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Seasonal variations in soil water in two woodland savannas of central Brazil with different fire history

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Summary Changes in soil water content were determined in two cerrado (*sensu stricto*) areas with contrasting fire history and woody vegetation density. The study was undertaken near Brasília, Brazil, from 1999 to 2001. Soil water content was measured with a neutron probe in three access tubes per site to a depth of 4.7 m. One site has been protected from fire for more than 30 years and, as a consequence, has a high density of woody plants. The other site had been frequently burned, and has a high herbaceous vegetation density and less woody vegetation.

Soil water uptake patterns were strongly seasonal, and despite similarities in hydrological processes, the protected area systematically used more water than the burned area. Three temporarily contiguous patterns of water absorption were differentiated, characterized by variation in the soil depth from which water was extracted. In the early dry season, vegetation used water from throughout the soil profile but with a slight preference for water in the upper soil layers. Toward the peak of the dry season, vegetation had used most or all available water from the surface to a depth of 1.7 m, but continued to extract water from greater depths. Following the first rains, all water used was from the recently wetted upper soil layers only. Evaporation rates were a linear function of soil water availability, indicating a strong coupling of atmospheric water demand and the physiological response of the vegetation.

Keywords: cerrado, evaporation.

Introduction

The Brazilian cerrado (*sensu stricto*) is a savanna characterized by dispersed trees and shrubs, small palms and a ground layer of grasses. It is the second largest ecosystem in Brazil, occupying two million km² in the central part of the country. The cerrado has distinct wet and dry seasons, with 90% of the mean annual rainfall of 1436 mm occurring from October to

April (Pereira et al. 1993). Seasonal variation in rainfall leads to seasonal changes in vegetation, with the herbaceous component drying out in the mid dry season and remaining dormant until the next wet season (Andrade 1998); whereas leaf expansion, flowering, rapid transpiration and fructification occur in woody species during the dry season (Pinto 1999, Meinzer et al. 1999, Oliveira and Gibbs 2000), indicating that woody vegetation has access to soil water during the dry season despite the lack of rain (Rawitscher 1948).

However, even woody species of the cerrado show a marked seasonality in physiological activity. For example, Miranda et al. (1996) reported significant reductions in surface conductance and associated ecosystem carbon fluxes during the dry season in a Brazilian cerrado and suggested that this was related to a significant reduction in photosynthesizing leaf area of both trees and grasses and a reduction in leaf-level gas exchange rate.

The prolonged dry season leads to frequent fires that reduce the woody component of the vegetation and increase the density of the herbaceous layer (Coutinho 1990), whereas exclusion of fire has the opposite effect. Such differences in vegetation structure may influence seasonal patterns in water use and the water balance of vegetation. Quesada et al. (2004) reported that frequent fires in campo sujo vegetation (savanna with some shrubs) increased evaporation rates for 7 months after fire, with reduced evaporation rates during the following dry months. This was presumed to be a result of the reduction in woody vegetation capable of accessing soil water at depth. By changing the vegetation structure, fire may also affect rainfall interception rates and, hence, regional-scale water balances.

We characterized patterns of soil water uptake, soil water recharge and discharge and the general water balance for two woodland savannas (cerrado *sensu stricto*) differing in fire history and associated vegetation structures. Tree and shrub litter-fall and seasonal variations in live and dead proportions of herbaceous layer and their relationships to soil water storage and

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†† Antonio Carlos Miranda died September 24, 2002

evaporation rates were measured and their relationships to soil water availability and ecosystem-level evaporation rates evaluated.

Material and methods

Site description

Soil water storage was measured between January 1999 and August 2001 in the core area of the cerrado at the Reserva Ecológica de Águas Emendadas, DF, Brazil (15°33' S, 47°36' W, 1000 m a.s.l.), 50 km north-east of Brasília. We chose two sites 8 km apart and at a similar elevation (about 1150 m). The sites are tropical, xeromorphic, semi-deciduous broadleaf tree and scrub woodland forms of cerrado (Eiten 1984) that differ markedly in fire histories. One site (burned cerrado) had been subjected to fires every 2 or 3 years for at least 30 years before 1987. After 1987, the Ecological Reserve was created and fires were successfully suppressed. The second site (protected cerrado) was a cerrado area naturally protected from human influence and anthropogenic fires by a marsh-like vegetation (*Veredas*, dominated by palms and grasses with flooded soils) that forms a natural barrier to fire invasion from nearby human settlements. The protected cerrado had been free of fires for at least 30 years (Nascimento 1992).

To characterize the vegetation during the study, a 100 × 100 m plot was established at each site. All woody individuals greater than 5 cm in circumference (1.6 cm diameter) at 30 cm height from the soil were recorded, mapped, identified and their diameters measured. Random samples of the herbaceous layer were collected twice a month from July 2000 to May 2001 in ten 50 × 50 cm quadrats and subsequently separated into live and dead grasses and dicotyledonous herbs. In addition, ten litterfall baskets were randomly positioned throughout the plot and woody plant litterfall determined every 30 days. Contents of the litterfall baskets were pooled before drying at 60 °C for 48 hours and weighing.

From the measurements of stem diameter at 30 cm height, biomass of the woody component was determined according to Abdala et al. (1998):

$$\log B = 0.9967 \log V + 2.587 \quad (1)$$

where B is wood dry biomass (g) and V is cylindrical volume (dm^3).

The soil at both sites is a well-drained reddish yellow oxisol with clay texture and a pH of less than 5. This soil type occupies 46% of the Brazilian cerrado (Reatto et al. 1998). Such soils have a low bulk density, typically between 0.8 to 1.1 g cm^{-3} , are deep, free of hardpan or other physical constraints, homogeneous and have a plant-available water-holding capacity of 0.10 to 0.15 m m^{-1} (Reatto et al. 1998, Quesada et al. 2004). Because there were no apparent differences in soil structure or physical properties between the plots, we assumed that any differences in water balance were caused by differences in rainfall or vegetation, or both. The water table is usu-

ally more than 40 m deep. The surface soil in the cerrado is highly permeable, and runoff was not observed. The slope at both sites was less than 2°.

Measurements

Soil water storage was measured with a neutron probe (Model IH II, Institute of Hydrology, Wallingford, U.K.). Three access tubes were installed to a depth of 470 cm, located 20 m apart, in an edaphically and vegetationally homogeneous area within each plot. Measurement depths were 5 and 20 cm, and then at 25-cm intervals to a maximum depth of 470 cm. Counting time was 16 s. Neutron probe calibration was based on the neutron capture model calibration method of Couchat et al. (1975) with a special gravimetric calibration applied for the 5-cm depth. To facilitate access without compaction of the surrounding soil during measurement, access tubes were equipped with a small steel mesh platform. Readings were taken weekly, commencing in January 1999, at the peak of soil water recharge. Before then, there had been 719 mm of rain from August 1998 to early January 1999.

Rainfall in each plot was measured with a pluviometer, located less than 50 m from the study plots in a large canopy gap.

Calculations

Evaporation losses were calculated as:

$$P - I = E + D + \Delta S + Q \quad (2)$$

where P is precipitation, I is interception loss, E is evaporation rate, D is deep drainage (below 4.7 m), ΔS is the change in soil water storage and Q is the surface runoff, all expressed in units of mm over the measurement interval.

Precipitation and interception was calculated from hourly rainfall measurements at the EMBRAPA CPAC weather station, located about 5 km from the plots, and an interception coefficient of 39% (Nascimento 1992). This value for calculating the interception loss for each period between soil water content measurements is an approximation because of variation in storm size and duration, and vegetation storage capacity. We assumed that intense rainfall events resulted in lower interception values (interception < 10%) and that brief events of light rain resulted in the 39% interception value of Nascimento (1992). Interception by light but prolonged rain was likely low because once the storage capacity of the vegetation is reached, interception is mostly related to evaporation from wet surfaces (Nascimento 1992).

Evaporation was estimated from the water balance during periods when drainage could be assumed to be negligible. Because oxisols are generally free draining (Sanchez 1976, Tomasella and Hodnett 1996), we assumed drainage below the 470 cm profile to be negligible from the mid dry season into the wet season until the wetting front reached 470 cm, which usually occurred in early January, 5 to 6 months after the onset of the rainy season.

Because peaks in soil water storage after heavy rainfall were not observed after the wetting front reached 470 cm, it was as-

sumed that drainage from the micro-aggregated, low density upper horizons ceased within 1 day of a heavy rainfall.

Daily drainage rates were estimated from water balance calculations for periods when evaporation and drainage occurred simultaneously. Because the soil water balance calculation results in an evaporation plus drainage value, daily drainage rates were estimated by subtracting a mean wet season evaporation value of 3.5 mm day⁻¹ from the evaporation plus drainage values.

Soil water storage was calculated from individual soil-layer water contents with runoff considered negligible because the soil surface is highly permeable. To perform correlations with soil water content, evaporation rates were converted to the ratio of actual evaporation rates (from the water balance) to potential evaporation rates (estimated based on data from the nearby weather station).

Available water capacity (A) was calculated as the difference between the profile water storage at field capacity and the minimum water storage value measured for each soil layer. The minimum water storage was taken to be close to the wilting point, because there were no further changes in water content in the late dry season. Field capacity in both plots was estimated from the profile water storage on January 12, 1999, about one day after the profile had been thoroughly wetted but with no further rain during the previous 24 hours.

We estimated the available soil water fraction (f) and related it to seasonal changes in evaporation rates and changes in vegetation fractions:

$$f = \frac{(S - S_{\min})}{A} \quad (3)$$

where f represents the available soil water fraction in the layer of interest, S is monthly mean soil water storage in that layer and S_{\min} is minimum soil water storage in that layer over the study period. The maximum available soil water in any layer (A) was calculated as:

$$A = S_{\text{FC}} - S_{\min} \quad (4)$$

where S_{FC} is maximum soil water storage at field capacity as defined above.

Six soil layers of increasing overall depth were considered in evaluating the relationship between evaporation and seasonal changes in f and vegetation cover: 0–45; 0–70; 0–95; 0–145; 0–170; 0–245; and 0–295 cm.

We acknowledge uncertainties in the available soil water fraction calculations. For example, the value of S_{\min} in this case representing the “wilting point,” might have been higher than the minimum soil water content at which the vegetation could extract soil water. Likewise, S_{FC} may have included some water above field capacity that eventually went to drainage. Nevertheless, because minimum and maximum storage values occupy the extremes of soil water storage, errors implicit in the calculations should be small. We also note that our approach represents a measure of the variation in soil water storage in the field experienced by the vegetation.

Results

Vegetation assessment

The contrasting vegetation structure between sites was reflected in the density of woody plants observed, being 6800 and 2620 ha⁻¹ for the protected and burned cerrado, respectively. Aboveground woody biomass was estimated at 40.4 Mg ha⁻¹ for the protected cerrado and 12.1 Mg ha⁻¹ for the burned cerrado.

Seasonal patterns in live and dead grass biomass, live and dead herbaceous dicotyledonous biomass, their totals and litterfall from trees and shrubs from July 2000 through May 2001 are shown in Figure 1. There was a strong seasonality in both live and dead grass biomasses, especially for the burned cerrado, which had more live grass than the plot at the protected site. Plot differences in dicotyledonous biomass were less consistent, although values tended to be higher at the protected site, especially during the rainy season (November–May). Nevertheless, with the exception of August 2000, total live herbaceous biomass was always greater in the burned cerrado plot. By contrast, rates of tree and shrub litterfall were consistently greater for the protected cerrado. Taking annual totals from Figure 1g, we estimated an annual woody plant litterfall rate of 2.1 and 5.6 Mg ha⁻¹ year⁻¹ for the burned and protected plots, respectively. Assuming leaf production and loss over a year to be in equilibrium, these values equate to the rates of new leaf production by trees and shrubs. Estimates of new grass production were 5.1 and 4.5 Mg ha⁻¹ year⁻¹ for the same two areas, obtained by summing the annual maximum values of live and dead biomass (Bulla 1996); no calculation was possible for the dicotyledonous layer because we were unable to separate soil leaf litter from dead dicotyledonous leaves. The relative proportions of live and dead herbaceous biomasses were strongly seasonal, with the production of green material peaking between January and May and the quantity of dead material increasing notably between July and October.

Soil water storage variations

Precipitation inputs and associated changes in the soil water storage profile to a depth of 470 cm were determined for the study period (Figure 2). Soil water storage was strongly seasonal with a mean change in profile between the wettest and driest days of 447.6 mm for the protected cerrado and 406.8 mm for the burned cerrado. The minimum soil water storage profile observed in the 1999 dry season was about 63 mm less than that in the 2000 and 2001 dry seasons, probably because of the extended dry season of 1999 (1 month longer than usual). However, mid-August values of the soil water storage profile, the dry season peak in average years, were similar in all three dry seasons despite large differences in rainfall (1010, 2443 and 1581 mm year⁻¹ in 1998–1999, 1999–2000 and 2000–2001, respectively).

Figure 2 shows that the patterns of change in soil water storage were similar between and within the study sites, but with subtle differences. For example, drying rates were always

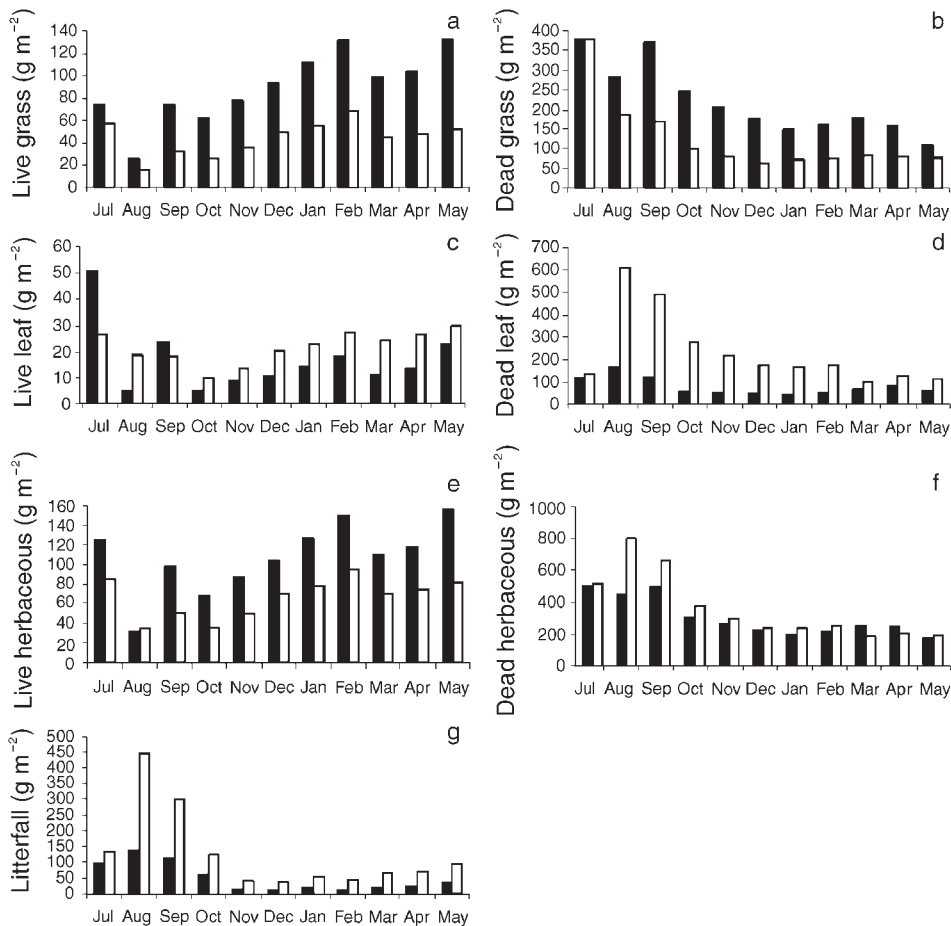


Figure 1. Seasonal changes in biomass of different components of the herbaceous layer and litterfall rates for July 2000–May 2001: (a) live grass; (b) dead grass; (c) live herbaceous leaves; (d) dead herbaceous leaves including leaf litter; (e) total live herbaceous biomass; (f) total dead herbaceous biomass; and (g) litterfall. Filled bars = burned cerrado, and open bars = protected cerrado.

higher in the protected cerrado than in the burned cerrado, as shown by the differences in cumulative water losses in Figure 3.

Changes in the water storage profile of successive soil layers were determined throughout the study (Figure 4). The top soil layer was dynamic, drying rapidly after rainfall events, and the protected cerrado plot dried sooner than the burned plot. As early as the first week of August 1999, 87 days after the last rain event, water storage in the top 70 cm of the soil in the protected cerrado ceased to decline and remained constant for 34 days until the end of the 1999 dry season, indicating that the vegetation had already used all available water in that layer (Figure 4a, Arrow 1a). At the burned site, drying of the top 70 cm of the soil occurred 14 days later than at the protected site (based on water balance calculations; see Figure 4b, Arrow 1b), and despite following the same pattern as the protected cerrado, systematically released less water by transpiration than the protected cerrado. However, in the 2000 dry season, only in the protected cerrado did the top 70 cm of the soil dry entirely (Figure 4a, Arrow 1c), whereas the burned area continually showed changes in soil water content in the top soil layer, never reaching the low values observed in 1999 (Figure 4b, Arrow 1d). These differences between the years are associated with a longer dry spell in 1999 than in 2000 (137 days versus 107 days). The longer dry season in 1999 re-

sulted in the drying out of the 70–170 cm layer in both plots, until all plant-available water had been used (Figure 4, Arrows 2a and 2b). In the 2000 dry season, the soil water content of the 70–170 cm layer never declined to the same value as in 1999, with the maximum depth of complete water depletion being 95 cm on July 21, 2000, after which it remained constant until the arrival of the wetting front during the next wet season (Figure 4, Arrows 2c and 2d). Even when water could no longer be extracted from the uppermost soil layers, both areas showed consistent water uptake from deeper soil layers at low but steady rates (Figure 4b, Arrow 3), and this pattern changed only after the first rainfall event.

Table 1 shows water balance calculations in each 1-m soil layer for four time periods in the protected cerrado, chosen to demonstrate the different uptake patterns. The first part of the dry season (May 27 to June 10, 1999 in Table 1; Figure 4) is characterized by water absorption throughout the profile (0 to 470 cm), but preferentially from the upper layers. The water absorption pattern changed as available water in the surface layers was depleted and water absorption increased at greater depths. This pattern of water uptake changed again after the upper soil layer dried out completely (June 26 to July 12 and August 23 to September 12, 1999 in Table 1; Figure 4), with soil water uptake occurring even deeper in the profile and, eventually, almost exclusively from below 170 cm. Calculated

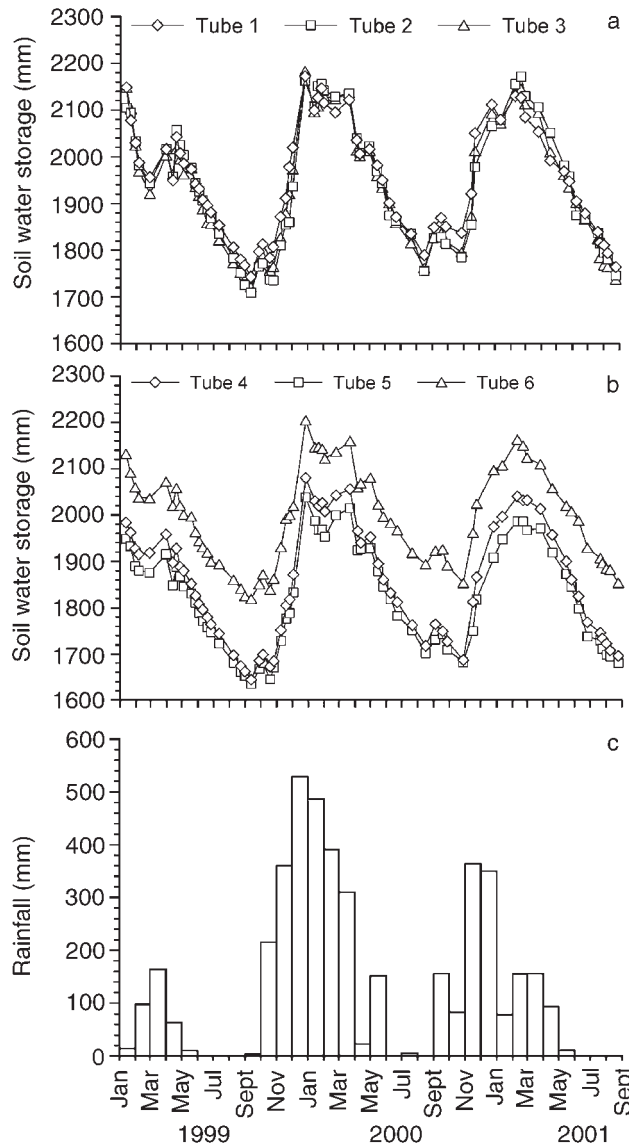


Figure 2. Seasonal changes in the soil water storage profile to a depth of 470 cm in the (a) protected and (b) burned cerrados. (c) Monthly precipitation at both sites.

mean evaporation rates for this period were 1.9 mm day^{-1} for the protected cerrado and 1.6 mm day^{-1} for the burned cerrado.

Another pattern of water uptake was observed after the onset of the first rains, strongly suggesting that, in response to changes in water availability, trees and shrubs are able to change rapidly the soil layer from which they take up water. As soon as there is significant rainfall (i.e., the first peak in water content in the 0–70 cm layer after the dry season, Figure 4) water uptake from deep soil layers ceases abruptly and community water uptake occurs mostly in the uppermost, recently wetted, soil layer (September 12 through October 5 in Table 1 and Figure 4). Water storage of deeper layers subsequently remained constant (Figure 4, Arrow 4) until the arrival of the wetting front several months later. In all study years, recharge

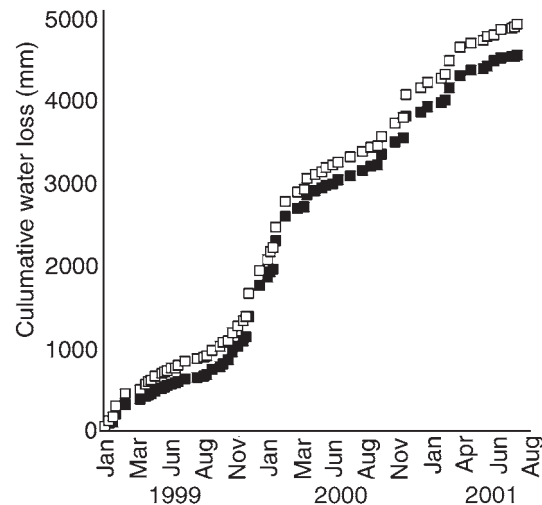


Figure 3. Cumulative water loss over the study period in the burned (■) and protected (□) cerrados.

of the entire profile occurred in either late December or early January, about three and a half months after onset of the rainy season. In the early wet season in 2000, vegetation of the burned cerrado plot showed no abrupt change in depth of water extraction zone, presumably because water content of the uppermost soil layers did not fall sufficiently that year to cause water extraction at greater depths.

Evaporation and vegetation dynamics in relation to soil water storage

Evaporation rates (expressed as actual evaporation as a fraction of potential evaporation; E/E_p) were a linear function of the available soil water fraction (Figure 5), the correlation increasing with increasing soil depth to 245 cm. Evaporation rates at both the burned and protected plots were best correlated with water content of the 0–245 cm layer (0.865, $P = 0.003$ and 0.775, $P = 0.014$, respectively), indicating that water was extracted mainly from this zone. Seasonal changes in the proportions of live grasses and herbaceous (dicotyledonous) biomass showed an increasingly close correlation with depth of water extraction. Similar patterns were not observed in changes in the dead herbaceous fraction. In general, dead fractions were unrelated to available soil water fraction. Seasonal variation in tree and shrub litterfall rates were strongly correlated with available soil water fraction, with litterfall in the burned cerrado being best correlated with the available soil water fraction in the 0–170 cm layer (-0.924 , $P < 0.001$), whereas litterfall of the protected cerrado was best correlated with the available soil water fraction in the 0–295 cm layer (-0.862 , $P < 0.001$). However, the correlations of litterfall rates and available soil water were significant at all soil depths, the strength of the correlation increasing with soil depth. Seasonal changes in green herbaceous biomass and changes in litterfall rates seemed best correlated with available soil water in the entire soil profile (both sites), indicating that both trees and herbaceous vegetation were exploring water to similar

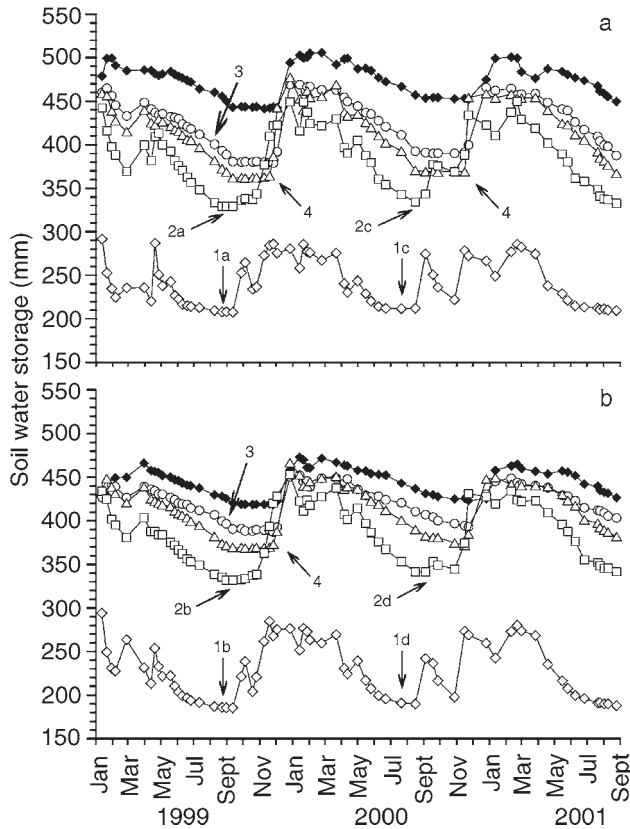


Figure 4. Storage profile changes in successive 1-m layers in the (a) protected and (b) burned cerrados. Symbols: \diamond , 0–70 cm layer; \square , 70–170 cm layer; \triangle , 170–270 cm layer; \circ , 270–370 cm layer; and \blacklozenge , 370–470 cm layer. See text for Arrows.

depths.

Figure 6 shows derived evaporation rates with missing values for measurement dates where drainage could not be excluded from the water balance calculation. The data show marked seasonality but little systematic difference between sites. Evaporation rates tended to decline from March–April

until September toward the end of the dry season, increasing again with the onset of the rainy season. Toward the end of the dry season, despite prolonged rainless periods, evaporation rates were estimated to be 1.5 mm day^{-1} for burned cerrado and 1.9 mm day^{-1} for protected cerrado. For wet season periods, when estimates of evaporation could be made, derived values were 2.6 and 2.7 mm day^{-1} , respectively (differences in wet season rates were not significant).

Soil water discharge and recharge patterns

Successive soil water content profiles from the wettest measurement day in the 1999 season (January 12, 1999) to the driest measurement day in the same year (September 12, 1999) are depicted in Figure 7. These data indicate that seasonal changes in soil water content become smaller with depth, implying only a small amount of water uptake from below 470 cm. Figure 7 indicates an almost even distribution of water uptake in the top 3 m of soil in the protected cerrado. In contrast, there was slightly higher water uptake from the top 2 m of soil in the burned cerrado. We estimated that, for the protected cerrado, changes in soil water content by soil layer from January–September 1999 were 27.8% in the top 1 m, 27.1% between 1 and 2 m, 23.4% between 2 and 3 m, 16.7% between 3 and 4 m and only 5.6% between 4 and 4.7 m. In contrast, the burned cerrado showed a different pattern with 44.6% of the changes in soil water content in the top 1 m, 26% between 1 and 2 m, 18.5% between 2 and 3 m, 9.5% between 3 and 4 m and only 1.4% between 400 and 470 cm. We estimated a mean available soil water content of about 117.3 mm m^{-1} in both plots.

Figure 8 shows the water content of the driest soil profile in September 1999 and successive profiles after the onset of the rainy season until the profile had been rewetted to below 470 cm. For the protected cerrado, 115 mm of rain was needed to recharge the top 1 m of soil, and after 521 mm of rain, the soil was fully recharged to 1.7 m. After 614 and 729 mm of rain, the wetting front reached 245 and 320 cm in the soil profile, respectively. The entire profile was not rewetted until late December after 1197 mm of rain. For the burned cerrado,

Table 1. Soil water storage (mm) of each soil layer in four periods and their percentage of the total storage change (in parenthesis). Early dry season May 27 to June 10, 1999, mid dry season June 26 to July 12, 1999, late dry season August 23 to September 12, 1999 and early wet season September 12 to October 5, 1999. Evaporation and rainfall between dates are also shown.

Soil layer (cm)	May 27–June 10	June 26–July 12	Aug 23–Sept 12	Sept 12–Oct 5
0–470	39.0	32.1	36.9	56.6
0–95	14.0 (35.9)	2.8 (8.7)	0.5 (1.3)	56.6 (100.0)
95–195	9.1 (23.3)	7.6 (23.7)	2.0 (5.4)	0.0 (0.0)
195–295	6.2 (15.9)	9.0 (28.0)	13.3 (36.0)	0.0 (0.0)
295–395	6.9 (17.7)	6.1 (19.0)	11.6 (31.4)	0.0 (0.0)
395–470	2.7 (6.9)	6.6 (20.6)	9.5 (25.7)	0.0 (0.0)
Rainfall (mm)	0.0	0.0	0.0	122.2
Evaporation + drainage (mm day^{-1})	2.8	2.0	1.9	2.5
Number of days	14	16	20	23

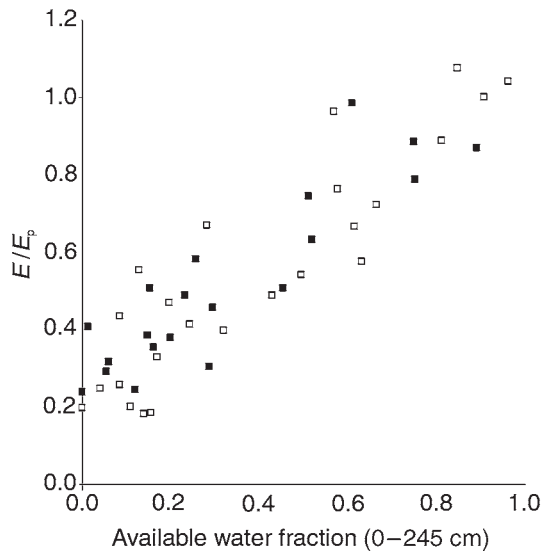


Figure 5. Evaporation rate relative to potential evaporation (E/E_p) as a function of available soil water fraction in the burned (\square) and protected (\blacksquare) cerrado plots.

100.5 mm of rain recharged soil water to a depth of only 70 cm and after 378 mm of rain the wetting front reached 120 cm. After 578 mm of rain a depth of 220 cm was rewetted, and only after 1107 mm of rain was the entire profile fully recharged (the soil in both plots was fully recharged 106 days after the onset of the rainy season). All profiles showed a well-defined wetting front without evidence of by-pass flow wetting the lower profile before the layers above were wetted. Once the wet season had begun, the water content below the wetting front changed little (Figure 8), indicating that no water uptake or drainage occurred, suggesting that deep water uptake at both sites ceased as soon as the upper soil layers had become rewetted with the onset of wet season rains.

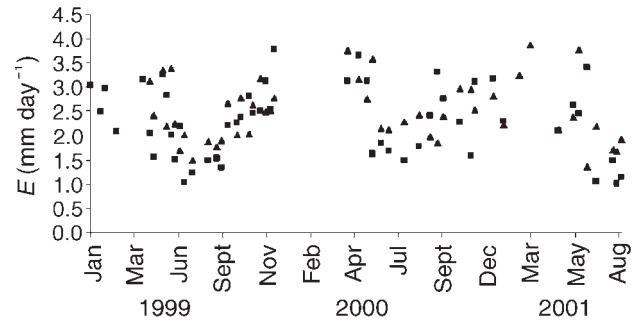


Figure 6. Observed evaporation rates (E) during the study period for the burned (\blacksquare) and protected (\blacktriangle) cerrado plots. Values are missing for dates when drainage could not be ignored.

Daily drainage rates are plotted against soil water storage to a depth of 470 cm for both protected and burned cerrado areas in Figure 9. Deep drainage (below 470 cm) occurred only when soil water storage had reached a threshold of about 2000 mm, confirming that storage values below that range allow accurate calculation of evaporation. There were several values with zero drainage rates, indicating that drainage must stop abruptly after rain events, even when soil water storage is high.

The general water balance calculations estimate that evaporation accounted for 43.5 and 41.1% of rainfall for the protected and burned plots, respectively. Similarly, in the protected and burned plots, drainage removed 14.5 and 17.7% of rainfall, respectively, and interception was 41.9 and 41.2%, respectively.

Discussion

The vegetation biomass and the number of woody individuals in our study were typical of burned and unburned cerrado ar-

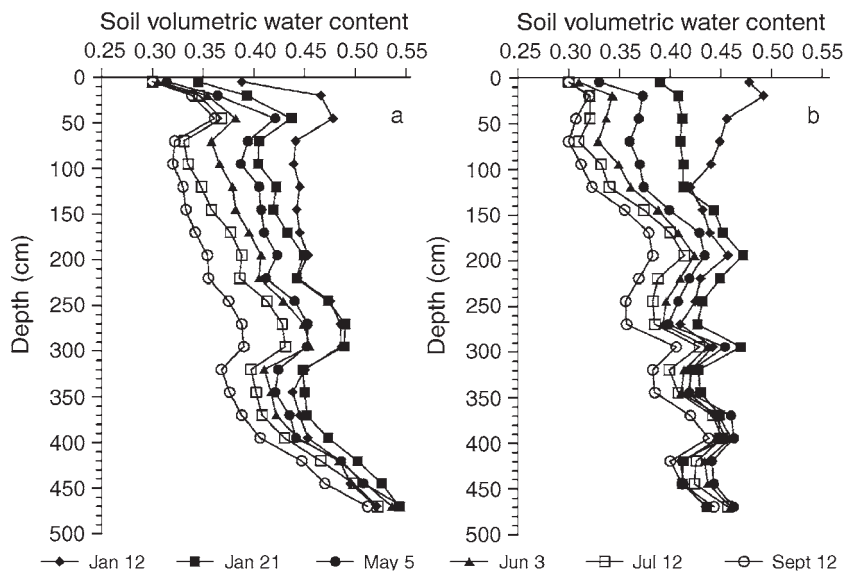


Figure 7. Soil water discharge patterns from the wettest (\blacklozenge) to the driest (\circ) day in 1999 in the (a) protected and (b) burned cerrados.

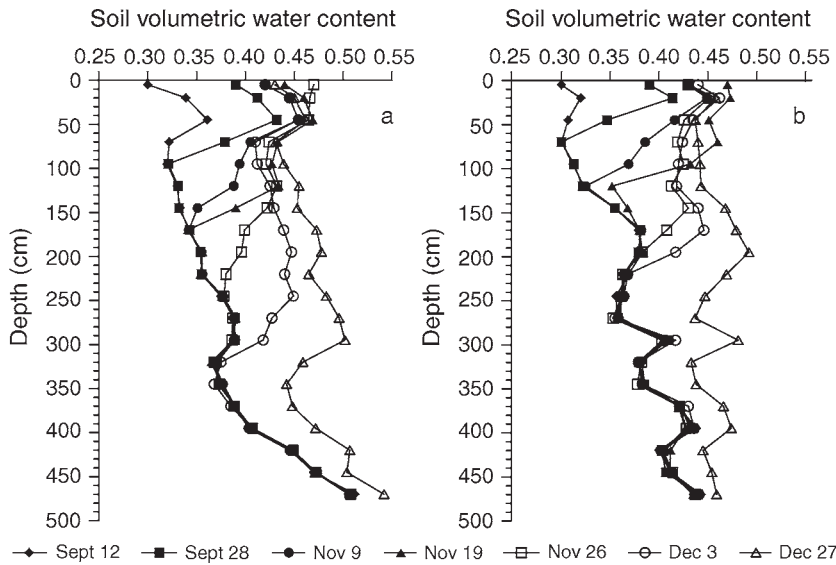


Figure 8. Soil water profile on the driest day (\blacklozenge), and following recharge (\triangle) in 1999 for the (a) protected and (b) burned cerrado plots.

eas. For example, Ottmar et al. (2001) reported a biomass of 42.9 Mg ha^{-1} for cerrado areas protected from fire for more than 20 years with $6258 \text{ woody individuals ha}^{-1}$. Based on the same study, they report aboveground biomass estimates for frequently burned cerrado areas ranging from 12.5 to 14.3 Mg ha^{-1} .

The patterns in litterfall that we observed were similar to published values. Pinto (1999), studying seasonal phenological changes in the cerrado, observed that leaf fall peaks for cerrado areas between July and September lead to a 53% reduction in leaf biomass during the dry season. Most of the reduction in leaf biomass observed by Pinto (1999) was associated with brevideciduous trees (leafless for only a short period), whereas evergreen cerrado trees keep at least 30% of their leaves during the dry season.

Besides large differences in the extent of woody plant leaf litterfall (Figure 1g), herbaceous biomass differed between the burned and protected sites, with the burned cerrado having twice as much grass as the protected cerrado (Figure 1a). Lloyd et al. (2008) used carbon isotopes to estimate the pro-

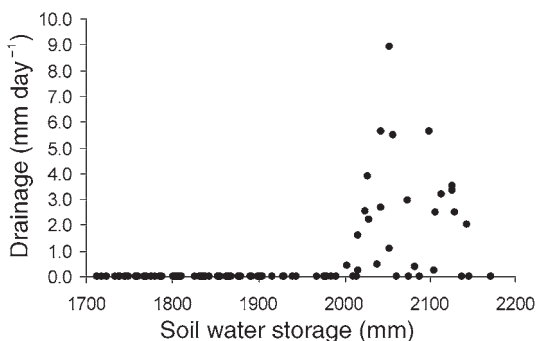


Figure 9. Relationship between daily drainage rates and soil water storage to a depth of 470 cm for both the protected and burned cerrado plots.

portions of productivity attributable to grasses versus trees in the same plots. For the protected area, they estimate that about 61% of overall ecosystem production was attributable to the woody vegetation compared with only 22% in the burned area.

Despite these large differences in vegetation structure, differences in soil water storage were similar between the study sites, reflecting large-scale similarities in rainfall, interception, surface and subsurface redistribution of water, runoff, deep drainage and, to a lesser extent, evaporation. Nevertheless, there were noticeable differences in water demand and depth of water use between the burned and protected plots, with the protected cerrado having a slightly higher demand for soil water than the burned cerrado (Figure 3). Higher water loss by the protected cerrado may be associated with its high density of woody vegetation and high leaf biomass, values similar to those reported by Oliveira et al. (2005). However, despite the contrasting vegetation structures, the differences in evaporation rates between the plots were small, with the greatest difference occurring during the dry season when a large fraction of the herbaceous layer was dead or dormant.

Depth variation in soil water storage was strongly related to seasonality, with surface layers drying out completely toward the end of the dry season. Quesada et al. (2004) report similar behavior for burned and unburned campo sujo areas. Nevertheless, for campo sujo vegetation, the maximum depth to complete drying (to the abstraction limit) was only 80 cm. Such differences between communities in maximum depth of water extraction are likely related to woody plant density and thus may be indirectly related to fire history (Coutinho 1990, Eiten 1994, Quesada et al. 2004).

Seasonal patterns in water availability across the soil profile, gave rise to three water uptake patterns (Table 1). During the early dry season, uptake occurred throughout the soil profile. However, the pattern of uptake during this period may not have been the same for all species. According to a study with deuterated water (Jackson et al. 1999), there are differences among cerrado tree species in the vertical pattern of soil water

uptake, which finding is consistent with the occurrence of competition between herbaceous and woody species for water near the soil surface, despite greater access by woody species to water in deep soil layers.

When the uppermost soil layer approached dryness, a second pattern of water uptake developed with water use restricted to deeper soil layers. This pattern implies that plants with roots confined to the surface soil layers are dormant or dead. Nevertheless, there was always some green vegetation in the herbaceous layer, indicating that not only trees and shrubs, but also some components of the herbaceous layer, have access to deep soil water.

A third pattern of water absorption was observed at the start of the wet season when deep soil water uptake ceased rapidly as water absorption by the entire community became concentrated in the recently rewetted upper soil layers, where extraction is subject to a lower gravitational limitation. The change in pattern indicates that at least some fine roots in the upper soil layers remain functional throughout the dry season and are immediately able to absorb water arriving with early wet season rains. Although we obtained no evidence of it, hydraulic lift may be important in maintaining live fine roots at the soil surface throughout the extended dry season.

The existence of dimorphic root systems that explore both surface and deeper soils appears to be an adaptive feature of cerrado species. However, the varying patterns of water uptake suggest competition for water among species and life forms (trees, shrubs and grasses) during some parts of the year. Plants that continue to photosynthesize during the dry season compete for deep water, but must also compete with grasses for water in the uppermost soil layers at the beginning of the rainy season and other times of the year when water is available in the uppermost soil layers. This, and the observation that woody vegetation must have taken water from the upper soil layers in direct competition with grasses during the early wet season, suggests that the niche separation theory (Walter 1969, 1979), sometimes used to explain stable coexistence of trees and grasses in savannas, does not account fully for the coexistence of woody and herbaceous layers in the Brazilian cerrado.

The niche separation theory suggests that herbaceous species extract water only from the surface soil layers and that woody plants avoid competition by exploring only deeper layers. Several studies have supported the niche separation theory in drier savannas, e.g., Knopp and Walker (1985) in South African savannas; Soriano and Sala (1983) and Golluscio et al. (1998) in the Patagonian steppes; Sala et al. (1992) and Dodd and Laurenroth (1997) in North American savannas; Brown and Archer (1990) in subtropical savannas; Jackson et al. (1995) in tropical forests; Akpo (1997) in semi-arid savannas from Senegal; Sarmiento and Monasterio (1983) in tropical savannas; and Medina and Silva (1991) and Sarmiento (1993) in northern Neotropical savannas.

Although other authors have also presented evidence in support of the niche separation theory (Vareschi 1960, Goldstein et al. 1986, Goldstein and Sarmiento 1987, San José et al. 1995), there are other explanations for the coexistence of trees and grasses. For example, Le Roux et al. (1995), working in

humid savannas of West Africa, reported that roots of the herbaceous layer and most of the woody plants were restricted to the upper soil layers with root distribution mainly determined by nutrient availability. Dawson and Pate (1996), working in Australia, reported the existence of trees with dimorphic root systems that extracted water from deep soil layers during the dry season and from surface soil layers during the rainy season, as was probably the case in our study. Le Roux et al. (1995) and Weltzin and McPherson (1997) concluded that trees and shrubs change their water uptake patterns depending on water availability. Scholes and Archer (1997) argue that the interactions among trees and the herbaceous layer cannot be explained by simple niche separation equilibrium models. Furthermore, several authors have reported niche superposition and competition for resources in savannas (Belsky 1994, Weltzin and McPherson 1997, Ludwig et al. 2004).

The ratio of actual to potential evaporation (E/E_p) was linearly related to available soil water in both plots (Figure 5), with the linear relationship between evaporation and soil water availability indicating a strong coupling of atmospheric water demand and physiological responses of vegetation. When soil water content was close to field capacity, E/E_p was controlled by atmospheric demand, but only small reductions in available soil water content were required to reduce E/E_p . This could be related to constraints in the soil–leaf pathway (cf. Meinzer et al. 1999), resulting in stomatal control of transpiration even at relatively high soil water supply. Miranda et al. (1997) reported that ecosystem-level water vapor fluxes for a cerrado *sensu stricto* were strongly coupled to the atmosphere, with evaporation rates largely controlled by stomatal response to atmospheric vapor pressure deficits.

Numerous attempts have been made to relate evaporation from vegetation surfaces to available soil water, but meteorological, plant and soil influences are hindrances. There are divergent schemes describing how evaporation varies with available soil water. Our data, and those obtained by Shepherd (1972), McNaughton and Black (1973) and Hutley et al. (2000), follow the Thornthwaite and Mather (1955) model, which predicts a linear reduction in E as a result of proportional reductions in available soil water. Our results disagree with those of Ritchie (1973) and Veihmeyer and Hendrickson (1955) who reported that E is similar to E_p until low values of available soil water are reached. Other studies show reductions in E when available water content is about 50%, and this has been related to soil properties, water availability in the root zone, root water potentials and variations in leaf area index (Penman 1949, Dunin and Aston 1984).

The evaporation rates reported here, which are derived from water balance calculations (Figure 6), were comparable with those derived by eddy covariance. Breyer (2001), who worked at the same sites, reported mean evaporation rates of 1.6 and 2.7 mm day⁻¹ for the dry and wet season, respectively, at the protected site and 1.5 and 2.5 mm day⁻¹, respectively, for the burned site. Similarly, Condé (1995) reported mean evaporation rates of 1.9 and 2.9 mm day⁻¹ for the dry and wet season, respectively, in another cerrado area near Brasília.

Despite similarities in overall evaporation rates and in the

relationship between E/E_p and available soil water between the burned and protected sites, the differences in the general water balance calculations, as well as the differences in depth of water uptake shown in Figure 7, can be related to vegetation structure. Dense woody vegetation in the protected cerrado plot resulted in higher water demand and more extensive root systems, whereas in the burned cerrado plot, high grass density led to water uptake mainly from the top 2 m of soil (about 70% of total water uptake was from the top 2 m). This is similar to results obtained for cerrado vegetation by Oliveira et al. (2005).

The differences in soil water recharge shown in Figure 8 may be related to rainfall distributions as well as to a time lag in subsoil recharge for the protected site, this being explained by the slightly greater water demand compared with the burned site. The higher evaporation rates of the protected cerrado would lead to a seasonal soil water storage deficit of about 60 mm, which may explain the time lag in deep recharge, as well as the lower estimated drainage values. Quesada et al. (2004) reported a similar pattern of soil water recharge in another oxisol under campo sujo vegetation, as well as a similar interruption in deep water uptake after the start of the rainy season. They calculated that 719.4 mm of water was needed to recharge to a depth of 360 cm.

The almost treeless campo sujo differs from the cerrado sensu stricto in concentrating its water uptake in the top 80 cm of the soil profile. This is a narrower soil layer than we found for herbaceous vegetation and suggests that depth of water use by the herbaceous layer may depend on the density of competing woody vegetation, presumably involving a preferential increase in biomass allocation to roots relative to shoots, suggesting an important mechanism by which woody vegetation density affects herbaceous phenology and biomass, production and allocation (Scholes and Archer 1997).

Rainfall in the 1999–2000 wet season was 70% above average, whereas the 1998–1999 wet season was the driest for 40 years, with only 1010 mm of rain, which is about 30% less than average. The 1999 dry season was one month longer than average. Nevertheless, despite the high rainfall input in 1999–2000, the low input in 1998–1999 and the extended 1999 dry season, the mean water uptake values for August were similar for all years. This implies that there is sufficient soil water to sustain the vegetation, even in years of low rainfall and with an unusually long dry season. In general, our results indicate that the cerrado is conservative in its water use and well adapted to dry years. Multiple conservation strategies in the cerrado such as deep root systems, dormancy of the herbaceous layer, stomata control, leaf abscission, low transpiration rates even when the soil water content is high and the ability to extract water from soil at different depths, combine to allow this vegetation to sustain itself, even in unusually dry years.

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