both the surface topography and bedrock topography [9].

4. Results

4.1. Soil moisture patterns

The hillslope remained relatively wet throughout the winter and early spring period (until mid-April) and dried quickly after (Fig. 3b). There was less variation in profile average soil moisture across the hillslope during the winter than during the summer months (Fig. 3b). Soil moisture responses to precipitation were distinct. From February to early April the hillslope drained to the same moisture level (~field capacity, ~70%) while further soil moisture depletion occurred after mid-April, the beginning of leaf out. The spatial soil moisture patterns at different depths below the soil surface at approximately 2-week intervals throughout the study period are shown in Fig. 4. During the winter and spring the hillslope was in a wet state (i.e. hillslope average soil moisture >70%), and changed into a dry state (i.e. hillslope average soil moisture <45%) rather abruptly in May. While soil moisture at some locations on the hillslope was persistently lower or higher than the hillslope average, there was only very little spatial structure in soil moisture when the hillslope was in the wet state (Fig. 4). Only during the drying down period (i.e. hillslope average soil moisture 45–70%: May 30–June 4 and June 10–24), was there some spatial structure in the soil moisture pattern. During the drying down period, soil moisture at 0.05 m below the soil surface was higher in the left (when looking upslope) upper corner of the hillslope and soil moisture at 0.30 m was higher in the midslope compared to other locations on the hillslope (Fig. 5). This location has deeper soils compared to the hillslope average. The spatial drying down pattern was persistent in time. The soil moisture pattern on June 4 (before the 50 mm June 4–6 storm) was repeated after the storm (Fig. 5). The grid resolution of soil moisture measurements did not allow for an accurate determination of the correlation length scale. Nevertheless, these data suggest that the correlation lengths (here defined as the distance where the standardized variance is 0.95) of soil moisture were very small at every depth below the soil surface (varying between less than 4 m and 10 m for both the omni-directional variogram and the directional variogram, with the largest correlation lengths during the drying down and dry period).

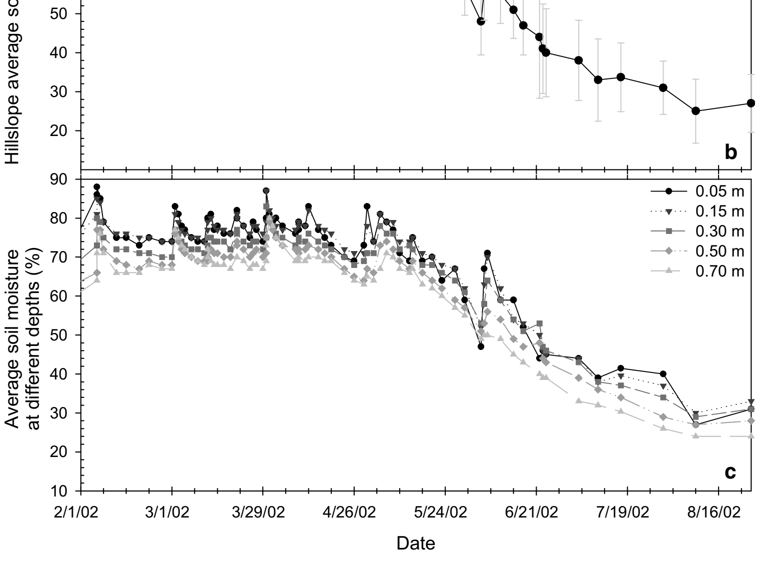

Fig. 3. Graphs of the daily precipitation (a), the hillslope average soil moisture during the study period and standard deviation of the profile average soil moisture on the hillslope (b), and the hillslope average soil moisture at different depths throughout the study period (c).

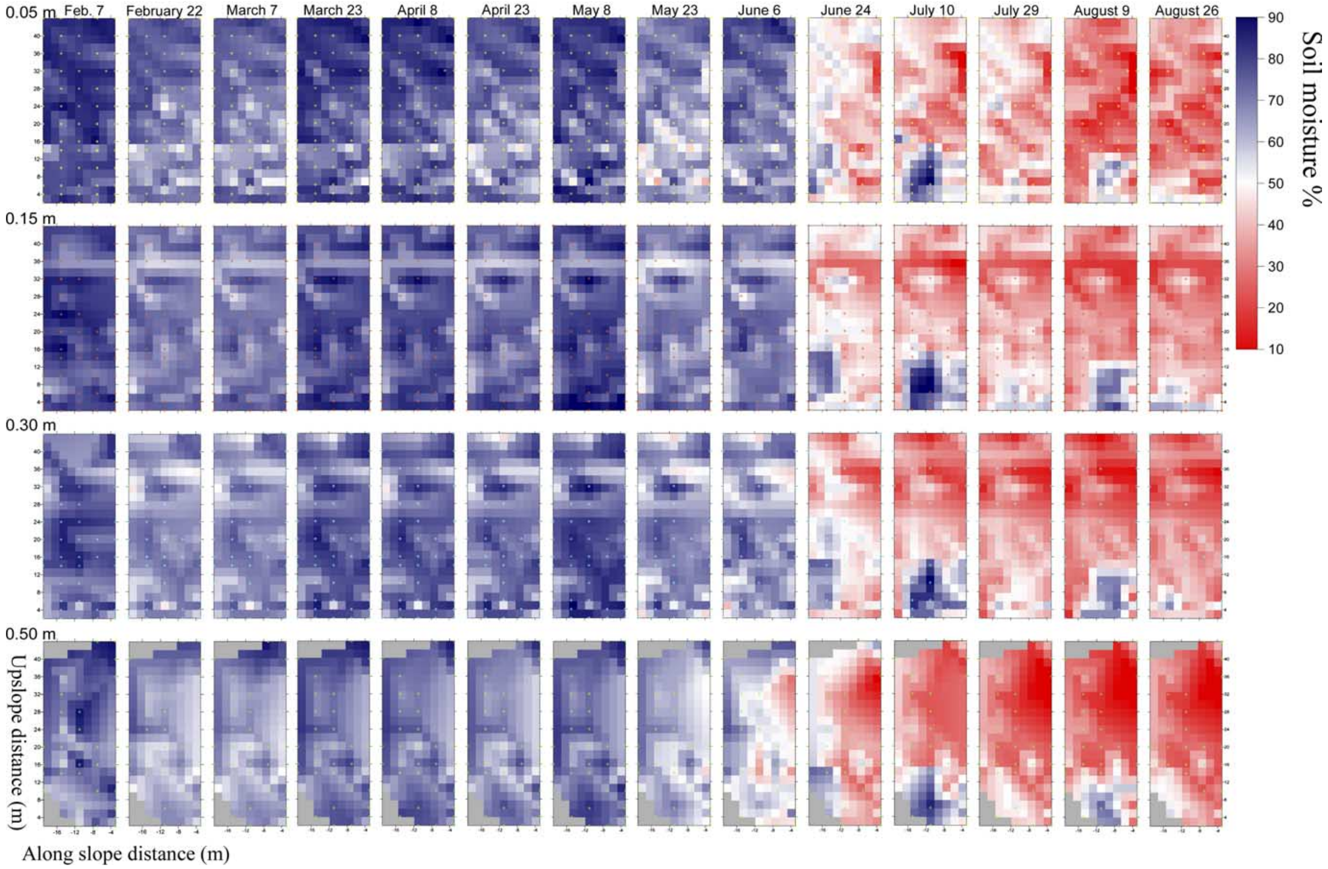

Fig. 4. Maps of soil moisture at different depths (0.05, 0.15, 0.20 and 0.50 m) below the soil surface on selected dates throughout the study periods. The diamonds represent the measurement locations. We used linear triangulation to interpolate between the measurement locations. The shaded grey area represents bedrock, where we could not interpolate the soil moisture measurements. Soil moisture at the lower 15 m of the hillslope during June 18–August 26 is influenced by sprinkling experiments and not included further analyses.

There was not only very little spatial structure in soil moisture across the hillslope but also little variation in the temporal pattern of soil moisture at different depths below the soil surface (Figs. 3c, 4 and 5). Soil moisture at the different depths was highly correlated to each other (Table 1). However, there was some stratification in soil moisture during and directly after storms during the drying down and dry period. Storms rewetted the upper soil layers but did not penetrate to the soil–bedrock interface, leading to stratification of soil moisture with depth during this period. The June 4–6, 2002 storm, for example, did not increase soil moisture at all locations at 0.30 m depth on June 5, 2002 10:00, while it had increased soil moisture at 0.20 m at all locations. By June 6, 2002 11:30, storm-induced increases in soil moisture were observed at 0.30 m below the soil surface at all measurement locations but soil moisture at 0.50 m depth remained unchanged at many locations.

Even though soil moisture was not stratified with depth below the soil surface for most of the study period, total water depletion between May 1, 2002 and August 26, 2002 (calculated as the sum of the negative soil moisture changes between consecutive measurement dates between May 1 and August 26, 2002) was almost twice as much from 0.05 m depth below the soil surface than from 0.5 m depth (Fig. 6) because of soil moisture replenishment during frequent storms that rewetted the shallow surface layers but not the deeper layers (Fig. 3c). For many measurement locations total soil moisture depletion during the May 1st and August 26th was also a bit higher near the soil–bedrock interface than at other deep soil layers (e.g. locations 7.16 and 11.24 in Fig. 6). The actual soil moisture depletion values are higher than the calculated values because of soil moisture depletion between the time of a (thunder)storm and the time of the actual soil moisture measurements. This affects the calculation for the upper soil layers especially because most storms during the growing season did not penetrate to more than 0.30 m below the soil surface.

4.2. Relation of soil moisture to topographic variables

Soil moisture was not well correlated to any of the computed topographic variables for the hillslope (Table 2). The exceptions were the relation between soil

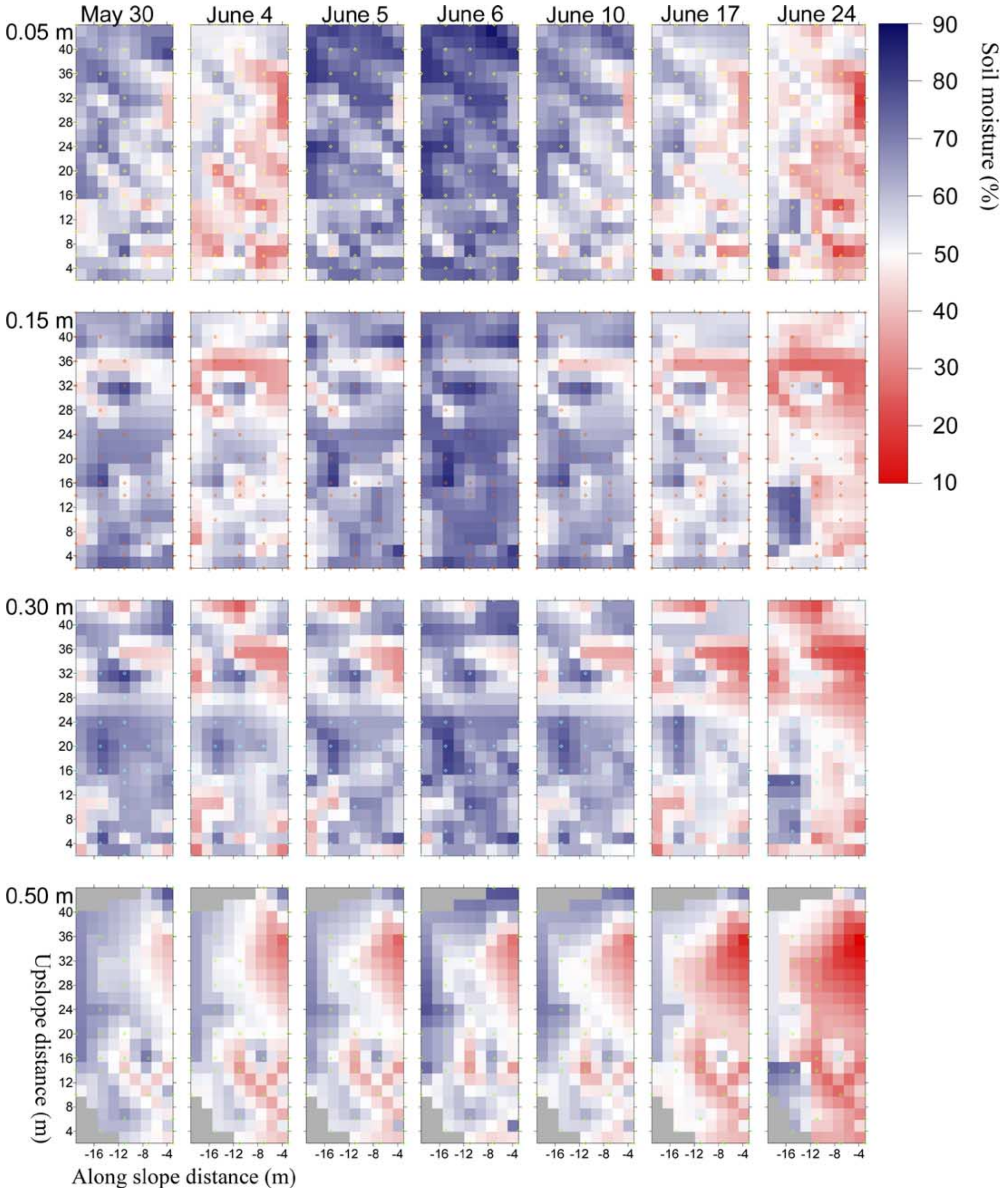

Fig. 5. Maps of soil moisture at different depths (0.05, 0.15, 0.20 and 0.50 m) below the soil surface on selected dates throughout the drying down period. The diamonds represent the measurement locations. We used linear triangulation to interpolate between the measurement locations. The shaded grey area represents bedrock, where we could not interpolate the soil moisture measurements. Soil moisture at the lower 15 m of the hillslope on June 24 is influenced by sprinkling experiments and not included in further analyses.

moisture at 0.30 m depth below the soil surface and soil depth and the relation between soil moisture at 0.30 m and upslope distance during the drying down and dry state. Not surprisingly, soil depth and distance upslope from the trench were correlated at the Panola hillslope. In general soils on the upslope part of the study hillslope were shallower than the soils on the midslope and lower slope. When the hillslope was in the wet state, soil moisture at 0.30 m below the soil surface was high and not correlated to soil depth (e.g. May 10 in Fig. 7c). During the drying down period (e.g. June 10 in Fig. 7c) soil moisture at 0.30 m below the soil surface decreased more rapidly at sites with relatively shallow soils, resulting in a relationship between soil depth and soil moisture at 0.30 m in the drying (e.g. June 10 in Fig. 7c) and dry state (e.g. July 10 and August 9 in Fig. 7c). This more rapid decrease in soil moisture at sites with relatively shallow soils was also observed (but was less clear) for soil moisture at greater depth (e.g. Fig. 7d).

Table 1
The r^2 of the relationships between the average soil moisture at different depths in the upper half of the matrix and the slope of the relationships between average soil moisture at different depths in the lower part of the matrix (in *italic*)

	0.05 m	0.15 m	0.30 m	0.50 m	0.70 m	Bedrock interface	Profile average
0.05 m	–	0.98	0.95	0.92	0.90	0.85	0.97
0.15 m	*1.03*	–	0.99	0.97	0.94	0.91	0.99
0.30 m	*1.11*	*1.08*	–	0.99	0.96	0.93	0.99
0.50 m	*1.07*	*1.05*	*0.97*	–	0.98	0.93	0.98
0.70 m	*0.98*	*0.96*	*0.88*	*0.91*	–	0.92	0.97
At bedrock interface	*0.77*	*0.76*	*0.70*	*0.72*	*0.77*	–	0.93
Profile average	*1.00*	*0.97*	*0.89*	*0.90*	*0.97*	*1.18*	–

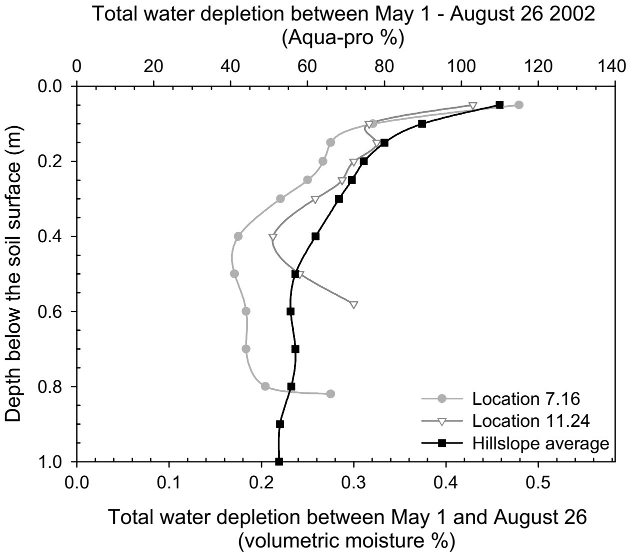

Fig. 6. Total water depletion between May 1 and August 26, 2002 as a function of depth below the soil surface. Total water depletion at a depth was calculated by adding all the negative changes between consecutive measurement dates during the May 1–August 26, 2002 period. Eq. (1) was used to convert the Aqua-pro values to volumetric moisture %.

4.3. Transpiration patterns

Average calculated transpiration was 2.6 mm/day for the May 1–August 24, 2002 period (Fig. 8). Daily solar radiation alone explained 55% of the observed variation in estimated hillslope average daily transpiration. Solar radiation, average relative humidity, average air temperature and soil moisture combined explained only 58% of the observed variation in estimated hillslope average daily transpiration rate.

Even though the value of the calculated hillslope average transpiration rate is uncertain (because we used the relationship between DBH and sapwood area from the Duke Forest in North Carolina rather than from PMRW), the difference between estimated throughfall (Eq. 2), measured subsurface stormflow and hillslope average transpiration matched the observed hillslope soil moisture changes well (Fig. 9b). We did not include understory or soil evaporation in the water balance calculations because of the sparse understory at the study hillslope and because understory evaporation is generally less than 10% of the total canopy fluxes during the growing season (e.g. [42]).

4.4. Influence of soil depth: comparison of upslope and midslope

The average soil depth of the midslope (14–25 m upslope from the trench) is 0.93 m while the average soil depth of the upslope (more than 25 m upslope from the trench face) is 0.51 m (Table 3). During the wet state the average soil moisture on the upslope was similar to the average soil moisture on the midslope (Fig. 10b). During the drying down and dry state the average soil moisture of the upslope was less than that of the midslope because of faster soil moisture decreases in the upslope section. The difference in the average soil depth of the two sections had a large effect on the calculated measure of total depth of water in the soil profile at the end of the wet state/dormant season (May 1, 2002) (Fig. 10c). During the drying down and dry state more water was removed from the midslope than from the upslope (Fig. 10d). Thus the shallower upslope contained less water than the midslope at the end of the dormant season due to differences in soil depth (Fig. 10c), dried down to a lower soil moisture level during the summer (Fig. 10b) but lost less total water during the growing season than the midslope (Fig. 10d). This is mainly due to the leveling off of soil moisture depletion on the upslope after early July while soil moisture depletion on the midslope continued throughout the summer (Fig. 10b and d). One could argue that soil moisture depletion in the midslope leveled off in late August as well. But this is highly influenced by the soil moisture measurements on August 26, 2002 and thus uncertain. There was 25 mm of precipitation in between the measurements on August 9 and 26, which could also be responsible for the apparent reduction in soil moisture depletion. Unfortunately we have no soil moisture measurements after August 26, 2002 to check if soil moisture depletion in the midslope continued with increasing drought conditions.

Table 2
The period average of the Pearson correlation coefficients for the relation between soil moisture at specific depths and topographic variables

Pearson correlation coefficients	Upslope distance	Topographic index—surface	Topographic index—bedrock	Soil depth	Weighted basal area
Wet state (February–April)					
0.05 m	0.30	−0.26	0.01	−0.06	−0.12
0.15 m	−0.22	0.13	0.03	0.14	−0.13
0.30 m	−0.05	0.04	0.09	0.37	0.09
0.50 m	0.25	0.03	−0.04	0.00	−0.13
0.70 m	0.11	0.14	0.03	−0.07	0.31
Profile average	0.06	−0.15	−0.14	−0.08	0.02
Transition period (May–June)					
0.05 m	0.24	−0.19	−0.05	0.02	−0.06
0.15 m	−0.23	0.13	0.00	0.19	−0.14
0.30 m	−0.10	0.08	0.05	0.42	0.04
0.50 m	0.17	0.01	−0.01	0.25	−0.11
0.70 m	0.04	0.07	−0.05	0.09	0.26
Profile average	−0.06	−0.09	−0.13	0.11	0.00
Dry state (July–August)					
0.05 m	0.13	−0.20	−0.01	0.18	0.21
0.15 m	−0.28	0.16	0.06	0.30	0.13
0.30 m	−0.52	0.26	0.13	0.50	0.20
0.50 m	−0.35	0.26	0.12	0.43	0.19
0.70 m	−0.40	0.13	0.05	0.22	0.47
Profile average	−0.37	−0.08	−0.02	0.28	0.29

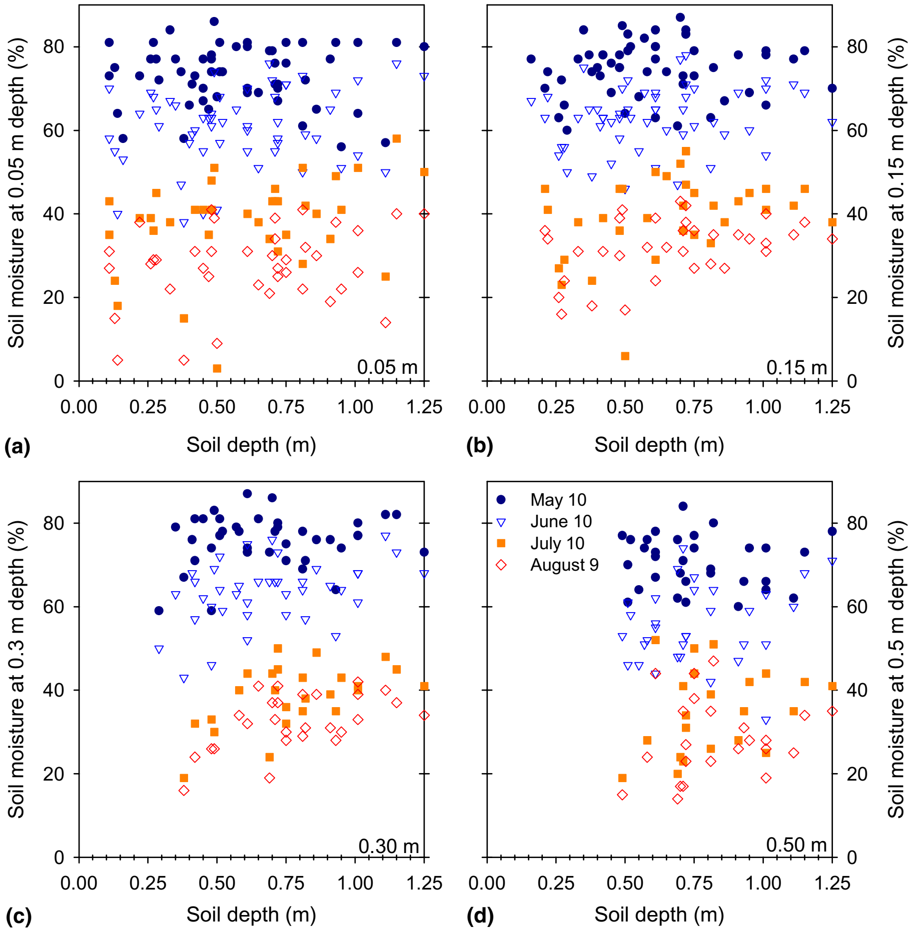

Fig. 7. Relationship between soil depth and soil moisture at different depths.

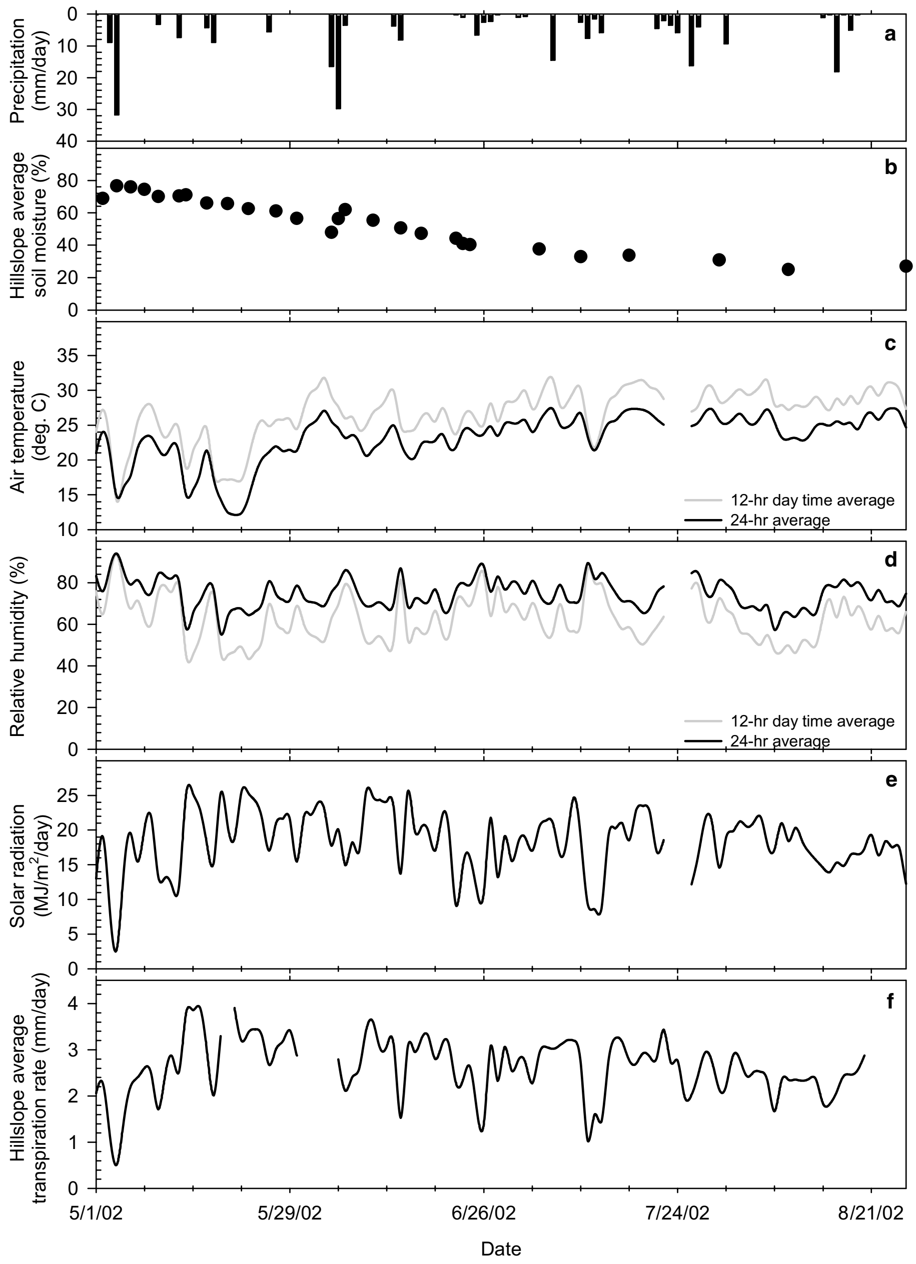

Fig. 8. Time series of precipitation (a), hillslope average soil moisture (b), the 12-h (6:00–18:00) and 24-h average air temperature (c), the 12-h and 24-h average relative humidity (d), daily solar radiation (e) and hillslope average transpiration estimated from the sapflow measurements (f).

During the early summer (until July) we observed no differences in sapflow across the hillslope. During the late summer however, maximum daily sapflow in trees on the upslope was reduced with time after the last rainfall event while maximum daily sapflow in trees on the midslope did not decrease (Fig. 11). Trees on the upslope showed a large increase in sapflow after a rainstorm while trees on the midslope and lower slope did not show such a large increase in sapflow after the storm (Fig. 11). Profile average soil moisture measured on August 9, explained 57% of the observed variation in daily sapflow per unit sapwood area on August 15 (before the storm) and only 1% on August 18 (after the storm) respectively. Thus, before the storm, when differences in average and shallow soil moisture were large, sapflow was related to soil moisture. After the storm, when soil moisture in the upper soils was replenished across the whole study hillslope, sapflow was no longer related to soil moisture before the storm. Soil moisture measurements were not made directly after the storm, thus we cannot determine if sapflow after the storm was related to the shallow soil moisture pattern directly after the storm.

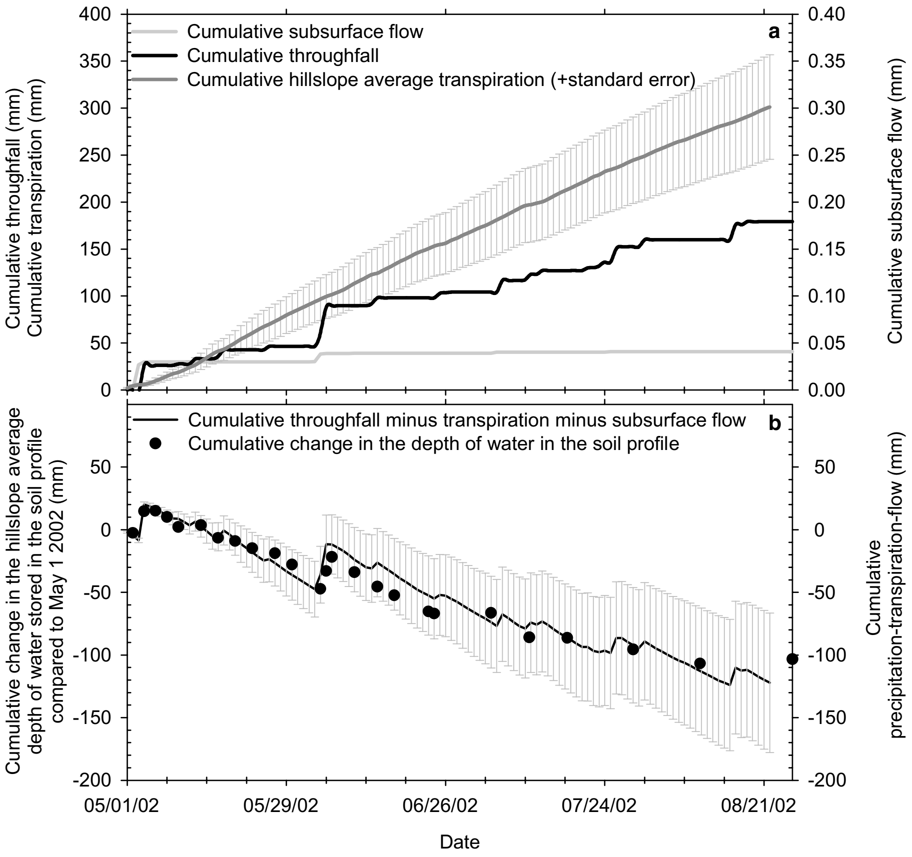

Fig. 9. Time series of cumulative throughfall, subsurface flow and hillslope average transpiration (estimated from the sapflow measurements) throughout the growing season. The error bars represent the cumulative standard error of hillslope average transpiration. Data from the lower part of the study hillslope that were affected by the artificial water applications were excluded from the analyses.

Table 3
Comparison of the lower slope, midslope and upslope

	Lower slope	Midslope	Upslope
Upslope distance (m from trench)	0–14	14–25	25–48
Average soil depth (m)	0.67	0.93	0.51
Median DBH (mm)	59	61	54
Average DBH (mm)	88	101	78
Average basal area (m^2/ha)	25.4	31.7	21.3
Contribution to hillslope total sapwood area (%)	33	27	40
Contribution to basal area by oak, hickory and loblolly pine (%)	96	95	85
Change in total water storage between May 1 and August 26 (mm)		123	87

Because of artificial water applications on the lower slope, the change in total water storage was not calculated for the lower slope.

The soil depth and upslope effect on soil moisture and sapflow could be responsible for the distribution of species and basal area across the hillslope (Table 3). The average basal area for the upslope is only 67% of the average basal area of the midslope (Table 3). The upslope is characterized by a larger number of chinkapin (*Castanea*), sparkleberry (*Vaccinium arboretum*) and other small trees with a more shrubby appearance beside Hickory trees (*Carya* sp.) while the midslope is characterized by a larger number and larger size hickory (*Carya* sp.) and oak (Q*uercus* sp.) trees (Fig. 12 and Table 3).

A weighted basal area was calculated for each location on the study hillslope by summing the multiplication of the basal area of every tree on and next to the hillslope by an exponential distance function between that point and the tree:

$$Wba = \sum_{\text{all trees}} (Ba_{\text{tree}} e^{\alpha L}) \tag{3}$$

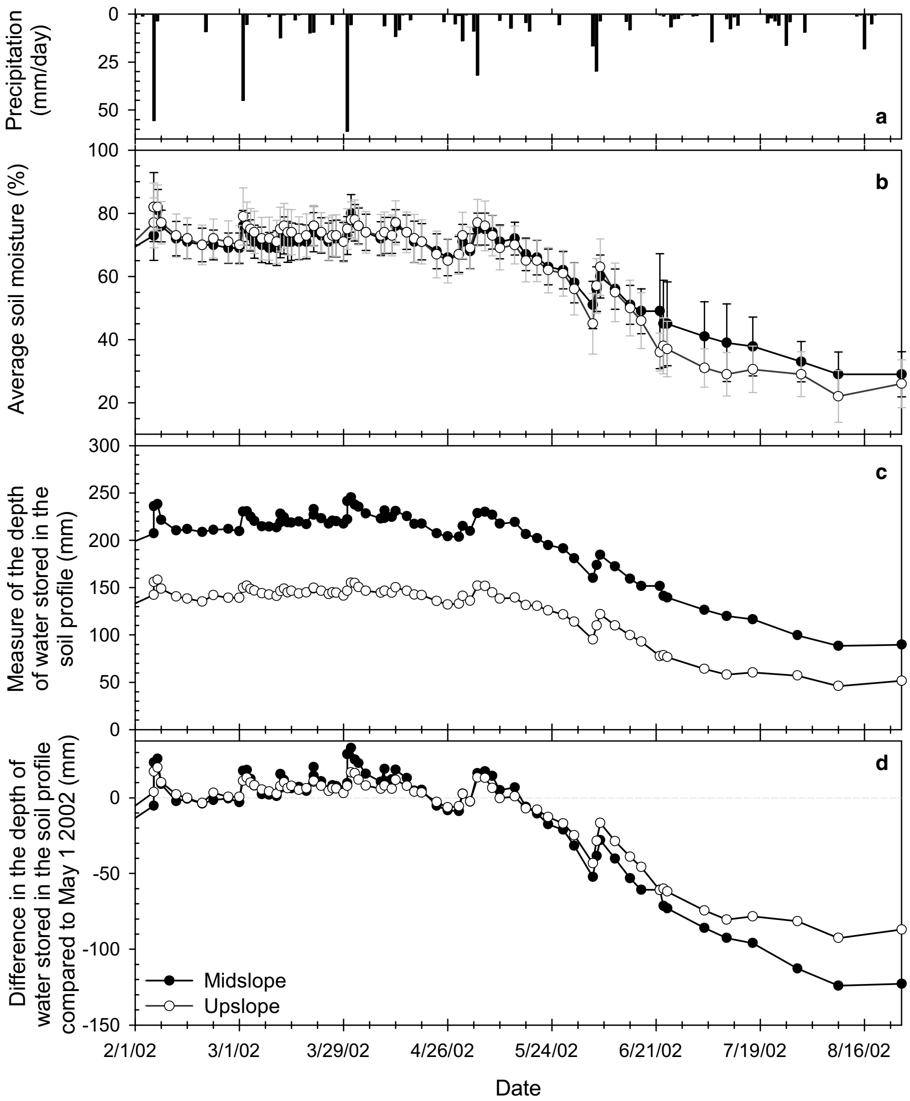

Fig. 10. Daily precipitation (a) and a comparison of the profile average soil moisture of the upslope and the profile average soil moisture of the midslope (b), of the depth of water stored in the soil profile (c), and the change in the total depth of water stored in the soil profile during the study period (d). The bars in (b) represent the standard deviation of the profile average soil moisture. Note that the measured depth of water stored in the soil profile shown in (c) is not the absolute depth of water stored in the soil profile because the Aqua-pro readings were converted to volumetric soil moisture values using only the slope of the relation between Aqua-pro readings and volumetric soil moisture content (not the intercept (b) in Eq. (1)).

where *Wba* is the calculated weighted basal area for a location on the hillslope, ba_{tree} is the basal area of a tree, L is the distance between the tree and the location for which the weighted basal area is calculated, and α is a constant determining how rapidly the weighting of a tree declines with the distance from the tree. Thus the basal area of a tree located close to a certain point counted heavily while the basal area of a tree located further away counted less. The value of α used in Fig. 12 is 0.2. This value was chosen so that the weight of a tree to areas outside the crown of the tree was less than 0.2 for the dominant trees on the hillslope. The r^2 of a linear relation between weighted basal area and soil depth and upslope distance together is 0.63.

5. Discussion

5.1. Preferred states of soil moisture

Like Grayson et al. [11], we observed two preferred states for soil moisture: wet (February–April) and dry (mid-June–August), separated by a relatively short drying period (May–mid-June). The transition from the wet state into the dry state lasted less than a month and occurred soon after full leaf out. The 50 mm rain event on June 4–6, 2002 temporarily moved the hillslope from the drying period back into the wet state, but after this storm the transition from the wet state on June 6, 2002 to the dry state occurred within 2 weeks.

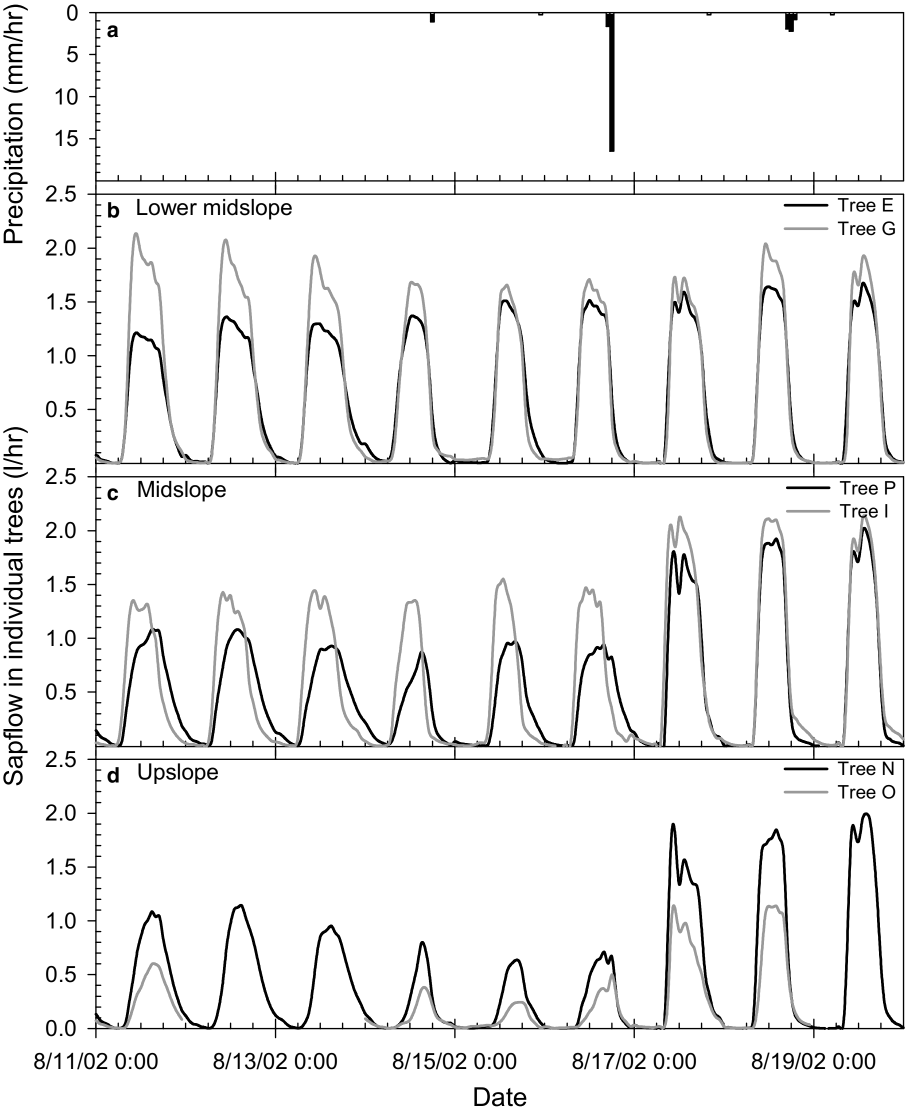

Fig. 11. Precipitation (a), sapflow response in trees on the lower part of the midslope (b), the midslope (c), and upslope during the late summer (d). The two lines in (b)–(d) represent sapflow measured in two different trees.

The drier than average 2002 study period, with smaller storms compared to the 1989–2001 period, probably resulted in less temporal variability and lower peak soil moisture values. The 2002 winter period was still wet enough that the hillslope remained in the wet state and drained to 'field capacity' in between storms (Fig. 3). The smaller and fewer storms during the summer, resulted probably in a more gradual drying of the hillslope, less temporal variability in soil moisture (i.e. fewer increases in shallow soil moisture), and a lower soil moisture level at the end of the summer compared to an average year. This in turn probably led to a more pronounced decline in sapflow compared to an average or wetter year.

Unlike Western et al. [40], who found a high degree of organization of soil moisture during the wet state, we found little spatial structure in our data. Western et al. [40] attributed the spatial structure in soil moisture during the wet period to (surface and subsurface) lateral redistribution of water and the lack of spatial organization during dry periods to a lack of lateral redistribution of water. Here we show that there was more (but still not a lot of) spatial organization in soil moisture across the hillslope during the drying and dry state than during the wet state, when soil moisture was highest in the deepest soil sections. Soil moisture variations were smallest during the wet state. Other studies have also found smaller variations in soil moisture at high soil moisture levels [15,39]. Even during the dry state the correlation length of soil moisture was never larger than 12 m and most of the time less than 8 m. The lack of spatial structure during the wet period may be caused by the scale of this study, uniformity of soil type and texture across the study hillslope and the absence of clear surface drainage

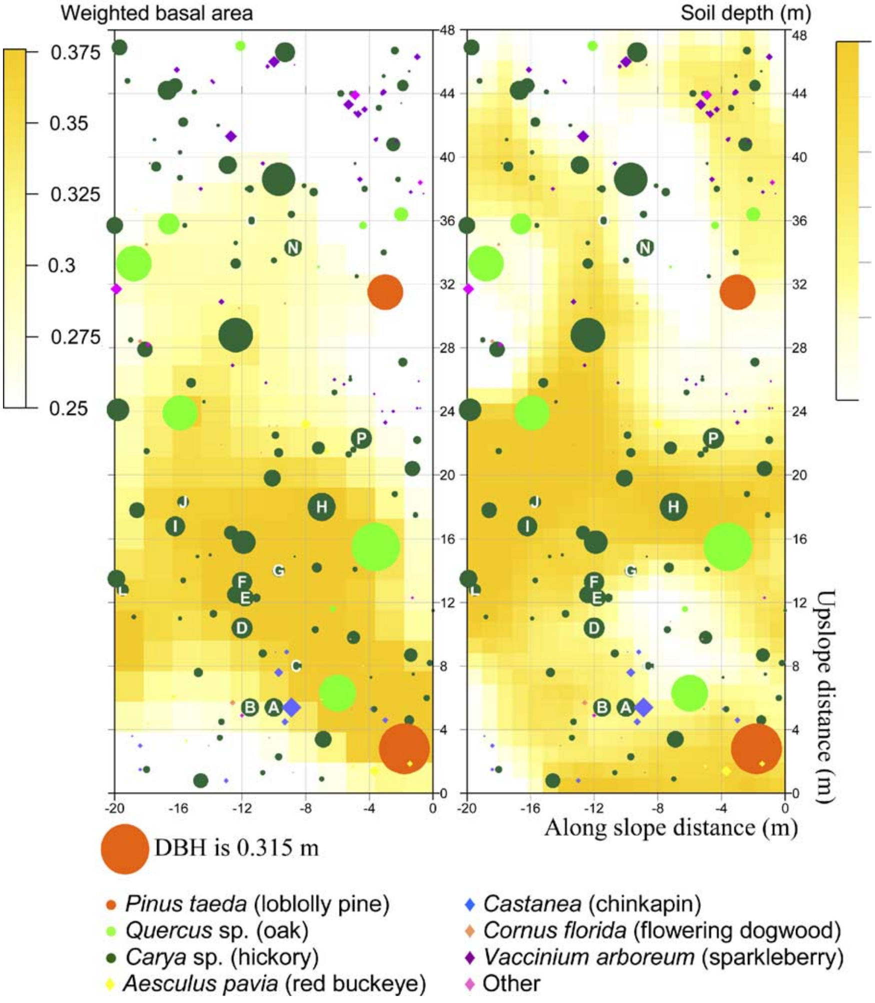

Fig. 12. Weighted basal area, species distribution and soil depth across the hillslope. The letters in the circles refer to the trees where sapflow was measured. The diameter of the circles represents the DBH of the trees.

lines on the hillslope. However, there is a clear subsurface drainage line in the bedrock topography at this hillslope [9,10,22, Fig. 2]. Even though we anticipated that lateral re-distribution of soil moisture at depth (near the soil–bedrock interface) would result in soil moisture patterns at depth that would reflect the bedrock topography, soil moisture in between storms (pre-event soil moisture) in the wet state, was not correlated to the bedrock topography, i.e. soil moisture at depth was not highest in areas of high bedrock accumulated area or high bedrock topographic index values (Table 2).

An alternative explanation for the lack of a spatial pattern in soil moisture during the wet state is that leakage to the bedrock results in predominantly vertical fluxes. This results in a lack of topographic expression in soil moisture. Western et al. [41] show a lack of a soil moisture pattern for the Point Nepean study site in Australia, which has very well drained deep sandy soils. Their variations in soil moisture at the 13 ha site are mainly due to variations in soil texture. At the Panola hillslope we did not observe any soil texture variations.

The observed persistent higher or lower soil moisture at certain measurement locations is probably due to the small Aqua-pro measurement volume [38]. A stone or an air bubble next to the access tube results in a lower Aqua-pro measurement value.

In addition to the lack of a soil moisture pattern across the hillslope, soil moisture was also very uniform with depth. The exception was during and directly after storms during the drying down and dry state when soil moisture close to the surface was higher than soil moisture at depth (e.g. June 4–6, 2002 in Fig. 3c). Stratification in soil moisture during and directly after storms was also shown by Wilson et al. [43].

Aqua-pro soil moisture values for the deeper soil layers were in general lower than the Aqua-pro soil moisture values for shallower soil layers, even when the soil drained to the constant soil moisture value (~field capacity) between storms in the wet state (Fig. 3c). We believe that this is not due to lower soil moisture at depth but rather due to a difference in the dielectric of the soil at depth compared to the dielectric of the soil closer to the soil surface, thus a different constant (b) in the relation between the Aqua-pro reading and actual volumetric soil moisture (Eq. 1). Yu et al. [45] show that the dielectric of the soil is mainly influenced by the surface area of the soil particles and only a little by soil solids, porosity or temperature. For the same soil composite dielectric constant, actual soil moisture is higher than calculated with the standard equation [36] when the porosity is lower, the dielectric of the solid is lower or the specific surface area of the soil particles is higher [45].

5.2. Transpiration patterns

While soil moisture at the different depths was similar at both the beginning of the drying down period and the end of the measurement period (i.e. August 26, 2002), total water depletion was higher from the upper 0.3 m of the soil profile and for many locations also directly above the soil–bedrock interface than from the other depths (Fig. 6). Frequent thunderstorms replenished soil moisture in the upper soil layer, but this water was transpired in a few days after the storm, such that there was no stratification in soil moisture with depth for the majority of the time during the drying and dry state. The depth distribution of total soil water depletion corresponded well with the observed root density pattern at the trench face, soil pits and holes dug for the installation of piezometers, wells and soil moisture access tubes. Even though roots were observed throughout the soil profile, there was a higher root density in the upper 0.3 m of the soil profile than at greater depth and also a slightly higher root density near the soil–bedrock interface. A few very fine roots were observed in the bedrock in the trench.

Hillslope average daily transpiration at the study hillslope was correlated to net radiation. This is comparable to the results from Oren and Pataki [26] for the Duke Forest in North Carolina, where daily stand transpiration increased linearly with the daily sum of photosynthetic radiation above the canopy. There, photosynthetic radiation above the canopy explained 59% of the variation in daily stand transpiration, while daytime mean vapor pressure deficit explained 22% and soil moisture deficit did not explain variations in measured daily stand transpiration when it was included in a multivariate regression with radiation and vapor pressure deficit.

Here we show that daily maximum sapflow in trees on the dry shallow upslope decreased with decreasing soil moisture and increased in response to precipitation. We also show that during the late summer the spatial pattern of daily sapflow per unit sapwood area was related to the soil moisture pattern before the storm. The increase in sapflow after a storm during dry conditions was also shown by Oren and Pataki [26] for white oak (*Quercus alba*) in the Duke forest.

Pataki and Oren [27] show for a hardwood forest that despite a severe drought during their study period only tulip poplar (*L. tulipifera*) (not Mockernut Hickory (*Carya tomentosa*), red oak (*Quercus rubra*), white oak (*Q. alba*), or sweetgum (*L. styraciflua*)) showed a decline in canopy stomatal conductance with decreasing soil moisture and that the primary effect of the drought for the species (except for the tulip poplar) appeared to be early autumn leaf senescence and abscission beginning in mid- to late-September. We observed that by late August that some trees on the upslope had reduced the sapflow flux and also shed their leafs while trees on the midslope and lower slope did not do this.

5.3. Feedbacks between terrain, soil moisture and plant transpiration

The depth of water stored in the soil profile at the end of the dormant season (together with summer throughfall) determined the total volume of water that was available for transpiration during the growing season. Because soil moisture at the end of the dormant season (wet state) was relatively similar across the hillslope, variations in the depth of total water available for plant use were determined by variations in soil depth. Even if there would have been some variation in soil moisture at the end of the dormant season, the variations in soil depth would be larger than variations in soil moisture such that variations in soil depth would still be the dominant factor in determining the variations in the total depth of water stored in the soil profile.

Measured sapflow was spatially uniform across the hillslope during the early summer. Thus, the same depth of water was transpired from the soil profile across the hillslope during the early summer. Because the total depth of water stored in areas with deeper soils was larger than the total depth of water stored in areas with shallower soils, the same depth of water could be removed from areas with deeper soils with less impact on soil moisture than from shallower soils. This resulted in a faster depletion of soil moisture in areas with shallower soils. This in turn increased the correlation between soil moisture and soil depth (Fig. 7c–d) and resulted in a spatial pattern in soil moisture during the drying down and dry state (Figs. 4 and 5). Frequent small storms that replenished soil moisture in the upper soil layers erased the relation between soil depth and soil moisture for the top soil (Fig. 7a–b).

Because more water was stored in the deeper midslope soils, more water could be taken out of the soil profile without lowering soil moisture to such low levels that transpiration became severely limited, as was the case for the shallower upslope (Fig. 11), so that at the end of the summer more water was removed from the midslope than from the upslope (Fig. 10d). The soil depth effect on soil moisture could also be responsible for the distribution of species and basal area across the hillslope (Fig. 12 and Table 3). During the dry summer periods, soil moisture limited transpiration rates in areas with shallow soils (on the upslope). This limits growth and resulted in a smaller basal area compared to areas with deeper soils (on the midslope and lower slope) where transpiration was not limited by soil moisture. In addition the lack of soil moisture could favor different species on the shallow soil sections (upslope) compared to the deeper soil sections (midslope or lower slope).

Part of the observed influence of soil depth and transpiration on the soil moisture patterns and vice versa could be larger than during an average year because the measurements were made during a drier than average year. Total rainfall between May 1 and August 31, 2002 was only 250 mm while the 12-year (1989–2001) average rainfall for the same period was 430 mm (Fig. 1).

It is often assumed that the spatially variable radiation influx is the main factor controlling the spatial variability of evapotranspiration [40]. We do not believe that climatic differences are responsible for the observed differences in soil moisture or sapflow at this hillslope because of the small scale of this hillslope, uniform slope and azimuth and thus uniformity of incident radiation and atmospheric forcing variables across the hillslope. In addition, we do not believe that the observed variations in soil moisture and sapflow were primarily due to drainage of water from the upslope to the midslope because of the low soil moisture and thus very low hydraulic conductivity of the soil during the drying and dry state. Thus we attribute the differences in soil moisture and sapflow between the midslope and upslope during the summer (dry state) to the differences in the total depth of water stored in the soil profile at the beginning of the drying down period, which is determined by differences in soil depth.

Unlike Western et al. [40], here we show that vegetation has a larger influence on soil moisture patterns than local surface or subsurface topography. Hupet and Vanclooster [15] showed for a flat corn field in Belgium that spatially variable vegetation growth within the field induced spatially variable evapotranspiration rates and consequently variable root water uptake rates, resulting in spatially variable shallow soil moisture. Here we show the effect of transpiration on soil moisture for almost all but the shallowest depths. We believe that this is due to the deeper rooting depth of the trees compared to corn and the frequent thunderstorms that replenish shallow soil moisture at this site. Here we also show a feedback mechanism between soil moisture and transpiration. Spatial variability in soil depth results in spatial variability in the total depth of water stored in the soil at the beginning of the growing season. Uniform transpiration rates in the early season result in spatial patterns of soil moisture, which in turn result in spatial patterns of transpiration during the late season. This in turn is responsible for the observed growth differences and species distribution. Thus soil moisture is both a cause and consequence of vegetation [32].

6. Conclusion

We show the importance of soil depth measurements to understand the relations between soil moisture, transpiration during the growing season and vegetation patterns. We also show the feedback between soil moisture and transpiration patterns at the hillslope scale. There are no spatial patterns in soil moisture with depth or across the hillslope during the dormant season (wet state). During the early summer, transpiration is uniform across the hillslope. Because more water is stored in the deeper soils, removing the same amount of water from a deep soil section and a shallow soil section, results in a faster depletion of soil moisture in the shallower soil section. This in turn results in a relation between soil moisture and soil depth after leaf out. Because soil moisture during the mid- to late-summer is lower on the shallow soil sections, transpiration on the shallower soil sections is reduced. This in turn determines growth, which determines the basal area and its competitive ability, which affects species distribution.

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